# Endemism and Richness in the Cape Floristic Region:

## Phytogeographic Patterns and Environmental Correlates in a Global Biodiversity Hotspot

by

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Late 19th centuary knowledge of the Cape, extracted from "Das Capland" by Von A Petermann (1868), kindly provided by the David Rumsey Collection

Consider the lilies, how they grow:
they neither toil nor spin;
and yet I say to you, even Solomon in all his glory
was not arrayed like one of these.
Luke 12:27

Finally: It was stated at the onset, that this system would not be here at once perfected. You can but plainly see that I have kept my word. But I now leave my Cetological System standing thus unfinished, even as the great Cathedral of Cologne was left, with the crane still standing upon the top of the uncompleted tower. For small erections may be finished by their first architects; grand ones, true ones, ever leave the copestone to posterity. God keep me from ever completing anything. This whole book is but a draught – nay, but the draught of a draught.
Oh, Time, Strength, Cash, and Patience!
Herman Melville, The White Whale.

Working on small parts of the system we find of course that
particularly the older volumes are very incomplete,
But this will also one day be the fate of the works of our day.
Weimarck, 1941

Dedicated to my parents:

Keith Wilfred Bradshaw

and

Bronwen May Bradshaw

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I am deeply indebted to my parents, who shouldered nearly all the financial burden of a fulltime student, for many years.

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# Declaration

I, Peter Lawrence Bradshaw

hereby

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# General Abstract

This study reports on an investigation of the phytogeographical patterns retrieved within the exceptionally species rich Cape Floristic Region (CFR), a global biodiversity hotspot in South Africa. Modern Analytical techniques, including a novel approach developed within this study, were used to identify Phytogeographical Centres. Moreover, the efficiency and optimality of these techniques were tested against each other using several different datasets. Endemism and species richness in the core CFR were assessed against contemporary environmental conditions, using a spatially sensitive regression technique.

A combined dataset of 4414 taxa was analysed, of which 4000 were recorded in the general CFR area. This represented 44.4% of the 9087 total taxa recorded in the CFR, and the largest dataset examined to date on floristic patterns in the CFR. The combined data (Combined Dataset), a relatively representative sample of the CFR flora, was used to establish overall phytogeographic patterns of endemism. Further, derivative subsets, based predominantly on phylogeny/taxonomy including taxa from eleven plant families, and two ecological guilds, Geophytes and Red Data Listed (RDL) Taxa, were also analysed. Differences between the derivative datasets revealed insights into taxonomically distinct floristic patterns, determined by the dominance of particular floristic/biotic elements within each dataset. This helped explain phytogeographical differences between previous CFR phytogeographical studies, which focused on different floristic/biotic elements.

In the Combined Dataset, nearly all Quarter Degree Square (QDS) cells were assigned to PCs in the core CFR, indicating endemism is common throughout the CFR. However, endemic taxa were concentrated in the high winter-rainfall west, and southwest areas. The large size of the dataset, and detailed analyses revealed additional finer phytogeographical sub-division, not previously recorded, including six Phytogeographical Provinces, 16 Centres, and 36 Sub-Centres; compared to five equivalent Phytogeographical Provinces and nine equivalent Centres of Weimarck.

Hierarchical analyses of the Combined Dataset displayed congruent patterns to the previous two comprehensive phytogeographical studies of Goldblatt and Manning, (2000) and Weimarck (1941). Within the core CFR phytogeographical provinces, common patterns across studies included choria being strongly associated with TMS mountain ranges. This highlighted the importance of substrate and topography explaining floristic patterns, consequent PC formation, and the numeric dominance of montane TMS 'fynbos' taxa. The latter was confirmed through habitat analysis of endemic taxa. However, PC development was also noted on the lower lying areas, notably the Agulhas Plains, and the lowland areas neighbouring the mountains of the Southwest Phytogeographical Province, and to a lesser extent, the Northwest Province.

The five analytical methods used to determine candidate PCs were evaluated for performance optimality. Bell Shaped Curve Weighting using UPGMA proved marginally more optimal than the other four methods, but differences between various weighting and clustering algorithms were less than anticipated. However, weighting was seen to be substantially better than not weighting. The novel technique of using a multiple clustering analysis approach was found to highlight areas of conflict, where floristic/biotic elements overlapped, and to supplement occasional poorly resolved trees. In addition, the approach of using GIS interrogation of candidate centres, substantially enhanced the endemic composition and size of PCs, and is strongly recommended. Moreover, post clustering GIS analyses may correct any marginal disadvantages of any single approach.

Significant correlations between endemism and PC size, and richness of non-endemics and PC size were found. However, certain PCs still contained more taxa than predicted by area alone, while others contained fewer. In these PCs with over- or under-represented richness, alternative explanations (either historical and/or environmental) were required to explain why these PCs differ from other PCs in the CFR, which was subsequently investigated.

Analyses of patterns of endemism and taxon richness against contemporary climatic and environmental variables using a regression technique which accounted for spatial variation in parameter estimates highlighted the importance of both the energy-water hypothesis, and the habitat heterogeneity hypothesis in the CFR. Potential evapo-transpiration and various measures of topographic heterogeneity provided much explanatory power. In addition, length of growing/rain season was particularly important in the western winter rainfall portion of the CFR, and is here retrieved for the first time as a strong predictor variable. Different input units and different floristic components of the dataset required different models for optimisation. The models were adequately able to account for much of the variability in richness ($r^2$ = 78.3-91.2%).

The Cape Floristic Region (CFR) – a global hotspot – proved an excellent area to study patterns of endemism, taxon richness, floristic patterns, and how environmental conditions affect richness because of its exceptionally high concentration of both richness and endemism, and high levels of beta and gamma diversity over relatively short geographic distances.

# Chapter 1: General Phytogeographical Introduction to the Cape Floristic Region

## 1.1 The CFR in a Global and Regional Context

The southwest tip of Africa is home to the Cape Flora (Goldblatt, 1978; Linder, 2003), remarkable for its very high species richness and dense concentration of range-restricted species. The region is unique in many ways and although only approximately 90 000 km$^2$ in area, it is home to 9087 species (Goldblatt, Manning and Snijman 2005). This richness is largely the result of a few large clades, with 50% of the species found in only 30 clades (Linder, 2003). Perhaps even more remarkable than this high level of diversity is the high level of species endemism in the Cape Floristic Region (CFR) (Cowling, Holmes and Rebelo, 1992) which approaches 68% (Goldblatt and Manning, 2000, 2002; Goldblatt, Manning and Snijman, 2005). This high level of endemism makes the flora highly distinct from the surrounding floristic regions. The development of a winter rainfall regime has undoubtedly contributed to its relatively independent development (Hendey, 1982). The distribution and diversity of the flora is positively correlated with winter precipitation levels. These extraordinary levels of diversity and endemism, confined within this small, non-island area, have prompted some biogeographers, for example, Takhtajan (1986) and Good (1974), to place the CFR in its own Kingdom (Figure 1). However, this phytogeographic elevation to kingdom status is not universally accepted (Cox, 2001). In addition, the CFR is recognized as one of 25 global biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca and Kent, 2000). Marloth (1908), Goldblatt (1978) and later Goldblatt and Manning (2002), delimited the core area of this flora as the Cape Floristic Region (CFR) (Figure 2), although Bayer (1984), and more recently Jurgens (1997) and Born et al., (2006) advocate Greater Cape Floristic Region, corresponding to the winter rainfall area, which includes the Succulent Karoo.

### 1.1.1 Vegetation and Floristics

The Cape Flora is concentrated in the southwest corner of South Africa, in an area referred to as the CFR (Goldblatt, 1978). Spatially, the CFR is largely congruent with the Fynbos Biome, which is defined as a relatively homogenous vegetation community, both structurally (consisting of microphyllous and sclerophyllous shrubs) and functionally (it has a winter rainfall and is fire adapted). The Fynbos Biome contains two principal vegetation units: Fynbos, found mostly on montane, oligotrophic sandstone derived soils; and Renosterveld, which generally occurs at lower altitudes, on nutrient rich, shale derived soils. At the regional level, the fynbos component is much more species rich than the Renosterveld component, comprising 70% of taxa (Cowling and Proches, 2005).

The Cape Flora has outliers both in the winter rainfall region to the northwest (notably the Kamiesberg (Helme and Desmet, 2006) (Figure 2) and possibly also in the Brandberg (Figure 9). Outliers are also found in the summer rainfall region, to the northeast, most immediately in the Grahamstown area (Weimarck, 1941) (see Figure 2), but extending further along the eastern escarpment and eastern high altitude areas of Africa, reaching as far north as Ethiopia and the Yemen in the Middle East (Levyns, 1938, 1964). While to the northwest, these outliers are small, fairly isolated and disjunct; the flora tapers off much more gradually to the northeast, especially in the more mesic montane habitats. Weimarck (1941) postulated that the arid Limpopo Valley seemed to have acted as a barrier to the northward migration of Cape elements, while the Rudolph interval between Kenya and Abyssinia acted as a barrier to the southward migration of species from the Northern Hemisphere.

Conversely, within the CFR are outliers of other floras. Throughout the CFR, in deep ravines that retain year round moisture and offer protection from fire, as well as on the coastal slopes and plateaux of the South Coast, are patches of evergreen forests. These are outliers of the Afromontane forests that have their heartland in the mountains of East Africa (White, 1983) and constitute the forest biome in the CFR.

Along the arid intermontane valleys, in the rain shadow of both the winter westerly fronts and the summer south-easterly rains, are elements of the Succulent Karoo Biome (Levyns, 1938; Goldblatt, 1978; Cowling and Hilton-Taylor, 1997), which shows its best development immediately north of the CFR in Namaqualand, and in the Little Karoo. The boundary between the CFR and the Succulent Karoo, towards the north and the interior, is both poorly defined and irregular, constituting a transitional area, where outlying populations of either vegetation group interdigitate (Goldblatt, 1978; Taylor, 1979). This is generally where winter rainfall decreases below 250mm (Levyns, 1964), although some authors use the 200mm isohyte (Goldblatt and Manning, 2000). Much of the rainfall is orographic and the annual rainfall can drop from 2000mm on the higher mountain slopes facing the coast to 200mm on the leeward slopes of the interior ranges (Goldblatt and Manning, 2000). Using mean annual rainfall data (Schulze, 1997), the top of the Keeromsberge received a projected 2473mm per annum, while six to seven kilometres away, in the region of Sandhills, the projected rainfall is only 98mm, a difference of 2375mm in six to seven kilometres. As a result, there is considerable floristic turnover at a much finer scale than the approximately 25km$^2$ QDS at which the data were analysed here. This association with winter rainfall produces notable geographic patterns and structures. In the Karoo, Fynbos is predominantly found on the high, southern slopes of mountains, which due to their aspect and altitude receive more moisture than the surrounding areas (Levyns, 1938; Weimarck, 1941). On the other hand, the Karoo vegetation of the Succulent Karoo Biome comprising leaf succulent and microphyllous shrubs, is found in lower altitude, drier areas, which receive less than 200mm of precipitation. They are also generally located on nutrient rich soils (Taylor, 1979; Goldblatt and Manning 2000). Finally, scattered throughout the CFR, predominantly on richer soils and on the coastal forelands, are forest thicket elements, consisting of *Rhus, Olea* and *Sideroxylon*.

### 1.1.2 Patterns of Species Richness

The high species diversity in the CFR is better explained by species turnover (beta and gamma diversity), rather than by alpha diversity alone (Latimer, Silander and Cowling, 2005; Cowling et al., 1992; Cowling, 1990; Simmons and Cowling, 1996), which is likely due to low migration (Latimer, Silander and Cowling, 2005). In addition, there are high levels of diversity and endemism with high turn-over (Cowling et al., 1992; Cowling et al., 1997) along steep ecological gradients (Goldblatt and Manning, 2000, 2002), resulting in abrupt changes in richness and floristic composition. Thus, one would expect substantial geographical structuring in the data. This would make the CFR an excellent choice to explore phytogeographic patterns. If there is congruence in the distributions of taxa, this may be explained by current environmental and/or historical processes. The CFR is an ideal area to study the relationship between richness and explanatory variables because it is relatively well known and explored botanically (Goldblatt, 1978; Goldblatt and Manning, 2000, 2002; Goldblatt, Manning and Snijman, 2005).

Although there have been recent phytogeographical analyses in the CFR, using comprehensive (Goldblatt and Manning, 2000) and well representative (Oliver et al., 1983) datasets, the last geographically detailed fine scale phytogeographic analysis was undertaken by Weimarck in 1941. However, Weimarck (1941) made use of a relatively small dataset of 462 taxa, excluding some of the largest representatives of cape clades as defined by Linder (2003). There is thus an urgent need to analyse phytogeographical patterns in the CFR, using a representative dataset, and modern techniques. This thesis primarily addresses this need. Further, techniques employed are critically and empirically assessed. Finally, patterns of richness, across the CFR, and within the identified phytogeographical units are regressed against contemporary environmental variables to explain richness patterns, using modern techniques that address issues of non-stationarity and spatial auto-correlation.

## 1.2 Summary of General Aims

1. To identify phytogeographical units within the CFR, and of individual clades both inside and outside the CFR

2. To investigate richness and areal properties of choria
3. To investigate the effectiveness of techniques employed
4. To determine environmental correlates of richness in the CFR (diversity and endemism).
5. To produce a list of taxa endemic to choria identified

Detailed aims and objectives are provided in the introductions of Chapters 2, 3 and 4.

## 1.3 Thesis Structure

### 1.3.1 Concise Breakdown of Thesis Chapters

Chapter 1: General introduction to the CFR, and the suitability of the area for analysis.

Chapter 2: A narrative monographic biogeographic account of phytogeographical patterns in the CFR (this chapter would appeal to readers with a strong interest in CFR biogeography, but who aren't necessarily interested in a technical evalution of the methods employed. Readers interested in a detailed evaluation of the methods would benefit from reading chapter Three first).

Chapter 3: An evaluation of the phytogeographical techniques employed in Chapter 2 (For readers interested in a detailed technical evaluation of the methods employed).

Chapter 4: Investigation of what environmental factors are correlated with, and could thus explain richness, at both the QDS level, and within the various smaller phytogeographical units identified in the biogeographic analysis (from Chapter 2).

Appendix I: Chapters 9-17: A concise narrative biogeographic account of phytogeographical patterns in each of the major taxonomic (Family) and functional (Geophytes; RDL Taxa) datasets.

Appendix II: Digital lists of taxa endemic to the phytogeographical units identified in the Combined (Chapter 2) and derivative datasets (Chapters 5-17).

Accompanying CD: Owing to the difficulties in reading values off certain maps (for example, the inverse weighting scores in Chapter 2, the place names off the 1250 000 Topocadastral maps for the core CFR PCs in Chapter Two, or the pseudo-t symbols and the legends of the GWR parameter maps in Chapter 4), high resolution images of all maps are provided on the accompanying CD, together with the digital list of chorial endemics (Appendix II).

### 1.3.2 Detailed Breakdown of Chapters

**Chapter 1**: General Introduction

The CFR is introduced, and discussed in a global to regional floristic context. Patterns of species richness are briefly described, as are the major phytogeographic studies in the CFR, with their shortcomings, to provide rationalization for the current study.

**Chapter 2**: Phytogeography of the CFR

Chapter 2 follows the style of classic biogeographic monograph studies (Weimarck, 1941; Goldblatt, 1978; Raven and Axelrod, 1978; van Wyk and Smith, 2001), being a narrative account of phytogeographical patterns, rather than a series of smaller chapters as suits more experimental biological studies. However, although narrative, it is based on rigorous and extensive statistical analysis.

The narrative biogeographic component of the thesis (Chapter 2) covers the following conceptual components: 1) Phytogeographical patterns; 2) Hierarchical relationships between phytogeographical patterns (choria) which ultimately form higher level phytogeographical patterns like Provinces and Regions; 3) Regression analysis of endemism, non-endemics and area of the phytogeographical units to identify over or under-represented richness in choria; 4) a habitat analysis of chorial (PC) endemics; 5) comparisons to previous studies; and 6) comparisons of how the phytogeographical patterns in the individual taxon/functional datasets (Chapters 5-17) differ from the general regional pattern (Chapter 2). I avoided separating these components into separate chapters to provide a more uninterrupted flowing narrative, and to avoid excessive internal cross referencing.

Section 2.1: Abstract.

Section 2.2: Introduction. This chapter introduces past phytogeographical classification in the CFR, and outlines newer developments in phytogeographic analysis.

Section 2.3: Methods. Properties of the dataset analysed and the analytical techniques employed are described and justified.

Section 2.4: Results and Discussion of CFR Phytogeography. An example is provided of how consensus was obtained from the dendograms of the different weighting techniques. Chorial units (PC and PSC) are identified, with descriptions linked to topographic and riverine features known to botanists in the CFR, to provide spatial context. The choria are compared to those of previous studies, and to those identified for derivative datasets (Chapters 5-17). The hierarchical relationships between choria are presented as dendograms, to illustrate how the choria form larger chorial entities (provinces). Habitat properties of the different PC endemics are also recorded and compared. Regression graphs of the relationship between PC endemics, PC non-endemics, and PC area are provided to highlight those PCs that deviate significantly from expected levels of diversity and endemism.

**Chapter 3**:

An assessment of the performance of methods as employed in Chapter 2 was undertaken. An important component of any study is to assess how analytical techniques of the study performed, and whether the methodology is justified and effective, and to provide advice for further potential studies. This is undertaken here. Further, the methods are placed in context, with comparisons to earlier and more recent techniques to retrieve phytogeographical patterns.

**Chapter 4**:

Environmental correlates of diversity in the core CFR, using a local regression (GWR) approach. Not only is it important to know where richness is distributed and what floristic patterns emerge, it is also important to know what potential environmental variables facilitate richness. I explore what contemporary environmental parameters (for example, topography and climate) correlate with richness, and thus how richness might be explained.

**Appendix I: Chapters 5-17**

An extensive study has also been made of the individual taxonomic (familial) and "functional" components of the dataset, in recognition of the fact that these are likely to show idiosyncratic patterns (Exell and Gonçalves, 1974; Currie, 1991; Currie et al., 1999; Jetz, Rahbek and Colwell, 2004). Included are a determination of their phytogeographical patterns; regression analysis on the relationship between endemism, non-endemic taxa and area; and an analysis of the habitats of endemic taxa where easily accessible. Although important to a greater understanding of floristic patterns, these taxonomic and functional datasets are placed in an Appendix (Appendix I), owing to space constraints, and their supplementary role in interpreting floristic patterns. These accounts are less formally written. Although there have been previous phytogeographical studies on individual taxa (Dahlgren, 1963; Nordenstam; 1969; Linder and Mann, 1998), there has as yet been no single consolidated study to compare the idiosyncratic patterns of individual taxa to that of the general phytogeographical patterns in the CFR, using the same objective techniques. Taxon specific patterns are identified here (Appendix I: Chapters 5-17) with a brief description, and discussed in comparison to the general CFR phytogeographical patterns in Chapter 2.

To avoid unnecessary repetition, methods sections are not provided for each of these chapters (5-17), as the methods undertaken here are identical to those undertaken in the Combined Analysis (see Chapter 2; sections 2.3.2-2.3.6).

**Appendix II**

A digital appendix is provided that lists taxa endemic to the various phytogeographical units identified, both within the combined dataset, and for the individual taxonomic/functional derivative datasets as well. In addition, habitat data associated with endemic taxa are also provided where available. I anticipate that this data should have use for both the biogeographical and ecological community. The list is provided in various digital formats, e.g. Excel (2003, 2007), CSV, Tab separated text, to facilitate easy dissemination.

# Chapter 2: Phytogeographical Analysis of the CFR

## 2.1. ABSTRACT

The aim of this chapter was to identify Phytogeographical Centres (PC) within the highly species rich Cape Floristic Region (CFR), South Africa. The study is unique in the CFR, as it analyses both a representative sample and individual taxonomic/functional datasets of the region.

A combined dataset of 4414 taxa were analysed, of which 4000 were recorded in the general CFR area. This represents 44.4% of the 9087 total taxa recorded in the CFR (Goldblatt and Manning, 2000, 2002; Goldblatt, Manning and Snijman, 2005), and the largest dataset examined to date on floristic patterns in the CFR. Data sampling was biased towards fynbos taxa, (the oligotrophic, Table Mountain Sandstone (TMS), montane taxa), which comprise the majority of taxa in the CFR, amounting to approximately 70% (Cowling and Proches, 2005). Taxa on shale, limestone and littoral sand deposits were also included.

The combined data (Combined Dataset) is a representative sample of the flora. It was used to establish overall floristic patterns of endemism, while the analysis of the subsections of the data was undertaken in order to identify taxon, or ecologically-specific endemism patterns. These data subsets were based predominantly on phylogeny/taxonomy and included taxa from the following families: Asteraceae, Bruniaceae, Ericaceae, Fabaceae, Orchidaceae, Poaceae, Polygalaceae, Proteaceae, Restionaceae, Rosaceae and Rutaceae. Furthermore, ecological guilds (Geophytes) and threatened Red Data Listed (RDL) Taxa were also used. It was found that although there is noticeable congruence between many of my different phylogenetic datasets, there are also notable differences. Floristic patterns are determined by the dominance of particular floristic/biotic elements within each dataset.

Numerous analyses were conducted on each dataset. An attempt was made to use analytical techniques that were both systematic and replicable. Parsimony Analysis of Endemism (PAE) and Sequential Agglomerative Hierarchical Nested Cluster Analysis (SAHN, using the Unweighted Pair-Group Method, Arithmetic Average (UPGMA)) were both employed as clustering algorithms. Unweighted and weighted data were analyzed, as it was discovered that slight adjustments in the weighting system often resulted in different biotic distribution patterns being emphasised in the same dataset. Such conflict occurred in the classification of the Quarter Degree Squares (QDSs) that contained significant interfaces between different environments, and subsequently different biotic elements. Congruence within the datasets of the different weighting and clustering analyses was established using a Geographical Information System (GIS). Where there was conflict, QDSs were assigned to PCs that maximized endemism.

Relatively large numbers of QDSs were assigned to PCs, thus indicating that endemism is common throughout the CFR. However, endemism is concentrated in the west, particularly the southwest and is congruent with high levels of winter rainfall. The combined dataset produced geographically smaller PCs, indicating the presence and congruence of numerous highly range-restricted taxa in numerous clades, as well as additional finer phytogeographical sub-division, not previously retrieved. Hierarchical analysis of the Combined Dataset revealed similar patterns to the two most significant and comprehensive previous phytogeographical studies by Goldblatt and Manning, (2000) and Weimarck (1941). PCs were found to cluster in the six traditional phytogeographical provinces (phytogeographical centres, *sensu* Goldblatt and Manning, 2000), the SWPP, NWPP, LBPP, APPP, KMPP and SEPP, forming the core CFR. Significant deviations included the classification of the Saldanha Peninsula and extreme western coastal areas with a southern Succulent Karoo cluster, which also included the Gifberg, Nieuwoudtville and Vanrhynsdorp PCs, outside the core CFR. Generally, within the core CFR phytogeographical provinces, choria are strongly associated with distinct TMS mountain ranges, indicating the importance of substrate and topography within the CFR for floristic patterns and consequent PC formation,

and the numeric dominance of montane TMS 'fynbos' taxa. However, there was also PC development on the lower lying areas neighbouring the mountains, notably the APPP and the Swartland and Rûens areas.

A more spatially resolved dataset would almost certainly result in higher endemicity values for the PCs, by removing conflict present at the QDS scale. It was found that the utilisation of multiple weighting techniques was highly beneficial. These illustrate congruence of the biotic elements of the different datasets, increasing confidence in the results, and I encourage similar such studies to make use of multiple analytical techniques.

I found significant correlations between endemism and PC size, and richness of non-endemics and PC size. However, certain PCs still contained more taxa than predicted by area alone, while others contained less. In these PCs with over- or under-represented richness, alternative explanations (either historical or contemporary environmental) are required to explain richness patterns.

Keywords: Centre(s) of Endemism (PC); Jaccard (SAHN, UPGMA); Parsimony Analysis of Endemism (PAE); Cape Floristic Region (CFR); Geographical Information Systems (GIS);

## 2.2. INTRODUCTION

### 2.2.1 Phytochorological classifications

Phytochorological classifications strive to divide regions into smaller floristic units, often termed biotic provinces (Linder, 2001; Rebelo, 1990; White, 1993), or Phytogeographical Centres (PCs) (Weimarck, 1941). Biogeographical centres or biochoria are used for the spatial interrogation of biodiversity, in historical interpretations (Major 1988, Rosen 1988), and in conservation planning (Platnick, 1992; Myers, Mittermeier, Mittermeier, da Fonseca and Kent 2000). Biogeographical centres are characterised by unique species compositions (Takhtajan, 1986; Good, 1974), and as such are similar to centres of endemism. The boundaries between centres indicate areas regions where there is a change in the species composition. Taxa mostly restricted or endemic to areas are arguably more indicative of evolutionary and environmental processes of the areas in which they are occur. Defined as such, not all species carry the same information for centre delimitation. Widespread species that occur in all possible centres carry no information relevant for centre delimitation, and centre specific interpretation, and may in fact have a negative effect on centre delimitation (Nelson and Platnick, 1981). In the past, when datasets were relatively small, visual inspection of individual ranges of taxa may have proved adequate to determine floristic patterns, for example, Weimarck (1941). Too many taxa may overwhelm this more intuitive method. Furthermore, this technique may also result in bias, because it is possible to be influenced by the taxa or floristic patterns that one is familiar with.

Utilisation of computerised clustering techniques resolves many of these problems. Two computerised clustering techniques that have been used in phytochorological classifications are Parsimony Analysis of Endemism (PAE) (Rosen, 1988; Morrone, 1994; Morrone and Crisci, 1995) and clustering based on similarity, using a coefficient such as the Jaccard similarity coefficient (Stehli and Wells, 1971; Linder and Mann, 1998; Linder 2001) or other less common techniques (Oliver, Linder, and Rourke, 1983). PAE clusters predefined geographic input areas, referred to as Operational Geographic Units (OGUs) (Crovello, 1981) into dendograms (analogous to taxon trees) and taxa in these geographic areas are treated as tree characters (Rosen, 1988). Autapomorphic tree characters represent the geographic endemic taxa.

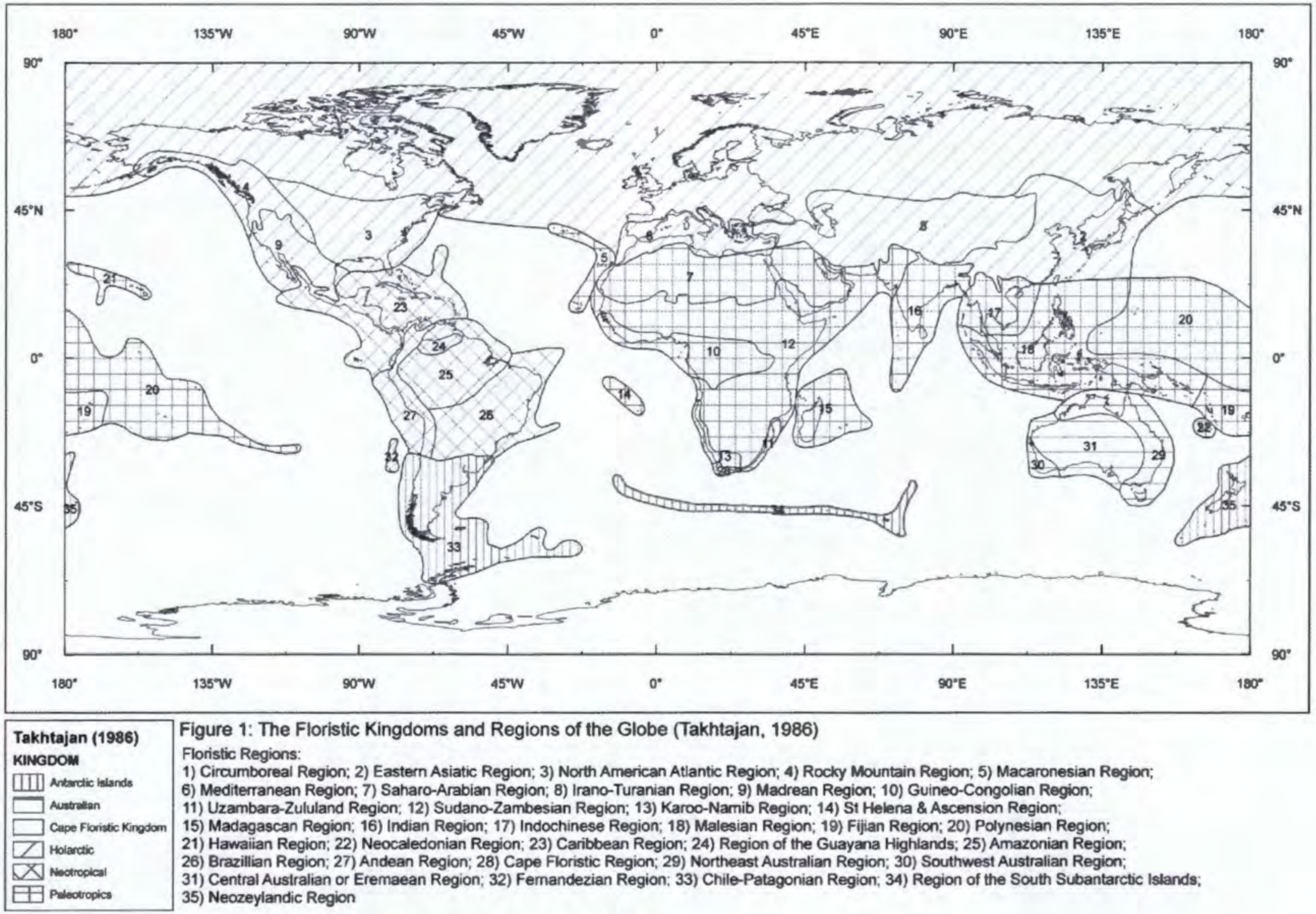


Figure 1: The Floristic Kingdoms and Regions of the Globe (Takhtajan, 1986)

Floristic Regions:
1) Circumboreal Region; 2) Eastern Asiatic Region; 3) North American Atlantic Region; 4) Rocky Mountain Region; 5) Macaronesian Region; 6) Mediterranean Region; 7) Saharo-Arabian Region; 8) Irano-Turanian Region; 9) Madrean Region; 10) Guineo-Congolian Region; 11) Uzambara-Zululand Region; 12) Sudano-Zambesian Region; 13) Karoo-Namib Region; 14) St Helena & Ascension Region; 15) Madagascan Region; 16) Indian Region; 17) Indochinese Region; 18) Malesian Region; 19) Fijian Region; 20) Polynesian Region; 21) Hawaiian Region; 22) Neocaledonian Region; 23) Caribbean Region; 24) Region of the Guayana Highlands; 25) Amazonian Region; 26) Brazillian Region; 27) Andean Region; 28) Cape Floristic Region; 29) Northeast Australian Region; 30) Southwest Australian Region; 31) Central Australian or Eremaean Region; 32) Fernandezian Region; 33) Chile-Patagonian Region; 34) Region of the South Subantarctic Islands; 35) Neozeylandic Region

Figure 1: The Floristic Kingdoms and Regions of the Globe (Takthajan, 1986).

A similarity measure such as the Jaccard Similarity can be used to calculate a similarity matrix between OGUs, which are then clustered together based on this similarity (Linder, 1999; Linder and Mann, 1998). Sequential Agglomerative Hierarchal Nested (SAHN) cluster analyses, using the Unweighted Pair-Group Method and the Arithmetic Average (UPGMA) (Sneath and Sokal, 1973) were then used to cluster the OGUs based on Jaccard similarity. I refer to this technique as UPGMA from here on. However, on its own, UPGMA is unable to specify which taxa may or may not be endemic to the PC. I used GIS to identify taxa that were endemic to the PCs (dendogram clusters). GIS was also used to refine the PC within the CFR, created from both PAE and UPGMA clustering algorithms. This was achieved by removing clusters that did not contain endemic taxa, thus removing QDSs that did not contain endemic taxa from PC.

Alternative techniques include various optimality criteria, focusing on congruence/co-occurrence of potential endemics, whether intrinsic during analysis (Szumik, Cuezzo, Goloboff and Chalup, 2002; Szumik and Goloboff, 2004), or by *a priori* filtering out those taxa whose distributions that are not significantly congruent (Mast and Nyffeler, 2003; Giokas and Sfenthourakis, 2008). These filtering techniques make use of randomly generated Monte Carlo matrices with the null model being used to test the probability of the observed distribution being higher than by chance alone (Mast and Nyffeler, 2003; Giokas and Sfenthourakis, 2008). Mast and Nyffeler (2003) reported a dramatic reduction in the number of dendograms generated after using a null-model to filter out taxa that did not co-occur significantly. The null-model technique also resulted in fewer and smaller candidate areas of endemism (Giokas and Sfenthourakis, 2008). While this may be desirable for historical biogeographic analysis, it is less useful for chorological delimitation, requiring further GIS refinement. However, these smaller candidate areas may be informative as core chorological areas, or PSCs. While co-occurrence is interesting, particularly for the delimitation of historically relevant units, it is less of a criterion for the delimitation of phytogeographical centres. For my study, endemism is more important. Currently, modern software generating null-models are limited to matrices of 300 by 800 (Gortelli and Entsminger, 2006), considerably smaller than many of my datasets, precluding its inclusion for comparison in my study. Null models have also been invoked to derive similarity matrices (Raup and Crick, 1979; McCoy, Bell and Walters, 1986), much like the Jaccard or other similarity coefficients (see Cheetham and Hazel, 1969).

Although the distributions of individual taxa are also important, focusing on individual taxa may detract from large scale, floristic regional biogeographical patterns, such as at the level of biotic provinces, regions, or kingdoms. Therefore, at regional scales it may be more informative to record, for example, that the Cape Peninsula, South Africa, has 2285 species, of which 158 are endemic (Helme and Trinder-Smith, 2006), rather than focusing on and describing the exact distributions of each species. In this instance, it would also be advantageous to consider the Cape Peninsula as a single historical entity. The effects of scale and an awareness of its implications are of critical importance to biogeographical analysis, especially in terms of diversity and endemism.

Centres of endemism facilitate the comparison of areas rather than individual species, so that species become characteristic of areas, rather than areas being an attribute of the species.

The high species diversity in the CFR is better explained by species turnover (beta and gamma diversity), rather than by alpha diversity alone (Latimer, Silander, Cowling, 2005; Cowling et al., 1992; Cowling, 1990), which is likely due to low migration (Latimer, Silander, Cowling, 2005). Thus, one would expect substantial geographical structuring in the data. This would make the CFR an ideal area to explore PCs and be conducive to the delimitation of these PCs. If there is congruence in the distributions of taxa, this may be explained by current environmental and/or historical processes. The study of Weimarck (1941) forms a distinct watershed in phytogeographical studies of the CFR, and I divide the studies accordingly below.

#### 2.2.1.1 The Pre-Weimarck Period

Although the uniqueness of the Cape Flora was already recognized by Linnaeus (1707-1778) and certainly by his student Thunberg (1743-1828) who spent a few years working on the flora of the Cape between April 1772 and March 1775 (Svedelius, 1944), its distinctiveness from the rest of the African flora was not yet appreciated (Goldblatt, 1978). Africa as a whole was relatively unexplored when Schouw (in 1823) produced his map (as cited in Taylor, 1978) of three floristic kingdoms, with his knowledge of African flora being restricted to the margins of the continent. Possibly due to absence of contrary evidence, many of the early biogeographers grouped the rest of southern Africa with the Cape Flora (Goldblatt, 1978), which had been known for a longer period (Figure 3: Schouw 1823).

The phytogeographical patterns in southern Africa were mapped in detail for the first time by Drége (1843), as an aid to documenting the plants he collected for the company of Ecklon and Zeyher in the period 1820-1830 (Figure 4). These professional collectors noted not only the remarkably high rate of change in the flora, but also the high level of endemism and range restrictedness of the flora (Drége 1843). Drége's (1843) map was atypical for the period, in that it recognised detailed internal sub-divisions of the CFR, within the fynbos and Renosterveld vegetation units. Most other maps of this early period focused on what are now regarded as biome level differences. A distinctive and insightful feature of Drége's map was the recognition of vegetation/floristic similarity associated with the topography within the CFR. For a long period afterwards, biogeographers seemed largely to ignore, or appeared to be unaware of Drége's (1843) map, with its internal sub-division of the CFR. Instead they tended to focus on its external floristic or vegetation (biome) boundaries. As a result, many of these maps contain substantially less detail (for example, Grisebach 1872; as cited by Taylor, 1978). Grisebach (1872) shifted the northern boundary of the Cape Flora to the political and geographical boundary of the Orange River. Grisebach (1872) grouped large areas of South African Flora with the Cape Flora (Figure 5). By this time however, other African elements were being identified, namely the interior floras of the

Kalahari and Sudan. Only with subsequent botanical exploration did it become apparent that the flora of the interior was significantly different from that of the winter rainfall south-western region.

Rehman (1880) (Figure 6) produced a substantially more accurate map than Grisebach (1872). His map of the Cape Flora showed distinct South-western Cape and Forest Regions, and the boundaries of the Cape Region were moved considerably further south. This was possibly the earliest reference to the South-western Cape, a phytogeographic delimitation still in use today. The Forest Region included the Outeniqua and Tsitsikamma Mountains, ending east of Port Elizabeth. Thus the Little Karoo and mountains such as the Swartberg and Kammanassieberg were excluded, and formed part of an extended Karoo Flora. Subsequent maps of the CFR recognised the disparate natures of the Cape and African Floras and these differences became more entrenched.

Engler (1882) (Figure 7) extended the South-western Cape Flora to include the North-western Phytogeographical Centre and shortened the eastward extension of the Southern Cape Flora, which was equivalent to Rehman's (1880) Forest Flora. His Karoo Flora was poorly defined and was detached from the Cape Flora.

Bolus (1886, 1905) produced two remarkably accurate maps. The 1886 map (Figure 8) included a large portion of the arid flats around Vanrhynsdorp (including the Knersvlakte and Hardeveld) into the CFR. These elements today form part of the Succulent Karoo Biome (Low and Rebelo, 1996; Mucina and Rutherford 2006). Significantly though, he also included the Nieuwoudtville Plateau in the CFR. On the interior side, in the west, he included the Swartruggens and Swartrugberge as part of the CFR, although he excluded the Witteberg. In the middle, Bolus included the Swartberg and Little Karoo; and in the east, the CFR boundary extended northwards to include the Grootrivierberge and Klein Winterhoekberge, although it ended short of Port Elizabeth. Bolus revised his map in 1905 (Figure 9) and his new map excluded the flats around Vanrhynsdorp and the Nieuwoudtville Plateau. He also excluded the drier inland slopes of the Cedarberg and the Swartruggens, and also the Swartrugberge. His central area remained relatively unchanged. He still excluded the Witteberg; and to the east, he excluded the Grootrivierberge and the Klein Winterhoekberge, shifting the boundary further south here. The eastern boundary of the CFR was also extended eastward to include the Elandsberg and Port Elizabeth.

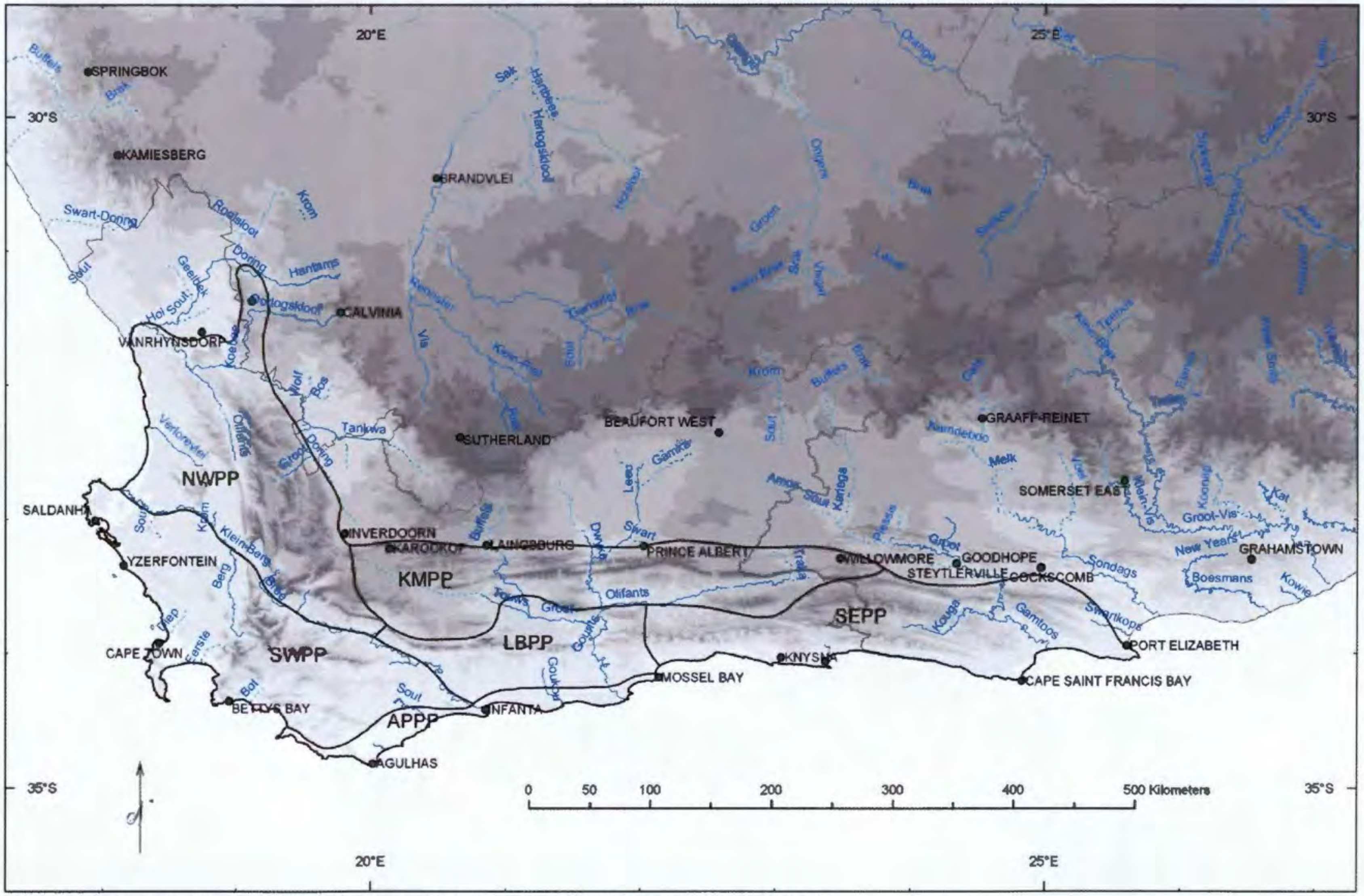


Figure 2: Phytogeographical Centres of the Cape Floristic Region (Goldblatt and Manning, 2000).
Codes used here are adaptations of those used by Goldblatt and Manning (2002); SWPP ≡ Southwest Phytogeographic Centre, NWPP ≡ Northwest PP, APPP ≡ Agulhas Plains PP, LBPP ≡ Langeberg PP, KMPP ≡ Karoo Mountain PP, SEPP ≡ Southeast PP. Locations of certain urban areas are provided to orientate the reader.

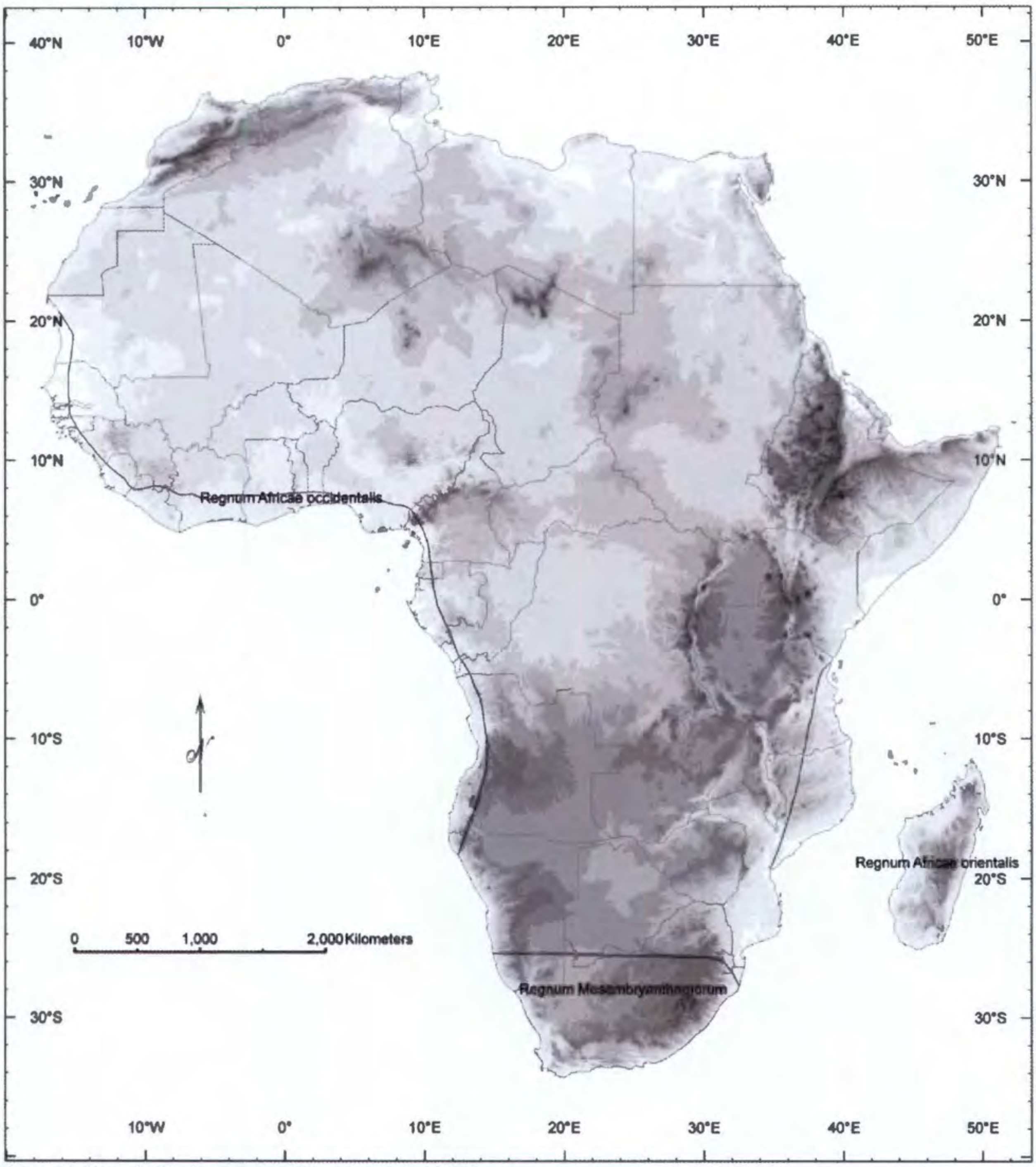


Figure 3: Floristic Regions according to Schouw (1823).

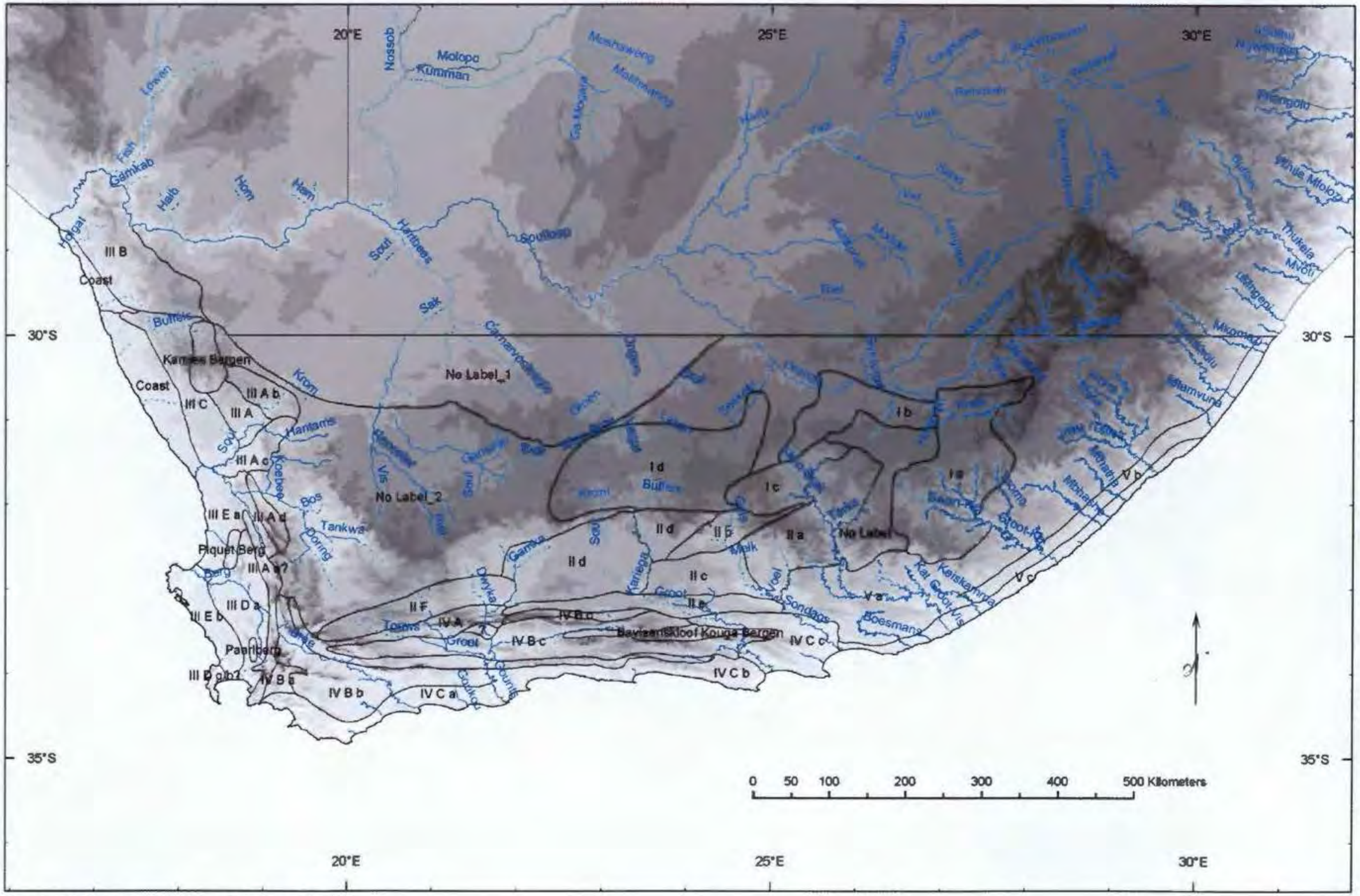


Figure 4: Floristic Divisions of Drége (1843).

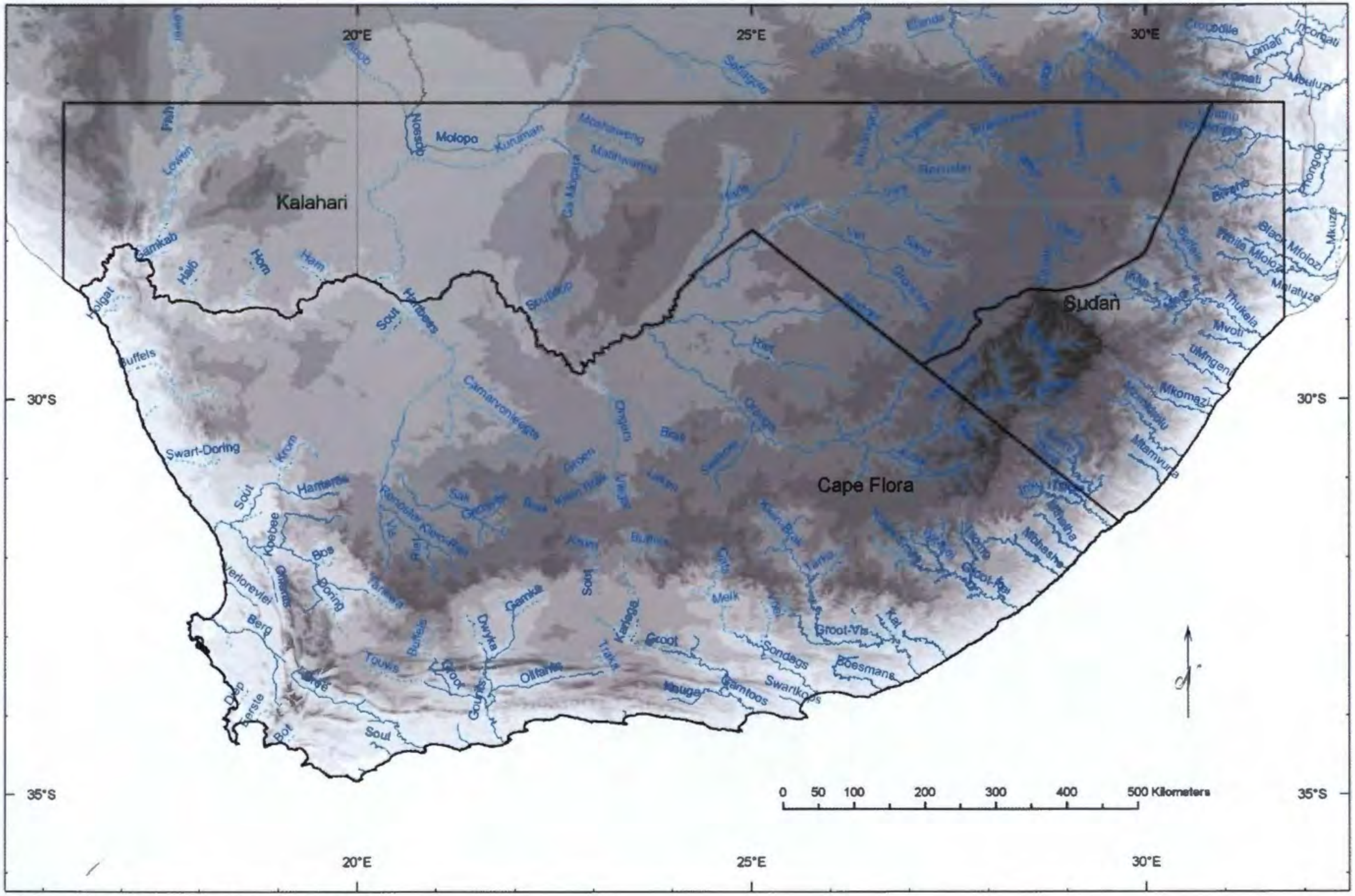


Figure 5: Floristic Divisions of Grisebach (1872).

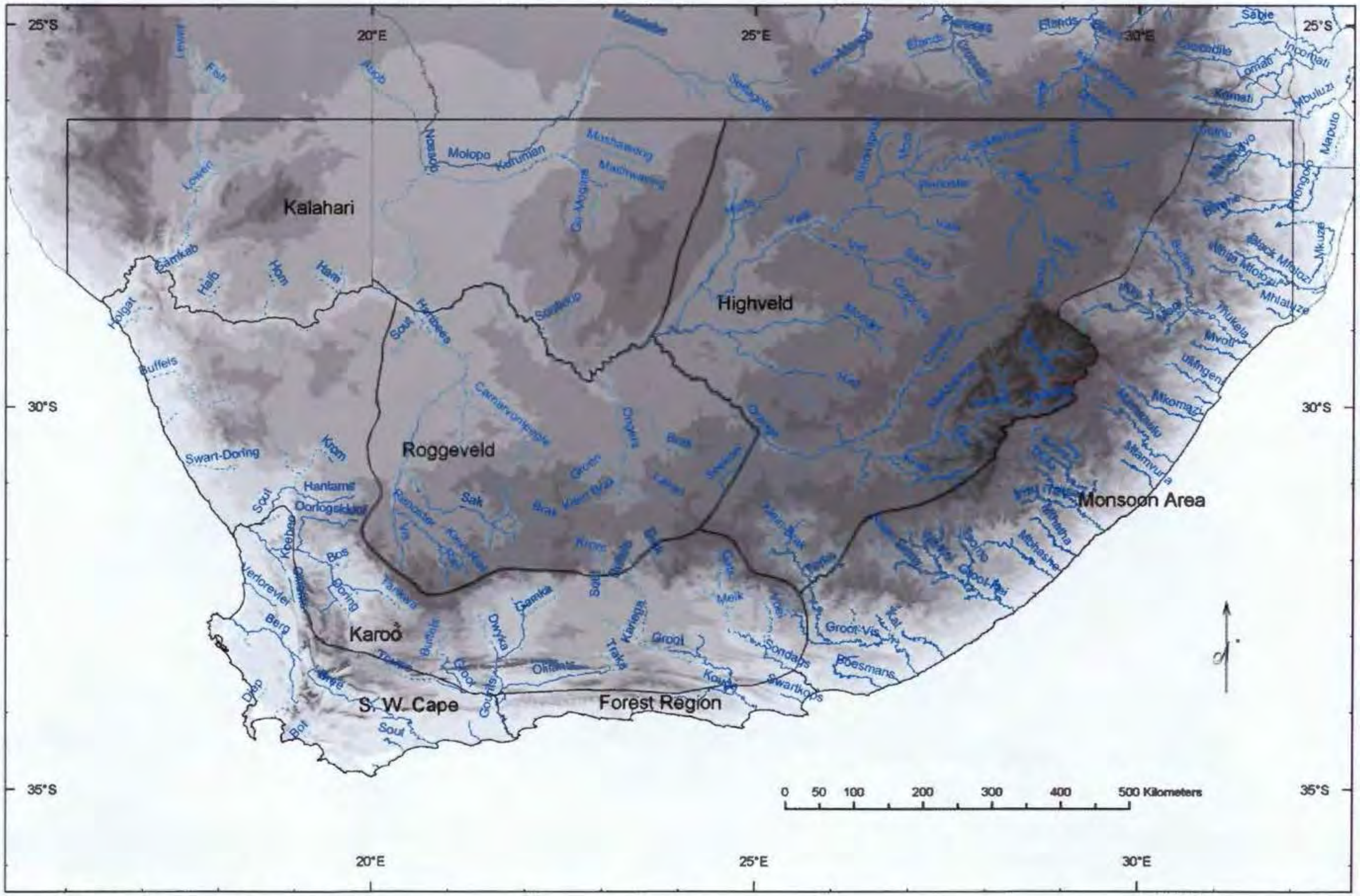


Figure 6: Floristic Divisions of Rehman (1880).

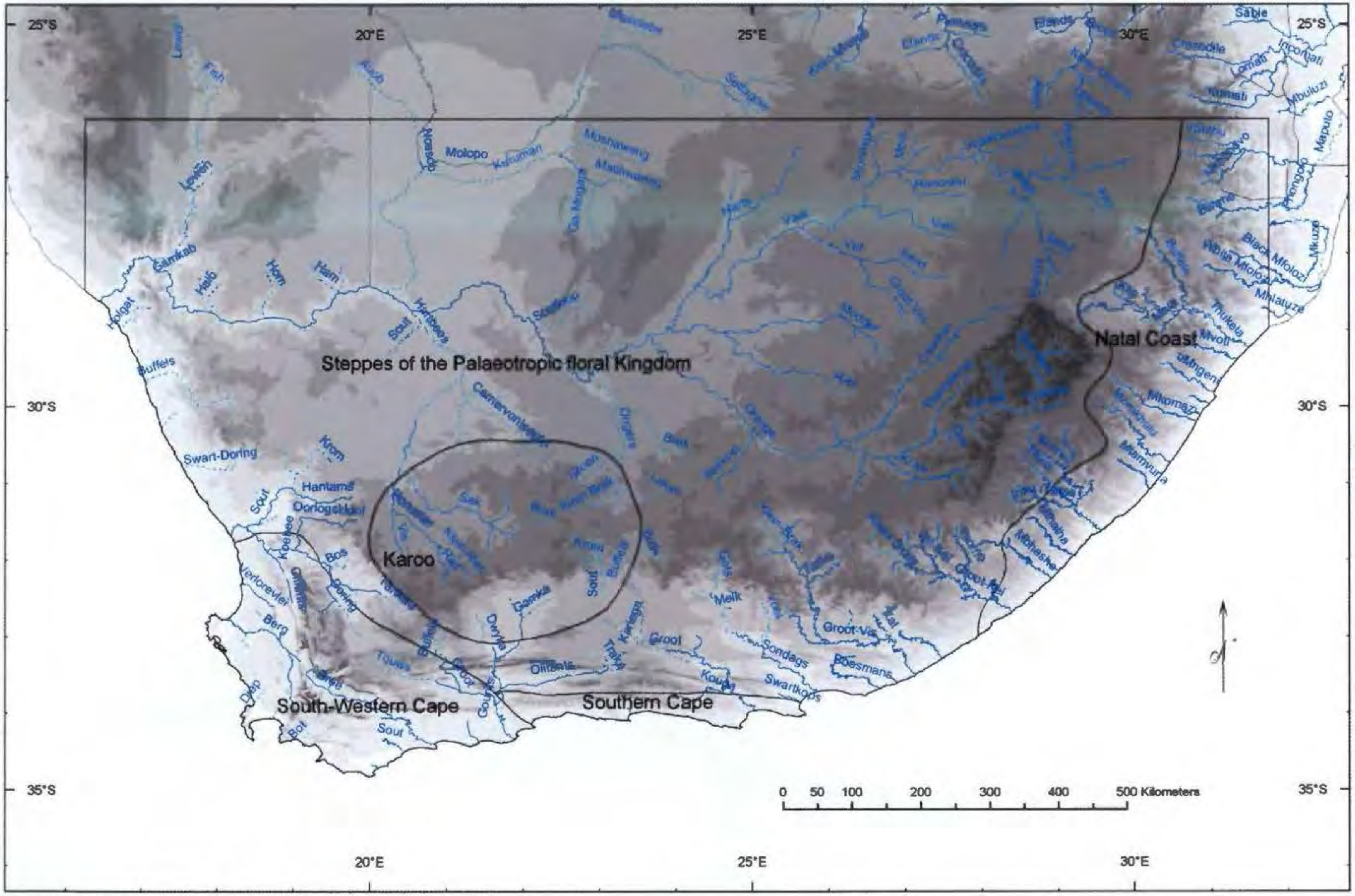


Figure 7: Floristic Divisions of Engler (1882).

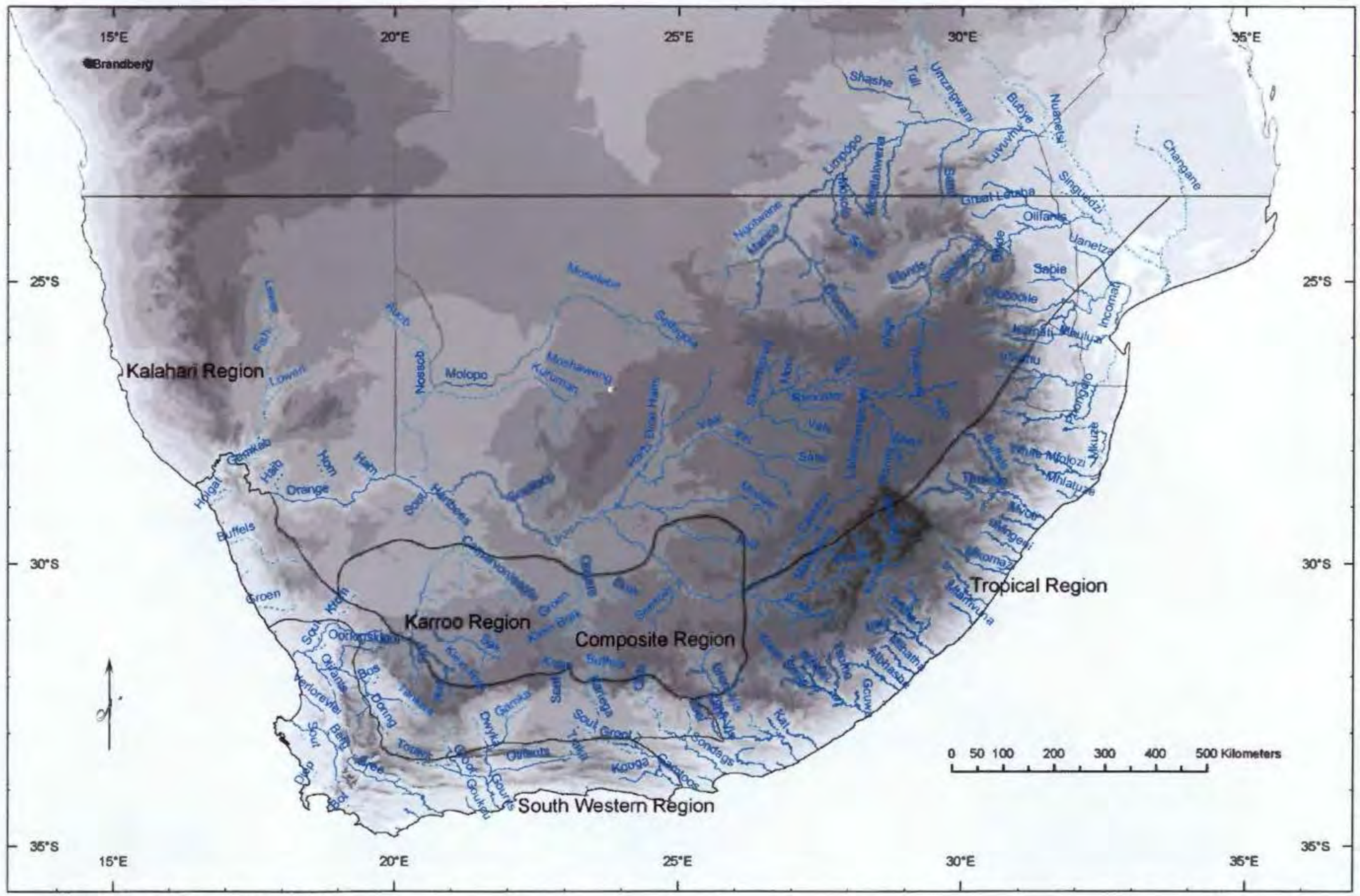


Figure 8: Floristic Divisions of Bolus (1886).

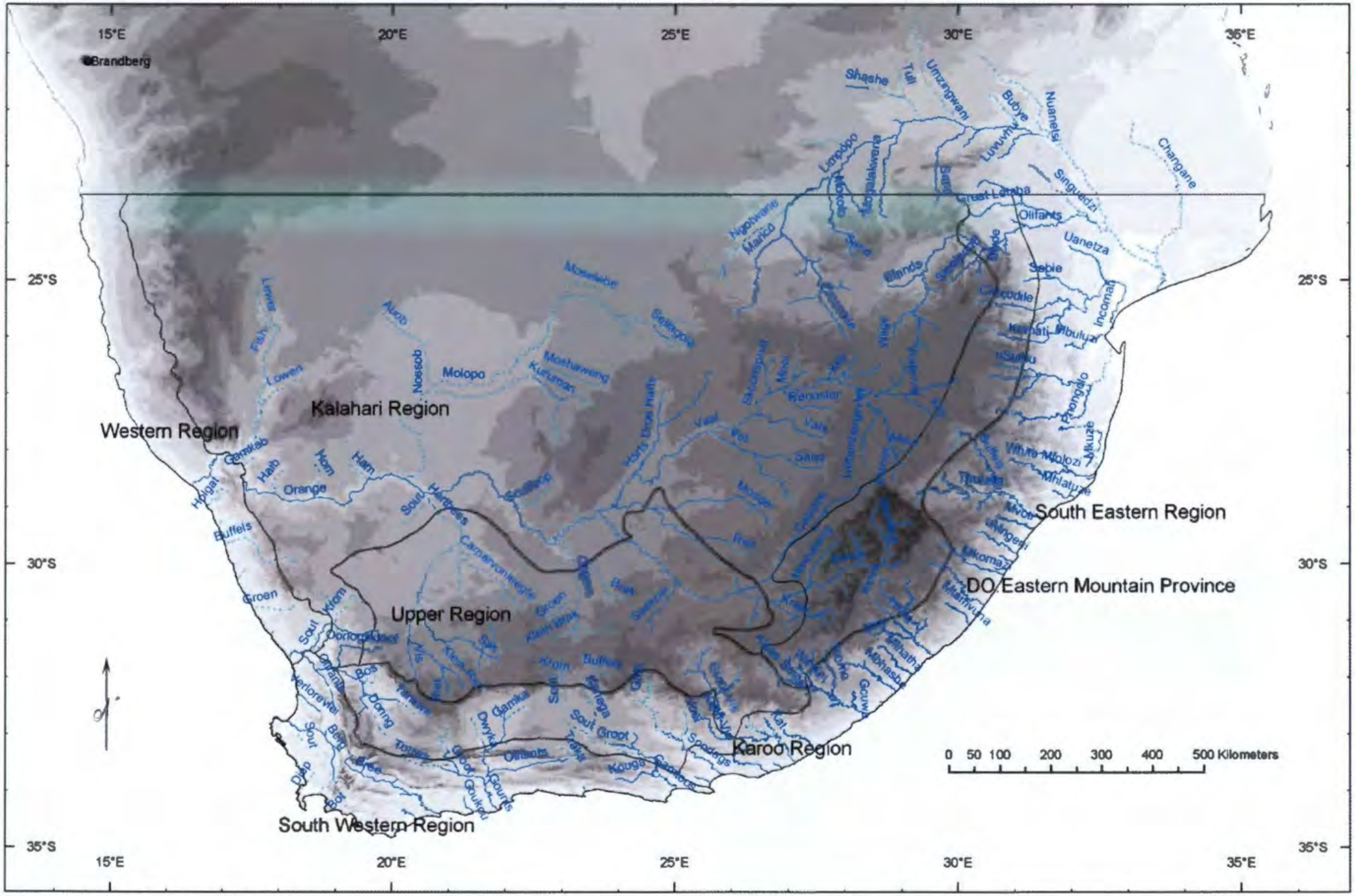


Figure 9: Floristic Divisions of Bolus (1905).

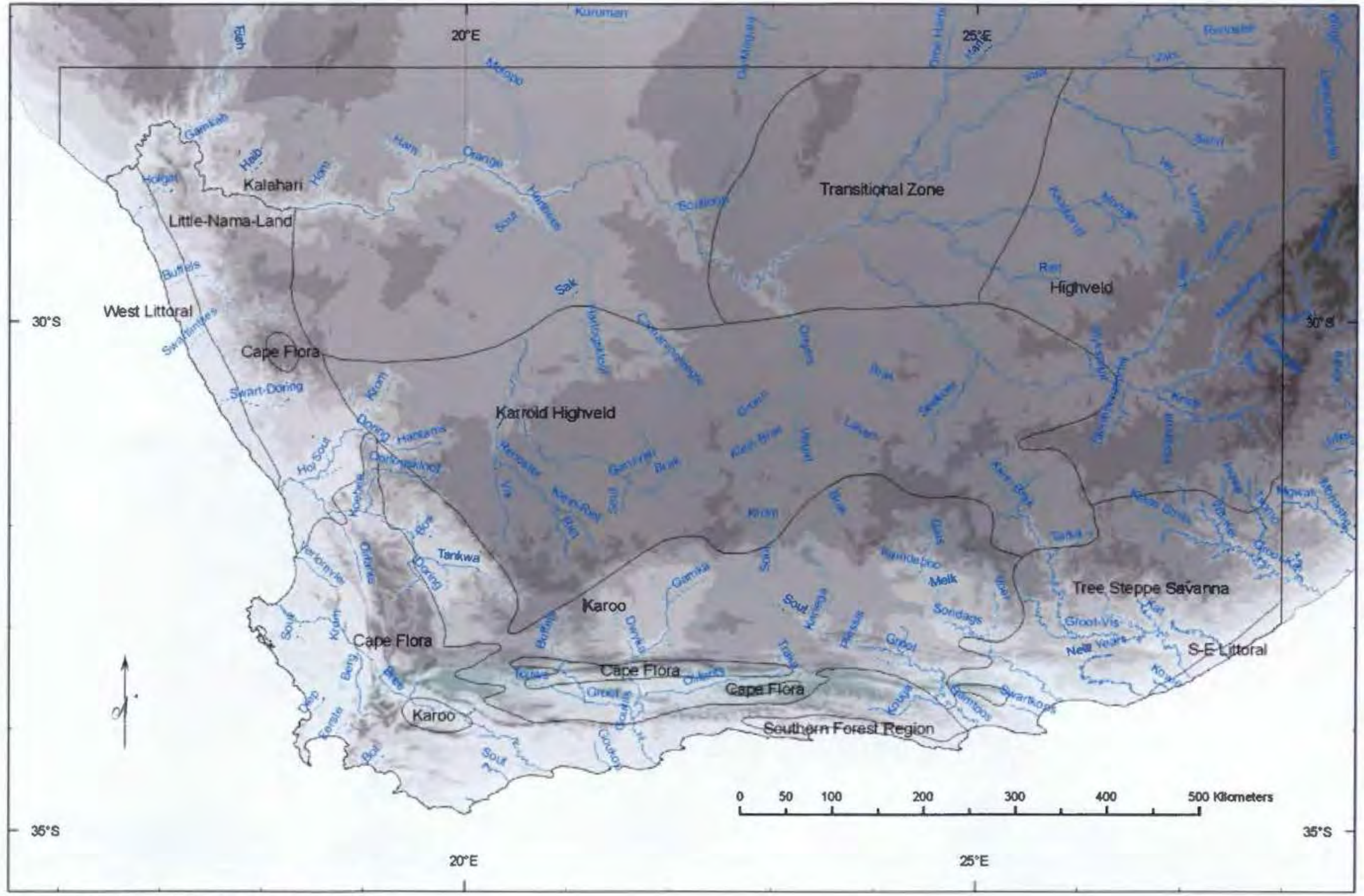


Figure 10: Floristic Divisions of Marloth (1908).

For a long time after Rehman's 1880 map, the flora of the South-western Cape was regarded as different from that of tropical Africa. However, it was not until 1908 when Marloth published his "Das Kapland" that the idiosyncratic nature of the Cape Flora began to be more fully appreciated. Marloth's 1908 map (Figure 10) was remarkably accurate and detailed. It recognised the interdigitation of the Fynbos and Karoo elements, especially the Little Karoo. It indicated that CFR flora occurred on the higher mountains of the Little Karoo, such as the Witteberg, Klein and Groot Swartberg, and also the Kammanassieberg. Marloth also identified outlying regions of Cape Flora, such as the Kamiesberg in northern Namaqualand and the Groot Winterhoek in the east. Further, Marloth (1908) showed considerable insight in identifying the Worcester-Robertson Karoo area.

#### 2.2.1.2 Weimarck (1941): The Phytochoria of the Cape Floristic Region; Figure 11

Weimarck's (1941) study of the CFR, '*Phytogeographical groups, centres and intervals in the Cape Flora*', represented a landmark in the study of the Cape Flora. Weimarck assembled a relatively small dataset by today's standards, comprising 462 types (taxa of species rank or lower) from 24 genera, which were largely centred in the area defined by Marloth (genera of the Cape element proper) and which at that time had been recently reviewed or monographed. These genera included: *Anthochortus*, *Aristea*, *Connomois*, *Chondropetalum*, *Cliffortia*, *Corymbium*, *Elytropappus*, *Hypodiscus*, *Hypolaena*, *Klattia*, *Leptocarpus*, *Lobostemon*, *Nivenia*, *Passerina*, *Phyllocomos*, *Restio*, *Staberoha*, *Stoebe*, *Thamnochortus*, *Willdenowia*, and *Witsenia*. It was remarkable that Weimarck was able to retrieve his Phytogeographical centres without the inclusion of taxa such as *Erica* and Proteaceae, which are dominant and characteristic CFR (particularly fynbos) taxa. Weimarck had benefitted from the Swedish, South African and Rhodesian Expedition (1930-1931), an extensive fieldtrip through southern Africa, undertaken in the company of Norlindh.

Table 1: Numbers of species identified from each of the natural floral groups, as proposed by Weimarck (1941). The Cape-Drakensberg floral groups have a number of sub-sets.

| Species endemic in the Cape Proper | | Species occurring (also) outside the Cape Proper | |
|---|---|---|---|
| Floral Group | Sp | Floral Group | Sp |
| Cape Ubiquists | 15 | Cape-Drakensberg | |
| Cape Ubiquists with a Knysna interval | 16 | Spp. restricted to Cape and Drak. centre | |
| The Karroo Mountains-W. Group | 17 | Ubiquists within the Cape | 5 |
| Southern Group | 26 | Southern within the Cape | 1 |
| Species with a Knysna interval | 4 | Spp. S. E. within the Cape | 3 |
| Western Group | 62 | Spp. Western within the Cape | 1 |
| Lange Berg-S. W. Group | 30 | Spp. extending from Cape over Drak. to mountains of tropical Africa | 3 |
| South Western Endemics | 149 | | |
| North Western Endemics | 42 | Drakensberg Endemics | 13 |
| Langeberg Endemics | 19 | Drak-Tropical Africa Mountain Group | 5 |
| Karroo Mountain Endemics | 13 | Montane Endemics within Tropical Africa | 13 |
| South Eastern Endemics | 13 | Madagascar Endemics | 9 |

During this fieldtrip they not only collected in South Africa, but they also travelled to the eastern escarpment mountains of modern-day Zimbabwe. Using a simple visual comparison of taxon distribution maps, he systematically classified the taxa into various distribution categories, some of which are nested within each other (Table 1).

In addition to centres, he also mapped disjunctions or intervals (Figure 11), expanding on the works of Marloth and others. In addition, Weimarck was able to identify subtle floristic differences within the CFR, leading to the establishment of phytogeographical provinces of endemism, many of which he subdivided into hierarchical sub-centres (Table 2). Earlier biogeographers, such as Drége (1843), Rehman (1880) and Engler (1882), documented differences in the flora of the CFR, and their classifications were largely based on physiognomic regions (Weimarck, 1941). However, Weimarck's level of resolution was far more detailed and floristic, because he was concerned with actual taxon distributions (Weimarck, 1941), rather than vegetation structure.

On the whole, the centre and sub-centre divisions of Weimarck are remarkably accurate and have only undergone minor revisions (*cf.* Figure 11 and Figure 2). Following is a brief description of the centres identified by Weimarck that are to be read in conjunction with the map. Firstly, there is the Southwest Centre, between the coast and the Berg – Bree River line. Secondly, to the north is the Northwest Centre, running from Cogmans Kloof to the Doorn River. Thirdly, in the centre is the Langeberg Centre, which includes the coastal plains between the Bree River and the Gouritz River. Fourthly, going inland is the Karoo Mountain Centre, which includes the mountains of the Little Karoo, notably the Little and Great Swartberg. Fifthly, is the area east of Plettenberg Bay (Keurbooms River), which extends to Grahamstown and inland to the Zuurberg, which forms the South-Eastern Centre. Weimarck excluded the Little Karoo (Karoo Interval) and coastal forest region between the Gouritz River and Plettenberg Bay (Knysna Interval) from his Cape Region, and he collectively referred to these areas as the Knysna Region (Figure 11).

Weimarck's (1941) classification also identified Cape elements beyond the borders of the CFR. These were named as follows: the Drakensberg Centre (30 species; 13 endemics); the Tropical African Mountain Centre (21 species; 0 endemics). He then listed the following sub-centres: Inyangani (10; 0); Mlanje (6; 0); Rungwe (9; 0); Katanga (4; 0); Kenya (7; 4 endemic to tropical Africa, one found in the Cape); Kivu (4; 0); Abyssinian (1; 0); Angolan (5; 0); Cameroon (4; 0); and finally the Madagascar Centre (9; 9).

Weimarck (1941) included the disjunct Kamiesberg and Hantam-Roggeveld as sub-centres of his Northwest Centre, even though they are disjunct from the CFR proper. This may have been largely due to the lack of detailed botanical knowledge of those areas at the time and consequently there was an absence of conflicting data. Weimarck (1941) may have also based these results on patterns observed in *Cliffortia* (Rosaceae), which he had revised (Weimarck, 1934). Interestingly, *Cliffortia* by itself still supports this association in my study.

Weimarck (1941) also recorded intervals or disjunctions in the distribution ranges of the taxa he dealt with, both within the Cape and between the Cape and the other Centres with Cape affinities. Intervals within the Cape include: the North-Western interval (12 species show this pattern strongly, another 6 less strongly, i.e. scattered individuals throughout interval); Doorn River (4); Tulbagh (8); Karroo (3); and the Knysna interval (21). Intervals outside the Cape are: the Kaffaria (1); Limpopo (8); Zambesi (5); Nyasa (6); East African Steppe (7); Rudolph (1); Upper Zambesi-Kassai (3); and the Congo Basin (4).

Table 2: The Centres and Sub-Centres within the Cape Flora, as identified by Weimarck (1941).

| Centre<br>Sub-Centre | No. of Species | No. of Endemics |
|---|---|---|
| South Western Centre | 315 | 149 |
| Cape Peninsula | 167 | 21 |
| French Hoek | 160 | 20 |
| Bredasdorp | ? | 24 |
| Hottentots Holland | 152 | 9 |
| | | |
| North Western Cape | 157 | 42 |
| Great Winterhoek | 107 | 8 |
| Cedarberg | 67 | 8 |
| Kamiesberg | 24 | 2 |
| Hantam-Roggeveld | ? | 2 |
| | | |
| Langeberg Centre | 133 | 19 |
| | | |
| Karroo-Mountain Centre | 55 | 13 |
| | | |
| South-Eastern Centre | 88 | 13 |
| Zitzikamma | ? | ? |
| Cockscomb | ? | 6 |
| Zuurberg | ? | 1 |

### 2.2.1.3 The Post-Weimarck Period

A number of subsequent, more taxonomically representative studies have been undertaken on the flora of the CFR (Oliver et al., 1983; Goldblatt and Manning, 2000). These have more or less supported the results of Weimarck. Ongoing taxonomic reviews and monographs continually increase knowledge of taxa and their distributional ranges, with the result that reassessment of phytochoria are necessary from time to time.

There are significant differences in the methodologies employed by Weimarck (1941) and Oliver et al., (1983). In the latter study, taxa were selected based on preconceived ideas of what constituted a Cape (fynbos) Clade. This essentially restricted the taxa analysed to those centred in montane areas, mostly on TMS substrates. Although including more numerous and diverse taxa, this was similar to the study of Weimarck, who also analysed this 'Cape element proper'. QDSs were clustered according to presence/absence similarity. Although these QDSs are dependent on the lines of longitude and latitude, they are essentially arbitrary, both geographically and topographically.

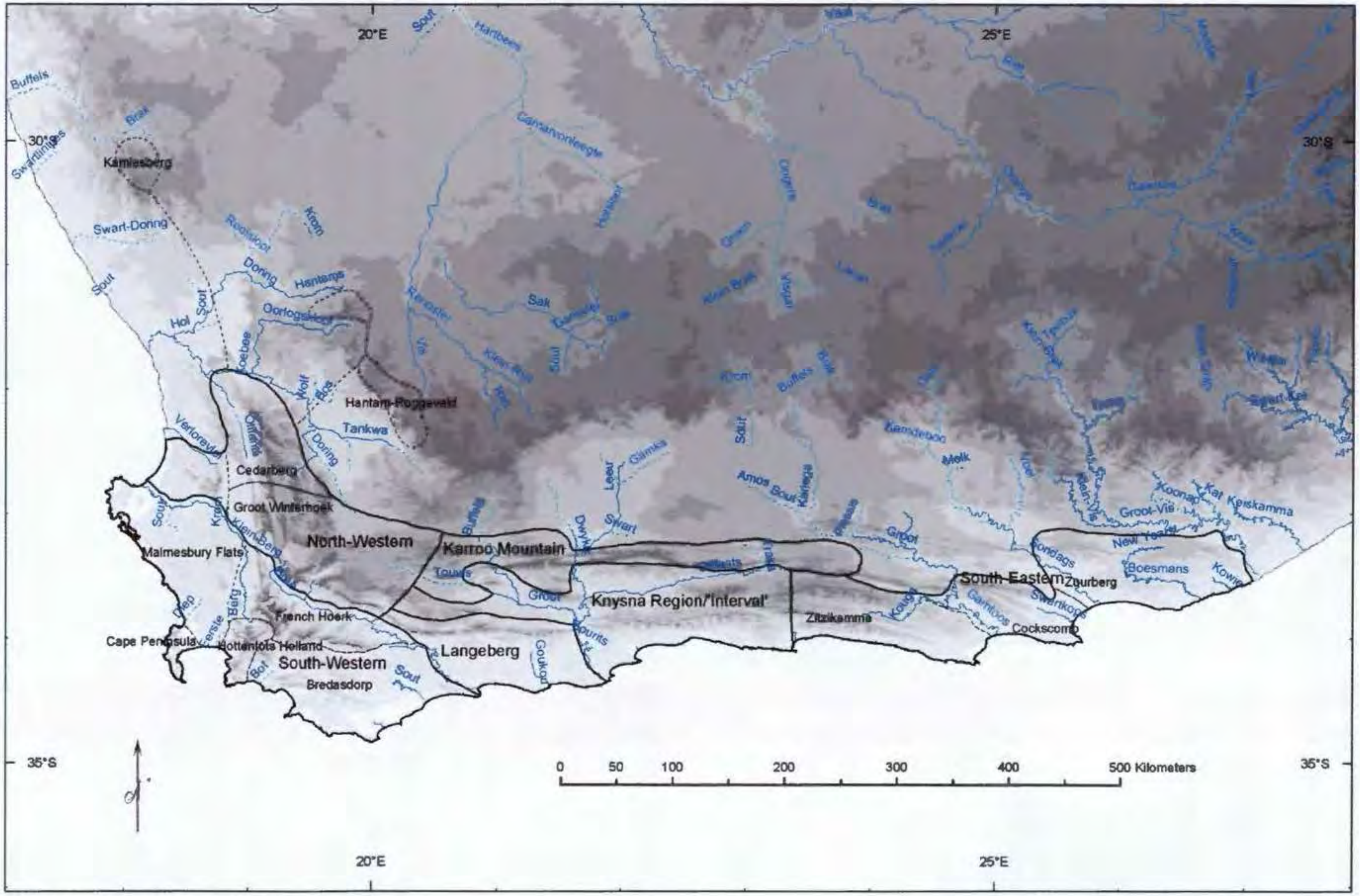


Figure 11: Floristic Divisions of Weimarck (1941).

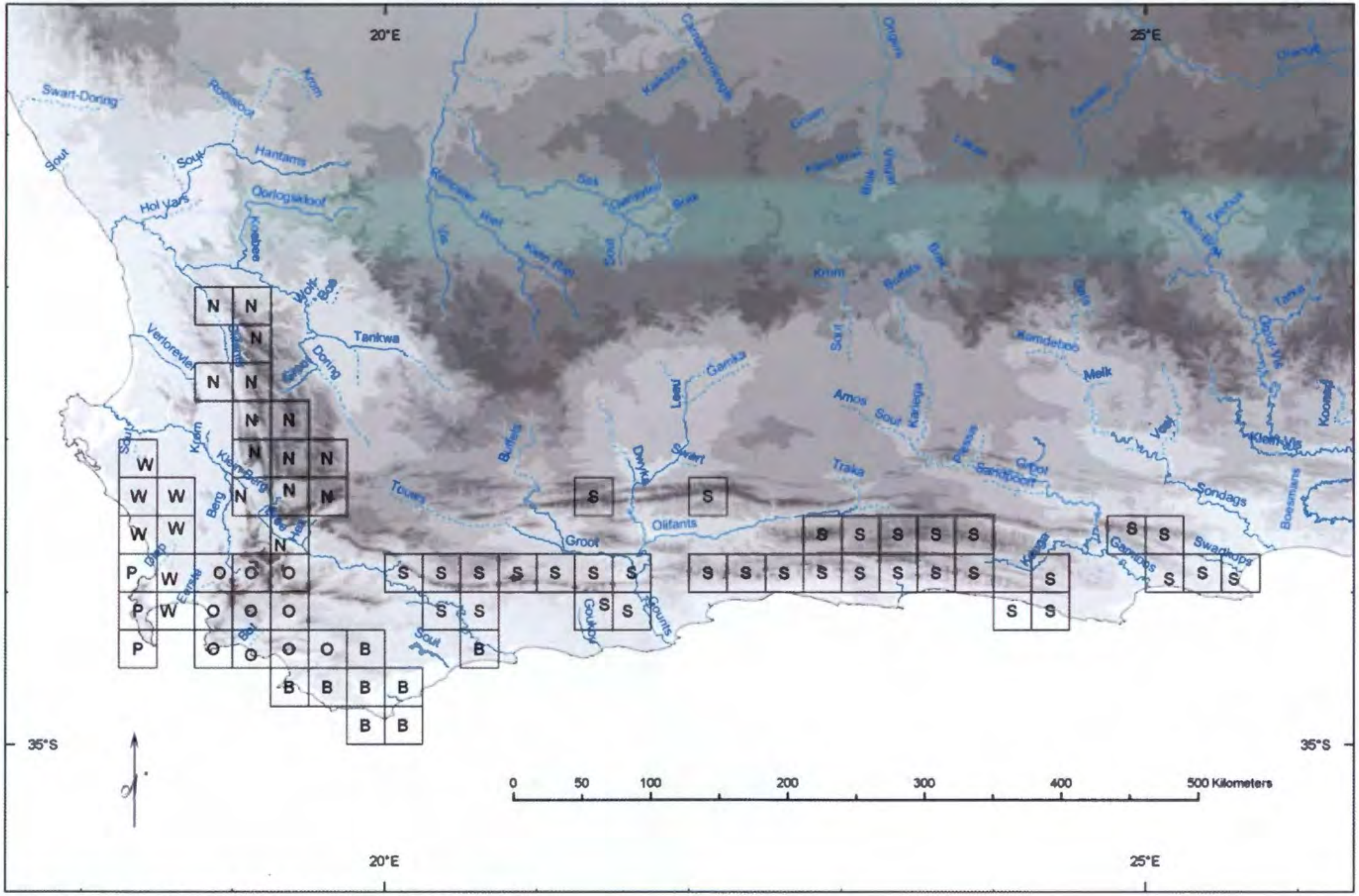


Figure 12: Floristic Divisions of Oliver, Linder, and Rourke (1983).
B = Bredasdorp; N = Northwest; O = South-western, S = Southern; W = West Coast

Advances in analytical technology have meant that increasingly larger datasets can be analysed, in more detail and in ways that were not previously possible. For example, in the study conducted by Oliver et al., (1983), 1936 species were analysed (analytical limit of 2000), using multivariate statistical approaches. The results of their study (Figure 12) were largely congruent with the results of Weimarck. No outlying centres were identified by Oliver et al., (1983), as boundaries for the CFR where predetermined, which excluded taxa and distributions outside these preconceived boundaries. There were no sub-centres in the North Western Centre, while Weimarck had three and the South Western Centre had three instead of five sub-centres. The Bredasdorp-Riversdale was delimited as an independent centre. Weimarck recognized it as a sub-centre of the South Western Centre. Further east, the Karoo Centre, Langeberg Centre and the South Eastern centre were all merged into a single, sparse centre.

Goldblatt and Manning (2000) did not detail the methods by which they produced their phytogeographical map of the CFR (Figure 2). However, their approach appears geographic in focus, working with a preconceived area, unlike Weimarck, who worked with preconceived Cape elements. Goldblatt and Manning (2000) sub-divide the CFR into phytogeographical centres (or units, perhaps better equating to phytogeographical provinces), based on the floristic affinities of all the taxa present. Thus, Goldblatt and Manning (2000) did not have Intervals in the same sense as Weimarck. Goldblatt and Manning (2000) listed all the taxa present in these centres, and noted which were endemic. Their Southwest Phytogeographical Centre (SWPP) was almost identical to that of Weimarck's (1941), except in the south, where Goldblatt and Manning (2000) recognised an independent Agulhas Plains Phytogeographical Centre/Province (APPP). The APPP also overlapped with the Langeberg Phytogeographical Centre and the western Knysna Region of Weimarck's along the coastal strip. The Northwest Phytogeographical Centre/Province (NWPP) of Goldblatt and Manning (2000) extended further north than that of Weimarck's to include the Nieuwoudtville Escarpment, Matsikammiesberg and the coastal plain north of Elandsbaai. Furthermore, it was reduced in the east, with the Witteberg and part of the Bontberg and Waboomsberg being assigned to the Karoo Mountain Phytogeographical Centre/Province (KMPP). One of the greatest differences was that Goldblatt and Manning (2000) included the Knysna Region in the CFR, which Weimarck did not assign to any centre, as it largely lacked fynbos element data in his study. Goldblatt and Manning (2000) partitioned the Knysna Region between the Langeberg Phytogeographical Centre/Province (LBPP), the KMPP and the Southeast Phytogeographical Centre/Province (SEPP). Thus, the LBPP and KMPP of Goldblatt and Manning (2000) were enlarged, compared to those of Weimarck. The LBPP included the Gamkaberg, while the Keeromsberg was added to the KMPP. The SEPP, of Goldblatt and Manning (2000) was similar to that of Weimarck, but only in its central regions. To the west, it included part of Weimarck's southeast Knysna Region and in the east it excluded the Suurberg Sub-Centre of Weimarck, but included the Baviaanskloofberge.

Bayer (1984) justifiably criticized a number of phytogeographical studies (Goldblatt, 1978; Oliver et al., 1983) for being "Cape Flora centred", because they ignored the rich leaf succulent and geophytic flora, which is partly adjacent to, and included within the "boundaries" of the CFR. The analyses of Weimarck and of Oliver et al., (1983) focused mainly on the montane, sandstone taxa, which are predominantly members of the fynbos vegetation (Weimarck's 'Cape elements proper'). The fynbos biotic element is numerically dominant within the CFR, comprising of 4800 species of the 9000 CFR species (Goldblatt and Manning, 2000). This could "drown out" the influence of other biotic elements in combined datasets, or at coarse geographical scales where a number of biotic elements are combined into single geographic entities like QDSs. Cowling and Proches (2005) calculated that this fynbos element could be as high as 70% of the CFR flora, or 6300 species. Bayer (1984) argued for a broader definition of "Cape" to include the Succulent Karoo component as well. Ecologically, this would mean a winter rainfall flora, rather than a sandstone flora. Jurgens (1991) also advocated a "Greater" Cape Flora, essentially combining the Succulent Karoo and Fynbos Biomes. Nonetheless, Goldblatt and Manning (2000) took over the Weimarckian phytogeography limiting their study to a more restricted geographical area (excluding Cape Flora outliers to the northwest and northeast). They combined their findings with Oliver et al., (1983), and intuitively produced a set of six centres for the Cape Floristic Region. van Wyk and Smith (2001) used "perception" or "intuitive discernment", and focused much more on the succulent flora, which produced a fairly similar and mostly congruent set of areas (van Wyk and Smith, 2001). Their Succulent Karoo Region was enlarged (especially within the CFR) and the distribution of succulents was emphasized, with the Fynbos Flora receiving less attention. Depending on the biogeographer's taxon of expertise and the resultant paradigm, different patterns may become apparent or emphasized.

Born, Linder and Desmet (2006) investigated the delimitation of the Cape Floristic Region, using a dataset of all species. They used taxon ranges tied to relatively large, subjectively predefined centres or areas, rather than QDSs. Their study revealed that the Succulent Karoo (Namaqualand) Flora is more closely related to that of the CFR than the adjacent tropical African Flora. Consequently, they suggested that a "Greater Cape Floristic Region" should be recognized. This region would combine the CFR and the Succulent Karoo Region (SKR) as sister areas, because they are more similar to each other than either one is to the rest of the African Flora, and as sister regions, they contribute higher numbers of endemic taxa.

### 2.2.2 Aims

I will be using a much expanded and improved dataset to explore the phytogeographical patterns in the Cape Flora, slightly biased towards Fynbos taxa. I aim to address the following issues:

1. To establish the spatial distribution of range-restricted Angiosperm species across the CFR.
2. To delimit Phytogeographical Centres (PC) within the CFR, to account for concentrations of range-restricted species.
3. To generate lists of taxa endemic to the PC, with their habitats, where known, that could be used for conservation planning and management.
4. To determine if there are hierarchical relationships between these PC and whether they can be grouped into larger entities, what these entities are, and whether they are congruent with higher level (chorological provinces and regions) floristic studies.
5. To determine if there is congruence in patterns of endemism between the different datasets (either taxonomic families or growth form guilds), and if not, what might account for these differences.
6. To determine if there is congruence between the present study and other major floristic studies undertaken on the CFR, principally Weimarck (1941), Goldblatt and Manning (2000), and Oliver et al., (1983).
7. To assess the correlation between endemism and species richness.
8. To briefly investigate the boundaries of the CFR, particularly in the northwest, where the fynbos and succulent Karoo biomes abut.
9. To identify potential disjunct Cape Clade elements outside the CFR.

# 2.3. METHODS

## 2.3.1 General

### 2.3.1.1 Taxa

A total of 4387 taxa (including 446 sub-specific taxa, mostly subspecies and varieties, and a few forms) in 399 genera in 64 families were used in my study. Approximately 91.6% of these taxa are represented in the CFR. Species distributions were opportunistically obtained from various sources including nearly all digital datasets used in previous biogeographical studies (such as Oliver et al., 1983), taxon specialists, the South African Red Data Lists (RDL) and the Protea Atlas Project. As RDL taxa are mostly range restricted and contains representatives of almost all taxa in the CFR, it represents a disproportionately large contribution of taxa that contribute most to establishing PCs, whilst omitting less informative widespread taxa. The taxonomic datasets assembled and digitised specifically for this study included Asteraceae, the two geophyte genera *Ferraria* and *Haemanthus*, and certain genera of the Tribe Diosmeae in Rutaceae. The comprehensiveness of the datasets varied from group to group, from 100% to only a small fraction (Table 3). As the RDL overlaps with many of the taxonomic datasets, considerable effort was employed to remove synonomous taxon names and localities, and use the most up to date nomenclature. While I attempted to produce a clean dataset for analysis, cleaning datasets of this size is an ongoing process, and is reflected in the slightly different dataset totals reported, which vary by about 2% in the Combined Dataset.

Table 3: Representation of taxa of the various datasets in the study, and the species diversity from Goldblatt and Manning (2000), and Goldblatt, Manning and Snijman (2005).
The figures for taxa in the study may exceed those of Goldblatt and Manning for two reasons. Firstly, Goldblatt and Manning list only species, while my study includes sub-specific taxa. Secondly, in this study, entire clades were analysed where possible, while Goldblatt and Manning list only taxa in their geographically predefined CFR.

| Dataset | Family | Total spp in CFR[1] | Taxa in study | Cape clade |
|---|---|---|---|---|
| Combined Dataset | All | 9 087 | 4 387 | Numerous |
| Asteraceae | Asteraceae | 1 048 | 431 | Numerous |
| Bruniaceae | Bruniaceae | 64 | 78 | Bruniaceae |
| Ericaceae | Ericaceae | 667 | 803 | *Erica* |
| Fabaceae | Fabaceae | 761 | 329 | Numerous |
| Geophytes | Numerous | 1 551 | 408 | Numerous |
| Orchidaceae | Orchidaceae | 227 | 454 | Disinae |
| Poaceae | Poaceae | 208 | 142 | Danthoniae |
| Polygalaceae | Polygalaceae | 142 | 119 | *Muraltia* |
| Proteaceae | Proteaceae | 330 | 403 | Proteae |
| RDL Taxa | Numerous | 1 549 | 1 549 | Numerous |
| Restionaceae | Restionaceae | 320 | 347 | African Restionaceae |
| Rosaceae | Rosaceae | 120 | 121 | *Cliffortia* |
| Rutaceae | Rutaceae | 273 | 279 | Diosmeae |

[1] Based on Goldblatt and Manning (2000), and Goldblatt, Manning and Snijman (2005)

The datasets differed in the method of their compilation. The Protea Atlas Dataset was based on a very thorough sampling regime. As a result, both widespread and rare species can be assumed to be completely mapped. The herbarium specimen-based datasets (Orchidaceae, Poaceae, Restionaceae), and the datasets assembled from taxonomic revisions, are likely to under-represent widespread taxa, while rare species are likely to have better representation. Finally, the remaining datasets are biased and include only range-restricted species (Asteraceae and RDL datasets), thus excluding more widespread species.

In order to determine whether patterns of diversity, endemism and PC formation are affected by phylogenetic properties, the data were divided into smaller sub-datasets, following taxonomic divisions where possible, usually at the family level. These family categories mostly represented some of the typical CFR clades (Table 3).

A widespread taxon may be problematic if it is the only taxon present in under-represented areas and may form artificial and geographically large PCs in the absence of more range-restricted taxa from neighbouring floras. In addition, these taxon localities may be very disjunct, forming disjunct PCs. It is difficult to determine, without thorough sampling of widespread taxa, whether they are under-collected across their distribution ranges, or are genuinely disjunct.

Table 4: List of widespread taxa ignored in the GIS analysis for modifying PC.

| Dataset | Taxon | PC |
|---|---|---|
| Geophyte Dataset | *Ferraria schaeferi* (13) | Namaqualand Centre |
| Geophyte Dataset | *Haemanthus namaquensis* (6) | Namaqualand Centre |
| Restionaceae dataset | *Thamnochortus glaber* (14) | Langeberg Centre |
| RDL Taxa Dataset | *Osteospermum pterigoideum* (4) | |
| RDL Taxa Dataset | *Dorotheanthus apetalus* (3) | |
| Orchidaceae Dataset | *Pterygodium hallii* (15) | Northern Centre |
| Orchidaceae Dataset | *Holothrix pilosa* (8) | South Coast Centre |
| Orchidaceae Dataset | *Holothrix grandiflora* (8) | South Western Centre |
| Orchidaceae Dataset | *Bonatea polypodantha* (2) | Widespread, (Drakensberg Remainder Endemic) |
| Poaceae Dataset | *Merxmuelleria dura* (13) | Namaqualand Centre |
| Combined Dataset | *Muraltia macowanii* (2) | Karoo Centre |
| Combined Dataset | *Pentaschistis airoides* ssp *jugorum* (15) | Drakensberg Centre |
| Combined Dataset | *Satyrium anomalum* (4) | Drakensberg Centre |

### 2.3.1.1.1 Asteraceae

Aside from the asterids listed in the RDL, no substantial geographical dataset existed for Asteraceae. Asteraceae has never been considered a typical CFR clade at higher (family or even tribal) taxonomic levels, although there may be CFR clades at lower taxonomic (generic) levels. However, it nevertheless contributes the largest number of species and genera of all the families present in the CFR. I therefore considered it important to include representatives of this diverse taxon, even though many of the revisions are dated. Furthermore, due to time constraints, only certain taxa were databased and analysed. As such, a more detailed breakdown of this previously unpublished dataset is provided here to highlight these potential biases. Globally, it is a significant family, particularly in semi-arid areas. Taxa were selected to include the species of all endemic genera and also species of limited range from all genera, supplemented by the RDL Asterids. The following complete genera (all taxa) were databased, giving both the herbarium from which the specimens were databased and the taxonomy that was followed: *Alciope* (BOL and Goldblatt and Manning, 2000); *Anaxeton* (BOL; RDL; Lundgren, 1972); *Anderbergia* (Nordenstam, 1996); *Anisothrix* (Anderberg, 1988); *Antithrixia* (Bremer, 1978); *Atrichantha* (BOL; Goldblatt and Manning, 2000); *Bryomorphe* (Goldblatt and Manning, 2000; BOL); *Cadiscus* (RDL; BOL); *Calotesta* (Karis, 1990); *Corymbium* (Weitz, 1989); *Dolichothrix* (Goldblatt and Manning, 2000; BOL); *Dymondia* (RDL; BOL); *Edmondia* (Goldblatt and Manning, 2000; BOL); *Gibbaria* (Goldblatt and Manning, 2000; BOL); *Gymnostephium* (Goldblatt and Manning, 2000); *Hippia* (RDL; BOL; Goldblatt and Manning, 2000); *Hydroidea* (Karis, 1990); *Lachnospermum* (BOL; Goldblatt and Manning, 2000); *Lamprocephalus* (BOL); *Langebergia* (BOL); *Lidbeckia* (BOL; Goldblatt and Manning, 2000); *Mairea* (Zinnecker-Wiegand, 1990); *Marasmodes* (RDL; BOL; Goldblatt and Manning, 2000); *Oligothrix* (Goldblatt and Manning, 2000; BOL); *Oreoleysera* (Bremer, 1978); *Osmitopsis* (Bremer, 1972); *Oxylaena* (Goldblatt and Manning, 2000); *Percidium* (BOL; Goldblatt and Manning, 2000); *Petalacte* (BOL; Goldblatt and Manning, 2000); *Phaenocoma* (BOL; Goldblatt and Manning, 2000); *Phaneroglossa* (Nordenstam; 1978); *Planea* (Karis, 1990; Goldblatt and Manning, 2000); *Poecilolepis* (Goldblatt and Manning, 2000; BOL); *Polyarrhena* (Grau, 1970); *Thaminophyllum* (RDL; Bond, 1980); *Vellereophyton* (Hilliard, 1983).

Partially databased genera included: *Amellus* (Rommel, 1977); *Amphiglossa* (BOL; RDL); *Arctotheca* (RDL); *Arctotis* (RDL); *Aster* (Goldblatt and Manning, 2000; BOL); *Athanasia* (RDL; Källersjö, 1991); *Berkheya* (RDL); *Cenia* (RDL); *Chrysocoma* (RDL; Bayer, 1981; Wijnands, 1985); *Comborhiza* (RDL); *Cotula* (RDL, BOL); *Cullumia* (RDL; Roesler, 1959); *Dicoma* (BOL); *Dimorphotheca* (RDL; Norlindh, 1943); *Disparago* (Goldblatt and Manning, 2000; BOL; Koekemoer, 1993); *Elytropappus* (RDL; BOL); *Eriocephalus* (RDL); *Euryops* (RDL; Nordenstam, 1969); *Felicia* (RDL; Grau, 1973); *Gazania* (RDL; Roessler, 1959); *Gerbera* (RDL; Goldblatt and Manning, 2000; BOL); *Haplocarpha* (RDL); *Helichrysum* (RDL; Goldblatt and Manning, 2000; BOL); *Heterolepis* (RDL); *Heterorhachis* (Goldblatt and Manning, 2000; BOL); *Lasiopogon* (BOL); *Metalasia* (RDL; Karis, 1989; Pillans, 1954); *Oedera* (RDL); *Oldenburgia* (RDL; Bond, 1987); *Oncosiphon* (RDL); *Osteospermum* (RDL; Norlindh, 1960); *Othonna* (RDL; BOL; Goldblatt and Manning, 2000); *Pteronia* (RDL; Goldblatt and Manning, 2000; BOL; Brusse, 1990); *Pterothrix* (RDL); *Relhania* (RDL; Bremer, 1976); *Senecio* (RDL; BOL; Goldblatt and Manning, 2000); *Steirodiscus* (RDL; BOL; Goldblatt and Manning, 2000); *Stoebe* (RDL; Levyns, 1937); *Trogophyton* (Goldblatt and Manning, 2000; BOL; Anderberg, 1991); *Ursinia* (RDL; Prassler, 1967); *Zyrphelis* (RDL; Zinnecker-Wiegand, 1990).

#### 2.3.1.1.2 Geophyte Data

Rovito et al., (2004) discuss Pliscoff's (2003) analysis of tree growth forms, thus analysis of functional groups in phytogeography is not unprecedented. Functional groups may be more inclined to face similar selective pressures, and may thus show convergence in distribution. Further, most CFR geophytes are members of Asparagales (Colchiaceae being the most notable exception), which represents an ordinal rather than familial taxa, but which is not monophyletic in this study, as Orchidaceae was analysed individually.

Many of the geophytic clades were poorly represented in my study and biased towards range-restricted species. In addition, the datasets were assembled from diverse clades. Due to the geographic bias in the construction of my Geophyte Dataset, it is possible that widespread taxa that occur inside and outside the CFR may contribute to endemism and the establishment of "artificial" PCs, especially on the periphery of the CFR. This may in turn cause an unrealistic increase in the geographic size of the PC, due to the absence of more range-restricted taxa, which could lead to the sub-division of these larger areas into smaller floristic units. For this reason, several taxa were excluded from GIS analysis for the establishment of PCs (Table 5). It is very probable that a more taxonomically complete dataset would reveal that these widespread taxa occur in a number of PCs and thus should not be considered for PC construction at smaller geographical scales. However, these widespread taxa may still be useful in determining the relationships between PCs.

Table 5: Geophytic taxa excluded from the analyses of PCs .

| Taxon | PC |
|---|---|
| *Haemanthus humilis subsp. humilis (53)* | E Southeastern Centre |
| *Haemanthus pubescens subsp. arenicolus (5)* | Namaqualand Centre |
| *Ferraria glutinosa (53)* | No Centre |
| *Haemanthus avasmontanus (1)* | No Centre |
| *Haemanthus carneus (5)* | No Centre |
| *Haemanthus deformis (10)* | No Centre |
| *Haemanthus humilis subsp. hirstus (44)* | No Centre |
| *Haemanthus montanus (27)* | No Centre |

### 2.3.1.1.3 Red Data List (RDL) Taxa

Due to the use of threatened or listed taxa in conservation planning, analysis of the phytogeographical patterns and distribution of endemics of this dataset may shed light on how these threatened taxa represent taxonomically based groups. This may shed light on how protection of threatened taxa which are used by conservation planners for conservation prioritisation may potentially preserve phytogeographic process and pattern of individual taxonomic groups. This would also help identify which taxonomic groups may or may not be preserved, due to similarity of phytogeographical patterns between the individual taxonomic datasets and the threatened (RDL) taxa dataset.

### 2.3.1.2 Unit Area

The Quarter Degree Square (QDS) was employed as the minimum operational geographical unit (OGU) in this study (Crovello, 1981). Although artificial and random environmentally, the QDS has been utilised for a long period as the standard level of geographical precision for capturing geographical data of specimens in South Africa (Morris and Leistner, 1971). Although point locality is becoming increasingly popular and available, due to the wider availability of GPS, point locality data cannot be used directly for the delimitation of PCs using clustering techniques, as these techniques attempt to group areas based on taxonomic similarity. If sufficient point locality data were available, it would be possible to convert the points to Broad Habitat Units (BHUs) (Cowling and Heijnis, 2001) or to Vegetation Units (Low and Rebelo, 1996; Mucina and Rutherford, 2006). These may be more biologically meaningful than QDSs for the analysis of these areas. The analysis of input data (Moline and Linder, 2006) revealed some meaningful improvements in the construction of PCs using BHUs rather than QDSs, but the differences were relatively small. Other studies have also made use of more natural OGUs (Conran, 1995; Borchsenius, 1997; de Mera et al., 1997; Tribsch, 2004), rather than grids as has been the general custom (Oliver et al., 1983; Rosen, 1988; Morrone, 1994; Morrone and Crisci, 1995; Linder and Mann, 1998; Linder, 2001; Crisp et al., 2001; Cavieres et al., 2002; García-Barros et al., 2002; Szumik et al., 2002; Szumik and Goloboff, 2004; Mast and Nyffeler, 2003; Rovito et al., 2004; Giokas and Sfenthourakis, 2008; Ramdhani et al., 2008), although not always at finer spatial resolution. Thus, the large number of datasets available in QDS format makes the QDS level of analysis is still the most accessible, convenient and objective way of analysing large datasets for delimiting PCs. However, due to the increased spatial resolution and flexibility of point locality data, this does represent a more desirable source of raw data, if initially somewhat more time consuming to prepare. In total, 1034 QDSs were analysed and of these roughly a quarter were from the CFR – the remainder were widespread throughout Southern Africa, but contained few taxa.

#### 2.3.1.2.1 Scale of Resolution

QDSs represent an area of approximately 644.4 km$^2$ in the CFR (min = 633.92 km$^2$; max = 660.929 km$^2$; mean = 644.4172 km$^2$; std. dev. = 5.4953 km$^2$; n = 206). As such, these may contain diverse environmental features, such as topography, precipitation, solar radiation, temperature, geological substrate and aspect. Thus, there may be numerous biotic elements in a single QDS. This may result in a measure of conflict in the process of cluster analysis, especially when assigning a QDS to particular PC. For example, a QDS situated between a predominantly montane PC and a predominantly low altitude PC, could have equal portions of both high and low altitude taxa. Therefore, the QDS may consist of equal or similar numbers of endemics when combined with either of the neighbouring PCs. Inevitably, one of the PCs would lose out, and this could lead to an overall decrease in the potential number of endemic taxa recorded. Thus, endemism in this study was probably under-represented. To record the diversity of biotic elements present in a QDS, a preliminary analysis of the habitat preferences of endemic taxa was undertaken (see section 2.3.7.3).

Levels of conflict can be somewhat interpreted by taking into consideration the total number of taxa in the PC, as well as the number of taxa with more than 50% of their ranges in the PC, and the number of PC endemics. This "conversion rate of diversity from near PC endemic to PC endemic" gives some indication of the conflict between the taxa in the PC. Typically, a low conversion rate may indicate higher levels of conflict. It is a simple procedure to calculate the ratio of endemism of taxa to particular PCs in a GIS. At a later stage, if desired, taxa that are nearly, but not quite endemic to a PC, can then be assessed in order to determine whether this conflict or geographic overlap is true, or if it is due to coarse levels of data capture, such as QDSs containing different biotic elements. Using environmental envelopes - such as BHUs proposed by Cowling and Heijnis (2001) - yielded improved results, by reducing the conflict between different biotic elements (Moline and Linder, 2006). However, as yet there are insufficient quantities high resolution taxonomic data.

A further problem of the relatively coarse geographical input data is the loss of endemism in neighbouring PCs. This is perhaps less obvious, but of considerable importance when assigning PCs and should be taken into consideration when dealing with data at the coarse scale of QDSs. Even if the QDSs are correctly assigned to PCs, the loss of endemism in neighbouring PCs, due to the conflict of different biotic elements, may result in a cascade effect, similar to phylogenetic islands in clustering algorithms (Swofford, 1998). This may reduce the overall endemism of the PC, as a PC becomes increasingly dominated by numerically superior biotic elements from surrounding PCs, thus making it smaller than it should be. This may ultimately result in the incorrect placement of phytogeographical boundaries. More accurate spatial data would be required to resolve this issue. This may be particularly important in the CFR, where 70% of the taxa are TMS montane taxa (Cowling and Proches, 2005). At the QDS scale of resolution, PCs may be somewhat complex ecologically, comprising of disparate biotic elements.

#### 2.3.1.3 Datasets

Apart from analysing a single combined dataset, representative of the entire region, I sub-divided the datasets into family categories (Table 6), and in addition, into two functional datasets: Geophytes (ecological guild) and RDL Taxa (threat status). Analysis of these derivative datasets was undertaken with the cognition that individual taxa may display phytogeographical patterns that differ from the whole, but that data, time and space constraints seldom allow for a full investigation of these differences (Exell and Gonçalves, 1974), as undertaken here. Further, there is mounting evidence that environmental conditions strongly affect individual taxon richness patterns differently, which results in differing geographic richness patterns (Currie, 1991; Currie, Francis and Kerr, 1999), which may have taxon specific phytogeographical/chorological implications, prompting investigation. In recognition of space constraints, the results of these derivative datasets are relegated to an Appendix (Appendix I).

Table 6: Taxa used in the study.
The table below lists the taxa (cleaned data) used in the study, together with the number of taxa sampled, and the source of the data. The # (Number) of Records and # of Taxa columns are not additive, as the RDL taxa are nested in the Clade datasets. Herb. Spec. = Herbarium Specimens.

| Dataset | Taxa | Herbarium | Source | # Records | # Taxa | # Grids | Notes |
|---|---|---|---|---|---|---|---|
| Combined Data | All Taxa Listed Below | | All Taxa Listed in Table Below | 37 115 | 4387 | 1033 | Old and New data |
| | RDL | | RDL | 4946 | 1538 | 233 | |
| Asteraceae | Taxon Details listed below | | Various, see below | 1618 | 431 | 212 | Newly Coded |
| | RDL | | RDL | 419 | 152 | 147 | |
| Bruniaceae | Combined | BOL, NBG, PRE | Oliver et al., 1983 | 639 | 78 | 116 | Old data set |
| | RDL | | | 60 | 17 | 39 | |
| Ericaceae | Combined Erica | BOL, NBG, STE, SAM, GRA, PRE, NH | Oliver et al., 1983; Oliver 1999, 2000 | 8017 | 803 | 459 | Old and New data |
| | RDL *Erica* | | | 378 | 112 | 97 | |
| Fabaceae | Combined | | | 2317 | 329 | 207 | Old and New data |
| | *Aspalathus* | BOL, NBG, PRE | Oliver et al., 1983 | 2140 | 271 | 202 | Old and New data |
| | RDL Taxa | | RDL | 328 | 112 | 127 | New Data |
| Geophytes | Combined | | | 1735 | 408 | 484 | Mostly new data |
| | RDL Taxa | | RDL | 933 | 359 | 170 | New data |
| | *Bobartia* | BOL, NBG, PRE | Oliver et al., 1983 | 189 | 20 | 100 | Old Data |
| | *Ferraria* | | De Vos, 1979 | 259 | 15 | 184 | Newly Coded Data |
| | *Haemanthus* | | Snijman, 1984 | 409 | 26 | 313 | Newly Coded Data |
| Orchidaceae | Combined | | | 4467 | 454 | 549 | |
| | Orchidaceae | BOL | Linder, 1999 | 7360 Herb. Spec. | | | New Data |
| | RDL | | RDL | 196 | 39 | 81 | |
| Poaceae | Combined, mostly Danthonieae | BOL, NBG, STE, SAM, GRA, PRE, C, NU, B, CANB, OXF, PR, BM | Peter Linder | 2683 (8003 Herb. Spec.) | 142 | 565 | 97% of taxa and 98% of records Danthonieae, |
| | RDL | | RDL | 18 | 4 | 13 | 2 taxa Not Danthonieae |
| Polygalaceae | Combined | | | 871 | 119 | 172 | |
| | *Muraltia* | BOL, NBG, PRE | Oliver et al., 1983 | 863 | 113 | 172 | Old Data |
| | RDL | | RDL | 62 | 28 | 45 | Existing Dataset |
| Proteaceae | Proteeae and *Brabejum* | | Protea Atlas Project | 5418 | 388 | 212 | Only 1 sp of *Faurea* |
| | RDL | | RDL | 747 | 124 | 163 | |
| RDL Dataset | Numerous | | RDL Taxa, John Donaldson | 4 977 | 1 549 | 235 | Existing Dataset |
| Restionaceae | Combined | | | 4288 | 347 | 236 | |
| | African Restionaceae | BOL | Linder, 1999 | 10 707 Herb. Spec. | | | New Data |
| | RDL | | RDL | 297 | 51 | 90 | |
| Rosaceae | Combined | | | 1743 | 121 | 373 | |
| | *Cliffortia* | BOL, K, PRE | Chris Whitehouse | 5860 Herb. Spec. | | | New Data |
| | RDL | | RDL | 85 | 19 | 55 | |
| Rutaceae | Diosmeae (Combined) | | | 1830 | 279 | 237 | |
| | *Agathosma* | BOL | Terry Trinder-Smith, pers.com. | 3433 Herb. Spec. | | | New Data |
| | *Adenandra* | BOL, NBG, PRE | Oliver et al., 1983 | 152 | 26 | 62 | Old Data |
| | Remaining Diosmeae | | Williams, 1981-1984 | 619 | 108 | 156 | Newly Coded |
| | RDL | | RDL | 291 | 86 | 122 | |

## 2.3.2 Taxon Weighting for Analysis

Widespread taxa do not contribute to the delimitation of PCs and can provide confusing or conflicting information (Nelson and Platnick, 1981). In order to reduce the impact of these widespread taxa, four different weighting methods where used to cluster QDS into PCs (Table 7). The weighting techniques were (1) uniformly weighted (unweighted) taxa, (2) Bell-shaped Weighting (Linder, 2001), (3) Integration Weighting, and (4) Modified Integration Weighting. The results of these different analyses were then combined and depicted graphically, using GIS, to delimit the PCs that best reflected the results of the different analyses. Performing multiple analyses gives insight into how much congruence there is amongst the taxa that occupy different geographical range sizes. Furthermore, finding the same patterns by different analytical methods suggests robust results. The weighting values of the taxa varied from a minimum of zero to a maximum of nine, in PAUP4.0b10Win (Swofford, 1998); and from one to nine for UPGMA clustering. The weighting of the taxa contributed to the cluster analysis.

### 2.3.2.1 Unweighted Analysis [Analysis 1]

Unweighted analysis of data was undertaken to determine the effects of not weighting the data. Consequently, in this derivative matrix, all the data is equally (uniformly) weighted, and contributes equal information to the formation of clusters.

Unweighted UPGMA analysis was also undertaken on the Combined Dataset PCs to determine the hierarchical relationships between the PCs. Effectively, all taxa obtained a weight of one and thus they contributed equal amounts of data to clustering.

### 2.3.2.2 Bell Weighted Analysis [Analysis 2 and Analysis 3]

A detailed explanation and evaluation of this weighting technique can be found in Linder (2001). The weighting of characters (taxa) is determined by the equation $y=e^{-axp}$ (Linder, 2001). 'y' is the weighting value of the taxon; 'x' is the taxon range in the QDS; 'a' varies the slope of the graph; and 'p' varies the length of the tail of the graph.

As there was no immediate way of evaluating the applicability of the relationship between the two variables 'a' and 'p' and a particular dataset, I used $a = -0.005$, and $p = 3$ in all analyses performed in this study. This is the higher of the two weighting parameters suggested by Linder (2001), to produce the best results for his study on Restionaceae. It was selected for my study due to the large number of range-restricted taxa in typical CFR clades, which these weighting parameters ($a = -0.005$, and $p = 3$) favour. These two parameters control the number of grids, which are weighted maximally, and the steepness of the reduction in the weighting beyond the maximally weighted plateau of the graph.

The variables 'a' and 'p' in the equation $y=e^{-axp}$ can potentially be adjusted to correspond more suitably with particular datasets. However, using fixed values saved considerable time, as analyses and parameters did not have to be re-evaluated. Evaluation was further complicated by the absence of universally accepted optimality criterion of centres.

Taxa that occupied a single QDS were given a maximum weight of nine, to help show candidate centre distinctiveness in a phylogram. Taxa occupying a single QDS were given a weighting of one in UPGMA as they do not contribute to QDS clustering.

The Bell Shaped Curve taxon weighted UPGMA analysis was also undertaken on the Combined Dataset PC, using the PCs as the OGUs, to determine the hierarchical relationships between the PCs.

#### 2.3.2.3 Integration Weighted Analysis [Analysis 4]

I found a consistent negative exponential relationship between a taxon range and the frequency of taxa in these ranges, which has also been noted by Simmons and Cowling (1996). This relationship can be exploited to objectively delimit weighting categories of taxa. I call this the Integration Technique (Int). A list of the Integration formulas and their Goodness of Fit ($r^2$) is shown in (Table 15).

Int integrates the relationship between the range of the species, i.e. the number of QDSs occupied and the frequency of the taxa in each range category. A line of best fit is then calculated, from which the equation was obtained. This was then integrated to calculate the area under the curve between one and the species with the largest range. This total area was then divided into nine equal area portions and the x-axis value was calculated at each division. Although any number of weighting categories could have been selected, using nine makes it comparable to the weightings available in PAUP4.0b10Win (Swofford, 1998), thus allowing comparison. Taxa of the QDS range values that fell within these equal area "divisions" were then weighted from 1 to 9, in descending sequential "division" order. They start at the division furthest away from the origin, with the weighting value increasing with decreasing range size.

The Int taxon weighted UPGMA analysis was also undertaken on the Combined Dataset PC, using the PCs as the OGUs, to determine the hierarchical relationships between the PCs and to establish hierarchical relationships between PCs.

In all cases, except one, the equation that best described the data was that of an exponential curve. Some complications arose due to the nature and shape of the curve. If the data set under analysis had a large left-handed (y-axis) tail, this increased the area dramatically under the curve to the left of the value one on the x-axis. This resulted in weight values of 9, 8, or even 7 being assigned to QDS areas less than one (theoretically). If this was the case, the species with the narrowest meaningful distribution, i.e. occupying two

QDSs, were assigned a weighting value of nine. This resulted in a gap in the weighting system, with not all weighting categories being used optimally. This was particularly notable in "unnatural" datasets, such as the RDL Taxa. Bell-shaped weighting has an advantage in that the curve shape is fixed, and reaches an asymptote near the y-axis. The second integration weighting technique (MInt) was utilised to determine if a more even distribution of weighting values would produce better PCs.

### 2.3.2.4 Modified Integration Weighting Analysis [Analysis 5]

The Modified Integration Technique (MInt) was devised as a modified version of the Integration Technique (above) to cope with datasets that have disproportionate numbers of range restricted taxa (for example the RDL Taxa dataset), which results in extreme handedness in the exponential graphs, and to offset any potential negative affects thereof. This handedness occurs when the area under the left portion of the graph next to the y-axis is large, while the right portion of the graph along the x-axis is low. In such cases, the drop-off in weighting values is too steep. To compensate, the area was integrated under the curve between two (x-axis) and the maximum area range value. This was justified, as only characters that occur in two or more Operational Geographic Units (OGUs) were useful in clustering OGUs together. If this still did not prove adequate to weight all taxa sequentially, the weighting values for the various areas were further subjectively adjusted to make full use of all weighting values between 1 and 9, by inspection.

The MInt taxon weighted UPGMA analysis was also undertaken on the Combined Dataset PC, using the PCs as the OGUs, to determine the hierarchical relationships between the PCs and to establish hierarchical relationships between PC.

### 2.3.2.5 Integration Weighting on PC Frequency for Hierarchical Analysis

To provide a further perspective on the hierarchical clustering of the PC OGUs from the Combined Dataset, additional weighting analyses were undertaken. Taxon range size was calculated by the number of PCs in which it occurred. The frequency of taxa in PC range sizes two to 28 was regressed against the range size category. Once the graph was plotted, a similar procedure was followed, as utilised in the MInt Analysis. The area under the curve was divided into nine equal areas and the weighting intervals calculated (Analysis 6.1). Cluster analysis was performed on this weighting technique. Due to the steep left hand side of the graph, not all weighting categories had values. In a further weighting technique, the data was subjectively "smoothed" between the different weighting categories in Analysis 6.2 (Table 7).

### 2.3.3 Clustering of QDSs and PCs into Phytogeographical Units

Six analyses were performed to cluster the QDS's into PCs (Table 7) and to avoid erroneous artefacts that could result from a single analysis. The first five clustering analyses were performed on the QDS input raw data. The sixth analysis was performed on on the consensus results of analyses one to five to cluster the PCs and PSCs to determine the hierarchial relationships between them. Although clustering techniques based on shared taxa are unable to make use of taxa restricted to single OGUs, later analysis in GIS would identify these taxa and areas, so this was not considered a serious impediment to the clustering approach undertaken.

Techniques utilised in this study were chosen due to their time efficiency and long established track record of utilisation and success in establishing phytogeographical patterns in biogeography. The clustering algorithms used included parsimony (Rosen, 1988; Morrone, 1994; Morrone and Crisci, 1995; Linder, 2001; Cavieres et al., 2002; Rovito et al., 2004; Tribsch, 2004; Ramdhani et al., 2008), implemented in PAUP4.0b10Win (Swofford, 1998) and UPGMA, using the Jaccard similarity co-efficient (Conran, 1995; de Mera et al., 1997; Borchsenius, 1997; Garcia-Barros et al., 2002; Tribsch, 2005; Hunter, 2005; Ramdhani et al., 2008), implemented in NTSyspc v 2.02i (Rohlf, 1998). Neither of these approaches takes shared absences into account, which is important considering the range restricted nature of the taxa analysed. As the Jaccard similarity coefficient is sensitive to large differences in species richness between OGUs (Born et al., 2006), I avoided implementing a generalised phenon-line to identify clusters (see below). PAE is very computing intensive, and was consequently only undertaken on the Bell-Weighted data, using the optimised variables identified by Linder (2001), which he found to be more effective than unweighted PAE and other weighting methods he employed. Conversely, as UPGMA is much more time efficient, it was implemented on all the weighting techniques that I employed. Further, both PAE and UPGMA techniques have proven success in the CFR (Linder and Mann, 1998; Linder, 2001), providing further support for their utilisation in this study.

PAE has received much criticism as a historical biogeographical technique (Brooks and Veller, 2003; Santos, 2005). In this study, the use of PAE is restricted to pattern retrieval, and does not include historical interpretation, for which phylogenies are required (Santos, 2005). Another criticism of PAE is the use of a hypothetical all-zero outgroup, which precludes a dispersalistic model (Santos, 2005). Due to the relatively short dispersal distances in fynbos (Linder, 1985b; Slingsby and Bond, 1985) reducing dispersal, and the regularity of fire as a potential vicariance mechanism (Linder, 1985b), this criticism may prove less of a theoretical hinderance in the fynbos biome.

Although promising, techniques like NDM (Szumik et al., 2002; Szumik and Goloboff, 2004) have not enjoyed widespread utilisation, and require a unique reference grid identification system. Matrix size limits of modern null model approaches (Mast and Nyffeler, 2003; Giokas and Sfenthourakis, 2008) discounted them from this study. Other avenues for analysis, particularly on larger datasets could include Primer (Clarke and Gorley, 2006) with Bray-curtiss similarity.

Other novel techniques that have been used to uncover centres of endemism that have not enjoyed widespread usage include corrected weighted endemism (Crisp et al., 2001) and spatial autocorrelation analysis (Getis and Ord, 1996). However, as these techniques do not necessarily delimit "hard geographic boundaries" between centres, lists of strict endemics cannot be generated. Thus, these methods were not utilised.

The choice of clustering technique may not be as critical if the approach is to obtain a consensus from a number of different techniques or analyses, rather than relying on a single analysis.

Table 7: Weighting and Analysis performed on the different Datasets to convert QDS to PC. Analyses marked with an asterisk (*) were also used in converting the PC of the combined dataset into Biotic Provinces.

| Analysis label | Weighting | Clustering Algorithm | OGU |
|---|---|---|---|
| Analysis1 | Unweighted | UPGMA | QDS |
| Analysis2* | Bell | PAE | QDS |
| Analysis3 | Bell | UPGMA | QDS |
| Analysis4 | Int | UPGMA | QDS |
| Analysis5* | MInt | UPGMA | QDS |
| Analysis6* | MInt on PC (Unsmoothed=6.1 and Smoothed=6.2) | UPGMA | PCs |

### 2.3.3.1 Parsimony Analysis of Endemism (PAE) [Analysis 2]

The data from each dataset (Table 6) were converted to NEXUS format and analysed in PAUP4.0b10Win (Swofford, 1998), using the PAE technique (Rosen, 1988; Morrone, 1994; Morrone and Crisci, 1995) to establish PCs. The entire distributional range of taxa was used. A major disadvantage of PAE is the long computing time (it can often take days) required to complete analyses. For this reason, only the Bell-Shaped Weighting Technique was implemented in PAE. A standard search algorithm, as outlined by Linder (2001) was used for each data set (Table 6), which included 300 Random Addition Sequence (RAS) inputs into the stepwise addition calculation. This was followed by Tree Bisection and Reconstruction (TBR) branch-swapping, keeping only five of the shortest trees for each replicate. The set of shortest trees obtained were then swapped with TBR until completion, or alternatively until an upper limit of 10 000 trees was reached. Once this figure was reached and in some cases earlier, the search was interrupted and the strict consensus tree calculated.

The following searches were not conducted to completion: For the Eastern (summer rainfall) Ericaceae Dataset, the second stage of the analysis (TBR swapping) was not performed. This probably resulted in only a minimal loss of analytical resolution, as *Erica* species densities are very low in the eastern part of the country. Unlike in the CFR proper, there would be minimal conflict between taxon distributions of *Erica* in these areas. Furthermore, in Bruniaceae, Geophytes, Proteaceae and Rosaceae, the TBR portion of the analysis was interrupted before reaching the predefined limit of 10 000 trees. I anticipated that further GIS analyses of these data sets would compensate for any lack of resolution due to the premature termination of these PAE analyses. In addition, the UPGMA part of the study (Analysis 1, 3, 4, and 5) would also cover these areas sufficiently and compensate for any loss of resolution in the incomplete PAE analyses. No TBR analysis was completed before the limit of 10 000 trees was reached.

The resulting clusters from the strict consensus tree were then encoded as PCs in the GIS packages: Arcview3.x or ArcMap9.x, for further analysis and refinement.

#### 2.3.3.2 Sequential Agglomerative Hierarchal Nesting (SAHN) - Unweighted Pair-Group Method, Arithmetic Average (UPGMA) [Analysis 1, 3, 4, 5, 6.1, 6.2]

NTSyspc (Rolf, 1998) is restricted to an input dataset of 500 Operational Taxonomic Units (OTUs). In two cases, namely Ericaceae and Orchidaceae, it was necessary to split the data sets into two groups, because of the large number of taxa and localities. Both were split east of the Port Elizabeth region (outside the CFR proper), roughly on the boundary between the all-year and the summer rainfall regions (Schulze, 1997). Asteraceae, Proteaceae and the RDL taxa were the only datasets that had a predefined area to select taxa for analysis. Locality data were not trimmed to predefined geographical boundaries, in order to avoid the possibility of circularity when establishing CFR boundaries.

As the UPGMA cluster analysis is relatively quick (taking hours as opposed to days), this enabled multiple UPGMA analyses to be undertaken. UPGMA clustering was undertaken on all four weighting techniques as outlined above (Table 7).

Unlike PAUP4.0b10Win (Swofford, 1998), NTSyspc v 2.02i (Rohlf, 1998) does not have a "built-in" facility for weighting taxa. To overcome this problem, the taxa (characters), were entered as many times as their calculated weight was specified. For example, if a taxon had a weight of nine, that data point (spreadsheet row) was entered nine times in the matrix.

In many cases, to further speed up analysis, QDSs that contained a single widespread taxon were excluded from the UPGMA analysis, while taxa that were restricted to one QDS only received a weighting of 1. Widespread taxa and taxa restricted to a single QDS are both uninformative for PC delimitation, and resulted in increased run times. QDSs containing a single taxon were retained if the taxon was range-restricted (taxon area of 2 to 5 QDSs), as these taxa contributed significantly to PC formation. In some cases QDSs with more than one widespread taxon were excluded from the cluster analysis, especially if the dataset contained few range-restricted taxa and many of its taxa occurred over larger geographical areas. This was applied most frequently to the UPGMA Bell-Shaped Weighting Technique, where clustering usually exceeded the 9 999 trees limit of NTSyspc v 2.02i (Rohlf, 1998). It is unlikely that this removal of QDS would have had a significant effect on the overall delimitation of the PCs, as subsequent GIS analyses would add taxa to the PCs if they would increase endemicity.

#### 2.2.3.2.1 Details of the Unweighted Pair-group Method, Arithmetic Average (UPGMA) Analysis

The Jaccard similarity coefficient for qualitative (nominal) data was used to compute a similarity matrix. Clustering was undertaken using Sequential Agglomerative Hierarchal Nested Cluster Analysis (SAHN), with the UPGMA method of computation, and all trees that were equally possible were retained. A strict consensus tree was calculated from the trees generated by UPGMA, containing only subsets that were present in all the trees that were included in the strict consensus tree (Rohlf, 1998).

## 2.3.4 Delimiting Phytogeographical Units: Spatial Analysis

### 2.3.4.1 Identifying clusters as potential Phytogeographical Units

Here I explain how I derived PCs and PSCs from my various cluster analyses, using Bruniaceae as an example to illustrate the process (Figure 13, Figure 14, Figure 15, Figure 16 and Figure 17), as it contained the fewest QDSs and thus the QDSs of the dendograms were legible on a single page.

Although PAE frequently presents neat, distinct geographic clusters, this is not the case with a UPGMA analysis. For this reason, it is advantageous to analyse the data using PAE first, despite its long analytical run times. The PAE clusters give an indication of possible cluster sizes and composition in the different areas under investigation. However, cluster congruence does not always occur between different analyses (Figure 13, Figure 14, Figure 15, Figure 16 and Figure 17). In the UPGMA, previous studies have made use of a cut-off phenon-line to identify clusters (Rosen, 1988, Linder and Mann, 1998; Linder, 2001). I chose not to use a phenon-line, as these phenon-lines are essentially arbitrary (Linder, 2001). Instead, logical clusters were intuitively grouped, based on geographic continuity, with an initial minimum cluster size of at least three QDSs, but more QDSs were added until a significantly large enough sister cluster was encountered. As a result clusters were based on their individual merits, not as an average of the entire dendogram, and consequently clusters with weaker representations of range restricted taxa were retained. This approach prevented the loss of clusters with lower taxon densities which have weaker similarity values. Interestingly, even though a phenon-line was not utilised, cut-offs often occurred in the same general region, as illustrated in my Bruniaceae example (Figure 13, Figure 14, Figure 15, Figure 16 and Figure 17), where the cut-off was mostly in the region of the 0.7 Coefficient Value. However, this varied depending on individual clusters and individual datasets.

I attempted to delimit small rather than large clusters, as these are easier to enlarge in subsequent GIS analysis if the addition of more OGUs results in an increase the number of species endemic to the relevant PC. This approach maximises the number of 'complete' clusters, without arbitrarily discounting basal QDSs on the dendogram. In the UPGMA analyses (Analyses 1, 3, 4, and 5: Figure 13, Figure 15, Figure 16 and Figure 17), remaining clusters of two QDSs were retained if they were basal/distinct, for example, 3318DB and 3321DA, or 3420CA and 3319BA. However, GIS analysis usually revealed that these clusters contained no endemics. An alternative approach may be to use a cut-off phenon-line for clusters and migrate up or down the tree branch adding single taxon branches (or two taxon branches, or whatever minimum is set), until one encounters a cluster that exceeds this value, or until one encounters the next cluster defined by the phenon-line cut-off.

Potential PC clusters from each of the five cluster analyses were identified on the dendograms and marked with ticks/characters (Figure 13, Figure 14, Figure 15, Figure 16 and Figure 17). In the unweighted analysis, more ticks were used compared to other UPGMA analyses. This increased the numbers of PCs, but reduced their geographic size, while in the Int and MInt analyses, the geographic size of PCs was increased, but the numbers of PCs correspondingly decreased (Figure 13, Figure 14, Figure 15, Figure 16 and Figure 17). It was anticipated that the different placements of ticks would complement each other and also facilitate the identification of sub-centres of endemism (PSC). Terminal clusters represented the PSC (higher cut-off values), while PCs were less terminal (lower cut-off values), and can potentially contain a number of PSC clusters. As many taxa in the CFR are endemic to a single QDS, PCs and PSCs may only be a single QDS in size.

#### 2.3.4.2 Cleaning and Refining Potential PCs

These ticked potential clusters where then investigated in a GIS. All spatial investigations, analyses and mapping were undertaken using ArcView3.x (ESRI, 2000) and ArcMap9.x (ESRI, 2005). The QDSs of the clusters that were identified were then plotted as areas on maps in GIS for each of the analyses. These potential PC clusters were then further refined in the GIS by:

1. Removing potential PC clusters that have no endemics.
2. Modifying the PC clusters to include only those QDSs that contain at least one of the endemics of the potential PC.

QDSs that contained taxa endemic to the respective clusters/PCs that were retrieved from the clustering analysis before GIS interrogation are marked with plus (+) signs in the dendograms (Figure 13, Figure 14, Figure 15, Figure 16 and Figure 17), to demonstrate how successful the clustering algorithms were at retrieving potential PCs, on their own, without further GIS analysis.

UPGMA analysis usually displays the hierarchical relationships between the PCs (for example, Figure 13, Figure 15 and Figure 17). However, occasionally there are exceptions, as illustrated by the Int Weighting analysis for Bruniaceae (Figure 16). This less nested type of dendogram was rare, and never occurred in more than one analysis per dataset. However, the retrieval of these less structured dendograms supports the advantage of undertaking multiple analyses. PAE produces fairly "flat", "grass roots" trees (Figure 14). The PAE dendogram was useful in identifying the sub-centres of the larger PCs as discreet units, as well as depicting the smaller PCs as distinct, whereas hierarchical relationships were forced in UPGMA, no matter how weak. However, PAE did not reflect the hierarchical relationships between the potential clusters that form PSCs or PCs.

#### 2.3.4.3 Establishing Consensus amongst Analyses

Once the potential PCs were cleaned, spatial congruence between the refined PCs obtained for the five different analyses was determined by visual inspection in the GIS, and consensus centres/sub-centres were established for each dataset. Where conflict arose between analyses with a QDS that showed affinity to two or more PCs, QDSs were assigned to those PCs that provided the highest overall endemicity for the dataset. If the endemicity contribution was equal in both PCs, then the endemic taxon with the smallest range was favoured. If this was also equivalent, the relative increase in PC endemicity (i.e. the percentage increase in the number of endemics in a PC) was also considered in some cases. PCs are established mostly by the absence of conflict or between the different analyses (taxa), while PSCs usually indicate some level of conflict, by the overlap of distribution ranges of some of the PC endemic taxa.

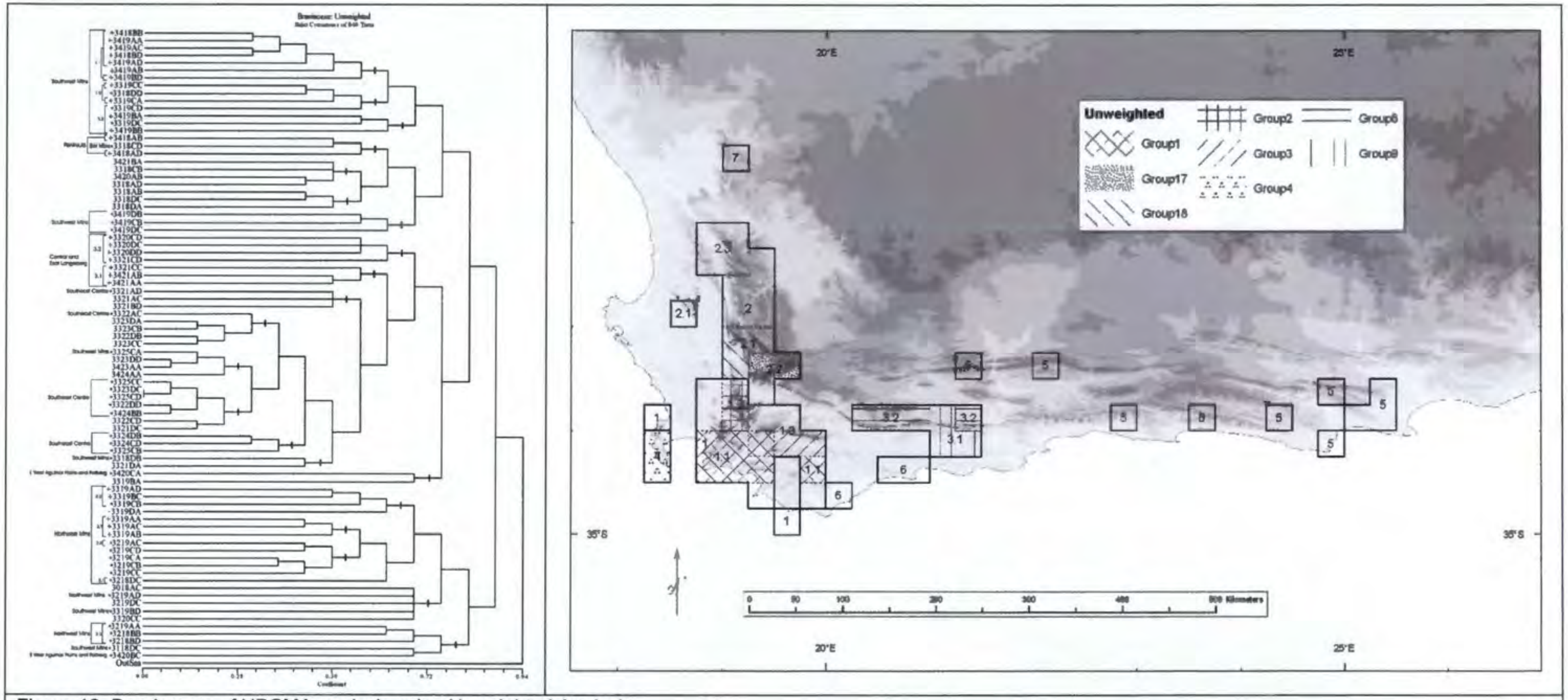


Figure 13: Dendogram of UPGMA analysis using Unweighted Analysis.
Dendogram ticks indicate candidate PC clusters identified from the dendogram; GIS was used to determine which of the QDSs in these clusters contained endemics, marked with +. Additional QDSs added based on further GIS analysis are marked with a *. QDSs nested within candidate PCs but containing no endemics are marked -. On the accompanying map, shaded QDSs indicate candidate PCs from cluster analysis, while final consensus PCs are outlined and numbered.

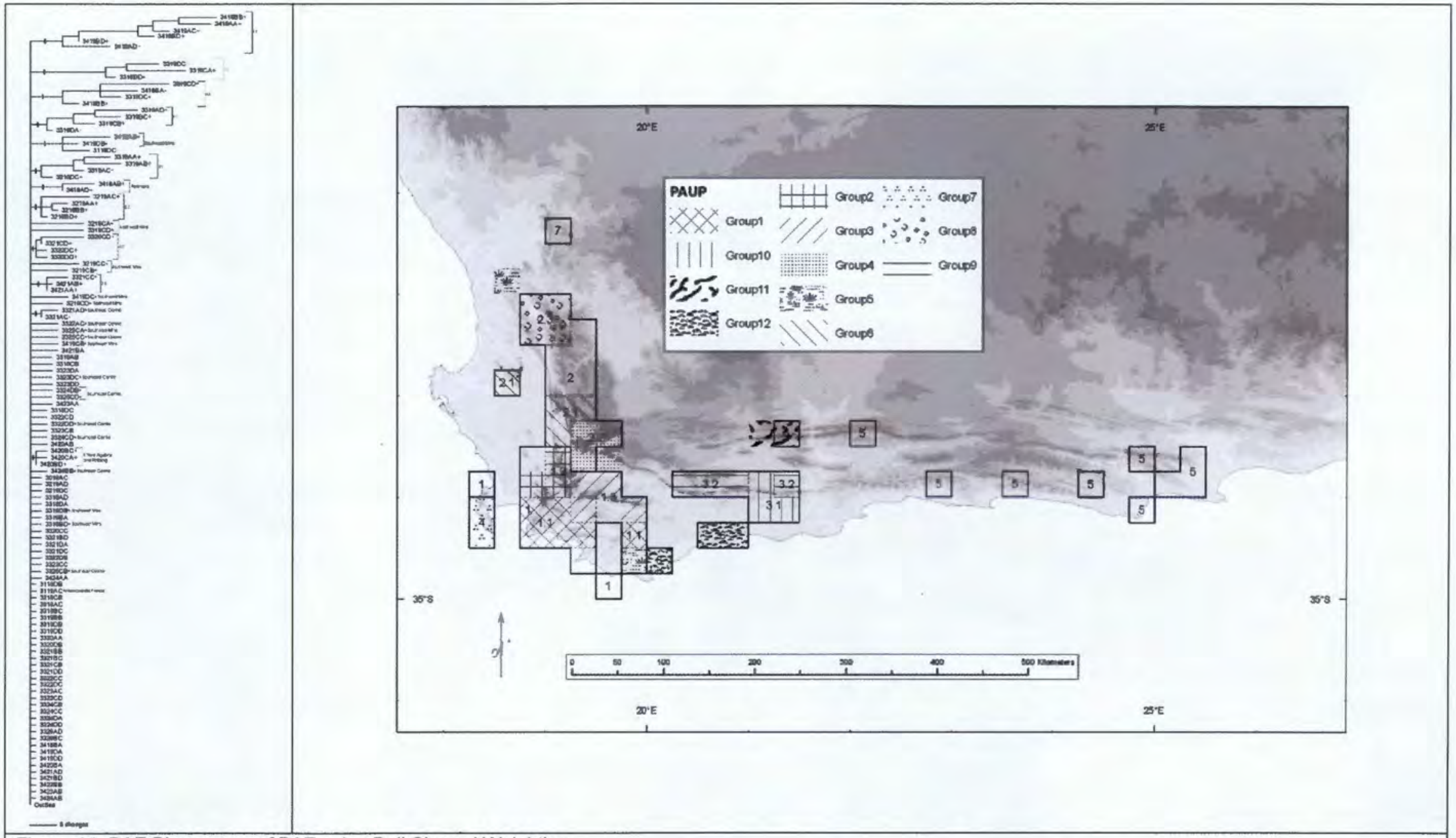


Figure 14: PAE Phenogram of PAE using Bell Shaped Weighting.
Dendogram ticks indicate candidate PC clusters identified from the dendogram; GIS was used to determine which of the QDSs in these clusters contained endemics, marked with +. Additional QDSs added based on further GIS analysis are marked with a *. QDSs nested within candidate PCs but containing no endemics are marked -. On the accompanying map, "Filled in" QDSs indicate candidate PCs from cluster analysis, while final consensus PCs are outlined and numbered.

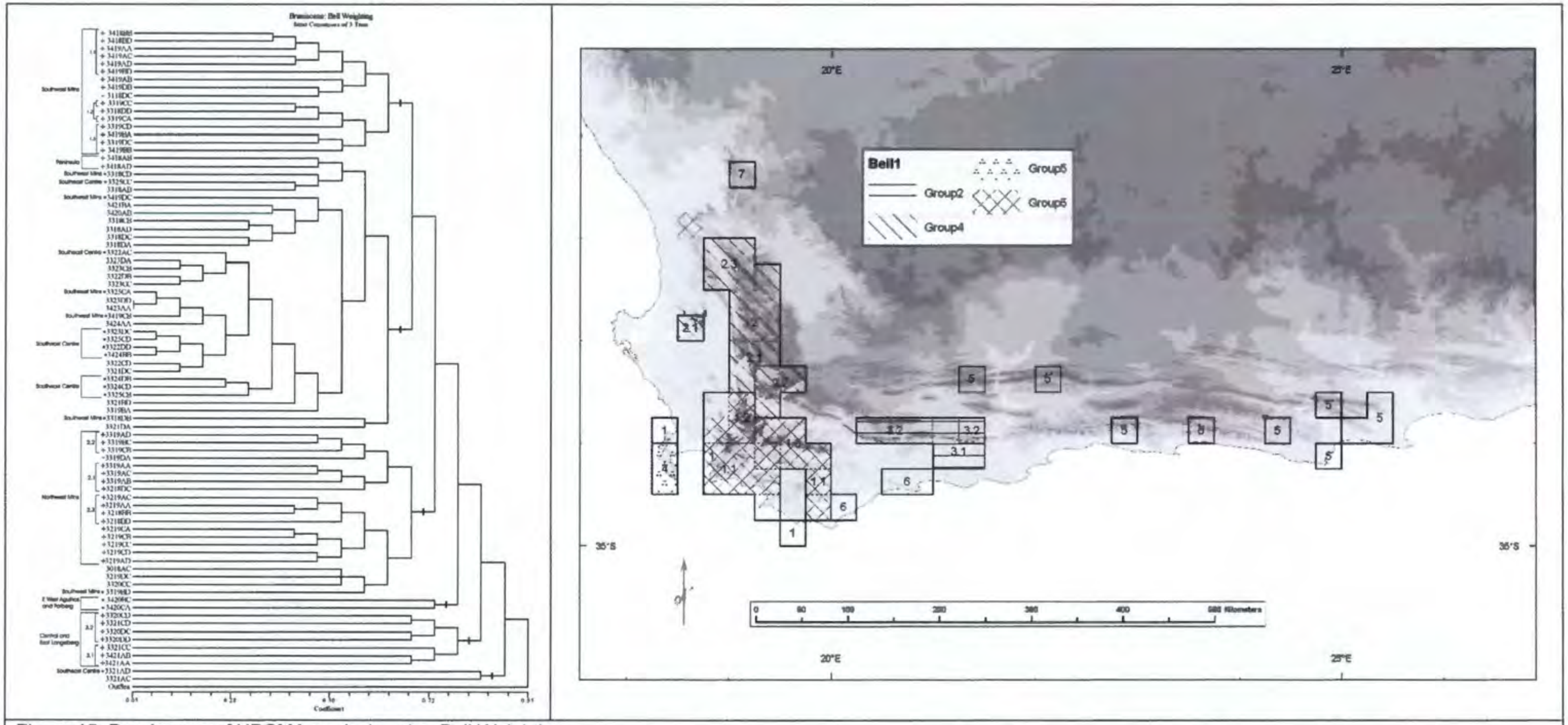


Figure 15: Dendogram of UPGMA analysis using Bell Weighting.
Dendogram ticks indicate candidate PC clusters identified from the dendogram; GIS was used to determine which of the QDS in these clusters contained endemics, marked with +. Additional QDSs added based on further GIS analysis are marked with a *. QDS nested within PCs but containing no endemics are marked -. On the accompanying map, shaded QDSs indicate candidate PCs from cluster analysis, while final consensus PCs are outlined and numbered.

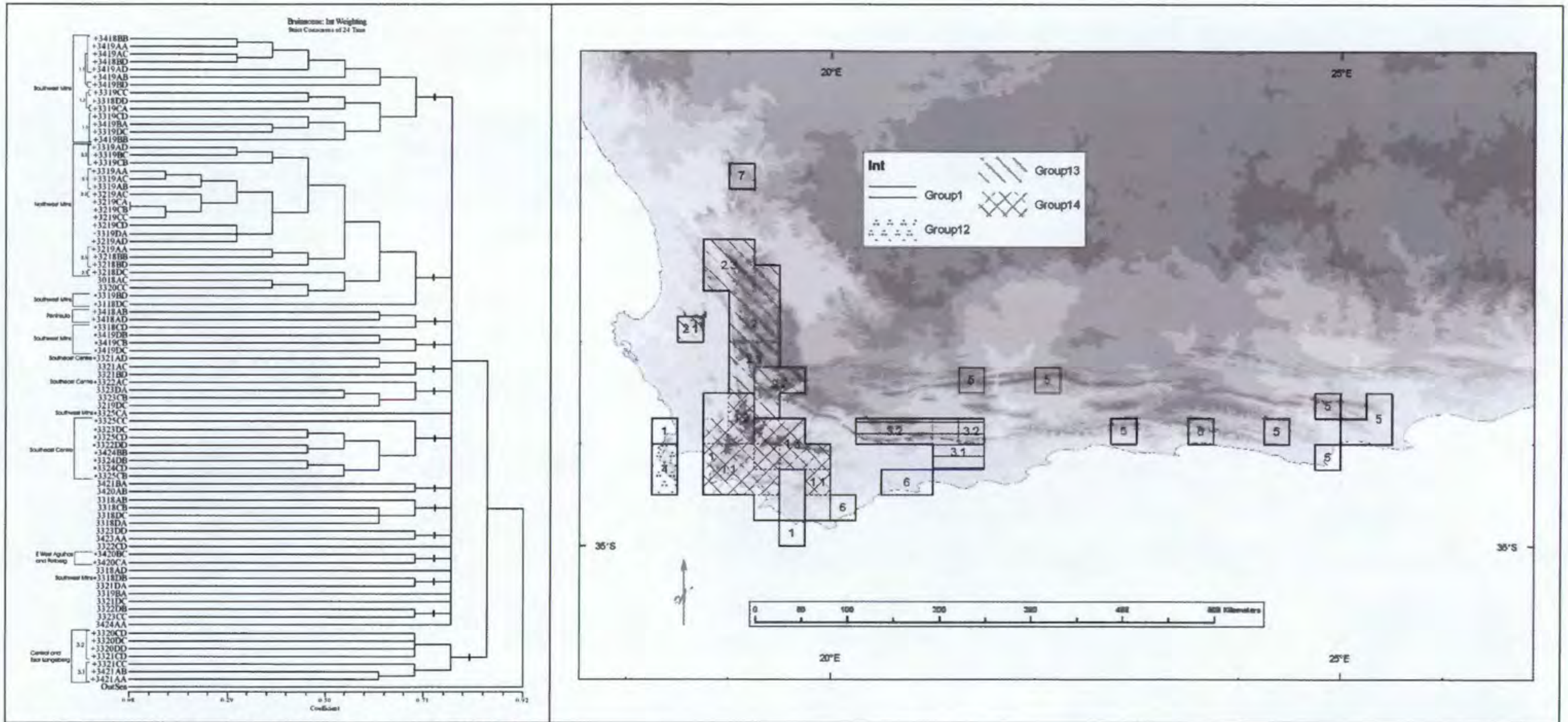


Figure 16: Dendogram of UPGMA analysis using Int Weighting.
Dendogram ticks indicate candidate PC clusters identified from the dendogram; GIS was used to determine which of the QDSs in these clusters contained endemics, marked with +. Additional QDSs added based on further GIS analysis are marked with a *. QDSs nested within PCs but containing no endemics are marked -. On the accompanying map, shaded QDSs indicate candidate PCs from cluster analysis, while final consensus PCs are outlined and numbered.

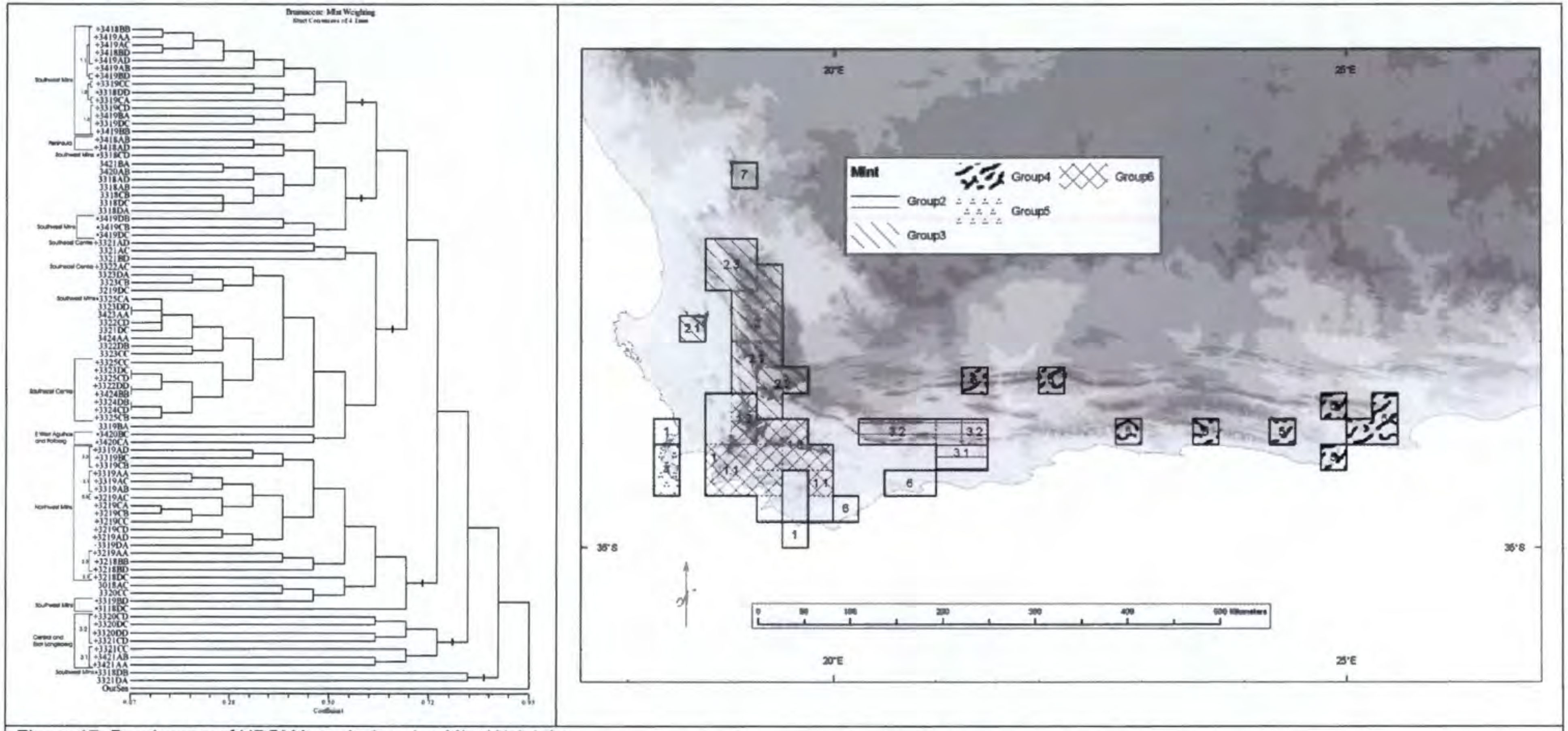


Figure 17: Dendogram of UPGMA analysis using MInt Weighting.

Dendogram ticks indicate candidate PC clusters identified from the dendogram; GIS was used to determine which of the QDSs in these clusters contained endemics, marked with +. Additional QDSs added based on further GIS analysis are marked with a *. QDSs nested within PCs but containing no endemics are marked -. On the accompanying map, shaded QDSs indicate candidate PCs from cluster analysis, while final consensus PCs are outlined and numbered.

### 2.3.4.4 Further Refinement and Enlarging of Consensus PCs

Finally, after consensus was established, additional spatial analysis was undertaken in the GIS package to determine if there were any taxa that could be added to the PCs to increase levels of endemism. This was always the case, as is depicted in the dendograms, where QDSs marked with an asterisk (*) were the additional QDSs that were not identified in that specific weighting clustering analysis, but were later added as a result of other analyses, or of later GIS analyses (Figure 13, Figure 14, Figure 15, Figure 16 and Figure 17). An example from Bruniaceae includes the E West Agulhas Plains (which was only retrieved in the PAE analysis - Figure 14), and the Southeast Centre (which was only retrieved in one UPGMA analysis - Figure 17), where the QDSs are marked with an asterisk (*), either of which could easily have been missed with fewer clustering analyses, or without GIS interrogation of datasets.

In the Bruniaceae example, there was fairly good congruence between the different weighting analyses, particularly in the Southwest Mountains PC, on the West Agulhas Plains and in the Central and East Langeberg PCs (Figure 13, Figure 14, Figure 15, Figure 16 and Figure 17). This congruence is positively correlated with a higher density of endemic taxa. This is generally the case in all datasets, where higher densities of endemic taxa result in more clearly defined and robust choria.

### 2.3.4.5 Statistical Summary of PC

Once the final, congruent PCs were established for each dataset, frequency analysis was undertaken to determine selected properties of the PCs and PSCs. This included total area (number of QDSs), total number of species, number of near endemics (species with half their ranges inside the centre) and the total number of endemics in the centre. Measures of congruency, as outlined by Linder (2001), were also calculated, including 'r', 'con', and 'CON'. The symbol 'r' is the sum of the ranges of all the endemic taxa in the PC. The symbol 'con'= $(\Sigma r)/(na)$, where 'a' = geographic size (number of QDSs) of the PC, and 'n' = the number of species endemic to each PC. This essentially measures how well the endemic taxa fit into the PC, or the sum of their congruence to the PC. Linder (2001) also proposed a modified form of the congruence index, 'CON' = $(\Sigma r\text{-}a)/(na\text{-}a)$, which gives a return value for poorer congruence. The lower the values, the poorer the congruence between the PC endemic taxa. A value of one indicates that all endemic taxa occupy the exact same range size/position and that they completely fill the area of endemism, i.e. complete congruence. Both these congruence values are included in the PC dataset tables.

### 2.3.5 The Relationships between the PCs of the Combined Dataset

Once PCs were constructed for the Combined Dataset of the CFR, further cluster analysis, using UPGMA, was undertaken to determine the hierarchical relationships between the PCs of the Combined Dataset. This essentially combined the PCs obtained in the Combined Dataset analysis into higher level hierarchical units or "Biotic Provinces". These hierarchical patterns were then compared to the phytogeographical patterns of previous studies.

I refer to these geographically larger areas (consisting of a number of PCs) as Phytogeographical Provinces in my study; these are equivalent to the Phytogeographic Centres of Goldblatt and Manning (2000), and the Centres of Weimarck (1941). I use the term Phytogeographical Provinces to avoid confusion between the geographically smaller phytogeographical centres of my study, and the larger phytogeographical centres of Goldblatt and Manning (2000), and the Centres of Weimarck (1941). However, the term "Phytogeographic Centres" may still be retained if referring specifically to the choria of Goldblatt and Manning (2000) and Weimarck (1941). Thus, Phytogeographical Provinces are hierarchically intermediate between my phytogeographical centres and the regions of other authors (Goldblatt and Manning, 2000), not unlike the use of Provinces in Rebelo (1990), or White (1993), but without the taxon representivity stipulations of the White (1993). Finally, at even higher hierarchical levels, the Phytogeographical Provinces (or PPs) are clustered into regions, such as the core CFR, with the neighbouring south Succulent Karoo and the Summer Rainfall areas (Figure 22, Figure 24, Figure 25 and Figure 26). This hierarchical classification system is summarised in Table 8.

Table 8: The various geographic units mentioned in the text, and their abbreviations.
The table is hierarchical, with the geographic units listed forming "building blocks" in the higher geographic units. Phytogeographic Centres are broadly equivalent to the Centres of Weimarck (1941), and Goldblatt and Manning (2000). Regions cover even larger areas, such as the CFR and Succulent Karoo.

| Name | Abbreviation | Definition/Data unit size |
|---|---|---|
| Quarter Degree Square | QDS | ca. 25km X 25km rectangles |
| Phytogeographical Sub-Centre | PSC | one to several QDS |
| Phytogeographical Centre | PC | One to several QDS or PSC |
| Phytogeographical Province | PP | One to several of the above |
| Region | Region | Several of the above |
| Kingdom | Kingdom | Several of the above |

Four different weighting techniques were used on the data to discern hierarchical relationships, to analyse the data from as many different perspectives as possible.

1. In the first analysis, taxa remained unweighted (Analysis 1).
2. Bell Shaped Curve weighting of taxa was implemented to weight taxa for hierarchical analysis.
3. In the third analysis, taxa were weighted according to the MInt weights for the Combined Dataset (Analysis 5).
4. Finally, a new type of weighting system was utilised (Table 7; Analysis 6.1 and 6.2). PCs established in the Combined Dataset analysis were used as OGUs, instead of QDSs and then

weighting and analysis proceeded as for other integration weighting techniques. Thus, the frequency of taxa occurring in one, two, three and up to 61 PCs were plotted, a best-fit graph obtained, and the equation integrated.

These analyses were only undertaken on the Combined Dataset, principally due to time constraints. Undertaking hierarchical analysis of all datasets would have been useful for comparing higher-level geographical patterns between the different datasets.

## 2.3.6 Mapping and Presentation of PCs

### 2.3.6.1 Recording and Presenting Phytogeographical Centres

The presentation of phytogeographical patterns in each dataset follows the same basic format. In most cases, a single map is used to display the PCs, which focuses on those centres in and immediately adjacent to the CFR. However, in cases where clade data extend far beyond the CFR, with possible Cape Clade taxa forming PCs outside the CFR, an additional smaller scale map was provided to display the positions of these centres. The PC maps depict the geographical position of the centres and have numerical labels that correspond to numeric labels on the accompanying tables. In the tables, the PCs are given a descriptive textual label and geographic size (number of QDSs) and taxonomic properties are given to each (see Statistical Analysis). The taxa endemic in each dataset for each PC are listed in Appendix II, together with their habitat data.

### 2.3.6.2 Mapping of different Phytogeographical Levels

One of the difficulties in displaying phytogeographical patterns is that floristic areas are hierarchically nested. This is observed in the nested clades in the dendograms produced by the cluster analysis (Figure 13, Figure 14, Figure 15, Figure 16, Figure 17, and Section 2.3.4.1), but it was difficult to depict clearly on a map. One possibility considered was to use isoflors to show the relationship between areas. Isoflors were used by Oliver et al., (1983) to link areas with similar species frequencies. An attempt was made to link QDSs using isoflors based on similarity in ArcView, using the results of the cluster analyses. However, this proved too complex and cumbersome. Consequently, two floristic levels are displayed on the phytogeographical maps, phytogeographical centres (PCs) and phytogeographical sub-centres (PSCs), equivalent to the mapping of Weimarck (1941).

### 2.3.6.3 Altitude Theme and core CFR Phytogeographical Centre Maps

An altitude theme was used as a backdrop to the PC maps, as topography is an important parameter in enhancing environmental heterogeneity (Goldblatt and Manning, 2000), and endemism is frequently associated with topography. In addition, most botanists working on the

CFR are familiar with its topography and it also presents a useful reference point for identifying where PCs are situated geographically. Data that was obtained from hole-filled Satellite Radar Topography Mission (SRTM) for the globe, Version 3, 90 metre DEM (digital elevation model) were utilised (Jarvis, Reuter, Nelson and Guevaraet, 2006).

Maps of each of the core CFR PCs are provided, with the official 1:250 000 Topo-Cadastral Maps (obtained from the Chief Directorate: Surveys and Mapping), to provide additional context, and to indicate geographic place names mentioned in the text.

### 2.3.7 Further Statistical Analyses

#### 2.3.7.1 QDS Diversity (Mapped)

The species richness at QDS level was mapped. Two diversity indices were used: 1) a simple count of the number of total taxa per QDS, as well as 2) the sum of the inverse taxon ranges of taxa present in a QDS (Williams, 1992; Linder, 2001). For the second method, each occurrence of a species in a QDS was weighted by the inverse range of the species, measured by the number of QDSs from which it had been recorded. Widespread species consequently contribute little to the species-richness value, while range-restricted species contribute more.

#### 2.3.7.2 The Relationship between Endemism, Richness and Area in PCs

Within PCs, levels of endemism are correlated with both diversity/richness (Jetz, Rahbek and Colwell, 2004) or non-endemic taxa (Exell and Gonçalves, 1974); and area (Anderson, 1994; Exell and Gonçalves, 1974) of PCs, and are all likely to be auto-correlated. In order to further investigate the relationship between endemism, diversity, and the area of PCs, regression analysis was performed to statistically gauge the strength of the relationships between: 1) endemic and non-endemic taxa in PCs; 2) between endemic taxa and the area of the PC; and finally, 3) the relationship between non-endemic taxa and the PC area. Graphed, this would also help to show where PCs contained significantly higher or lower levels of endemic and non-endemic taxa, when taking these other variables into account.

I chose to regress endemic taxa against non-endemic taxa, rather than total PC diversity, to avoid pseudo-replication and the artificial strengthening of the relationship. I also chose to regress non-endemic taxa against the PC area, rather than the total PC diversity against the PC area. I did this as I used non-endemic taxa in the first regression analysis (endemic versus non-endemic taxa). Non-endemic taxa also represented the least likely taxa to correlate positively with area, producing the "worst fit", as most of the range-restricted taxa fell into the endemic taxon category. Thus, if there was a significant relationship between non-endemic taxa and PCs, there would be an even stronger correlation between PC diversity and the PC area. The statistical patterns of the graphs were discussed and interpreted, where possible, in the light of environmental or historical factors.

I used log transformed data for all analyses, to easily facilitate comparisons between the regression analyses in the different datasets. I tested for normality using Kolmogorov-Smirnov and Lilliefors tests, which showed that log transformation produced more normally distributed data.

#### 2.3.7.3 Endemic Habitat Frequency Tables

Tables of habitat frequencies of taxa that were endemic to the PCs were generated to supplement the discussions of PC phytogeographical patterns. Unfortunately, records of taxa collected do not equally or systematically describe ecological or microhabitat site collection data. This precludes a more rigorous statistical analysis of the ecological properties and habitat frequency representations of PCs, and the endemic taxa of the datasets that I analysed. Thus, I echo the sentiments of Linder (2005), who called for a more systematic documentation of the ecology of Cape plants.

Goldblatt and Manning (2000) was the primary source of information on habitat data that I analysed, being succinct, up to date, and in electronic format. Some of the datasets, particularly those with PC endemics outside the core CFR, were supplemented by additional sources of habitat data, where recent taxonomic treatments have been undertaken, for example: Orchidaceae (Linder and Kurzweil, 1999); Restionaceae (Linder, 1985a); and Poaceae (Linder and Ellis, 1990).

I make use of various habitat categories, which are most consistently mentioned in Goldblatt and Manning (2000). I include both a qualitative (descriptive) and a quantitative (500 metre interval) altitude description, as altitude is not treated consistently, nor is always known accurately. I also recorded the seven most frequently mentioned soil/rock types (remaining minor types were grouped into a remainder category), the topography/terrain, the local microhabitat and the vegetation type in which the endemic taxon occurs. Some of my categories are subjective and may overlap with others slightly. However, I feel that there is sufficient data to justify my elected categories.

Scoring of the frequencies is additive and not exclusive for each endemic in each of the PCs for each habitat category. For example, if a single endemic occurs in lower slopes, hills and flats, all three of these topographic/terrain categories (slopes, hills, flats) received a score of one. This gives an indication of where endemic taxa are concentrated, but it also indicates the other habitats in which they occur. Hence, in my frequency tables, the frequencies are the number of presence records of endemic taxa in a particular habitat category. Thus, table totals are not total numbers of endemics, but total numbers of habitat occurrence records of PCs endemic taxa.

As Goldblatt and Manning (2000) were dealing primarily with fynbos clades in the CFR, many of the contributing authors did not always explicitly state whether their taxa occurred on sandstone, or in fynbos vegetation, for example, the Ericaceae treatment (Oliver, 2000). However, most taxa do occur on sandstone substrates, or in fynbos vegetation, in the CFR, estimated at 70% (Cowling and Proches, 2005). Thus, the occurrence of taxa on sandstone in fynbos appears to have been frequently omitted by them. It appears that rock type and vegetation were more consistently recorded when they were not sandstone or fynbos. Therefore, it is highly probable that most of the PC endemics from fynbos clades, or from taxa endemic to the core CFR, occur on sandstone, in fynbos vegetation.

As the main focus of my study is endemism in the CFR and habitat data is not readily available for taxa outside the CFR, the PC habitat frequencies for these geographically extraneous taxa were largely omitted from my study.

### 2.3.7.3.1 Habitat Tables Comparisons

I developed a comparative table of the habitat frequencies of the different datasets that were analysed. I compared the relative percentage distribution of each of the dataset's PC endemic taxa habitat frequencies, in order to obtain relative percentage values (Table 13). These percentage values that were calculated within each dataset were then compared to the percentage values obtained in the other datasets, to determine if there were notable differences in the frequencies of PC endemic habitat data. The omission of definitive records on vegetation and rock type data, (typically the fynbos vegetation category and the sandstone rock type category), was again apparent, and where I felt datasets were drastically under-represented, I used strikethrough text formatting. Where there was low representation of PC endemic taxa, in a particular habitat for a dataset, compared to the average, I indicated this with a smaller italic font, in grey squares. I used a bold font to indicate where the numbers of PC endemic taxa were very high in a particular habitat.

### 2.3.7.3.2 Biotic Elements, Phytogeographical Centres, Corridors, and Barriers

Phytogeographical centres, by the definition used here are delimited by the congruent distributions of taxa that are endemic to the centre. This implies that there is reasonable gene flow amoungst the species that define the centre, to maintain the integrity of the species, although molecular techniques would be required to test this emipirically. This also implies that there are barriers or inhibitors to gene flow between PCs. Two significant and often extreme ecological barriers to gene flow in the CFR are altitude (correlated with rainfall/moisture (Levyns, 1964; Lechmere-Oertel and Cowling, 2001), and geology, which frequently contain distinct biotic elements. The majority of the taxa in the CFR fit a particular profile, comprising fynbos, which is mostly found on montane, oligotrophic sandstone derived soils, which at the regional level comprises as much as 70% of taxa (Cowling and Proches, 2005). Thus, if the majority of a PC contains endemic taxa of a certain biotic element, (for example, montane TMS taxa on the Cape

Peninsula), which is surrounded by less favourable habitat (such as the more xeric Cape flats consisting of littoral deposits), inferences can be made regarding barriers to gene flow of these taxa. As Weimarck (1941: 60) observes: "The plains east of and north-east (the Malmesbury flats) {of the Peninsula} constitute an important obstacle (≡ barrier) to the spreading of montane species". These potential altitudinal and geological barriers are alluded to in the text, but to re-emphasise, molecular techniques would be required to test these hypothesise empirically.

Conversely, the extension of similar habitats into divergent ecological areas may facilitate dispersal of particular biotic elements along these corridors, which may be spatially contiguous or not. Examples of this would include, a TMS ridge or mountain chain extending into a different rock/soil type (littoral sand, limestone, or shale), or a moist high altitude area extending through a more xeric area. This has been explored at a regional level by Galley et al., (2006). Where the perceived congruence in the distributions of a number of taxon distributional ranges – alluding to the potential of continuous gene flow (and thus corridors) – is encountered, attention is drawn to this fact, to highlight potential areas of further research. Phylogenies and modern phylogeographic research would be required to verify these patterns more empirically.

# 2.4. RESULTS AND DISCUSSION

## 2.4.1 General

The analysis of the Combined Dataset reveals the overall or most dominant patterns in the flora. Phytogeographical boundaries and the distribution of diversity and endemism in my Combined Dataset closely match the phytogeographical patterns in the literature (Goldblatt and Manning, 2000; Weimarck, 1941; Oliver et al., 1983). This is despite the fact that many of the earlier biogeographers (Weimarck and others) used much fewer taxa, which were less well collected. Congruence between the results of my Combined Dataset, my different clades/datasets (especially the montane Cape (fynbos) clades) and the results of earlier phytogeographers suggests that these patterns are robust. As this study focused on identifying PCs, rather than on identifying biotic elements, I did not categorise taxa by distribution patterns, as was done by Nordenstam (1969), Dahlgren (1963c) and Weimarck (1941).

This is the first study on the CFR that uses the same techniques and procedures to analyse the similarities between areas based on total taxonomic endemism, as well as on the endemism in different clades. The results of the latter are presented and discussed in Appendix I. Weimarck (1941) analysed phytogeographic patterns of a sample (24 genera and 462 'types') of the Cape Flora; but although he identified different biotic elements he did not analyse the patterns of the different clades separately. Dahlgren (1963c) and Nordenstam (1969) focussed on *Aspalathus* and *Euryops* respectively, relating their geographical patterns to those reported by Weimarck. By analysing the phytogeographical patterns of both the entire dataset and separate taxonomic groups, and by using the same techniques, I could identify the regional scale phytogeographical patterns peculiar to particular taxa. For example, the Asteraceae and Fabaceae are relatively well developed at lower altitudes, while *Erica* is dominated by montane elements.

The centres and sub-centres derived from the Combined Dataset are listed in Table 9, where their essential floristic attributes are reported, and mapped in Figure 18 and Figure 19.

Table 9 (PC 1 - 14): Taxonomic properties of the Centres identified for the dataset Combined Dataset (The labels correspond to PC labels in Figure 18 and Figure 19).

| Label | Centres<br>Sub-Centres | Area | Family # | Genus # | Diversity | Spp >=0.5 | Endemics | r | con | CON |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Hottentots-Kleinrivier | 8 | 37 | 172 | 1381 | 439 | 158 | 340 | 0.27 | 0.26 |
| 1.1 | Hottentots-West Kleinrivier | 5 | 36 | 168 | 1313 | 364 | 131 | 245 | 0.37 | 0.37 |
| 1.2 | East Kleinrivier | 3 | 21 | 87 | 439 | 22 | 6 | 8 | 0.44 | 0.33 |
| 2 | Greater Langeberg | 14 | 41 | 173 | 958 | 257 | 152 | 306 | 0.14 | 0.14 |
| 2.1 | East Langeberg | 5 | 30 | 122 | 574 | 90 | 46 | 65 | 0.28 | 0.27 |
| 2.2 | Central Langeberg | 5 | 31 | 122 | 543 | 86 | 38 | 52 | 0.27 | 0.25 |
| 2.3 | West Langeberg Plains | 2 | 26 | 85 | 269 | 27 | 12 | 13 | 0.54 | 0.50 |
| 2.4 | Central Langeberg Plains | 2 | 26 | 71 | 283 | 14 | 7 | 8 | 0.57 | 0.50 |
| 3 | Groot Winterhoek-West Langeberg | 11 | 39 | 187 | 1167 | 276 | 117 | 199 | 0.15 | 0.15 |
| 3.1 | Hexriver-West Langeberg | 6 | 34 | 155 | 873 | 131 | 54 | 75 | 0.23 | 0.22 |
| 3.2 | Groot Winterhoek | 4 | 29 | 135 | 768 | 92 | 43 | 58 | 0.34 | 0.32 |
| 3.3 | Riebeek-Kasteel | 1 | 15 | 31 | 87 | 1 | 1 | 1 | 1.00 | - |
| 4 | Agulhas Plains | 11 | 33 | 130 | 759 | 224 | 101 | 235 | 0.21 | 0.20 |
| 4.1 | West Agulhas Plain | 8 | 27 | 115 | 642 | 147 | 58 | 121 | 0.26 | 0.25 |
| 4.2 | Potberg | 3 | 27 | 88 | 331 | 45 | 25 | 36 | 0.48 | 0.46 |
| 5 | Southeastern Centre | 46 | 39 | 147 | 655 | 206 | 102 | 248 | 0.05 | 0.04 |
| 5.1 | Grootwinterhoek-Vanstadens | 12 | 30 | 105 | 386 | 64 | 33 | 50 | 0.13 | 0.10 |
| 5.2 | Springbokvlakte | 6 | 20 | 41 | 80 | 18 | 13 | 19 | 0.24 | 0.18 |
| 5.3 | Tsitsikamma | 5 | 17 | 71 | 337 | 12 | 10 | 15 | 0.30 | 0.22 |
| 5.4 | Slypsteenberg-Antoniesberg | 6 | 22 | 47 | 114 | 14 | 7 | 11 | 0.26 | 0.14 |
| 5.5 | Kouga | 4 | 20 | 62 | 228 | 18 | 5 | 8 | 0.40 | 0.25 |
| 5.6 | Baviaanskloofberge | 3 | 18 | 51 | 152 | 6 | 4 | 8 | 0.67 | 0.56 |
| 5.7 | NW Baviaanskloofberge | 1 | 10 | 12 | 21 | 1 | 1 | 1 | 1.00 | - |
| 5.8 | Grootrivierberge | 1 | 9 | 12 | 15 | 1 | 1 | 1 | 1.00 | - |
| 5.9 | Remainder | 8 | 14 | 64 | 210 | 2 | 0 | 0 | - | 1.00 |
| 6 | Stellenbosch-Bainskloof Mtns/Sandveld | 13 | 36 | 184 | 1288 | 295 | 100 | 207 | 0.16 | 0.15 |
| 6.1 | Stellenbosch-Bainskloof Mtns | 4 | 31 | 152 | 1073 | 153 | 50 | 74 | 0.37 | 0.36 |
| 6.2 | Sandveld | 9 | 29 | 114 | 539 | 106 | 36 | 76 | 0.23 | 0.21 |
| 7 | Karoo Mtn Centre | 16 | 35 | 136 | 597 | 191 | 98 | 190 | 0.12 | 0.11 |
| 7.1 | Klein Swartberg-West Touwsberg | 5 | 29 | 94 | 339 | 57 | 30 | 52 | 0.35 | 0.32 |
| 7.2 | Groot Swartberg-Anysberg | 6 | 26 | 94 | 358 | 53 | 26 | 40 | 0.26 | 0.23 |
| 7.3 | Rooiberg | 2 | 24 | 56 | 168 | 21 | 13 | 15 | 0.58 | 0.54 |
| 7.4 | Kammanassieberg | 2 | 19 | 51 | 168 | 12 | 10 | 11 | 0.55 | 0.50 |
| 7.5 | East Touwsberg | 1 | 14 | 21 | 40 | 4 | 3 | 3 | 1.00 | 1.00 |
| 8 | Cedarberg | 12 | 39 | 151 | 808 | 224 | 93 | 183 | 0.16 | 0.15 |
| 8.1 | Cedarberg Core | 6 | 37 | 138 | 736 | 174 | 58 | 88 | 0.25 | 0.24 |
| 8.2 | S Koebeeberge-Boegoeberge | 2 | 18 | 33 | 61 | 7 | 6 | 7 | 0.58 | 0.50 |
| 8.3 | Southeast Cedarberg-Skurweberge | 2 | 18 | 75 | 335 | 18 | 5 | 8 | 0.80 | 0.75 |
| 8.4 | Remainder | 2 | 3 | 3 | 3 | 0 | 0 | 0 | - | 1.00 |
| 9 | Peninsula | 3 | 29 | 145 | 801 | 162 | 87 | 148 | 0.57 | 0.56 |
| 10 | RZE | 6 | 29 | 148 | 1061 | 199 | 79 | 128 | 0.27 | 0.26 |
| 11 | Nieuwoudtville Plateau | 4 | 34 | 102 | 264 | 98 | 69 | 83 | 0.30 | 0.29 |
| 12 | Greater Witteberg | 18 | 34 | 137 | 483 | 106 | 51 | 82 | 0.09 | 0.07 |
| 12.1 | Witteberg Core | 5 | 25 | 76 | 242 | 29 | 12 | 17 | 0.28 | 0.22 |
| 12.2 | Southwest Karoo | 2 | 24 | 49 | 96 | 18 | 11 | 13 | 0.59 | 0.55 |
| 12.3 | Southeast Cold Bokkeveld-North Waboomsberg | 4 | 27 | 83 | 293 | 22 | 9 | 12 | 0.33 | 0.25 |
| 12.4 | Karookop-Klein-Roggeveldberge | 2 | 7 | 8 | 8 | 3 | 3 | 4 | 0.67 | 0.50 |
| 12.5 | Swart Ruggens | 2 | 18 | 38 | 87 | 6 | 2 | 3 | 0.75 | 0.50 |
| 12.6 | Inverdoorn | 1 | 6 | 8 | 8 | 2 | 2 | 2 | 1.00 | 1.00 |
| 12.7 | Droekloof | 1 | 7 | 7 | 7 | 3 | 1 | 1 | 1.00 | - |
| 12.8 | North Tankwa Karoo | 1 | 6 | 7 | 7 | 1 | 1 | 1 | 1.00 | - |
| 13 | Drakensberg | 94 | 8 | 36 | 229 | 101 | 48 | 313 | 0.07 | 0.05 |
| 13.1 | Northern Drakensberg | 35 | 7 | 29 | 174 | 42 | 20 | 112 | 0.16 | 0.12 |
| 13.2 | South and Southwest Drakensberg | 17 | 8 | 24 | 115 | 7 | 5 | 21 | 0.25 | 0.06 |
| 13.3 | East Drakensberg | 4 | 5 | 22 | 79 | 4 | 2 | 5 | 0.43 | 0.14 |
| 13.4 | Sekameng | 1 | 3 | 4 | 5 | 1 | 1 | 1 | 1.00 | - |
| 13.5 | Remainder | 37 | 7 | 31 | 143 | 5 | 0 | 0 | - | 1.00 |
| 14 | Piketberg-Swartberg-Sandveld | 11 | 37 | 141 | 558 | 112 | 43 | 79 | 0.17 | 0.15 |
| 14.1 | Piketberg | 4 | 22 | 90 | 379 | 53 | 24 | 38 | 0.40 | 0.37 |
| 14.2 | Swartberg-Sandveld | 4 | 34 | 107 | 324 | 40 | 9 | 13 | 0.36 | 0.28 |
| 14.3 | Graafwater | 1 | 14 | 28 | 60 | 2 | 2 | 2 | 1.00 | 1.00 |
| 14.4 | West Piketberg Sandveld | 1 | 14 | 21 | 42 | 1 | 1 | 1 | 1.00 | - |
| 14.5 | Remainder | 1 | 13 | 18 | 28 | 0 | 0 | 0 | - | 1.00 |

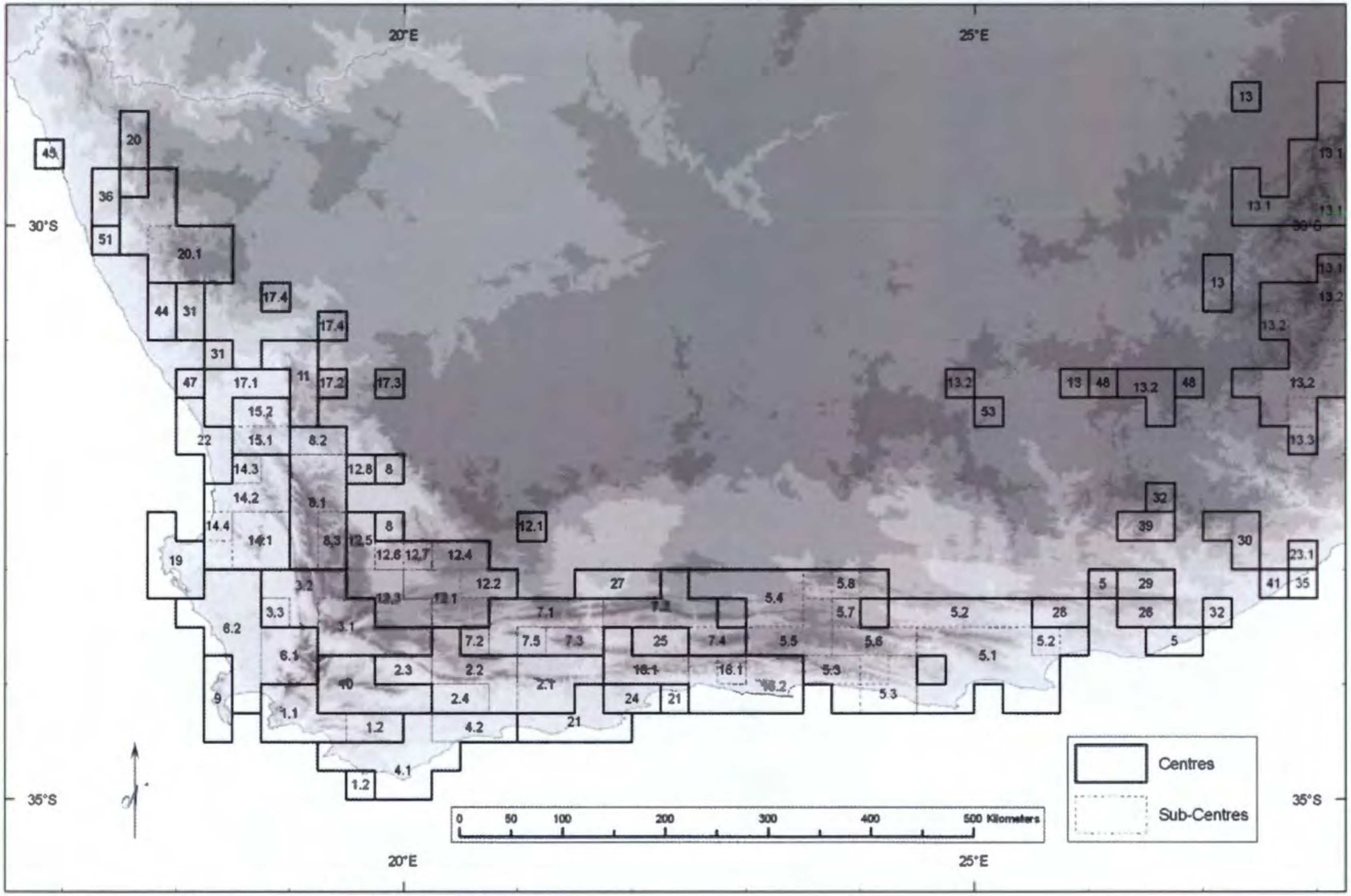


Figure 18: PCs and PSCs for the Combined Dataset in the CFR.

Table: (cont'd; PC 15 - 58)

| Label | Centres<br>Sub-Centres | Area | Family # | Genus # | Diversity | Spp >=0.5 | Endemics | r | con | CON |
|---|---|---|---|---|---|---|---|---|---|---|
| 15 | Gifberg | 4 | 31 | 95 | 256 | 76 | 41 | 60 | 0.37 | 0.35 |
| 15.1 | South Gifberg | 2 | 31 | 84 | 200 | 43 | 23 | 24 | 0.52 | 0.50 |
| 15.2 | North Gifberg | 2 | 24 | 49 | 108 | 32 | 10 | 13 | 0.65 | 0.61 |
| 16 | West Southeastern Centre | 12 | 28 | 106 | 578 | 88 | 37 | 64 | 0.14 | 0.12 |
| 16.1 | West Outeniqua | 5 | 27 | 87 | 451 | 43 | 22 | 31 | 0.28 | 0.25 |
| 16.2 | East Outeniqua-West Tsitsikamma | 7 | 20 | 81 | 379 | 27 | 12 | 22 | 0.26 | 0.19 |
| 17 | Vanrhynsdorp | 8 | 27 | 58 | 109 | 49 | 37 | 50 | 0.17 | 0.15 |
| 17.1 | Vanrhynsdorp Core | 4 | 23 | 44 | 80 | 43 | 33 | 45 | 0.34 | 0.32 |
| 17.2 | Soetlandsfontreinrivier | 1 | 8 | 12 | 12 | 4 | 2 | 2 | 1.00 | 1.00 |
| 17.3 | West Hantamsberg | 1 | 8 | 16 | 21 | 1 | 1 | 1 | 1.00 | - |
| 17.4 | Harslagkop-Kubiskouberge | 2 | 2 | 3 | 4 | 1 | 1 | 2 | 1.00 | - |
| 18 | Northeastern Escarpment | 24 | 6 | 32 | 143 | 24 | 19 | 50 | 0.11 | 0.06 |
| 18.1 | Pilgrims Rest | 8 | 5 | 21 | 74 | 9 | 7 | 17 | 0.30 | 0.19 |
| 18.2 | Barberton | 5 | 5 | 20 | 84 | 8 | 5 | 9 | 0.36 | 0.20 |
| 18.3 | Wolkberg | 5 | 4 | 18 | 55 | 3 | 2 | 6 | 0.60 | 0.20 |
| 18.4 | Remainder | 6 | 6 | 22 | 60 | 2 | 0 | 0 | - | 1.00 |
| 19 | Kamiesberg | 12 | 13 | 38 | 98 | 22 | 15 | 35 | 0.19 | 0.14 |
| 19.1 | Kamiesberg Mtns | 6 | 13 | 36 | 87 | 17 | 12 | 22 | 0.31 | 0.24 |
| 19.2 | Remainder | 6 | 8 | 15 | 36 | 5 | 0 | 0 | - | 1.00 |
| 20 | Saldanha Peninsula | 5 | 21 | 50 | 100 | 25 | 14 | 25 | 0.36 | 0.31 |
| 21 | East Agulhas Plain | 6 | 23 | 72 | 262 | 36 | 11 | 19 | 0.29 | 0.23 |
| 22 | West Coast | 4 | 21 | 42 | 68 | 22 | 11 | 16 | 0.36 | 0.30 |
| 23 | Natal Coast | 26 | 7 | 43 | 147 | 14 | 11 | 37 | 0.13 | 0.04 |
| 23.1 | Natal Coast1 | 13 | 7 | 36 | 106 | 9 | 8 | 17 | 0.16 | 0.04 |
| 23.2 | Natal Coast2 | 3 | 6 | 23 | 39 | 2 | 1 | 3 | 1.00 | - |
| 23.3 | Remainder | 10 | 7 | 25 | 66 | 2 | 0 | 0 | - | 1.00 |
| 24 | Far East Agulhas Plain | 2 | 16 | 44 | 135 | 8 | 4 | 5 | 0.63 | 0.50 |
| 25 | East Little Karoo | 2 | 20 | 33 | 65 | 7 | 4 | 4 | 0.50 | 0.33 |
| 26 | South Grahamstown | 2 | 13 | 47 | 136 | 4 | 3 | 5 | 0.83 | 0.75 |
| 27 | South Groot Karoo | 3 | 17 | 26 | 46 | 5 | 2 | 4 | 0.67 | 0.33 |
| 28 | East Suurberg | 2 | 12 | 23 | 54 | 2 | 2 | 3 | 0.75 | 0.50 |
| 29 | North Grahamstown | 2 | 11 | 16 | 36 | 2 | 2 | 3 | 0.75 | 0.50 |
| 30 | Transkei | 3 | 6 | 28 | 97 | 2 | 1 | 3 | 1.00 | - |
| 31 | Bitterfontein-Garies | 3 | 7 | 11 | 21 | 2 | 1 | 3 | 1.00 | - |
| 32 | Katberg | 2 | 9 | 21 | 44 | 1 | 1 | 2 | 1.00 | - |
| 33 | West Transvaal | 4 | 3 | 10 | 31 | 1 | 1 | 4 | 1.00 | - |
| 34 | Northern Natal | 2 | 3 | 13 | 27 | 1 | 1 | 2 | 1.00 | - |
| 35 | East London | 1 | 6 | 7 | 15 | 1 | 1 | 1 | 1.00 | - |
| 36 | Buffelsbank-Komaggas | 2 | 6 | 9 | 13 | 1 | 1 | 2 | 1.00 | - |
| 37 | East Soutpansberg | 1 | 3 | 8 | 12 | 1 | 1 | 1 | 1.00 | - |
| 38 | N Barberton | 1 | 3 | 7 | 11 | 1 | 1 | 1 | 1.00 | - |
| 39 | Tarkastad-SADA | 2 | 4 | 7 | 11 | 1 | 1 | 2 | 1.00 | - |
| 40 | Willowvale | 2 | 4 | 7 | 9 | 1 | 1 | 2 | 1.00 | - |
| 41 | Kiwane | 1 | 4 | 5 | 7 | 1 | 1 | 1 | 1.00 | - |
| 42 | NE Wolkberg | 1 | 2 | 5 | 7 | 1 | 1 | 1 | 1.00 | - |
| 43 | South Namibia | 5 | 2 | 5 | 7 | 1 | 1 | 5 | 1.00 | - |
| 44 | Garies-Kotzesrus | 2 | 3 | 5 | 6 | 1 | 1 | 2 | 1.00 | - |
| 45 | McDougall's Bay | 1 | 4 | 5 | 6 | 1 | 1 | 1 | 1.00 | - |
| 46 | Swartkop | 1 | 3 | 4 | 6 | 1 | 1 | 1 | 1.00 | - |
| 47 | Moedverloorberg | 1 | 4 | 5 | 5 | 1 | 1 | 1 | 1.00 | - |
| 48 | South Drakensberg | 2 | 5 | 5 | 5 | 1 | 1 | 2 | 1.00 | - |
| 49 | Brandvlei | 1 | 2 | 2 | 3 | 1 | 1 | 1 | 1.00 | - |
| 50 | Windhoek | 1 | 3 | 3 | 3 | 1 | 1 | 1 | 1.00 | - |
| 51 | Koingnaas | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1.00 | - |
| 52 | Lebombo | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1.00 | - |
| 53 | Joubertsberge | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 54 | Mbazwana | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 55 | SE Barberton | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 56 | N Botswana-Okavango | 6 | 2 | 2 | 3 | 1 | 1 | 6 | 1.00 | - |
| 57 | East Tanzania | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 58 | West Tanzania | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 59 | Outside | 600 | 19 | 87 | 443 | 45 | 0 | 0 | - | 1.00 |

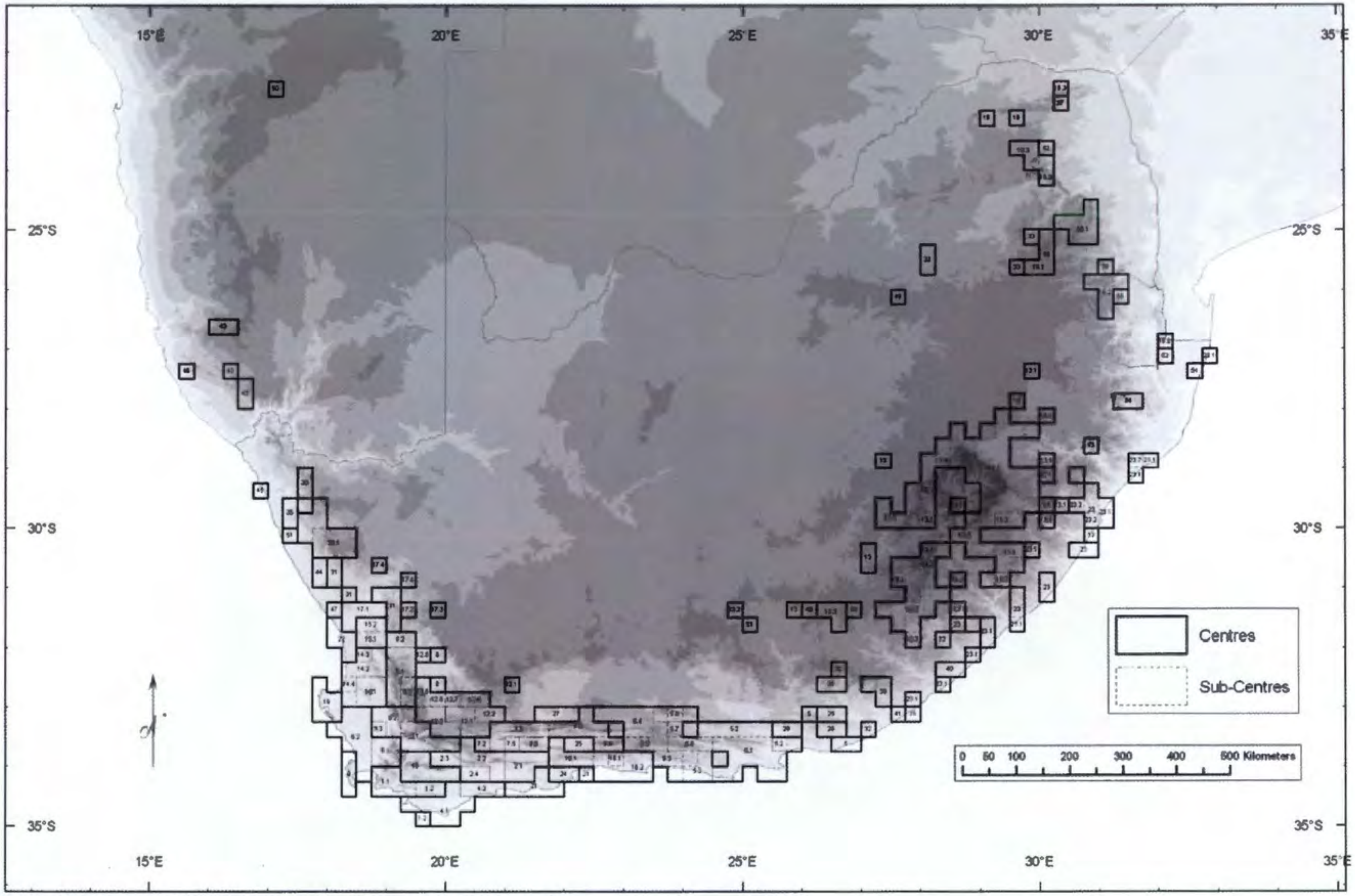


Figure 19: PCs and PSCs for the Combined Dataset in Southern Africa.

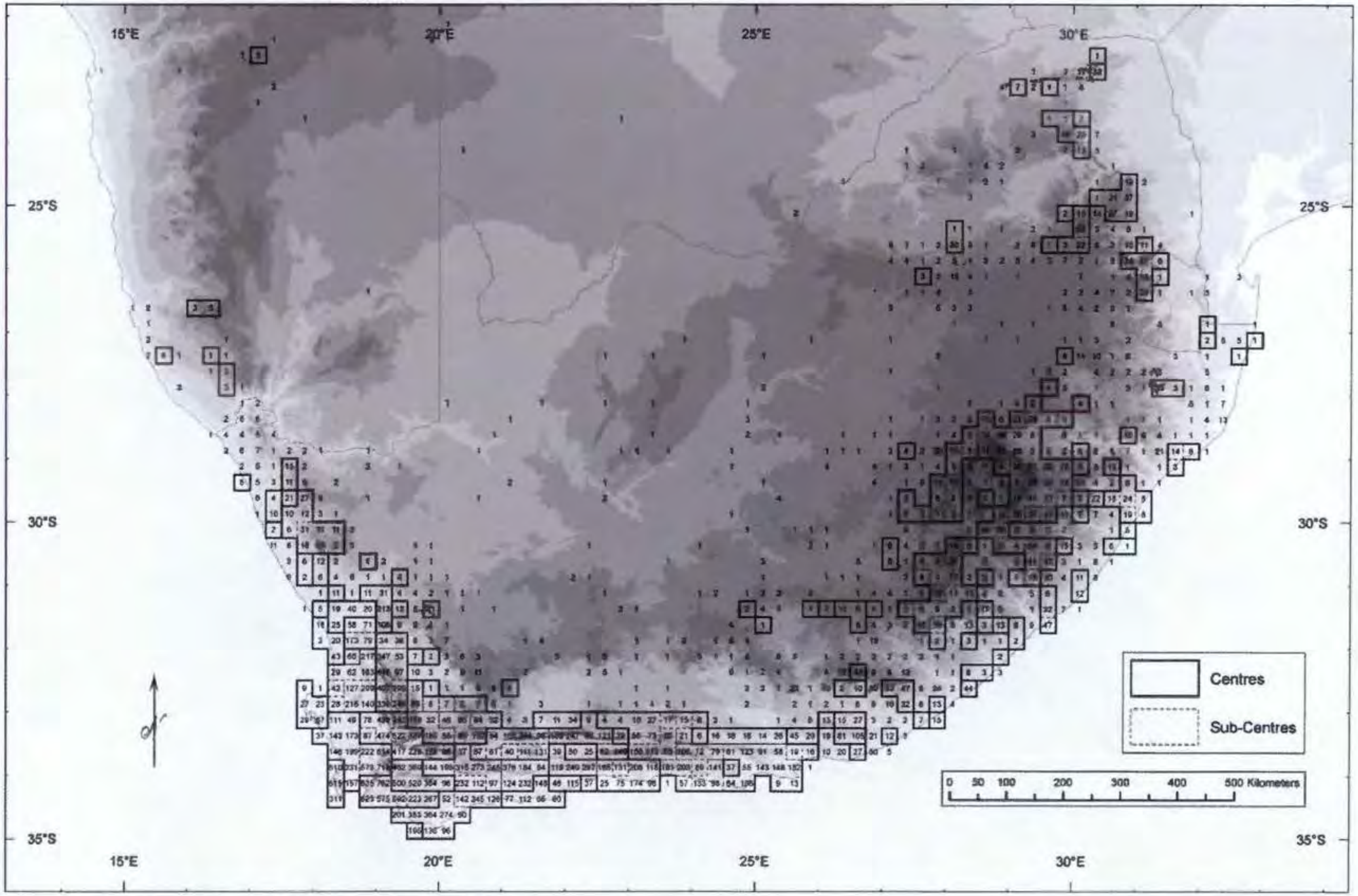


Figure 20: QDS Diversity for the Combined Dataset in Southern Africa.

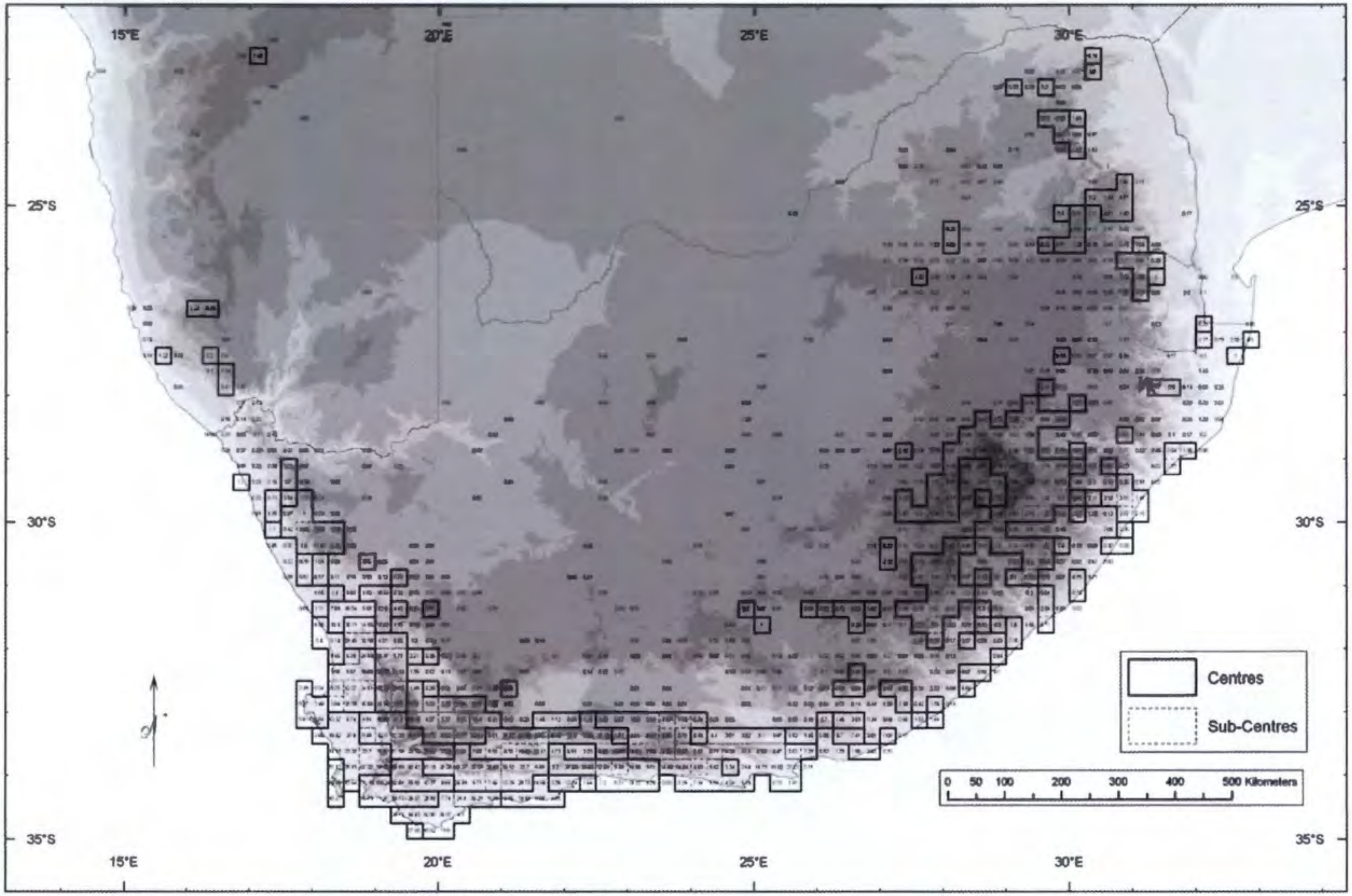


Figure 21: Sum of the Inverse Taxon Ranges for the Combined Dataset in Southern Africa.

#### 2.4.1.1 Hierarchical Clustering

Five different data weighting techniques were used to cluster the PCs and these produced dendograms that broadly conformed to the phytogeographical boundaries that are traditionally recognised in the CFR (Weimarck, 1941; Oliver et al., 1983; Goldblatt and Manning, 2000). However, there are some differences between the five analyses employed here, as well as when compared to patterns that were previously reported (*cf.* Weimarck, 1941; Goldblatt and Manning 2000); and see Table 14). Overall, congruence in the dendograms that was derived from the five different weighting techniques was good (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). The Bell, MInt, and Unsmoothed PC Frequency weighting techniques generally gave similar results, while the dendogram based on the Unweighted and Smoothed PC Frequency weighting technique differs in the placement of the Agulhas Plain Centre.

At a broader geographic scale, the hierarchical analysis clustered PC into two principle areas: the winter rainfall area and the summer rainfall area (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). With only minor differences, the montane regions of the CFR are divided into the phytogeographical provinces that were identified by Goldblatt and Manning (2000) (discussed in more detail below). The delimitation within the core CFR is slightly ambiguous, due to the placement of the Agulhas Plains, which either forms an APPP cluster (Figure 23, Figure 24, Figure 25), or is divided amongst the SWPP and LBPP (Figure 22, Figure 26). Sister to the core CFR, are three south Succulent Karoo PCs ((Vanrhynsdorp (PC 17), Gifberg (PC 15), and Nieuwoudtville (PC 11)), two Karoo PCs (East Little Karoo (PC 25) and South Groot Karoo (PC 27)) and the two West Coast PCs (Saldanha Peninsula (PC 20) and West Coast (PC 22)). It is likely that a more precise spatial delimitation of these areas might separate out lowland succulent or coastal PCs from neighbouring montane regions, especially along the Gifberg and Nieuwoudtville escarpments. The Greater Cape Floristic Region of Born et al., (2006) is almost exactly retrieved. This includes all the regions with winter rainfall. In the Unweighted Analysis, the three eastern Archipelago PCs (South Grahamstown, North Grahamstown, and East Suurberg) are included in this Greater CFR (GCFR), while in my three weighted analyses these eastern outliers are included in the general eastern summer rainfall area.

Cape (fynbos) elements do not provide much support for Weimarck's geographically extensive Zuurberg Sub-Centre in my study, although isolated and disjunct Cape elements do occur in the region, and gradually diminish in abundance towards the east. Additional analysis of thicket and other sub-tropical elements may retrieve the expanded Zuurberg Sub-Centre (Weimarck, 1941), or the Albany Centre (Croizat, 1965; van Wyk and Smith, 2001), but perhaps with lower CFR affinities.

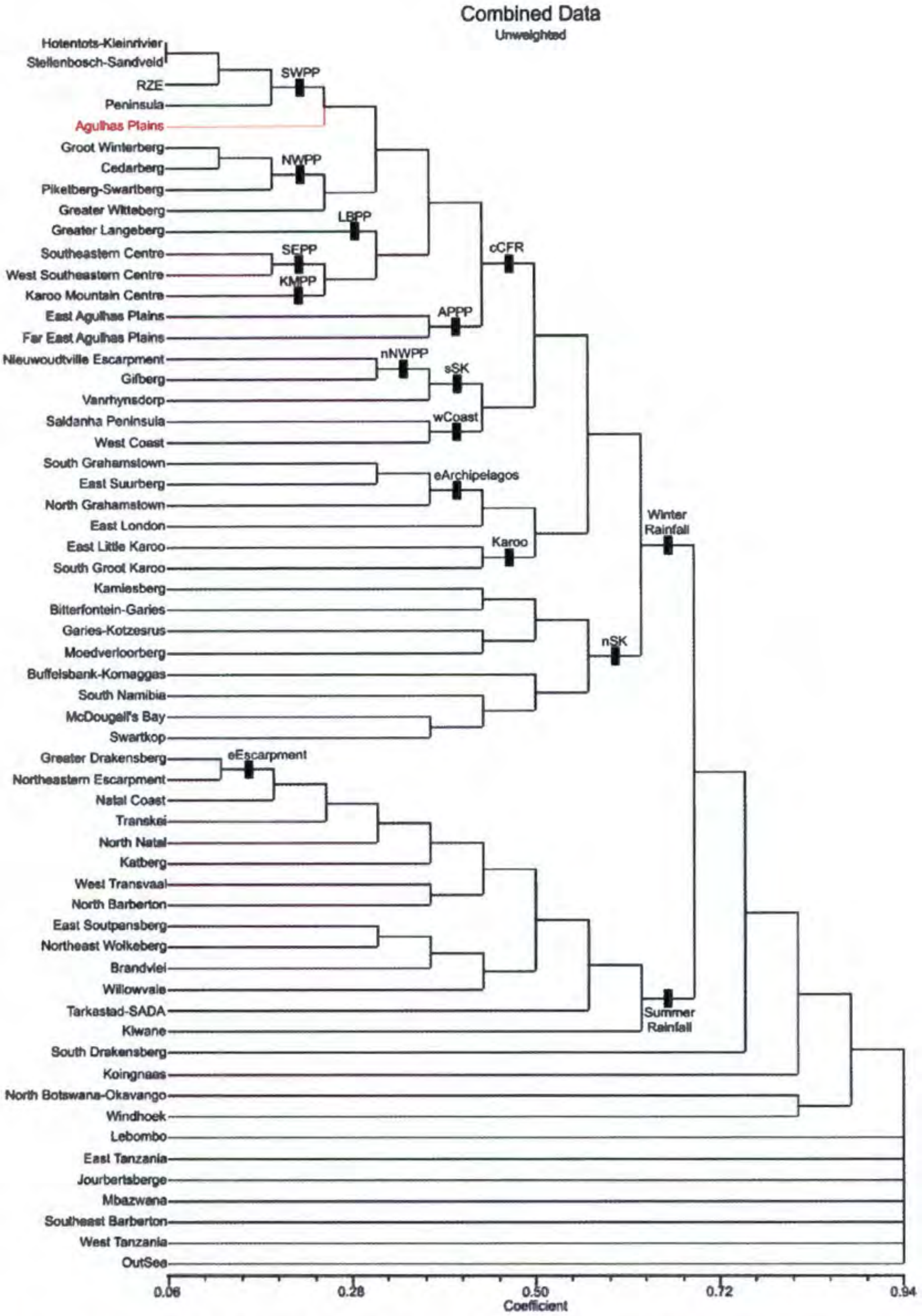


Figure 22: UPGMA analysis of the relationships between the PC for the Combined Dataset, using Unweighted Characters (taxa).
The marks on the dendogram indicate higher level phytogeographical or environmental boundaries. OGUs in red indicate conflict with the other hierarchical analyses, or OGUs whose position should be investigated further.

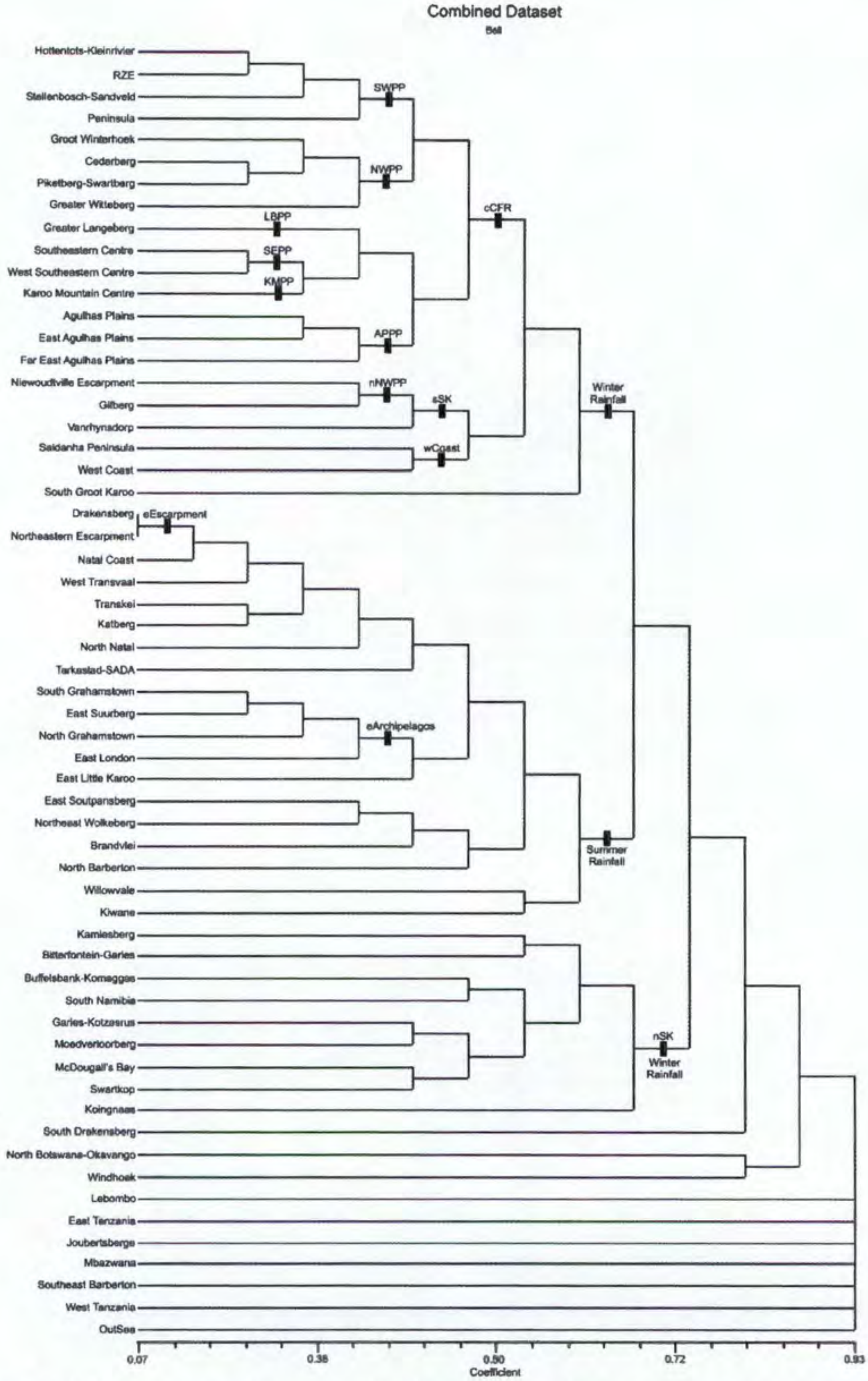


Figure 23: UPGMA analysis of the relationships between the PC for the Combined Dataset, using Bell Weighted Characters (taxa).
The marks on the dendogram indicate higher level phytogeographical or environmental boundaries.

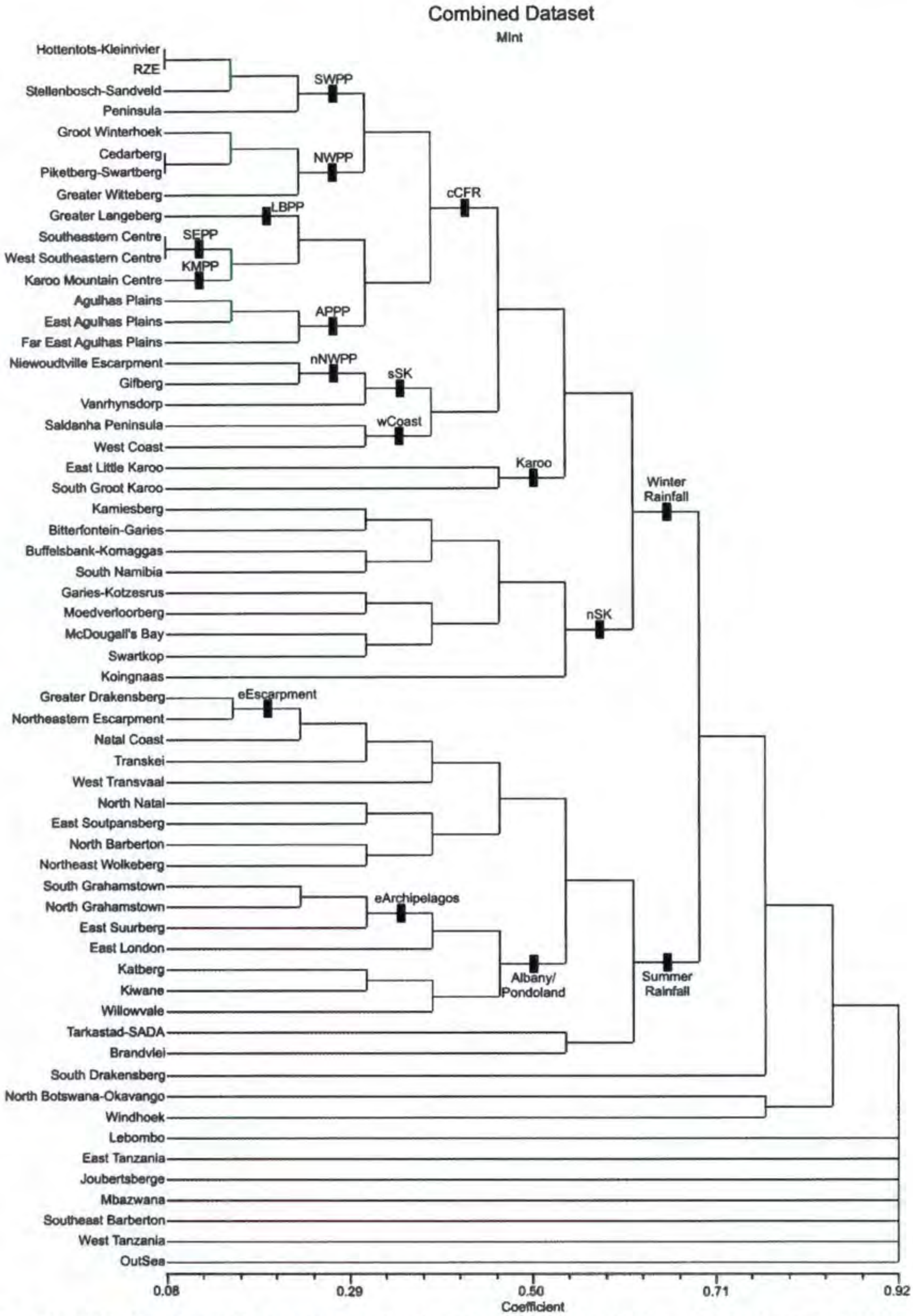


Figure 24: UPGMA analysis of the relationships between the PC for the Combined Dataset, using MInt Weighting on the taxa.
The marks on the dendogram indicate higher level phytogeographical or environmental boundaries.

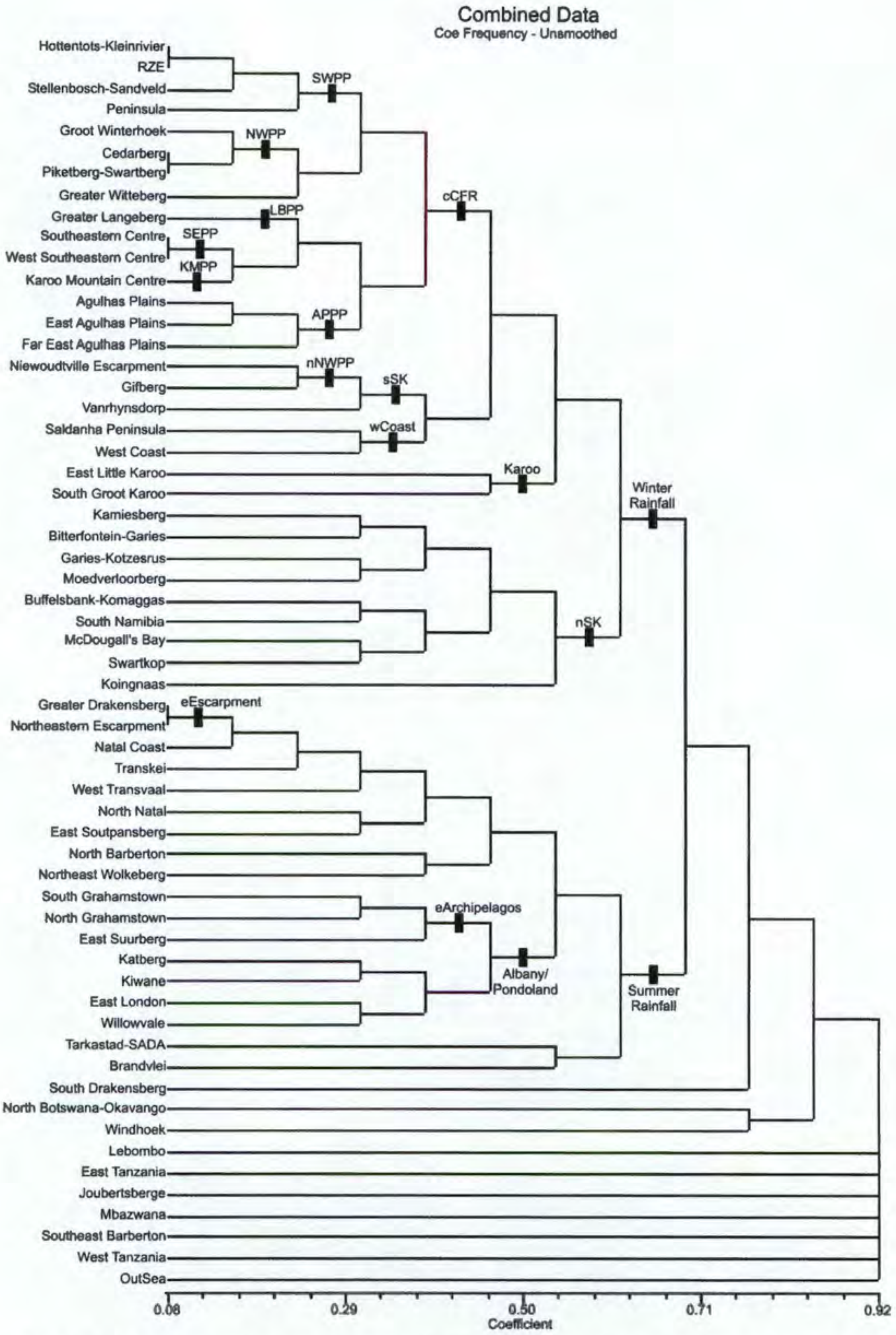


Figure 25: UPGMA analysis of the relationships between the PC for the Combined Dataset, using Unsmoothed Centre Frequency Weighting.
The marks on the dendogram indicate higher level phytogeographical or environmental boundaries.

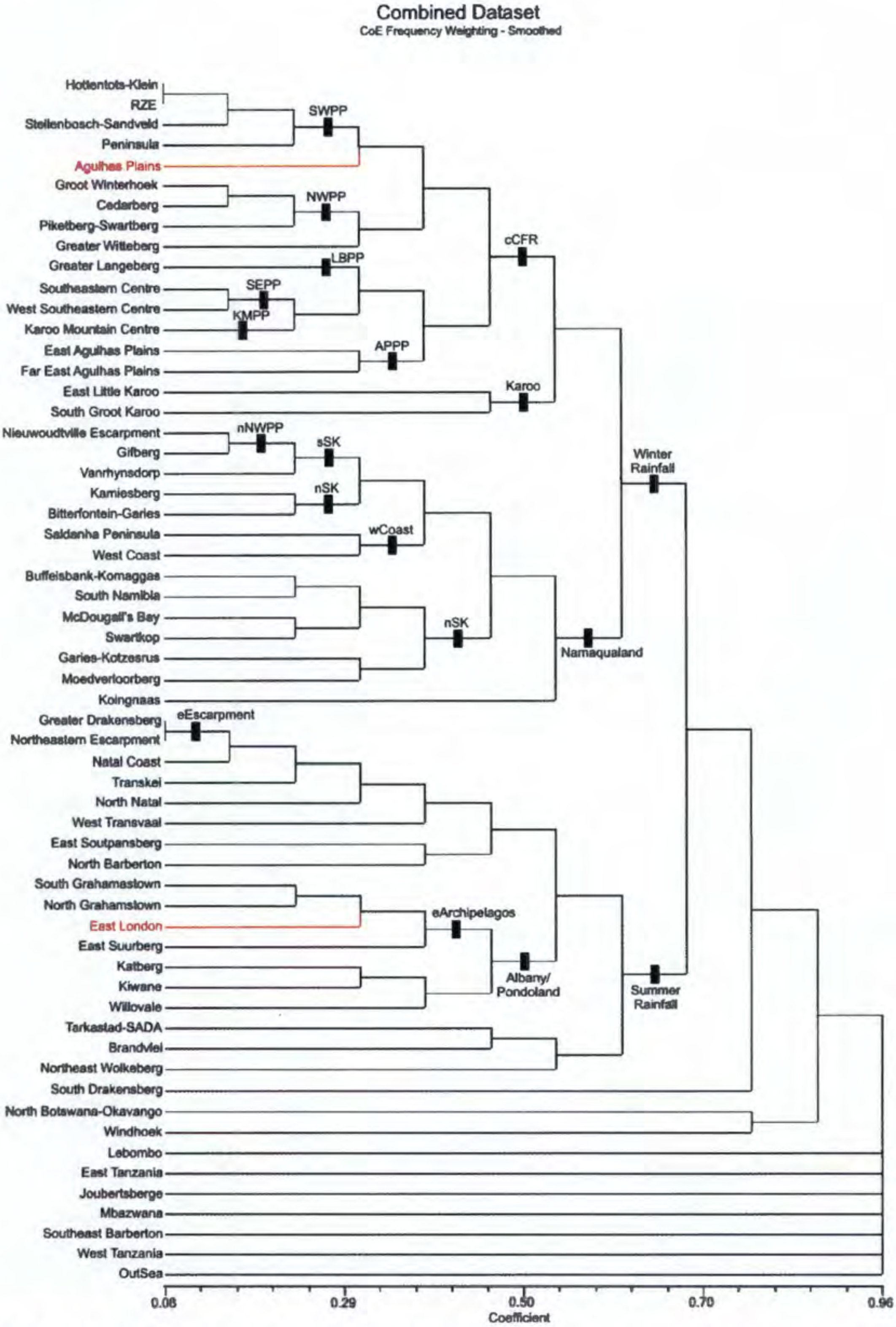


Figure 26: UPGMA analysis of the relationships between the PC for the Combined Dataset, using Smoothed Centre Frequency Weighting.
The marks on the dendogram indicate higher level phytogeographical or environmental boundaries. OGUs in red indicate conflict with the other hierarchical analyses, or OGUs whose position should be investigated further.

The phytogeographical patterns I retrieved may change slightly with a more complete dataset, although this is unlikely to result in major changes in the PCs, especially in the core CFR areas. It is hoped that a more complete dataset will bring more stability to PCs that appear to be weakly supported, or appear in conflict in the different analyses, and particularly to PSCs, which were less stable. Regions geographically removed from the core CFR produced less robust results, reflecting the small number of species of Cape elements found in these spatially distant areas.

#### 2.4.1.2 Spatial Differences in the Combined Dataset Phytogeographical Centres versus Individual (Taxon or Guild) Datasets Centres

When a comparison was made between the PCs formed in the Combined Dataset, to those of the Clade/Group Datasets (Appendix I), it was noted that the PCs of the Clade/Group Datasets were typically larger. This was observed mainly in the Southwest Centre and to a lesser extent in the Northwest Centre. These areas are particularly mountainous and often form a single continuous PC in the Clade/Group Sub-datasets. However, in the Combined Dataset, they form much smaller phytogeographical areas. Occasionally, the reverse is true for the Southeast Centre and this is possibly due to fragmentation of suitable habitats, and/or under-collection. This may also occur because of the higher numbers of range-restricted taxa in the Combined Dataset from different floras, which lack spatial congruence, grouping more QDSs together in a domino effect.

In the Combined Dataset, the PCs are generally geographically smaller in the Southwest Region, and have higher numbers of endemics, particularly in the more mountainous regions (Cowling and Lombard, 2002). There are higher numbers of montane biotic elements here and conflict between taxa is minimal. This is equally true for the Combined Datasets and for the Individual (Taxon or Guild) Datasets.

In the Southeast Region, there is a lower ratio of montane elements to low altitude elements (Table 12, PC 5), particularly in the RDL Dataset (Table 54, PC 10). This increase in the numbers of lower altitude endemics in the RDL Dataset contributes to the relatively high numbers of endemics in the Combined Dataset PCs in the southeast of the CFR. In datasets with predominantly montane biotic elements, smaller, scattered, disjunct PCs were observed in the SEPP and these appeared to be restricted to montane habitats. This may occasionally result in a disjunct grouping of these habitats in different Phytogeographical Centres, for example, the Karoo Mountain Phytogeographical Centre (KMPP), the Langeberg Mountains Phytogeographical Centre (LBPP) and the Southeast Phytogeographical Centre (SEPP), in Orchidaceae and Bruniaceae. In the Combined Dataset, the PC in the SEPP Region was considerably enlarged. This may be due to the increased number of low altitude biotic elements and elements from other floras (thickets), which may merge the disjunct montane elements into a consolidated PC. Thus, the Southeast Centre (PC 5) in my Combined Dataset may be floristically and ecologically artificial.

The RDL Dataset is similar to the Combined Dataset in that it contains phylogenetically and ecologically diverse taxa. RDL taxa generally have small ranges, and the dataset lacks the slightly more widespread taxa that may have contributed to the large size of the SEPP in the Combined Dataset by grouping the smaller phytogeographical units together. Disjunct PCs were also observed in the Orchidaceae and Bruniaceae, possibly due to restriction to more moist habitats.

Thus, the observed spatial patterns of taxa and the congruence of distributions may be more important in determining the size of centres, rather than simply determining the number of endemics per se. In the Combined Dataset, the overwhelming number of montane taxa with very similar phytogeographical distributional patterns may produce less conflict in the more mountainous centres, such as the NWPP and SWPP. In less mountainous centres, such as the SEPP, conflict may be greater, due to the lesser or non-existent dominance of montane taxa, ultimately resulting in larger PCs.

A further complication that could result when comparing PCs occurs when the complexity of the hierarchical relationships between the PCs are reduced. These relationships are recorded as multidimensional in the similarity table and two-dimensional in the dendograms. Additionally, dendograms are very hierarchical, but for mapping purposes they were reduced to two floristic levels in my study (Section 2.3.6.2). The phytogeographic levels of these groupings may be different in the different datasets, much like taxonomic levels in taxonomy (Stevens, 2001). In other words, the sub-centres of the Clade/Group Datasets may be equivalent to the centres of the Combined Taxa Dataset. Thus, pattern and congruence should be emphasised and compared to a greater extent than the ranks of centre or sub-centre. In all probability, the larger centres of the Clade/Group Datasets could be congruent with the mega-centres (hierarchical clustering) of the Combined Taxa Dataset, which ultimately form the SWPP, NWPP, LBPP, APPP, KMPP and SEPP, as indicated in the literature (Weimarck, 1941; Goldblatt and Manning, 2000).

## 2.4.2 Phytogeographical Patterns

### 2.4.2.1 The Winter Rainfall Clusters

#### 2.4.2.1.1 Core CFR Centres

The SWPP most frequently contains the highest diversity and endemism of the CFR Phytogeographical Centres in the datasets I analysed. This has been noted in previous studies (Levyns, 1962, 1964; Goldblatt and Manning, 2000, 2002). In Bruniaceae, *Erica,* Orchidaceae, Polygalaceae, Proteaceae and Restionaceae, there is at least twice the number of endemics in the SWPP as in the NWPP, which is usually the next richest Phytogeographical Centre. In my Asteraceae, Poaceae and Rosaceae Datasets, the SWPP and the NWPP contain almost equal numbers of endemic taxa, although the SWPP usually contains slightly more. Depending on how the hierarchical affinities of the Rosaceae PCs are classified, namely, whether PC 2 is assigned to the NWPP or SWPP, Rosaceae could have double the numbers of endemic taxa in the SWPP than NWPP, or nearly equal numbers of endemic taxa in the SWPP and NWPP. The NWPP contains more endemic taxa than the SWPP in the Fabaceae, Geophytes, the RDL Taxa and Rutaceae Datasets. Rutaceae has nearly twice the number of endemics in the NWPP as compared with the SWPP. The other Phytogeographical Centres performed less consistently and their rank depended on the clade/group being analysed. Generally, levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, NWPP, SEPP, KMPP, SEPP, LBPP and APPP.

The six centres currently recognised in the CFR (Goldblatt and Manning, 2000) are grouped together in all analyses, although in slightly differing ways, forming the core CFR (denoted as cCFR in the dendograms; Figure 22 - 26). The PCs identified for the Northwest Centre (NWPP) are sisters to the PCs of the Southwest Centre (SWPP) and comprise the western centres with the most seasonal concentration of winter rainfall. The remaining centres (Langeberg Centre (LBPP), Karoo Mountain Centre (KMPP), Southeast Centre (SEPP) and Agulhas Plains Centre (APPP)) mostly group together, forming the eastern and southern component, as sister to the western centres. The greatest deviation is in the unweighted hierarchical analysis: here the eastern APPP (PCs 21 and 24) is sister to the rest of the core CFR (Figure 22).

The results of the hierarchical relationship between the two Southeast Centres (PC=5 and 16) are identical in all analyses. The relationship of the Greater Langeberg Centre (PC=2) and the Karoo Mountain Centre (PC=7), are identical, namely ((SEPP, KMPP), LBPP), with no conflict between analyses. The close relationship between these three centres is also observed in the individual clade/group datasets, where they are often grouped into single floristic units, for example, the KMPP and SEPP in Bruniaceae and Geophytes, and the SEPP and LBPP in Orchidaceae.

###### 2.4.2.1.1.1 Southwest Phytogeographical Province (SWPP; PC 1, 6, 9, 10)

The Southwest Province of my Combined Dataset corresponds well to the Southwest Centre circumscribed by Weimarck as well as that of Goldblatt and Manning (2000). The greatest difference in my study is that the Saldanha PC (PC 20) forms a cluster with the West Coast PC (PC 22), outside the core CFR cluster and has closer affinities to the Southern Succulent Karoo cluster (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). In addition, there are some minor boundary deviations. The southern boundary of the Southwest Province moves further north near the Agulhas Plains, as more of the lowlands are incorporated into Agulhas Plains Centre (PC 4). Quoin Point (PSC 1.2) is combined with the Kleinrivier Sub-centre (PSC 1.2), which may have been a favoured collecting locality. Attention is drawn to this pattern in taxa (datasets) where this is apparent.

The Southwest Province may be regarded as the heart of the CFR. Parts of these mountainous areas constitute the wettest part of the winter rainfall area of Southern Africa (Schulze et al., 1997). In addition, this area has some of the steepest moisture gradients of the CFR. The SWPP contains high numbers of endemics with a preference for mesic habitats (Table 12). It may also be the centre least affected by the southerly displacement of the rain-bringing westerly anti-cyclonic cold fronts, during drier fluvial cycles (Meadows and Baxter, 1999; Cowling and Lombard, 2002). This may make it the most robust refugia in the CFR for species, which cannot tolerate much drought and may lead to less extinction among these species in other areas of the CFR. This may account for its notably high levels of endemism, as compared to the other Phytogeographical Centres (*cf.* Cowling and Lombard, 2002). A dated phylogeny would better able to determine the ratios of neoendemics and palaeoendemics. More of the latter would indicate the effectiveness of the area as a refugia.

Seven PCs are retrieved in my Southwest Province in the different datasets that I analyse. These include: (1) the Hottentots Holland-Kogelberg-Kleinrivierberge, (2) the Stellenbosch-Bainskloof Mountains, (3) the Cape Peninsula, (4) the Riviersonderend Mountains (RZE), (5) the SWPP Sandveld and (6) the Saldanha Peninsula. These centres are all rich in typical fynbos taxa. In addition, the (7) Berg-Bree River Valley is recognised as a PC rich in Fabaceae, Geophytes and RDL Taxa Datasets.

#### 2.4.2.1.1.1.1 Hottentots Holland – Kogelberg – Kleinriviersberge (PC 1)

The importance of this area (Hottentots Holland–Kogelberg–Kleinriviersberge) has been known for a long time (Levyns, 1964). It has previously been referred to as the Caledon Centre (Levyns, 1964) due to its location in the Caledon Magisterial District. Levyns (1964) noted that the highest diversity of Cape Flora is usually found here, which decreases to the north and east.

Linder (2001) retrieved this centre by using a Restionaceae Dataset, based on a weighted analysis of endemism. In my study, I retrieved it again. For many groups, this area is usually the heart of the SWPP (at the PC and QDS level), which is itself the heart of the CFR. It is centred in the west in the Hottentots-Holland-Kogelberg Mountain axis and usually trails off to the east along the Kleinrivierberge (Figure 27), the extent of which is often dependent on the development of the Western APPP. Neither Oliver et al., (1983) nor Weimarck retrieved this PC. The latter has a completely different set of delimitations in this area, which included the area between the Palmiet River and the Gouritz River into his Bredasdorp sub-centre, without further sub-division or refinement. Weimarck's boundaries divided the western region of my Hottentots–West Kleinriviersberge (PSC 1.1).

The Hottentots Holland–Kogelberg–Kleinriviersberge area forms an independent PC in the Combined Dataset and in Proteaceae. Although semi-independent in Rutaceae, but including part of the Cape Peninsula, the PC is much reduced in size, diversity and endemicity, and does not have the same status as in other fynbos groups. In Bruniaceae, *Erica* and Restionaceae, the region forms a distinct phytogeographical area (sub-centre) in a much larger floristic unit, which includes many other parts of the SWPP Mountains. In Poaceae, there is very little sub-centre differentiation in this region and even less in Orchidaceae.

In a number of datasets (Asteraceae, Proteaceae, the RDL Taxa and Polygalaceae) only the western QDSs are assigned to this centre, while the eastern parts of the Kleinrivierberge Range are included in the APPP. In Rosaceae and Rutaceae, PC development is restricted to the west, but additionally the APPP is also relatively weakly developed.

In Fabaceae, RDL Taxa and Polygalaceae, there is an unusual PC development, where the Hottentots Holland, Kogelberg and West Kleinrivierberge are combined with the southern RZE, rather than with the more southerly eastern Kleinrivierberge. The latter is combined into an enlarged APPP. A cursory analysis of the habitats of the taxa in the Fabaceae dataset indicates that very few of the taxa that are endemic to this enlarged APPP are limestone endemics (Table 39, PC 2). This raises some interesting questions about speciation of TMS taxa in this centre (Fabaceae PC 2). They appear somewhat isolated from the western Kleinrivierberge and RZE

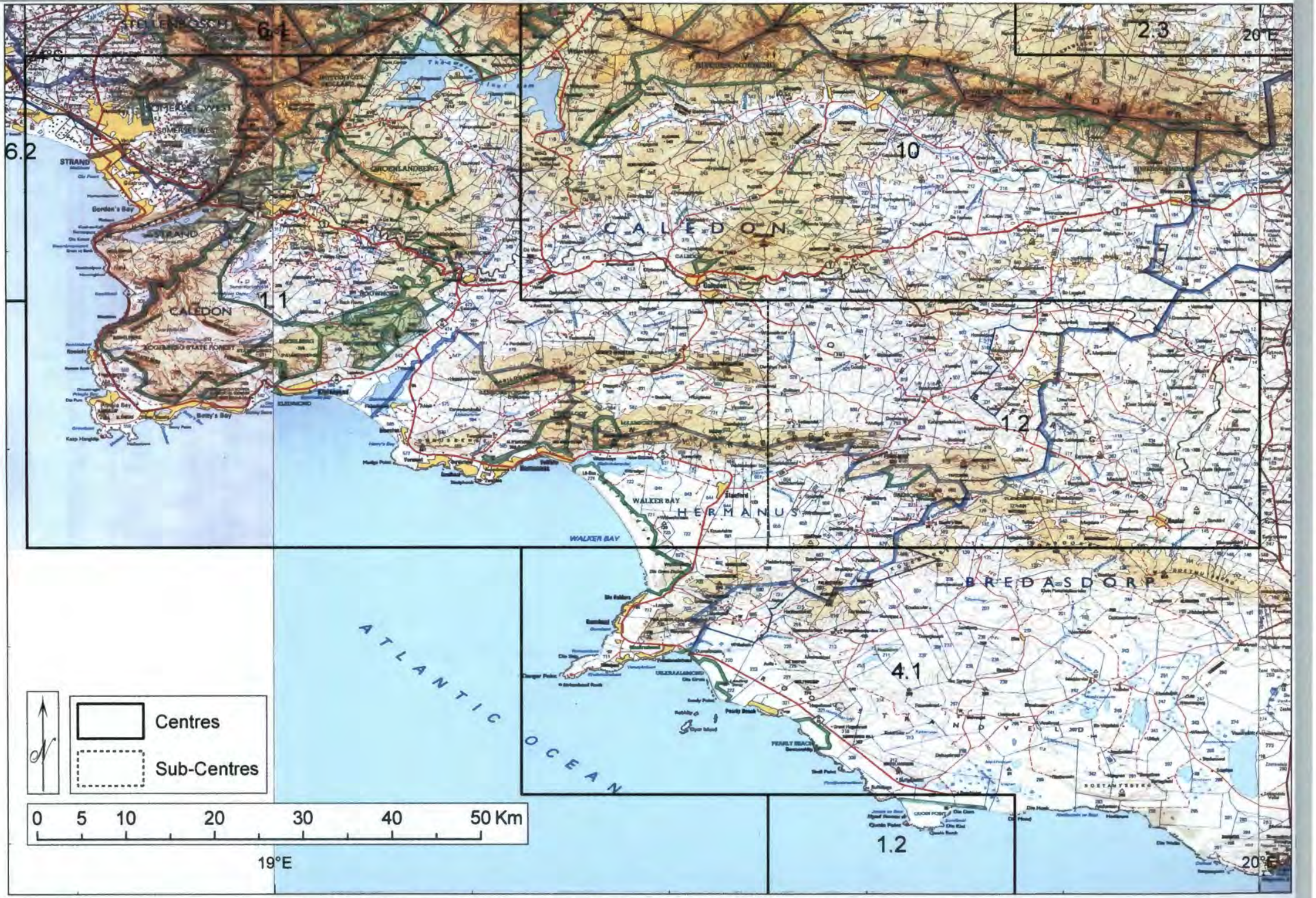


Figure 27: Position of the Hottentots Holland - Kogelberg - Kleinrivierberge Phytogeographical Centre (PC 1)

TMS taxa, or there may be some sort of barrier that is not apparent or effective in the other datasets. My Geophytes have a similar phytogeographic pattern to Fabaceae, combining the Hottentots Holland, Kogelberg, West Kleinrivierberge and the southern RZE, but also including the more southerly eastern Kleinrivierberge, with a reduced APPP PC.

### 2.4.2.1.1.1.2 Stellenbosch-Bainskloof and SWPP Sandveld (PSC 6.1 and PSC 6.2)

The SWPP Sandveld/lowland region (PSC 6.2 of the Combined Dataset) shows very strong affinities with the Stellenbosch-Bainskloof Mountains (PSC 6.1), merging the two sub-centres into a single PC. This may be the result of a common flora on the granite hills of the Paardeberg, Paarlberg and Darling areas, as well on the granite foothills of the Drakenstein Mountains (Figure 28). Granite Endemics form a strong component of this centre (Table 12). However, the endemics of each of the sub-centres show distinct habitat preferences. Endemics of the Stellenbosch-Bainskloof Mountains (PSC 6.1) have a higher representation in montane sandstone habitats (Table 12), while there are a high proportion of endemic taxa in low altitude littoral sand habitats in the SWPP Sandveld/lowland region (PSC 6.2) (Table 12). Thus, the combining of these two areas (PSCs 6.1 and 6.2) may be as a result of interdigitisation of disparate habitats in QDSs.

### 2.4.2.1.1.1.2.1 Stellenbosch-Bainskloof (PSC 6.1)

The relationship between the coastal Hottentots-Holland-Kleinrivier Mountains and the western inland Bainskloof-Du Toitskloof Mountains and the eastern Riviersondereinde Mountains, remains unresolved. The Combined Dataset recognizes them as three distinct PCs (6.1, 1 and 10). However, there is much conflict in the literature regarding the different clade/group datasets analysed here (Appendix I), which indicates that the area is difficult to classify floristically. Linder (2001) showed that there is a close relationship between Bainskloof and the Riviersonderend Mountains and Weimarck grouped them as the Frenchhoek Sub-centre. In Oliver et al., (1983), the western part of the Riviersonderend Mountains is included with the Bainskloof Mountains, as part of their much more narrowly defined South-Western Centre (Bainskloof, Hottentots Holland and Kleinriviersberge). In my study, the Stettynsberg, which are directly east of the Slanghoek-Du Toits Mountains, are included as part of the Riviersonderend Centre (PC 10). The boundaries between the Riviersonderend, Stettyns, Du Toits and Slanghoek Mountains are not phytogeographically clear and they might be better regarded as a gradual transition, rather than a definite boundary.

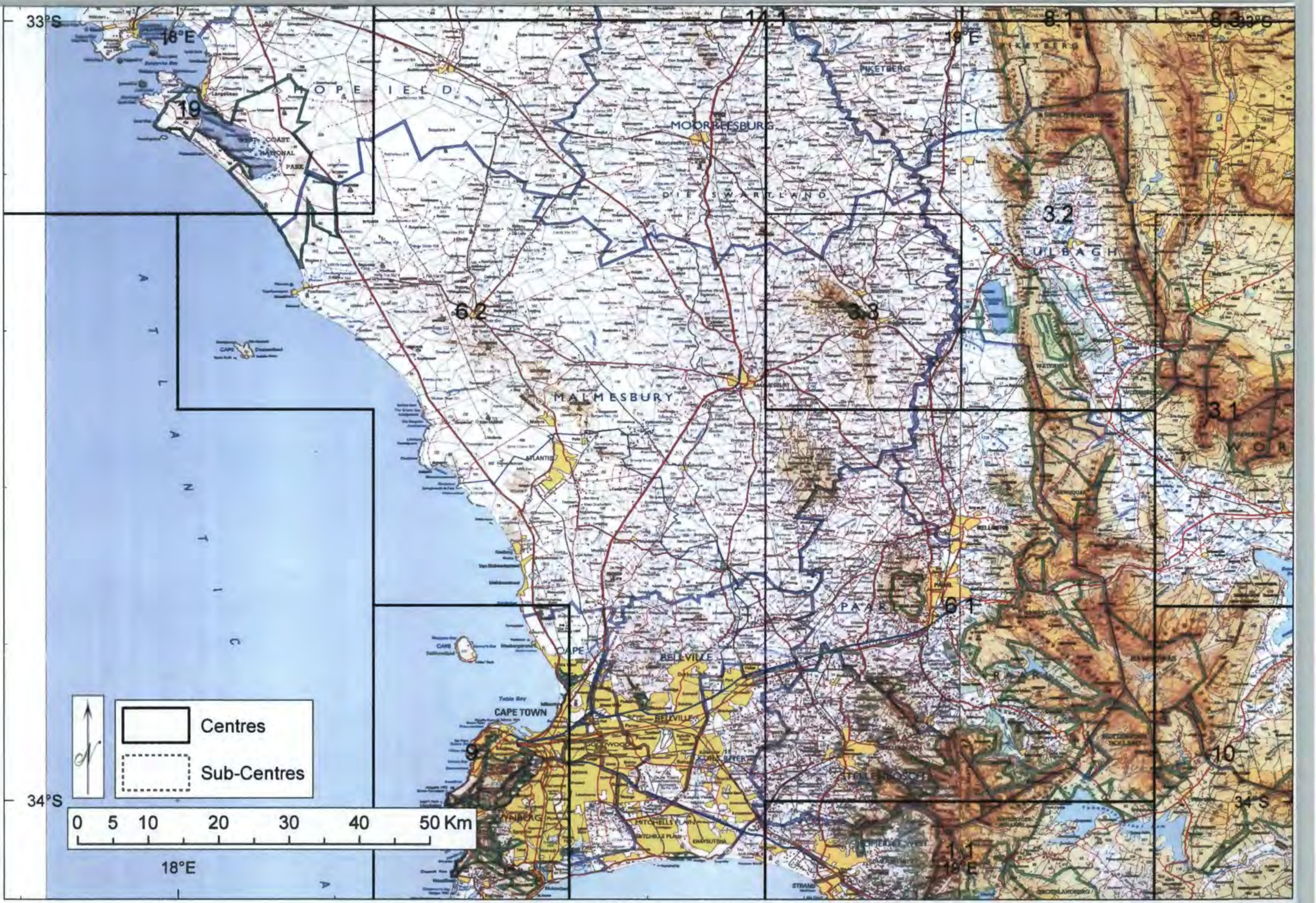


Figure 28: Position of the Stellenbosch-Bainskloof and SWPP Sandveld Phytogeographical Centre (PC 6)

The Stellenbosch-Bainskloof Mountains form an independent PC in the Fabaceae, Proteaceae and RDL Taxa Datasets, while in the Combined Dataset and Polygalaceae, it is strongly associated with SWPP Sandveld. In Asteraceae, Bruniaceae and *Erica,* it usually forms an independent sub-centre, combined to varying degrees with the rest of the central Southwest Centre Mountains, but usually excluding the Kleinrivierberge, and occasionally including the Hottentots-Holland Mountains. The Cape Peninsula is amalgamated with this larger PC in Poaceae, Polygalaceae and Restionaceae, although only in the latter three is there differentiation into mountain range-specific sub-centres.

In Orchidaceae, Rutaceae and Rosaceae, the Stellenbosch Mountains combine with the rest of the SWPP Mountains. However, the Bainskloof QDS is associated with the Hexrivier, West Langeberg and Groot Winterhoek (only in Rosaceae) Mountains in the NWPP, across the Berg River Valley.

#### 2.4.1.1.1.2.2 The SWPP Sandveld (PSC 6.2)

The Sandveld Sub-Centre (PSC 6.2 of the Combined Dataset) is also recognised by Oliver et al., (1983) and Linder (2001). Weimarck's sub-centre boundary nearly bisects the QDS (3318DC), combining the Perdeberg with his Malmesbury Flats Sub-Centre, and the Paarlberg with his Frenchhoek Sub-Centre. The current configuration, namely, the grouping of QDSs 3318DB (which includes both Paarlberg and Perdeberg) with the Stellenbosch/Bainskloof Mountains Sub-Centre (PSC 6.1), only results in one more endemic taxon being added to the combined total number of endemics for the two sub-centres, than if 3318DB was combined with the Sandveld Sub-Centre (PSC 6.2). QDS 3318DB has diverse biotic elements, which may occupy different ecological niches. These different biotic elements are likely to have conflicting affinities in both sub-centres. There are a number of exposed granite intrusions in the Stellenbosch/Bainskloof Mountains Sub-Centre (PSC 6.1), especially in 3318DB, which form the Perdeberg (758m) and Paarlberg (729m). These may have associations to both the Groenberg (942m) near Bainskloof (3319CA) in the Stellenbosch/Bainskloof Mountains Sub-Centre (SC 6.1) and to the hills around Darling (e.g. Dassenberg, 567m) in the Sandveld Sub-Centre (PSC 6.2). The granitic elements (Table 12) may also have further affinities south, along the lower slopes of the mountains to the Helderberg.

Interestingly, Kasteelsberg (946m), which is surrounded by lower lying areas, also shows inconsistent affinities. Kasteelsberg contains no granites, consisting entirely of sandstone. This may account for the floristic link to the Groot Wintershoek in the Combined Dataset and the general NWPP in *Erica,* although the Fabaceae Dataset indicates affinities to the SWPP.

The SWPP Sandveld PSC contains endemics in several vegetation types, including littoral sand plains fynbos, shale Renosterveld, TMS fynbos, and granitic elements (Table 12).

Figure 29: Position of the Peninsula Phytogeographical Centre (PC 9)

#### 2.4.2.1.1.1.3 Peninsula (PC 9)

The floristic and phytogeographic significance and distinctiveness of the Cape Peninsula has long been recognised (Drége, 1844; Weimarck, 1941; Oliver et al., 1983; Linder, 2001; Helme and Trinder-Smith, 2006; Trinder-Smith, Cowling and Linder, 1996). In almost every dataset, there is some sort of distinct phytogeographical development on the Cape Peninsula and in most cases (excluding Orchidaceae, Rosaceae, and Rutaceae) it is significantly distinct enough from surrounding areas to form its own PC.

Although the mountains of the Cape Peninsula (Figure 29) are isolated from the inland mountains of the Southwest Cape by a 40 km wide, low lying littoral sand plain, it has strong hierarchical affinities to the Hottentots-Holland-Kleinrivier Mountains are apparent in a number of taxa, for example, Bruniaceae, Geophytes, *Erica,* Orchidaceae, Poaceae, Restionaceae, Rutaceae and Aizoaceae. It has less affinity with the other mountains of the SWPP to the north of the Hottentots-Holland-Kleinrivier Mountains, including those around Stellenbosch and the Bainskloof-Limietberg Range.

The Cape Peninsula contains both montane and lower altitude taxa, with strong TMS substrate preferences (Table 12). The montane elements show affinities to the other SWPP Mountains, while the lower altitude taxa show affinities to the South Sandveld and indirectly to the Stellenbosch Mountain QDSs.

#### 2.4.2.1.1.1.4 RZE (PC 10)

Despite being a well-defined mountain range, which in the CFR would suggest a distinct endemic flora, the RZE has not often been treated as an independent PC, but is usually grouped with the rest of the northern SWPP Mountains (Weimarck, 1941; Linder and Mann, 1998; Linder, 2001; Moline and Linder, 2005). Occasionally, the western and eastern portions of the RZE have not been treated together (Drége, 1844; Oliver et al., 1983). In the Combined Dataset, it is identified as a distinct PC (PC 10), although it includes portions of the Stettynsberge in the west and the Caledon Swartberg in the south (Figure 30). The RZE is thought to have very close affinities to the remaining northern SWPP Mountains, hence its frequent classification with those mountains. Only Drége (1844) indicated that the affinities of its eastern region might lie elsewhere. In my study, the RZE has greater affinities to the southerly Hottentots-Holland-Kleinrivierberge in four of the five hierarchical analyses (Figure 23, Figure 24, Figure 25 and Figure 26), while in the unweighted hierarchical analysis (Figure 22) it is sister to (Hottentots-Holland-Kleinrivierberge;

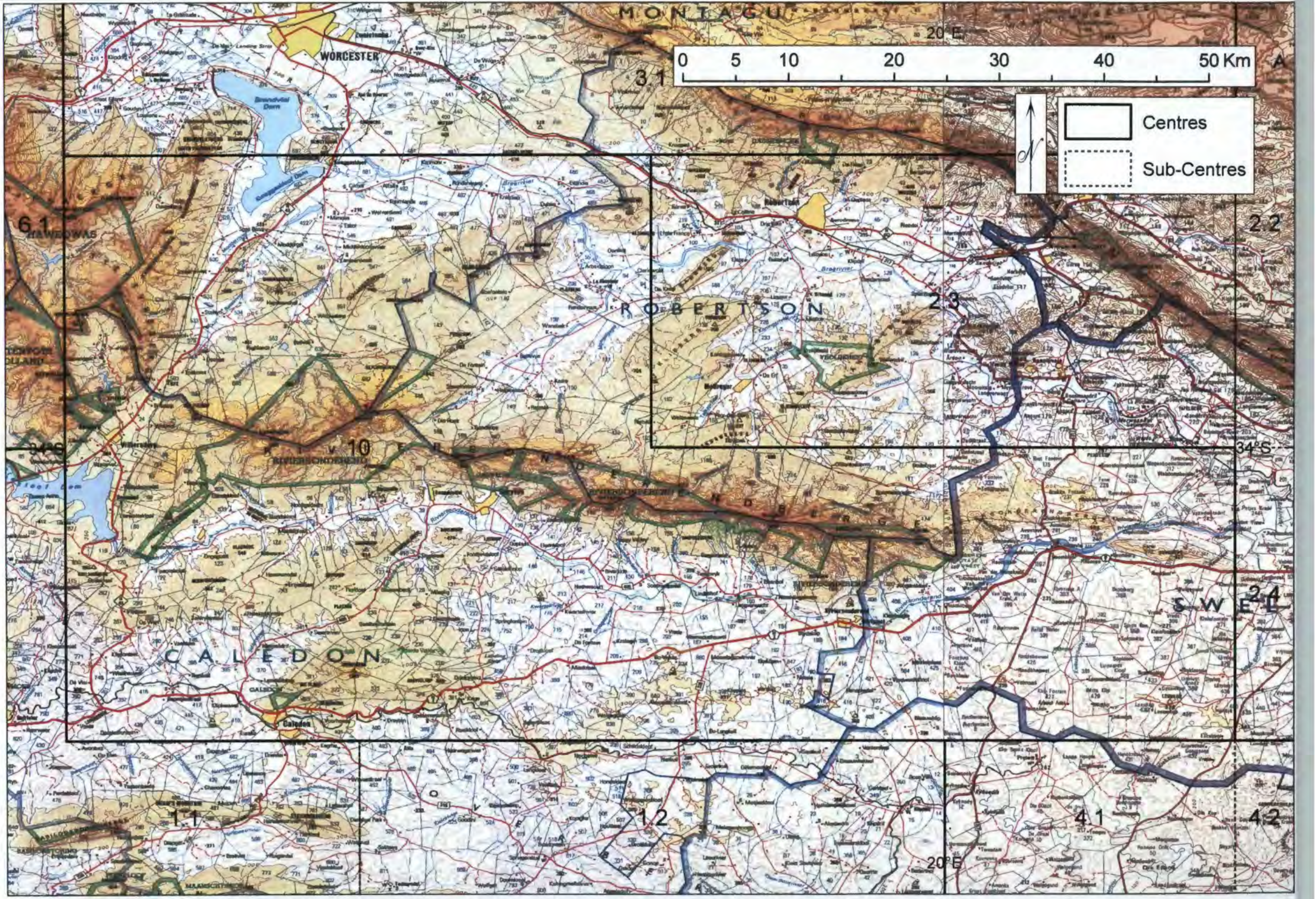


Figure 30: Position of the Riviersonderend Phytogeographical Centre (PC 10)

Stellenbosch-Bainskloof-Sandveld). This is in agreement with the findings of Moline and Linder (2005), although it contradicts those of others (Drége, 1843; Weimarck, 1941; Linder and Mann, 1998; Linder, 2001), which indicated stronger affinities to the more northerly Frenchhoek and Bainskloof Mountains.

The RZE PC is distinct and independent of the surrounding PCs in the Combined Dataset, Proteaceae and Rutaceae. In Asteraceae, Bruniaceae and *Erica,* the RZE forms a sub-centre in a much larger PC, centred on the central SWPP Mountains. In Poaceae, the pattern is less clear, with no sub-centre development.

An interesting pattern is observed in Fabaceae, the RDL Taxa, Polygalaceae and to a lesser extent, the Geophytes. In these datasets, the RZE splits along its ridge, with PC formation to the north and south of the ridge, rather than centred on the mountain range itself. In most cases, the southern floristic unit extends from the Hottentots-Holland-Kogelberg to the eastern RZE, while this pattern is less clearly developed in Polygalaceae. The patterns on the northern side are less consistent. This seems to indicate the presence of a lower altitude flora or biotic element. Most of these datasets have appreciable numbers of non-sandstone and non-fynbos elements (Table 39, Table 42, Table 49 and Table 54), which may undermine the dominance of fynbos TMS patterns. In Orchidaceae and Rosaceae there is no clearly identifiable pattern.

### 2.4.2.1.1.1.5 Hierarchical Relationships between SWPP PCs

In the Combined Dataset hierarchical analysis, the four PCs comprising SWPP are identical in all analyses. The SWPP consists of: the Hottentots-Holland-Kleinrivier Centre (PC 1), the RZE Centre (PC 10), the Stellenbosch-Bainskloof Mountains-Sandveld Centre (PC 6) and the Cape Peninsula (PC 9). The hierarchical relationships between them are nearly identical, except in the Unweighted Analysis (Figure 22), where the RZE and the Stellenbosch-Sandveld swap positions. The Cape Peninsula is the most distantly related to the four centres, and it includes the greatest barrier to gene flow, namely, the low altitude Cape Flats. The West Agulhas Plains forms a sister sub-centre to the core SWPP in the Unweighted and Smoothed PC Frequency Weighting Analyses, as in Weimarck's study. This lack of node stability may indicate conflict between different biotic elements, for example, montane and lower altitude elements shared between the SWPP and the APPP (Table 12).

#### 2.4.2.1.1.2 The Northwest Phytogeographical Province (NWPP) (PC 3, 8, 12, 14)

Drége (1843) was the first botanist to designate a phytogeographical boundary between the more mesic southwest and the more arid northwest CFR. This distinction was largely ignored (Rehman, 1880; Engler, 1882; Bolus, 1886; Bolus, 1905; Marloth, 1908) until Weimarck's landmark study confirmed Drége's subdivision. The NWPP, as delimited by Goldblatt and Manning (2000), and Weimarck, and also in my study, together with the SWPP and APPP, are the major phytogeographical provinces in the CFR that almost exclusively receive winter rainfall.

The NWPP occupies and defines the north-western area of the CFR. Although the Northwest Centre has usually been centred on the Groot Winterhoek, the Hexrivier, and the Cedarberg Mountains, its geographical extent and thus the external boundaries of the NWPP and north-western CFR have fluctuated. Drége (1843) used the lower Olifantsrivier as the north-western boundary and the Nieuwoudtville Escarpment Centre was included in his NWPP as well. Rehman (1880) excluded the majority of the Nieuwoudtville Escarpment and the Cedarberg from his Southwest Cape Region (equivalent to his definition of the northern CFR boundary), while Engler (1882) included all of the Gifberg and Cedarberg, but excluded the Nieuwoudtville Escarpment (equivalent to his definition of the northern CFR boundary). Bolus' (1886) eastern boundary, in the region of the NWPP of the CFR, was remarkably accurate, but his northern boundary was very far north and erroneously included the Hardeveld and the southern Knersvlakte as part of the CFR. In a later map (1905), Bolus shifted the eastern and northern boundaries considerably to the west and south respectively, with the result that the entire Nieuwoudtville Escarpment and the eastern half of the Cedarberg were excluded from the CFR. Marloth's (1908) map is extremely accurate for the external boundaries of the NWPP and one of the few to recognise the Cape affinities of the Kamiesberg. Marloth's northern boundary began at the Verlorenrivier Mouth on the coastal plains and included the Matsikammaberg/Gifberg and Nieuwoudtville areas of the escarpment, and recognised the Cape affinities of many of these northerly mountain ranges.

Weimarck, who like Marloth (1908), concentrated on Cape Temperate elements and taxa centred in the Cape, defined a much-reduced Northwest Centre that excluded the Gifberg and Nieuwoudtville Escarpment, as did Oliver et al., (1983).

The external boundary of the CFR, around the NWPP of Goldblatt and Manning (2000), has much in common with Marloth (1908) except on the coastal plains, where Goldblatt and Manning (2000) used the more northerly Olifantsrivier as a floristic boundary.

In my Combined Dataset, the boundary between the Southwest and Northwest occurs in the region between the Groot Winterhoek and Elandsberg Mountains, and is a little further south than in Weimarck and Goldblatt and Manning (2000), both of whom used the course of the Little

Berg River/Roodezand Pass as a floristic boundary. I include both the Elandsberg and the Kasteelsberg, which lie south of the Little Berg River, in the Northwest Centre. The Elandsberg and Limietberg probably contain a mixture of NW and SW elements and so constitute a transition zone where these elements interdigitate. The lower northerly slopes of the Kasteelsberg (PSC 3.3), just west of the town Riebeek-Kasteel, may include more arid adapted species from the Cedarberg and Piketberg. The other inselbergs to the south of Kasteelsberg (Paardeberg and Paarlberg) are granitic and show a closer affinity to the SWPP (PC 6 of the Combined Dataset).

Many studies have used the Olifantsrivier as the northern boundary of the CFR (Drége, 1844; Rehman, 1880; Engler, 1882; Bolus, 1905; Goldblatt and Manning, 2000). This, like the Little Berg River, constitutes a convenient border, but the Olifantsrivier splits my Combined Dataset West Coast PC (PC 22). The West Coast PC includes the sandy plains north of Elands Bay and has no fynbos elements endemic to it (Appendix II: Combined Dataset, PC 22). The analysis of Oliver et al., (1983) also did not group this area with the NWPP, although their "unplaced" area included the whole Swartland, Piketberg, and the Saldanha Peninsula. My delimitation of the NWPP on the coastal plain is consistent with that of Marloth (1908) and Weimarck.

Curiously, in the Tankwa Karoo, there are two QDSs that show affinities to the Cedarberg PC (8). These QDSs are disjunct across the arid Tankwa Karoo basin and occur where the escarpment starts to rise on the eastern side of the Tankwa Basin. The taxa responsible are *Erica eremioides* subsp. *eglandula* (3) and *Agathosma pubigera* (4) in the northern and southern QDSs respectively, and perhaps indicate a tentative link between the NWPP and the Hantam-Roggeveld.

Diversity and endemism are usually high in the NWPP in most Cape Clades and it usually ranks second after the SWPP (Table 9) (Weimarck, 1941; Goldblatt and Manning, 2000). In Rutaceae and to a lesser extent, Fabaceae, the NWPP contains more endemics and higher diversity than the SWPP. In the Geophytes Dataset, the difference between the number of endemics and the diversity between the NWPP and SWPP, is not as marked as in more exclusively Cape Clades, which may indicate that geophytes are not as concentrated in the SWPP as are many Cape 'fynbos' Clades.

Apart from Weimarck and Drége (1843), previous studies (Oliver et al., 1983; Linder, 2001; Goldblatt and Manning, 2000) did not identify internal divisions in the NWPP. Weimarck identified two sub-centres within the CFR proper, the Cedarberg Sub-Centre and the Great Winterhoek Sub-Centre, the latter of which includes large southerly areas of my Greater Witteberg Centre (PC 12). Although the Piketberg-NWPP Sandveld formed part of Weimarck's

NWPP, it was unassigned to a sub-centre. Drége's (1844) subdivisions appear to focus mainly on the differences between the montane and lowland floras.

I recovered six major PCs in the NWPP, a few neighbouring PCs and other minor PCs. The number of endemics they contain and the relationships between them vary, depending on which clade/guild group is being analysed. The major PCs from my Combined Dataset are: the Hexrivier (PSC 3.1 in part); the West Langeberg (PSC 3.1 in part); the Groot Winterhoek (PSC 3.2); the Cedarberg and North Bokkeveld Mountains (PC 8); the North Sandveld, including the Piketberg and Olifantsrivierberg (PC 14); and finally, the Greater Witteberg (PC 12), which was found to be sister to the rest of the NWPP in the hierarchical clustering analysis (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), and whose inclusion in the NWPP is contentious.

#### 2.4.2.1.1.2.1 The Groot Winterhoek PC and Hexrivier-West Langeberg PC (PC 3)

In the Combined Dataset of my study, the belt of mountains stretching from the Groot Winterhoek in the west to Cogmans Kloof (between Ashton and Montagu) in the east, and including the Skurweberg, Witzenberg, the Hexrivier Mountains, and the western Langeberg, are delimited as the Groot Winterhoek-West Langeberg PC (PC 3; Figure 31). It is largely congruent with the southern part of Weimarck's Groot Winterhoek Sub-Centre, but does not include the more northerly and easterly arid areas, which I include in the Greater Witteberg PC (PC 12). In this regard, they may have greater similarities to the western parts of the IVa area of Drége map (1843). Three sub-centres were identified: the Hexrivier-West Langeberg (PSC 3.1), the Groot Winterhoek (PSC 3.2), and the Riebeek-Kasteel (PSC 3.3). No phytogeographical division was recovered between the Hexrivier and West Langeberg. In my Combined Dataset, the three QDSs that contain the Hexrivier Mountains contain 38 of the PSC's 57 endemics and 97 of the PSC's 131 near endemics. By comparison, the three QDSs that make up the West Langeberg area only contribute 11 endemics and 19 near endemics; which may indicate a potentially unrecovered sub-division between these areas in the Combined Dataset, but is apparent in some of the clade/guild datasets, hence their separate treatment here.

##### 2.4.2.1.1.2.1.1 The Hexrivier PSC (PSC 3.1 in part)

The Hexrivier Mountains usually form a distinct or nearly distinct sub-centre within a larger northwest PC. This is apparent in my Combined Dataset (despite being merged with the west Langeberg), Asteraceae, Bruniaceae, *Erica,* Restionaceae and to a lesser extent, Polygalaceae.

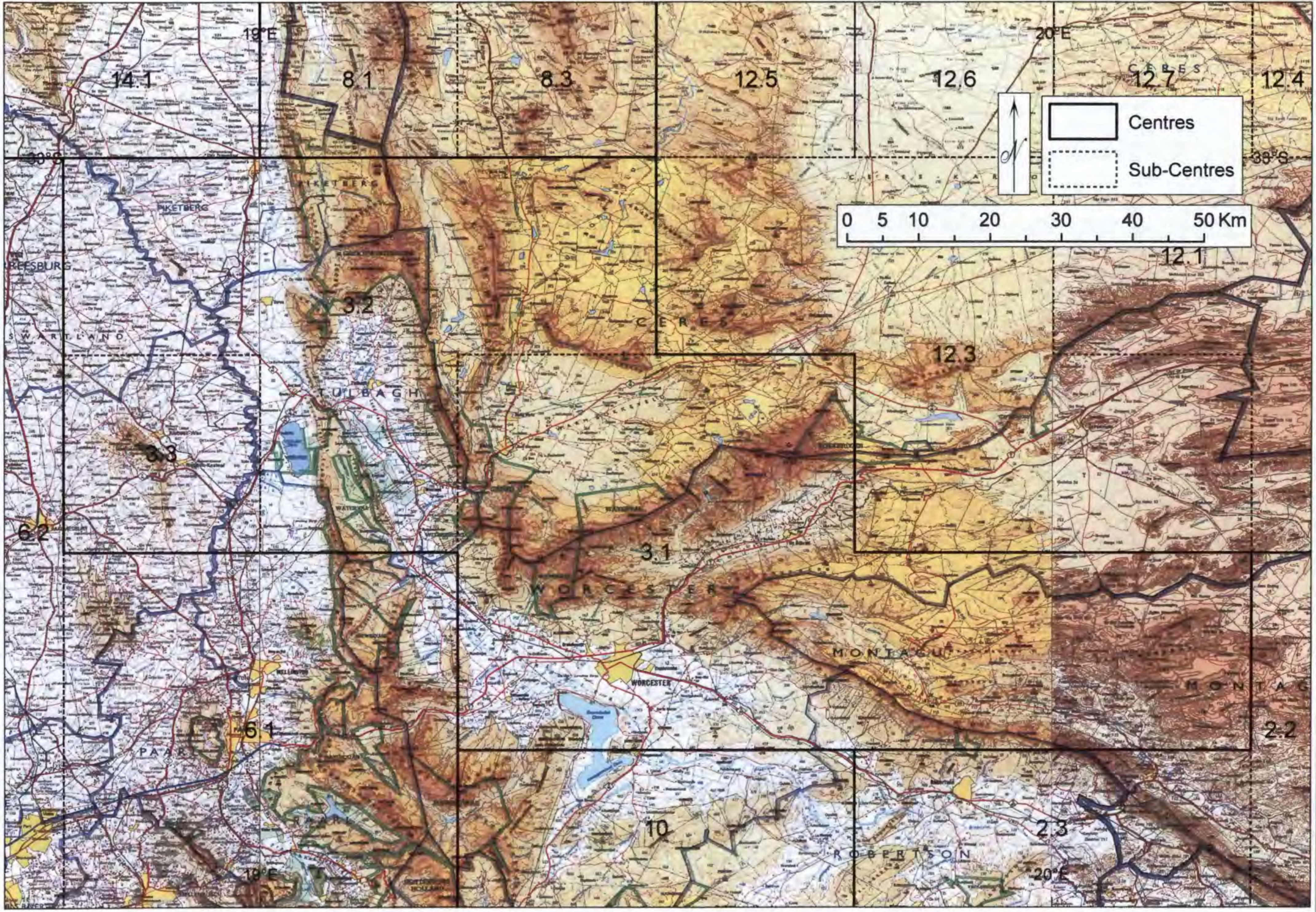


Figure 31: Position of the Groot Winterhoek PC and Hexrivier-West Langeberg Phytogeographical Centre (PC 3)

In Orchidaceae, the Hexrivier is contained within the NWPP, but there is no apparent differentiation of the area from the rest of the southern NWPP sub-centre. Most of these groups, aside from Asteraceae, represent the more temperate Cape Clades. In Rosaceae and Rutaceae, the Hexrivier Mountains also form distinct sub-centres, but where its strongest phytogeographical affinities lie in these groups (i.e. SWPP or NWPP) is less clear.

In the remaining datasets, the Hexrivier Mountains do not form a consolidated area. In the Fabaceae and the RDL Taxa, the Hexrivier is split along a north-south axis. In Poaceae, there is an east-west split into different PCs, while in the Geophyte Dataset there is an east-west split into different sub-centres. In Fabaceae, at least, there seems to be a significant low altitude (<1000m) biotic element (Table 39), which may have contributed to this split pattern. The Geophyte Dataset also has appreciable numbers of non-sandstone (non-montane) elements in this area (Table 42).

Surprisingly, in Proteaceae, a well known montane Cape element, the Hexrivier is split three ways. Firstly, there is an east-west division; then, in the western portion, there is a further north-south division. The reasons for this are not entirely clear. It may be that the Hexrivier is poor in endemic Proteaceae resulting in the various QDSs of the Hexrivier being grouped with more dominant neighbouring PCs.

#### 2.4.2.1.1.2.1.2 The West Langeberg (PSC 3.1 in part)

The West Langeberg shows complex and often conflicting patterns and affiliations between the different datasets. This is most likely a result of its phytogeographical location on the junction of four large phytogeographical provinces (SW, NW, LB and KM). In the Combined Dataset, Restionaceae and Rutaceae, the West Langeberg shows an affinity to the NWPP. In the latter two groups, it forms a definable sub-centre within a larger southern Northwest PC. In Polygalaceae, the West Langeberg forms the southernmost extension of the NWPP, as it does in *Erica,* although it forms a distinct sub-centre there. In Rosaceae, the western portion forms part of the Hexrivier and the eastern portion joins with the Central Langeberg. In Proteaceae, the Western Langeberg and Central Langeberg form sub-centres within a larger PC, which includes the eastern Hexrivier Mountains.

The importance of the Berg-Bree River Valley is emphasised in Fabaceae and the RDL Taxa and to a lesser extent, in the Geophytes. The RDL Dataset in particular, shows much conflict in the assignment of QDSs to PCs in this area, with little congruence between the different analyses. This is probably due to the large number of different biotic elements in the RDL Taxa Dataset (Table 54 and Table 56).

The arid affinities of Asteraceae are displayed by the merging of the southeast Hexrivier and West Langeberg sub-centres and are included within an extended Western Karoo PC that also includes the Witteberg and Klein Roggeveld.

#### 2.4.2.1.1.2.1.3 The Groot Winterhoek (PSC 3.2)

The Groot Winterhoek area is usually well-defined floristically and in most cases, shows strong affinities to the NWPP. It forms an independent PC in Rutaceae, which is slightly enlarged in Proteaceae. This northern enlargement is extended in the RDL Taxa, where it occupies most of the Koue Bokkeveld and Southern Cedarberg (Figure 31). In the Combined Dataset, its most immediate affinities are to the southeast, in the Hexrivier and West Langeberg, but ultimately to the rest of the NWPP.

The Groot Winterhoek forms a well-defined sub-centre within a larger Northwest PC in *Erica,* Bruniaceae, Restionaceae and Asteraceae, situated south of 33°S. In Fabaceae, Poaceae and Polygalaceae, the Groot Winterhoek form part of a much larger central NWPP phytogeographical region, but has less fine scale phytogeographical subdivisions. In Geophytes, Orchidaceae and Rosaceae, the affinities of the Groot Winterhoek are less clear, with PCs within these groups occurring in both the NWPP and SWPP areas.

#### 2.4.2.1.1.2.1.4 The Riebeek-Kasteel (PSC 3.3)

Kasteelsberg (946m) is a near mountain, surrounded by lower lying areas, and showing inconsistent affinities. It contains no granites, consisting entirely of sandstone. This may account for its link to the Groot Wintershoek in the Combined Dataset and the NWPP in general in *Erica,* although the Fabaceae Dataset indicates affinities to the SWPP. Kasteelsberg is species poor in most datasets, which represents under-collection, and results in its QDS being unassigned in 12 of my datasets.

Weimarck and Goldblatt and Manning (2000) used the course of the Little Berg River/Roodezand Pass as a boundary between the NWPP and the SWPP, and thus they included the Kasteelberg in the SWPP. Oliver et al., (1983) and Rebelo (1990) did not assign it to a floristic unit. I include both the Elandsberg and the Kasteelsberg, which lie south of the Little Berg River, in the NWPP (Figure 31). The Elandsberg and Limietberg probably contain a mixture of NW and SW elements and so constitute a transition zone where these elements interdigitate. The other inselbergs to the south of Kasteelsberg (Paardeberg and Paarlberg) are both granitic and show a closer affinity to the SWPP.

Figure 32: Position of the Cedarberg Phytogeographical Centre (PC 8)

#### 2.4.2.1.1.2.2 The Cedarberg PC (PC 8)

In my Combined Dataset, the Cedarberg Centre (PC 8), and in particular, two of its PSCs: the Cedarberg Core PSC (PSC 8.1) and Southeast Cedarberg-Skurweberg PSC (PSC 8.3) correspond fairly well to Weimarck's Cedarberg Sub-centre. However, I found that the closely adjacent, narrow and lower altitude Olifantsrivierberge are classified with the Piketberg-Swartberg-Sandveld PC (PC 14). The Cedarberg Core PSC (PSC 8.1) corresponds to the southern part of Drége's (1843) "III A d" area. In my study, the northeast boundary of the Cedarberg Centre is further northeast than in Weimarck's study and includes the Boegoeberge (PSC 8.2), across the Doring River Valley, as part of the Greater Cedarberg area (Figure 32). Interestingly, the Doring River Valley does not form a floristic boundary here. While three sub-centres are recognised, the Cedarberg Core PSC contains an order of magnitude more endemics than the remaining two sub-PCs in the Cedarberg PC (Table 9).

In several datasets (for example, Asteraceae, Bruniaceae, Fabaceae, Geophytes, Orchidaceae, RDL Taxa and Restionaceae) the Cedarberg is divided into northern (Pakhuis) and southern floristic areas, although the boundary between the two sub-divisions is not consistent in the different datasets.

In Polygalaceae, the NWPP Sandveld is slightly more dominant numerically, at the expense of a montane Cedarberg PC. In Rosaceae, there are no entirely independent phytogeographical units in the NWPP, which is most likely on account of its very low local endemism in the area.

#### 2.4.2.1.1.2.3 NWPP Sandveld (Piketberg and Olifantsrivierberg Mountains, PC 14)

I also retrieved a previously unrecognised NWPP centre, the Piketberg-Swartland-Sandveld Centre (PC 14). Although appearing simple topographically, this region is complex edaphically. The area includes the low altitude sandstone ridges of the Piketberg and the northern Olifantsrivier Mountains; Quaternary littoral sand deposits and to a lesser extent, shales (Figure 33). Most of the endemic taxa that I have habitat data for occur on the sandstone ridges, while the majority of the remainder occur on the littoral sand deposits (Table 12). This edaphic complexity may help explain the conflicting patterns in the different datasets.

Curiously, Weimarck included this area in his NWPP, but it was not assigned as part of the four sub-centres (two internal, two disjunct) that he identified. He noted that the Piketberg was very species poor, with one known endemic species at that time. Possibly due to its low species diversity, he left it unclassified. Drége (1843) identified a discrete Piketberg region, surrounded by two lower altitude areas, "III E a" to the north and "III D a" to the south, although I am unaware whether he identified taxa endemic to these areas.

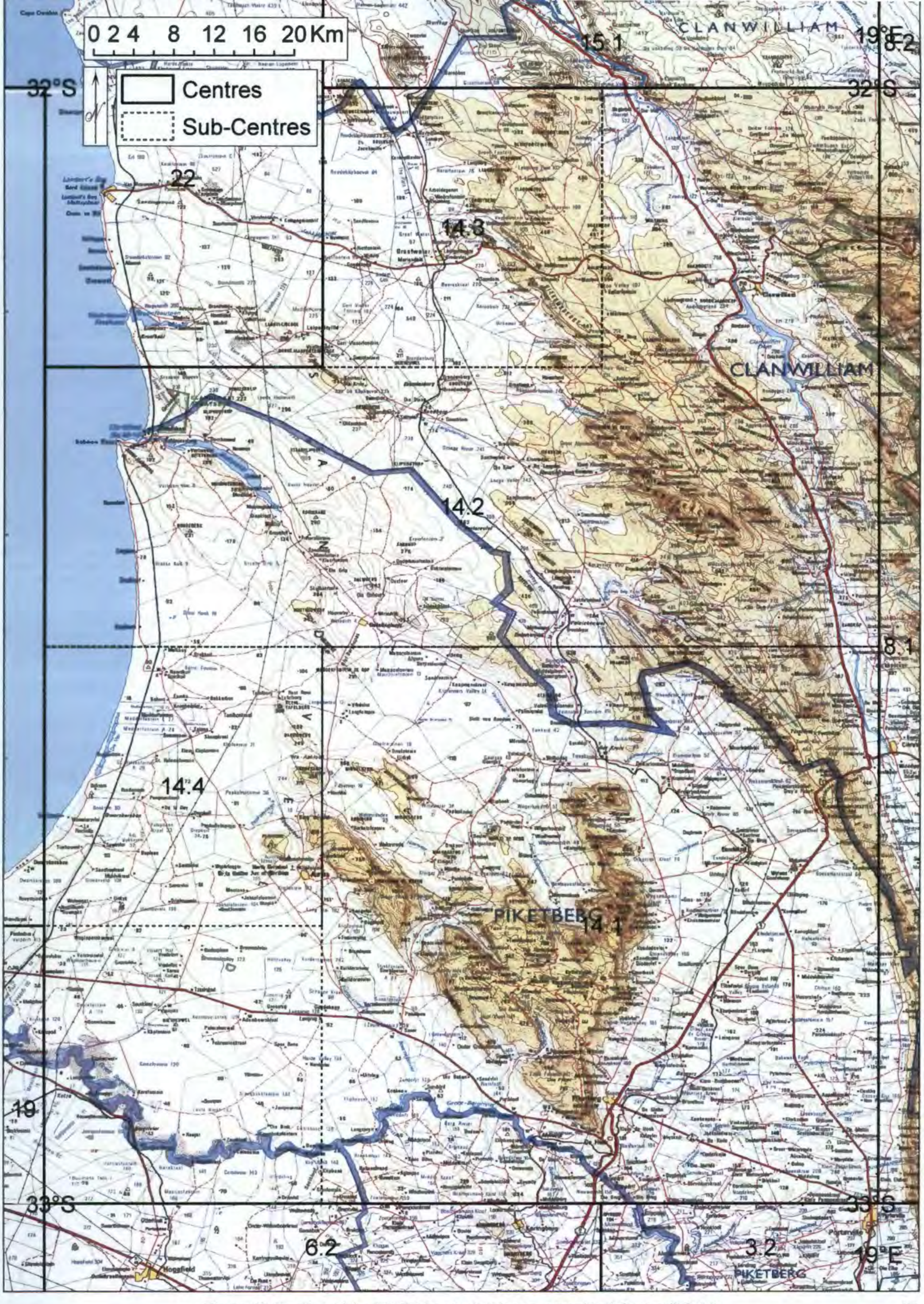


Figure 33: Position of the NWPP Sandveld Phytogeographical Centre (PC 14)

In the Combined Dataset and the Proteaceae, the Sandveld, Piketberg and Olifantsrivier Mountains form a single PC, although in the Combined Dataset, numerous sub-centres divide the area into smaller floristic units, the most significant of which is centred on the Piketberg Range. Frequently, portions of the NWPP Sandveld form sub-centres within a larger NWPP floristic unit, in my datasets where QDSs of this western region are assigned to PCs. The Rutaceae PC/PSC includes both the Piketberg and lower altitude areas, while the *Erica* sub-centre is more restricted to the Piketberg itself, with the lower lying QDS not assigned to a sub-centre in *Erica*. NWPP PC development in Poaceae is mostly restricted to montane areas, with the Piketberg having links to the southeast Gifberg. Similarly, in the RDL Dataset, the NWPP Sandveld combined with the Northern Cedarberg/Pakhuis region into a single PC, but these areas are in different sub-centres. In Orchidaceae, the affinities of the Piketberg are split between the Northern Cedarberg/Pakhuis and another independent minor PC. In Polygalaceae, the NWPP Sandveld forms a sub-centre within a larger NWPP, but here, unusually, the lower altitude Sandveld Sub-Centre is the largest and most dominant sub-centre, although this is primarily due to conflict and numerical dominance of the lower altitude taxa over montane elements in the QDSs here. Finer scale geographical data may alleviate this conflict, resulting in montane and lower altitude PCs with good representations of endemic taxa.

In Bruniaceae and Geophytes, the NWPP Sandveld shows a stronger relationship to the Groot Winterhoek region, rather than to the Cedarberg. The relationship in Bruniaceae is montane (*Thamnea hirtella*), and is disjunct over lower lying QDSs. In Geophytes, lower altitude QDSs between the Piketberg and the Olifantsrivierberge are assigned to PCs, due to the renosterveld taxon *Moraea neopavonia*.

In Asteraceae and Fabaceae, the NWPP Sandveld and SWPP Sandveld form a consolidated floristic area. This indicates stronger affinities between the lowlands within the NWPP and the SWPP, rather than between the lowlands and highlands within either the NWPP or the SWPP. This may indicate the presence of a well-developed low altitude biotic element, which may be of historical interest (Asteraceae: Table 33; Fabaceae: Table 39). In both Asteraceae and Fabaceae, the NWPP PC development is most advanced in the Piketberg and Olifantsrivierberg, with the Piketberg designated as a distinct sub-centre in both groups.

In Restionaceae and especially Rosaceae, there is no definite NWPP Sandveld development. However, in Restionaceae, the NWPP Sandveld area has outliers of SWPP taxa, which are Sandveld elements of the Sandy Coastal Flats (Goldblatt and Manning, 2000). This introduces an additional potential source for floristic elements in the NWPP Sandveld (the other possible sources being the montane NWPP or SWPP, or the Succulent Karoo). The Restionaceae SWPP Sandveld elements in the NWPP Sandveld may indicate the origins of the Asteraceae and the

Fabaceae NWPP Sandveld elements, which combine the NWPP and SWPP Sandveld into a single PC, but may have originated in the south.

#### 2.4.2.1.1.2.4 The Greater Witteberg PC (PC 12)

In my Combined Dataset, I recognize a "Greater Witteberg PC", which includes the Swartruggens from the Katbakkies Pass to Karoopoort (PSC 12.5), Bonteberg (PSC 12.6), Voetpadsberg (PSC 12.7) and the Moordenaarskaroo and Klein Roggeveldberge (PSC 12.4), as well as the Witteberg and Anysberg (PSC 12.1) (Figure 34). The affinities of the Swartruggens, Swartrugberge and Baviaansberg to the Greater Witteberg (PC 12) may be explained by the presence of shared narrow endemics, which was also detected with analysis of phytogeographical patterns by Linder (2001) and Linder and Mann (1998). There are a number of Restionaceae taxa that are represented in and endemic to the CFR mountains, forming the western and southern borders of the Tankwa basin (Figure 97; and see Linder and Mann, 1998). My Greater Witteberg Centre (PC 12) shows affinities both to the NWPP and the KMPP. Taxa shared with the NWPP may be numerically dominant, due to my dataset bias towards montane TMS "fynbos" Cape elements. In all the weighted analyses presented here, the Greater Witteberg Centre is basal to the NWPP. This is in contrast with Goldblatt and Manning (2000) who place this area in the KMPP, and closer to the delimitation of Weimarck. The close alliance of the Greater Witteberg Centre to the NWPP may be due to a number of factors. There is some evidence to suggest that the presence of a high altitude corridor may be connecting these centres together (Linder and Mann, 1998). This corridor is especially noticeable in my Restionaceae and Rutaceae (Diosmeae) datasets, and has been highlighted in Linder and Mann's (1998) discussions. As this may be a corridor of genetic exchange between the NWPP and KMPP, it has potentially high conservation importance. This possibility should be investigated from a phylogenetic/phylogeographic perspective, to determine if sister taxa occur across this proposed corridor. Xerophytic taxa may also make use of this corridor along the eastern NWPP and the northern KMPP, but in more xeric, lower altitude azonal habitats. I maintain the Greater Witteberg in the NWPP, but acknowledge that my datasets are biased towards Cape (fynbos) Clades, which would favour the current classification. I anticipate that a more comprehensive dataset, or a dataset that focuses on or includes more non-fynbos elements (such as succulents, or possibly even geophytes), may result in the fragmentation of my Greater Witteberg PC, and stronger affinities of some of the Greater Witteberg areas to the

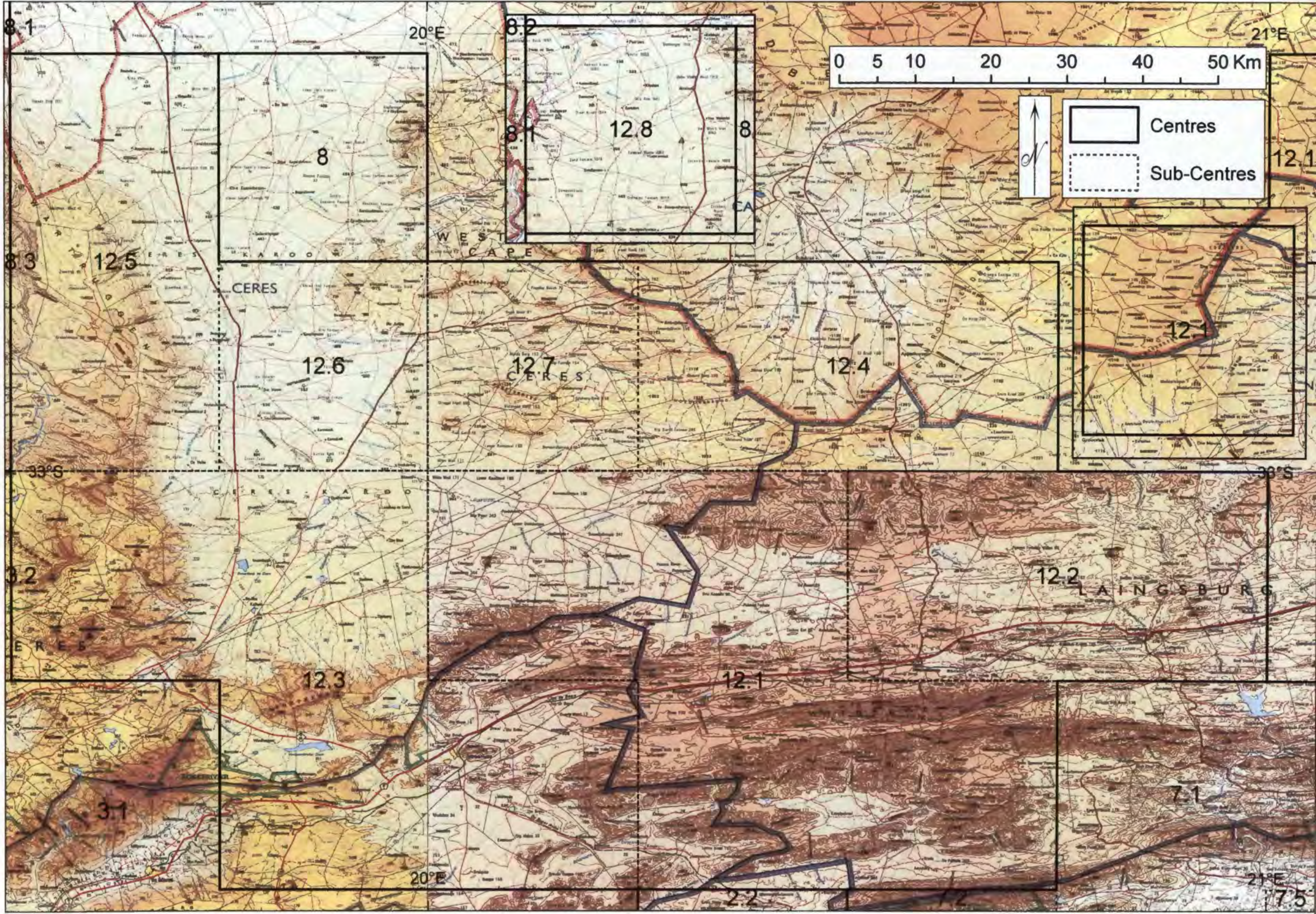


Figure 34: Position of the Greater Witteberg Phytogeographical Centre (PC 12)

KMPP. In addition, finer spatial analysis may show that only the higher lying areas of the Greater Witteberg display NWPP affinities, while the lower lying areas may display stronger KMPP affinities. This may also possibly occur in the Southern Succulent Karoo cluster and the Eastern Archipelago cluster.

The most significant PSCs of the Greater Witteberg Centre (PC 12) are: the Witteberg (PSC 12.1); the Southwest Karoo (PSC 12.2); the Southeast Cold Bokkeveld-North Waboomsberg (PSC 12.3); the Karookop-Kleinroggeveldberg (PSC 12.4); and the Swartruggensberge (PSC 12.5). The two southern sub-centres (PSC 12.1 and 12.3) of the Greater Witteberg contain the greatest number of CFR endemics (Appendix II) and offer the most temperate mesic montane environments (Schulze, 1997). These two PSCs (12.1 and 12.3) were also largely included in the NWPP of Weimarck. The Greater Witteberg Centre extends the NWPP further north and east in my study to include the Kleinroggeveldberge (PSC 12.4). However, the endemic taxa in this sub-centre are not Cape elements (Appendix II). The inclusion of these northern arid areas may be due to sampling biased to CFR clades. By sampling additional taxa from areas outside the CFR, the boundary may be shifted south again, as these borderline areas of weak Cape Floral representivity would then be incorporated into the surrounding floras.

#### 2.4.2.1.1.2.4.1 Witteberg, Karookop-Klein Roggeveld and Roggeveld Areas

Although the Witteberg (PSC 12.1), Karookop-Klein Roggeveld (PSC 12.4) and Roggeveld contain scattered CFR elements (Appendix II), only the Witteberg PSC (12.1) has Cape Clade elements endemic to it (Appendix II). Weimarck did not elucidate the affinities of the Klein-Roggeveld specifically, but recorded the affinities of the Roggeveld to the NWPP. Frequently in my study, the PCs of CFR clades didn't reach as far as the Klein Roggeveld, but stopped in the Karookop QDS (3220CD), which contained part of the CFR boundary of Goldblatt and Manning (2000) and Weimarck. Additional datasets of non-CFR clades would likely reveal that this area has greater floristic affinities to phytogeographical areas outside of the CFR.

Groups that show PC development in the Greater Witteberg PC area, but only extend as far as Karookop (not to the Kleinroggeveldberge) are: Poaceae, Proteaceae and Restionaceae. Proteaceae is the only group to have an exclusive PC development in the Greater Witteberg PC. In Poaceae and Restionaceae, the floristic development on the Witteberg shows strong floristic affinities to PCs in the NWPP. The Poaceae PC is disjunct to the Swartrugberge and northeast Hexrivier. In the Geophytes and Proteaceae, parts of the Greater Witteberg PC and southern NWPP (Proteaceae) are combined with the Western and Central Langeberg, while in Restionaceae, the NWPP extends eastwards into the Greater Witteberg PC area. These Cape Clades may explain why in my study, the Greater Witteberg is more strongly associated with the NWPP, rather than the KMPP.

Asteraceae, Geophytes (with LBPP affinities) and the RDL Taxa PCs extend as far as the Klein Roggeveld. Fabaceae has two independent, single QDS PCs (PC 15 and 19) in the Karookop and Klein Roggeveld areas respectively. In Rosaceae, the phytogeographical patterns are less clear, although there is a Karookop QDS affiliated with a widespread disjunct PC. There is a complete absence of independent PC development in this area in Bruniaceae, *Erica* and Rutaceae. In Rutaceae, the Waboomsberg is associated with the Hexrivier and southern NWPP, reminiscent of the pattern in Restionaceae. In both Restionaceae and Rutaceae, these sub-centres may contain elements with stronger KMPP affinities.

The Karookop-Klein Roggeveld phytogeographical unit (PSC 12.4) is best developed in the Combined Dataset, forming an independent sub-centre in an enlarged Greater Witteberg PC. This is probably due to the large number of contributing taxa in the Combined Dataset, which are not all exclusively Cape Clades (Linder, 2003).

#### 2.4.2.1.1.2.4.2 Swartruggens, Swartrugberge and Baviaansberg

An understudied floristic component of the NWPP/KMPP are the arid areas to the east of the Cedarberg, here in the western Greater Witteberg PC (PSC 12.5 and 12.3 in part), which includes the small relatively low altitude mountains of the Swartruggens, the Swartrugberge and the Baviaansberg. The affinities of this area are ambiguous, with the different datasets indicating links to either the NWPP or KMPP.

The two most frequent patterns appear to be of either no PC development (for example, in Bruniaceae, Geophytes, Orchidaceae, Polygalaceae and Proteaceae), or an association with the NWPP (indicated by *Erica,* Fabaceae, RDL Taxa, Restionaceae and Rutaceae). Asteraceae has two independent PCs in this area, whose affinities were not determined.

In the Combined Dataset, the Swartruggens Mountains seem to have been invaded from and sequestered into the Greater Witteberg (PC 12). This pattern is a little confusing, considering that many datasets group this area with the NWPP. The inclusion of the Swartruggens and Swartrugberge into the Greater Witteberg (PC 12) may have increased the Greater Witteberg's affinities to the NWPP, resulting in the current classification. However, the inclusion of xeric taxa, from Aizoaceae, Apocynaceae and possibly some geophytes, is most likely to have resulted in this area being grouped with the western KMPP. Thus, there may be two significant biotic elements present here, causing conflict.

#### 2.4.2.1.1.2.4.3 The Hexriver-Witteberg High altitude corridor

In Restionaceae and Rutaceae, interesting phytogeographical patterns were observed in the boundary between the NWPP/SWPP and KMPP, although with slight variations. There appears to be a high altitude corridor (mountain-bridge) joining the Hexrivier Mountains to the Witteberg.

In Rutaceae, it joins the Hexrivier to the south-western Witteberg, Keeromsberg/Waboomsberg. In Restionaceae, a similar mountain-bridge is observed. However, the Swartruggens, Swartrugberge and Baviaansberg are joined via the same mountain-bridge to the south-western Witteberg, before the area extends north and further east. In both cases, the mountain-bridge occurs in the same QDSs, namely 3319BD and 3320AC, possibly extending from Saalberg to the Bonteberg and finally from the Voetpadsberg to the Witteberg, as discussed for the Restionaceae.

#### 2.4.2.1.1.2.5 PCs Previously Classified in the NWPP

Adjacent to the Core CFR area (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26) is a cluster of PCs that has dual affinities, to both the southern Succulent Karoo, and to the northern CFR. This clade includes an inland cluster, consisting of the Nieuwoudtville Escarpment (PC 11), the Gifberg (PC 15) and the Vanrhynsdorp Centre (PC 17). Coastal areas clustering here include portions of the West Coast (PC 22) near the Olifant's River Mouth, which has occasionally been placed in the NWPP (Goldblatt and Manning, 2000) and the Saldanha Peninsula (PC 19), which has previously been placed in the SWPP (Weimarck, 1941; Goldblatt and Manning, 2000).

Other PCs that display affinities to the NWPP include the Kamiesberg Centre (PC 20), although floristically this is even more distantly related to the NWPP and is included in my northern Succulent Karoo area (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). Weimarck recognized both the Kamiesberg and the Hantam-Roggeveld as sub-centres of his NWPP. I recognise the Kamiesberg to have greater Succulent Karoo floristic affinities and propose the Hantam-Roggeveld to be a potentially distinct PC – I discuss these PCs in detail under their appropriate sections.

#### 2.4.2.1.1.2.6 Relationships between NWPP PC

The relationships among NWPP PCs are often ambivalent. In two analyses, the Groot Winterhoek (PC 3) and Cedarberg (PC 8) are sister OGUs. However, in the other two analyses, the Cedarberg and Piketberg Centres (PC 14) are grouped together. It appears that the Cedarberg and the Groot Winterhoek PCs may share more taxa (Figure 22 and Figure 26), but that the Cedarberg and Piketberg-Swartberg-Sandveld may have more range restricted taxa in common, explaining why they are grouped together when weighting techniques are employed (Figure 23, Figure 24 and Figure 25). The Greater Witteberg (PC 12) was retrieved as the most distant PC in the NWPP in all five of my hierarchical analyses.

### 2.4.2.1.1.3 Langeberg Phytogeographical Province (LBPP, PC 2)

The LBPP is spatially unique in the CFR, as it is the only phytogeographical province to border all the other phytogeographical provinces of the CFR. All other floristic provinces only border either two (the AP and SE phytogeographical provinces) or three (NW, SW and KM phytogeographical provinces) other phytogeographical provinces. There might thus be considerable scope for floristic overlap of the LBPP from neighbouring centres. This could dilute its character and distinctiveness, as an independent phytogeographical province on an equal hierarchical level as the other centres. The LBPP consists of a single PC, the Langeberg Phytogeographical Centre (LBPC).

I define the LBPC as the area centred on the Langeberg Mountain Range, east of Cogmans Kloof between Ashton and Montagu and west of the Gouritsrivier, including the associated lowlands lying to the south, but north of the Eastern APPP (Figure 35). In the west, there is strong congruence between this study and those of Weimarck and Goldblatt and Manning (2000). East of Gysmanshoekpas, in what I refer to as the East Langeberg, there are notable differences. In the far east of this area, my results are more congruent with those of Weimarck who placed the boundary on the Gouritsrivier, rather than on Robinsons Pass (Klein-Brakrivier), as did Goldblatt and Manning (2000). The Gouritsrivier has a long history of being used as a phytogeographical boundary (Drége, 1844; Rehman, 1880 and somewhat haphazardly by Engler, 1882). This boundary makes intuitive sense when viewing the underlying topography of the centre and sub-centre boundaries. However, the more eastern Robinson Pass boundary marks the start of almost continuous forests, especially on the coastal plateau. Different biotic elements and/or taxonomic groups have different barriers to gene flow and this should be borne in mind when interpreting phytogeographical patterns, including the conflict between datasets and within datasets. The valley created by the Gouritsrivier may pose a significant barrier to montane taxa. Furthermore, the abrupt habitat change caused by near closed canopy continuous forests may be a significant barrier to lower altitude non-forest taxa.

The southern boundary of the Langeberg Centre is similar to that of Goldblatt and Manning (2000), due to their recognition of the Agulhas Plains Centre. However, in my study the Langeberg Plains are more restricted, with the southern boundary shifting north in the west, and eastern boundary moving west. Drége (1844) sought to combine the entire length of the east-west axis mountains (Langeberg, Outeniqua, Tsitsikamma, Swartberg) into a single centre, which ran south of the Waboomsberg and continued up along the Witzenberg, but excluded the Groot Winterhoek Mountains. The Langeberg Centre of Linder (2001) is confined to the

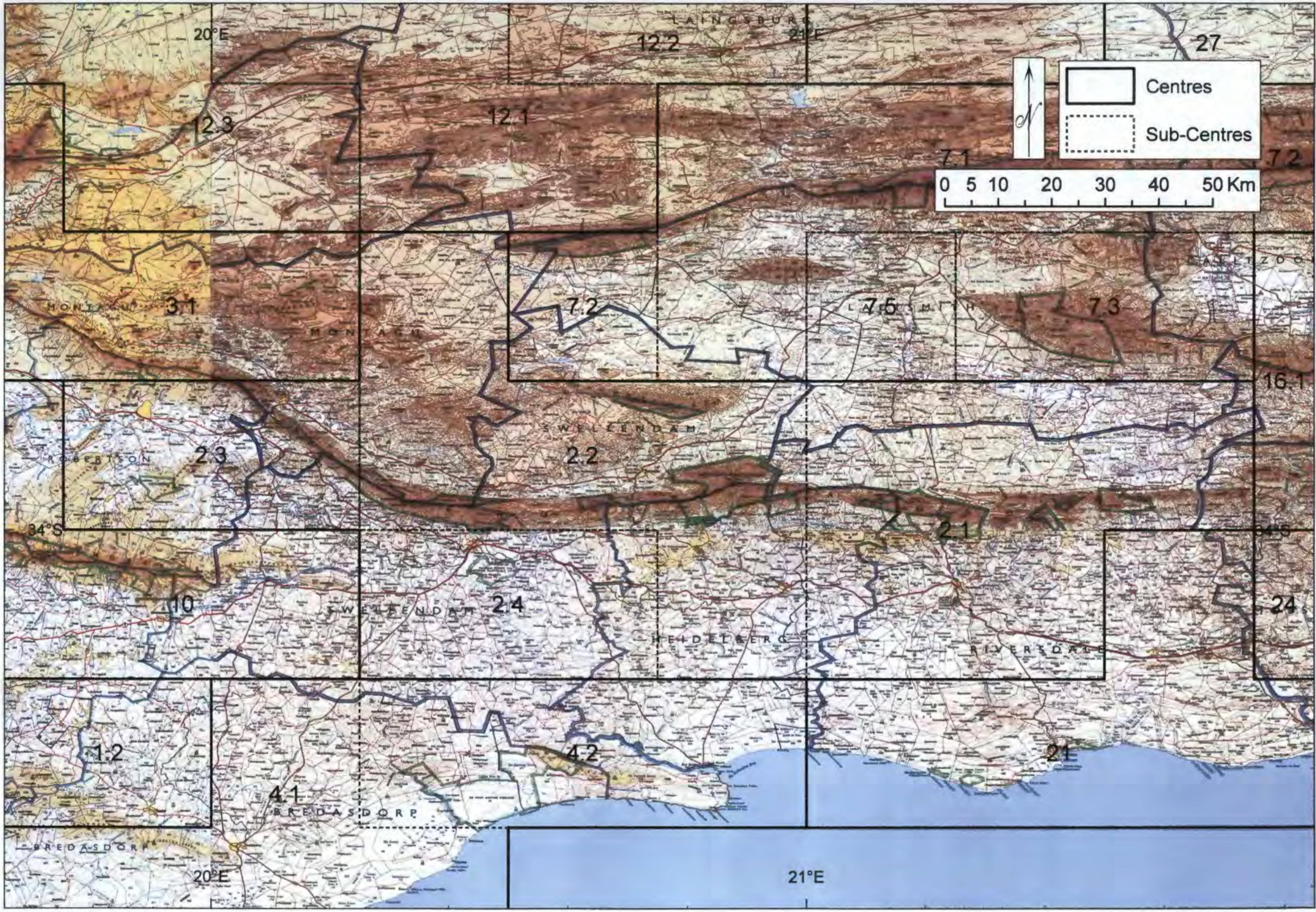


Figure 35: Position of the Langeberg Phytogeographical Province and Centre (PC 2)

mountains proper, while Oliver et al., (1983) did not identify it as a distinct centre, but rather merged the area with parts of the Karoo Mountain Centre and Southeast Centre. Here, as with previous studies (Weimarck, 1941; Goldblatt and Manning, 2000), the western Langeberg (west of Cogmanskloof, PC 3.1) is part of the NWPP (PC 3) and not of the LBPP to the east. This floristic unit (PSC 3.1) also includes the arid Waboomsberg and the high Hex River Mountains, resulting in my naming it the Hexrivier-West Langeberg Sub-Centre (PSC 3.1).

Previous investigators have not divided the LBPP into smaller choria, except for Drége (1844) who partitioned the mountains from the plains. In my Combined Dataset, the Greater Langeberg area forms a single nested, floristic unit (PC 2), which contains smaller, distinct phytogeographical units (PSC). The formation of a single PC may be due to the compact and smaller geographical size of the Langeberg, or because of the more uniform, or more continuous and uninterrupted nature of the habitats there. The Langeberg also does not contain the topographical extremes and disjunctions of the NWPP and SWPP.

In the Combined Dataset, I subdivide the Langeberg into four units: the Central Langeberg (PSC 2.2) and its associated plains (PSC 2.4), the East Langeberg (PSC 2.1) and its associated plains (PSC 2.3). My clade/group datasets produce conflicting patterns in the Langeberg and for this reason the PSCs are not discussed individually in the LBPP, as with the other phytochorial centres. Where there is LBPP sub-division, there are frequently two major themes, which produce four phytogeographical areas in the LBPP. Firstly, in some datasets, there is phytogeographical differentiation between the mountains and the plains (as depicted by Drége, 1844). Secondly, some of my datasets differentiate the Langeberg into eastern and western LBPP sub-regions, either in the mountains, and/or on the plains. This is usually in the vicinity of Gysmanshoekpas, though this is not always consistent. Ultimately, this may potentially lead to four major phytogeographical areas, the Central Langeberg Mountains, the East Langeberg Mountains, the Central Langeberg Plains and the East Langeberg Plains. Due to the complexities of geographical patterns, it is difficult to make precise generalisations, but a few patterns seem to emerge for the LBPP. Although not tested, there does appear to be a positive correlation between the development of distinct east-west LBPP sub-centres and phytogeographical development on the LBPP plains, and this is most likely due to a general increase in endemics in the area.

As with the APPP, there is ample evidence in many of my clade/group datasets to support the delimitation of a Langeberg Centre. While the Langeberg PC development is very weak in Poaceae, with only a single endemic, Orchidaceae is the only group that does not have an independent PC in the Langeberg. In Orchidaceae, the LBPP and SEPP form a single floristic unit, much like the results of Oliver et al., (1983).

In Asteraceae, Fabaceae, Poaceae, Polygalaceae, Restionaceae and Rutaceae, there is no clear eastern and western floristic differentiation in the LBPP. Concomitantly, in most of these groups, there is very little floristic development on the lower lying areas south of the Langeberg Mountains, directly associated with the Langeberg. One possible exception is Bruniaceae, with some plains development, but with no distinct east-west differentiation. In some cases, this lack of east-west endemism differentiation, or low altitude endemism development in the LBPP, may be simply a result of low taxon numbers, as in Poaceae and to a lesser extent in Fabaceae. However, it is not the case in all these groups, which may possibly indicate the stronger montane preferences of the endemics in this area. Polygalaceae is unusual in that it associates the LBPP with the Potberg.

Distinct east-west LBPP phytogeographical development was found in the Combined Dataset, *Erica*, Proteaceae, the RDL Taxa and Rosaceae. In most of these groups, there is fairly substantial phytogeographical development in the southern lower altitude area, except in the central region of Proteaceae, where there is a distinct gap. Proteaceae represents quite an extreme case of east-west LBPP differentiation, where the east and west LBPP are in different PCs. In Proteaceae, the east Langeberg shows stronger affinities to the Outeniqua Mountains to the east, rather than to the Central Langeberg to its west. In both Proteaceae and Geophytes, the Central LBPP has affinities to the West Langeberg and Waboomsberg Mountains. A similar pattern might also occur in the RDL Taxa, but hierarchical analysis would be required to determine this.

A rather unusual feature occurs in the *Erica* and Geophyte Datasets. Here, the valleys between the Klein and Groot Swartberg, the Rooiberg and the East Langeberg merge together into a single floristic unit along the Gouritsrivier Valley, suggesting KMPP affinities. A vaguely similar pattern is also apparent in the Restionaceae, joining the Rooiberg and part of the east Langeberg, but this is slightly west of the Gouritsrivier and more centred in the LBPP.

#### 2.4.2.1.1.4 Southeast Phytogeographical Province (SEPP; PC 5, 16)

In my Combined Dataset, I retrieved the SEPP as a nearly continuous area, from about the Gouritsrivier to around the Sundays River. East of the Sundays River, enclaves of the Cape Flora become increasingly scattered and disjunct, as the environment becomes increasingly tropical. There is also a transition from a Mediterranean to summer rainfall regime, which has a pronounced effect on floristic composition (see Appendix II), particularly at lower altitudes. This pattern continues until the higher lying temperate areas of the eastern escarpment are encountered. Montane areas in the summer rainfall area usually contain elements with Cape affinities (Carbutt and Edwards, 2002; Carbutt and Edwards, 2006; Galley, Bytebier, Bellstedt and Linder, 2006), as do some of the coastal areas (van Wyk and Smith, 2001).

Goldblatt and Manning (2000) treat the area from Robinsons Pass (Klein-Brakrivier) to the area around Port Elizabeth as a single continuous floristic unit. Weimarck's Southeast Centre excluded the western portion between the Gouritsrivier and Keurboomsrivier (Knysna Interval) and extended from the Keurboomsrivier to the Groot-Visrivier, and was subdivided into three sub-centres. However, he noted that areas east of the Sundays River "constitutes an extreme outlier of the Cape", and stated that many authors considered that the CFR proper does not extend beyond the Sundays River (Ecklon, 1830; Bolus, 1886, 1905; Marloth, 1908; as cited by Weimarck). More recently, Goldblatt and Manning (2000) espoused similar views, truncating the CFR short of the Sundays River.

Here I treat the SEPP as two distinct PCs: the West Southeast Centre (PC 16) and the East Southeast Centre (PC 5), generally separated by the Keurbooms-Palmiet River. In the Hierarchical Analyses (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), these two PCs always clustered together, with the Karoo Mountain Centre (PC 7) always occurring as an outgroup. This indicates very strong node stability.

Generally, the eastern CFR floristic units are relatively poorly developed compared to those in the western CFR. CFR clades decrease in diversity and levels of endemism as one proceeds further east (Levyns, 1964; Cowling and Lombard, 2002). This correlates with the decrease in temperate conditions and decreasing winter rainfall, and an increase in summer rainfall, until the temperate (summer rainfall) Eastern Escarpment is reached. In my Combined Dataset, the East Southeast Centre (PC 5) has more endemics than the West Southeast Centre (PC 16), but this is purely as a result of the differences in size of the PCs. The West Southeast Centre (PC 16) has 36.3% of the number endemics and amazingly, 88.2% of the diversity that the East Southeast Centre (PC 5) contains, but only occupies 26.1% of the area. Thus, per unit area, the more westerly PC has higher numbers of endemics and considerably higher diversity (*cf.* Colwing and Lombard, 2002). However, the western Kouga region of the East Southeast Centre (PC 5) has lower numbers of endemics than the more easterly region that is centred on the Elandsberge and Groot Wintershoekberge, and this is clearly shown in the Combined Dataset and RDL Taxa. This represents a slight deviation from Levyns (1964) who described a tapering of diversity and endemism to the north and east in the CFR.

The Combined Dataset displays the best coverage of the east SEPP area, due to the higher numbers of taxa represented in the area. Most of the clade-based datasets have notable gaps and disjunctions, due to the western winter rainfall area bias of Cape Clades, and under collection. Even so, some broad patterns are discernable. There appears to be fairly consistent east-west differentiation of the SEPP into distinct floristic units, with the interval most commonly centred on the Keurbooms-Palmiet River system, though this is not always constant, with numerous instances of overlap. In some cases, there is also a Gamtoos interval to varying degrees, but the same PC is disjunct across the interval, for example, Asteraceae, *Erica* and Orchidaceae. Rosaceae is the only group that appears unaffected by this interval.

There is also evidence of a north-south interval, across the Langkloof Valley, separating the more coastal Outeniqua-Tsitsikamma Mountains from the inland Kouga Mountain, which is in the rain shadow of the former. This interval appears to get weaker to the east, as the height differential between the valley floor and mountaintops decrease. Datasets that have PCs that largely ignore this potential barrier include: Fabaceae, Rosaceae and Geophytes (but not at the sub-centre level for the latter).

There are three main areas of phytogeographical development in the east SEPP: the Outeniqua-Tsitsikamma Mountains, the Kouga-Baviaanskloofberg and the Groot Winterhoek-Van Stadens-PE area, which includes the Suurberg (sometimes Zuurberg). The first two areas could be divided further, into east and west sub-centres and the third into montane and lowland (roughly north and south) sub-centres.

Generally, the PCs of the SEPP have an east-west orientation in the western SEPP parallel to the mountains and the coast. It then begins to bend southward to a northwest-southeast orientation nearer the coast, in the Cape St. Francis and Port Elizabeth areas in the east, following the orientation of the mountains in this area. QDS diversity seems to follow this pattern quite loosely (Figure 20). Part of the reason for this orientation may be due to the position and orientation of the mountain ranges in these areas. Climate may also play a factor. Inland penetration of the winter rainfall bearing cold fronts become less pronounced as one travels from west to east and south to north, although altitude can compensate very significantly for geographical position. This is also observed in the RDL Dataset, whose taxa may have contributed to the pattern here in the Combined Dataset.

#### 2.4.2.1.1.4.1 West Southeast Centre (PC 16)

The Afromontane or forest region of the CFR has long been recognised as a distinct phytogeographical unit (Rehman, 1880; Engler, 1882; Marloth, 1908; White, 1993). In my study, the West Southeast Centre corresponds most closely to the southeast part of Weimarck's Knysna Interval – a region which, according to Weimarck, lacked endemic Cape taxa. Many of the Cape taxa he analysed that showed a Knysna interval, seemed to have the majority of their collection records from the lowland coastal plateau regions, containing biotic elements that may be excluded by forest elements, hence the disjunction. Most of the endemic taxa (14 of 21) identified in my study were montane (Appendix II) and were distinct members of the Cape Flora (Linder, 2003). It may be that the mountain flora of this area (Figure 36) was less well known to collectors at the time of Weimarck's publication. Weimarck explained his Knysna interval by hypothesising that the Afromontane forests would have outcompeted fynbos in wetter geological periods, resulting in a decrease in fynbos diversity and endemism in the Knysna area. Weimarck is the only other floristic biogeographer to have proposed a floristic boundary in the Keurbooms-Palmiet River area, between the West Southeast Centre (PC 16) and the East Southeast Centre (PC 5). Most other phytogeographical studies combine the area of my West Southeast Centre (PC 16) with the remainder of the East Southeast Centre (Drége, 1843; Rehman, 1880; Engler, 1882; Marloth, 1908; Oliver et al., 1983; Goldblatt and Manning, 2000), forming a single, large continuous centre.

The western boundaries of my West Southeast Centre (PC 16) correspond fairly well to that of Goldblatt and Manning (2000), although my PC extends further west by one QDS. Goldblatt and Manning (2000) included 3321DD in the LBPP and about half of QDS 3321DB in the LBPP and KMPP (the difference between using the more westerly Gouritsrivier, or the easterly Robinsons Pass as the boundary (Figure 36)). Here, 3321DD and 3321DB combine with the West Southeast Centre. Linder's (2001) analysis of Restionaceae did not identify any centres of endemism east of the Gouritsrivier, although my analysis of Restionaceae revealed PC development on the Outeniqua, Tsitsikamma, and Kammanassie Mountains. The West Southeast Centre broadly coincides with Acock's (1988) Knysna Forest Vegetation and Cowling and Heijnis' (2001) Knysna Afromontane. The Afromontane Flora in this area is generally species poor, with relatively low endemism (Geldenhuys, 1993). There are very few Cape elements in this flora. Geldenhuys (1993) lists 40 Cape Clade elements. However, none of these taxa were found to be endemic to the focused PCs of this study. However, there are Cape Clade elements endemic to this general area, though these endemics occur outside the Afromontane Vegetation, mostly in the mountains to the north (Table 12).

From my Combined Dataset, I identified two sub-centres in my West Southeast Centre. The West Outeniqua Sub-centre (PSC 16.1), and the East Outeniqua-West Tsitsikamma Sub-Centre (PSC 16.2).

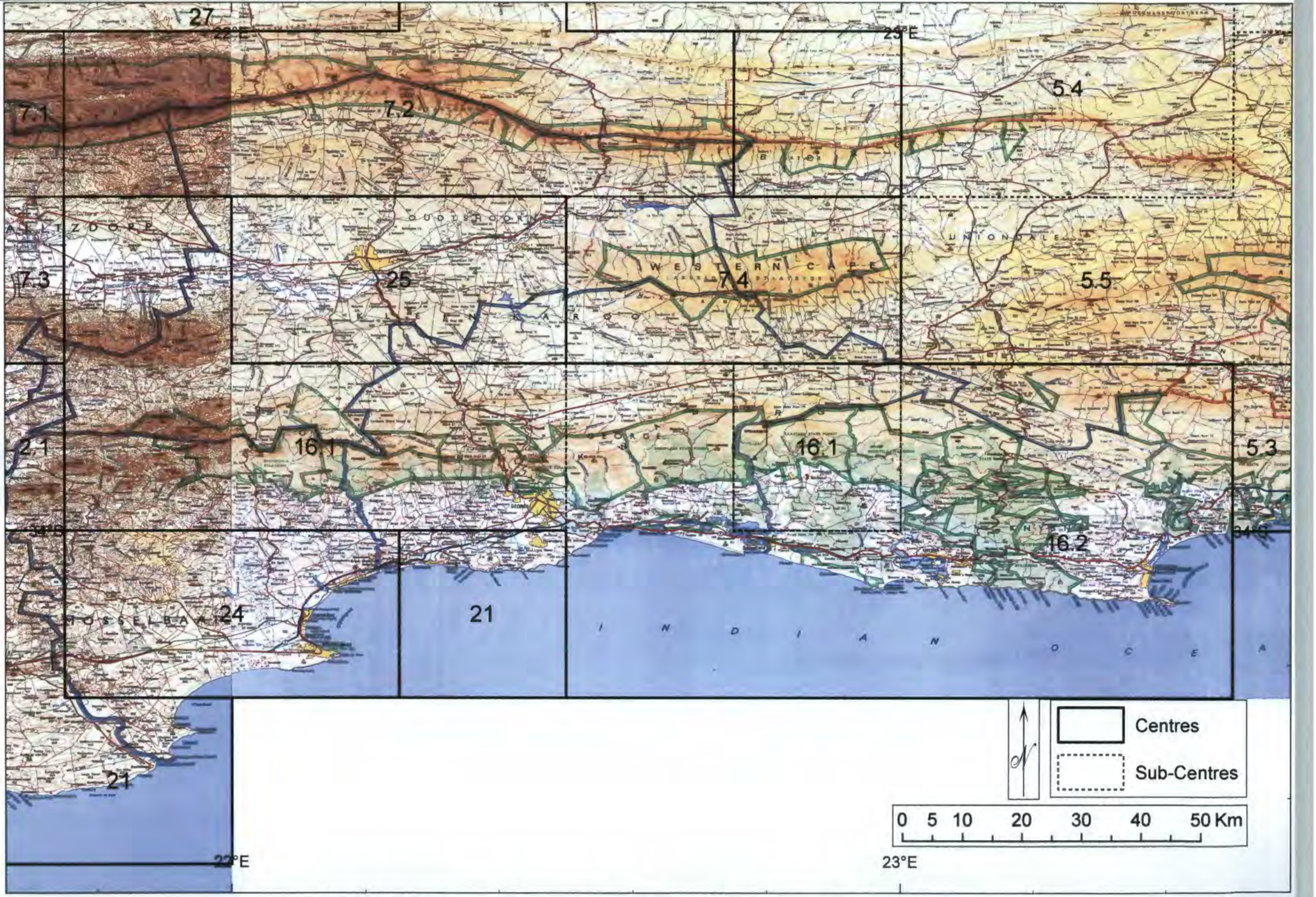


Figure 36: Position of the West Southeast Centre Phytogeographical Province and Centre (PC 16)

Although these two areas are often identifiable at different floristic levels in the different datasets, either at the centre or sub-centre level, they usually show the greatest affinity to each other. In the Combined Dataset and the RDL Taxa, the Tsitsikamma area has greater affinities to the north (possibly Kougaberge), rather than to the west (Outeniquaberge).

The Outeniqua PC is usually better developed, with more endemics than the Tsitsikamma PC. This is possibly because of its more westerly location and subsequently stronger Mediterranean climate, although Asteraceae is an exception. The only dataset in which the Outeniqua area shows very little floristic development is Bruniaceae. The Tsitsikamma area is impoverished in Bruniaceae, Proteaceae, Polygalaceae and Poaceae, although it is well developed in Restionaceae and *Erica*. There appear to be transitional elements in the Outeniqua area, showing affinities to the SEPP, LBPP and KMPP.

That the phytogeographical boundary between the LBPP and SEPP is an area of floristic contention is evident by comparing my different datasets. The Combined Dataset, Fabaceae, Polygalaceae and the RDL Taxa support a more westerly boundary, in the region of the Gouritsrivier, similar to Weimarck. Asteraceae, *Erica* and Geophytes (the latter at the sub-centre level) seem to indicate a boundary in the region of Robinsons Pass, similar to Goldblatt and Manning (2000). Proteaceae, Restionaceae, Rosaceae and Rutaceae suggest a boundary even further east, possibly in the region of the Outeniekwapas, or the Montagu Pass.

#### 2.4.2.1.1.4.2 East Southeast Centre and Outliers (PC 5)

The East Southeast Centre of my study corresponds to the central and eastern areas of Goldblatt and Manning's (2000) Southeast Centre and combines and matches the Tsitsikamma and Cockscomb Sub-Centres of Weimarck's study reasonably well. Here, it is enlarged in the northwest and includes the far eastern parts of the Groot Swartberg Range (Figure 37 and Figure 38). At the sub-centre level, the Grootwinterhoek-Van Stadens Sub-Centre (PSC 5.1) is equivalent to Weimarck's Cockscomb Sub-Centre. The Tsitsikamma Sub-Centre (PSC 5.3) is nested in the southern part of Weimarck's Tsitsikamma Sub-Centre, while the northern part is further divided into two minor sub-centres (PSC 5.7 and 5.8), which do not contain Cape (fynbos) elements (Appendix II).

I retrieved some disjunct elements further east, but nothing as substantial or continuous as Weimarck's Zuurberg Sub-Centre. This is in agreement with many biogeographers (Bolus, 1886, 1905; Marloth, 1908; Weimarck, 1941; Goldblatt and Manning, 2000). Further, my Grootwinterhoek-Van Stadens Sub-Centre (PSC 5.1), which is equivalent to Weimarck's

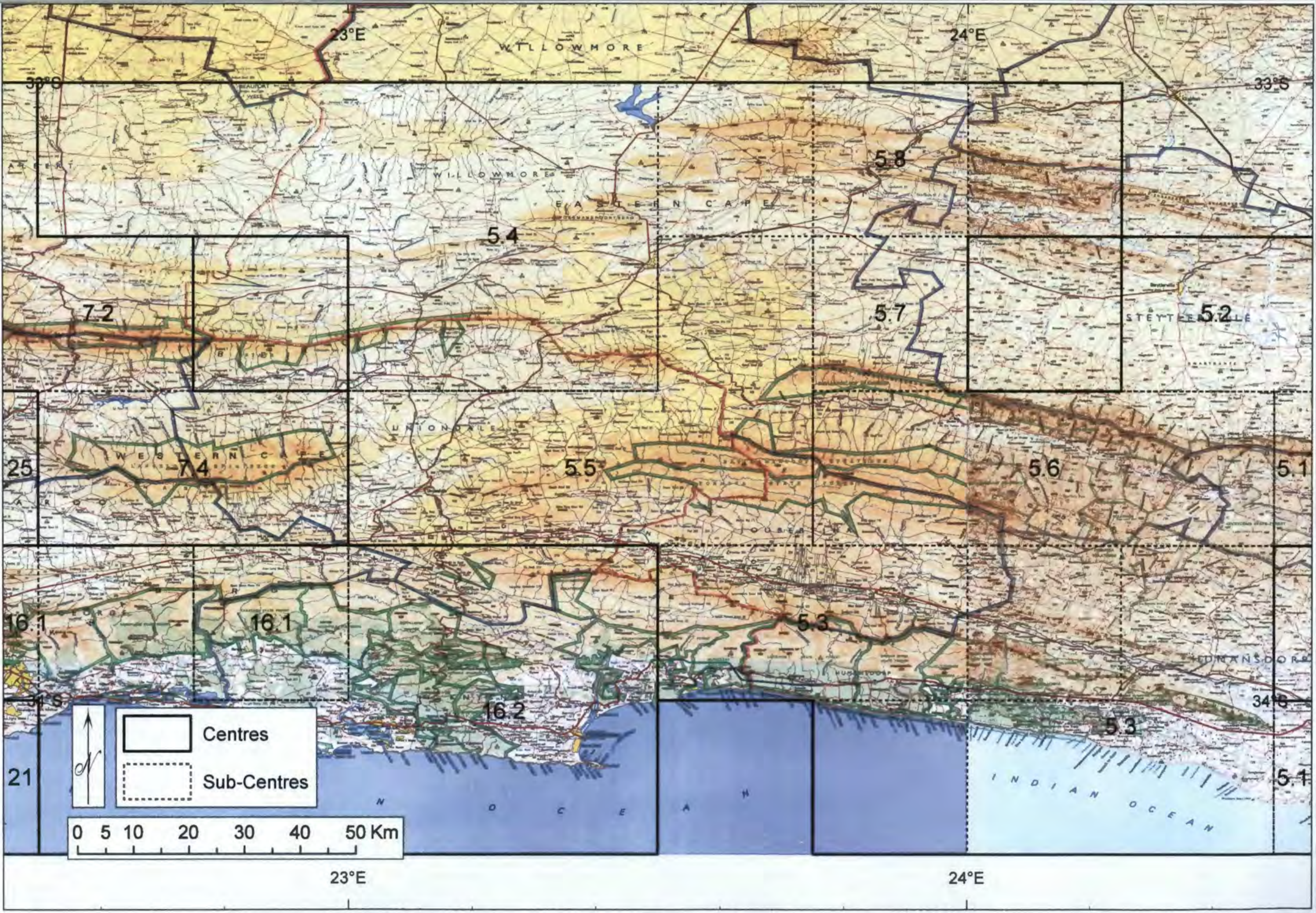


Figure 37: Position of the East Southeast Phytogeographical Centre (PC 5 western portion)

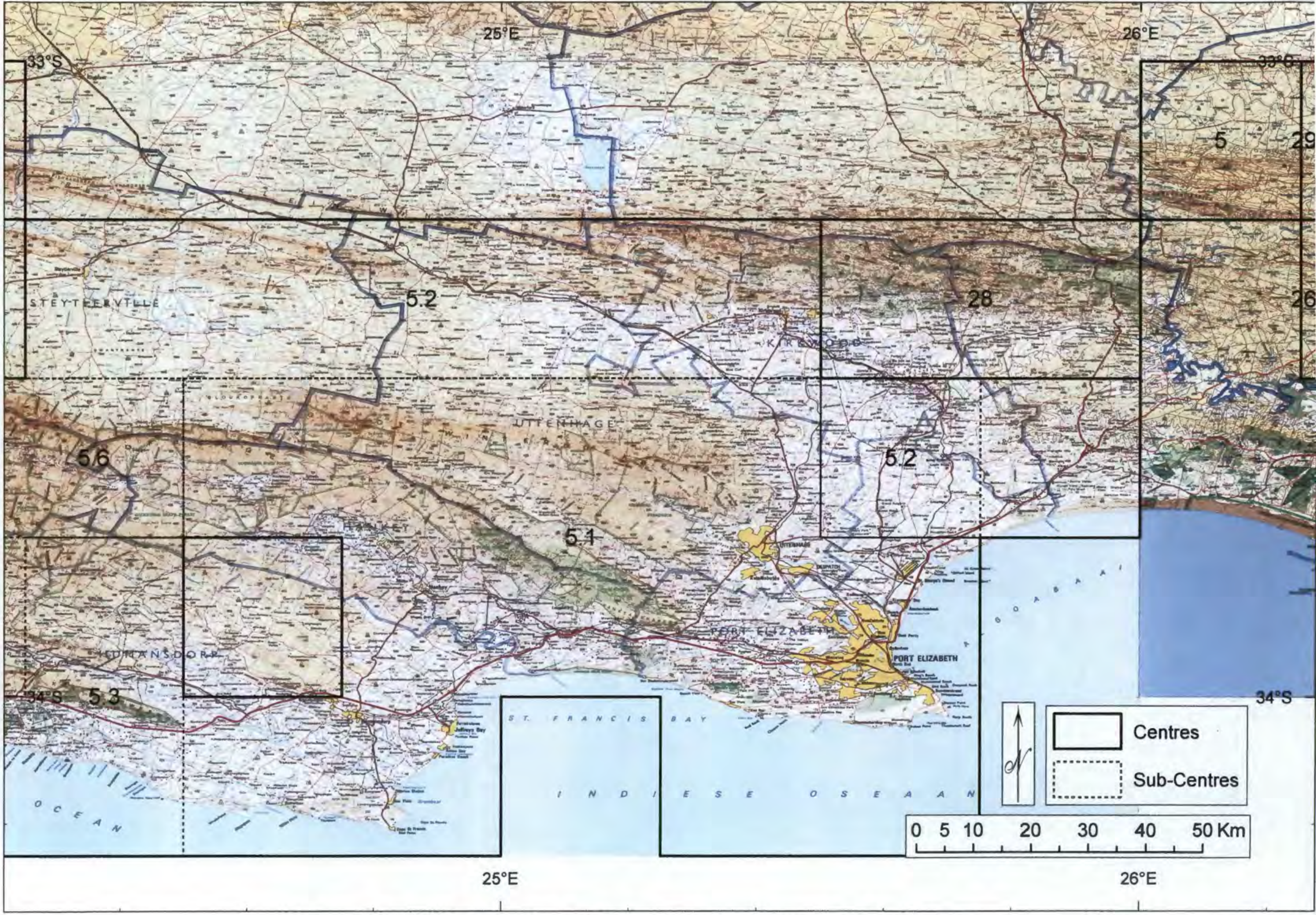


Figure 38: Position of the East Southeast Mountain Phytogeographical Centre (PC 5 eastern portion)

Cockscomb Sub-Centre, is the eastern most extent of the more geographically continuous Cape Region. East of this, disjunct parts of the East Southeast Centre (PC 5) occur, and some other minor PCs, such as the East Suurberg Centre (PC 28), the South Grahamstown Centre (PC 27) and the North Grahamstown Centre (PC 29), and occasionally the East London PC (35). I refer to these latter three PCs as the Eastern Archipelago Centres in the hierarchical analysis (eArchipelago, Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), due to their disjunct nature. Disjunct Cape Clade elements in these PCs (Appendix II) may be overwhelmed by the contemporary summer rainfall floras in the east, in much the same way as the Kamiesberg and Northern NWPP floristic units are in the north-western regions of the CFR by geophytes and xerophytes. This may account for these easterly PCs being classified in the Summer Rainfall OGU (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), rather than being nested with the winter rainfall cluster. By themselves, these minor centres have very few CFR endemics, but if combined with the rest of the CFR, they could result in an increased number of endemic taxa, or clades (especially genera).

There does not appear to be any evidence from my data to suggest an Albany Centre as substantial as that proposed by van Wyk and Smith (2001) and Croizat (1965). The Albany Centre is most likely based largely on succulent taxa, such as Euphorbiaceae (Croizat, 1965), Apocynaceae and to a lesser extent on Aizoaceae. My sampling consisted largely of non-succulent Cape Clade taxa (Linder, 2003). The taxonomic diversity of the Cape taxa in this region is relatively low. The inclusion of xerophytic taxa, prevalent in summer rainfall areas, such as *Euphorbia* (Croizat, 1965) and *Haworthia,* would undoubtedly reveal some interesting and potentially conflicting floristic patterns here.

My study indicates an apparent realignment in the boundary between the Karoo Mountain Centre (PC 7) and the East Southeast Centre (PC 5). My East Southeast Centre boundary is situated further west, along the Slypsteenberg and Antoniesberg, traditionally placed in the northern KMPP (Weimarck, 1941; Goldblatt and Manning, 2000). This westward extension of my East Southeast Centre (PC 5), to the north of the traditional boundary of the KMPP, may be due to edge effects and the incorporation of taxa from neighbouring floras would probably restore the original boundaries, as argued for in the Witteberg Centre (PC 12).

##### 2.4.2.1.1.4.2.1 Groot Winterhoek-Vanstadens-PE area (PSC 5.1)

This phytogeographical area corresponds to the Cockscomb Sub-Centre of Weimarck and constitutes the eastern boundary of the CFR, according to many biogeographers (Bolus, 1886, 1905; Marloth, 1908; Goldblatt and Manning, 2000). The *Erica* and Rosaceae datasets suggest that this area is an extension of the Kouga-Baviaanskloofberg PC. In the Combined Dataset, the

Proteaceae and the RDL Taxa, this floristic unit contains equal or nearly equal areas of montane and lowland area, without any spatial differentiation between them at the QDS scale. In Geophytes and Rutaceae, where there are distinct PCs, they are either restricted to the lowlands, or to the montane areas.

In Asteraceae, Fabaceae and Polygalaceae, the floristic development in this area is restricted to the lower lying areas. Others, such as Bruniaceae, Orchidaceae, Poaceae and surprisingly Restionaceae, show no floristic development in this area.

###### 2.4.2.1.1.4.2.2 Kouga-Baviaanskloofberg (PSC 5.5 and 5.6)

The Kouga-Baviaanskloof area is situated in the central northern region of the SEPP, though in some cases it shows affinities to surrounding areas like the eastern KMPP, or to other parts of the SEPP. Although Weimarck combined the Kouga-Tsitsikamma areas into a distinct floristic unit, he did not recover the Langkloof sub-division. Weimarck largely excluded the Baviaanskloofberge from the CFR, which I found to occur in the SEPP. In the Combined Dataset, there is a division into west (PSC 5.5) and east (PSC 5.6) sub-centres.

In the various clade/guild datasets, the area varies from being well defined phytogeographically, even extending beyond the core area, to having no PC development. The area is very well defined in the Combined Dataset and Rutaceae, where there is east-west differentiation. The area is also well defined in the RDL Taxa, Proteaceae and Rosaceae, although in these groups there is no internal sub-division. It covers an enlarged area in Proteaceae and Rosaceae. *Erica* and Orchidaceae show distinct floristic development in the west, while Asteraceae has good development in the central areas.

There is no distinct PC development in Bruniaceae, Poaceae, Polygalaceae and Restionaceae. In Geophytes, the area is not distinguishable from the larger PC in which it occurs.

###### 2.4.2.1.1.4.2.3 Suurberg

It is debatable whether the Suurberg (Zuurberg in older publications) region belongs in the core CFR or not. Weimarck supported its inclusion, but noted its weak affinities, while many others did not include it (Bolus, 1886, 1905; Marloth, 1908; Goldblatt and Manning, 2000). A compromise between the two is perhaps the best solution, much like the Southern Succulent Karoo Cluster (Section 2.4.2.1.2.2.1). While the montane areas frequently contain a few Cape Clade elements, the lower lying areas support thicket of a more sub-tropical origin, which are frequently numerically superior to their CFR counterparts.

Where my datasets show distinct PC development in the Suurberg floristic area, the most common pattern indicates a more montane flora, such as in the Combined Dataset, Asteraceae, Poaceae, Polygalaceae, RDL Taxa and Rutaceae. In Fabaceae and Rutaceae, phytogeographical development includes both montane and lower altitude areas. There is no distinct Suurberg PC development in Rosaceae, although the area is included in a more widespread Summer Rainfall PC. There is a complete lack of PC development in Bruniaceae, Geophytes, Orchidaceae, Proteaceae and Restionaceae. In Geophytes, this may be due to the absence of adequate data.

In summary, certain higher altitude areas of the larger Suurberg Sub-Centre of Weimarck that contain Cape Flora should be treated as outliers of the Cape Region, while the remaining lower altitude areas may be better placed in the summer rainfall floras.

### 2.4.2.1.1.5 Karoo Mountain Phytogeographical Province (KMPP; PC 7)

Drége (1843) was the first to map the importance of the west-east mountain ranges of the Langeberg and Swartberge and their floristic significance and distinctiveness from the surrounding lower lying areas. Rehman (1880) recognized a distinct Karoo Centre, separate from the CFR and included the Swartberge as part of this centre, while Engler's (1882) Karoo Centre is a somewhat detached area, vaguely centred on the Roggeveld-Hantamsberge. Bolus (1886, 1905) included the Swartberge as part of his Cape Region, while Marloth (1908) very accurately recognized the Swartberge as having Cape affinities surrounded by low-lying Karoo vegetation. Similarly, Weimarck recognized the importance of the Swartberge as a Cape floral centre, with much of the Little Karoo forming part of his Knysna Interval, as it tends to lack TMS "fynbos" montane Cape floral elements, except on the mountains. Goldblatt and Manning (2000) expanded the KMPP of Weimarck by including the plains and inselbergs of the Little Karoo in it. Oliver et al., (1983) failed to differentiate between the KMPP, LBPP and SEPP, instead grouping all three together, probably due to a lack of data in their study. Acocks (1988) referred to this vegetation mostly as False Fynbos. Most vegetation biogeographers recognise different floras in this phytochorial centre, noting that higher altitude areas have fynbos vegetation and lower altitude areas contain Succulent Karoo vegetation (Levyns, 1964; Taylor, 1979; White, 1993; Acocks, 1988; Rutherford and Westfall, 1994; Low and Rebelo, 1996; Cowling and Heijnis, 2001; Mucina and Rutherford, 2006). This supports Marloth's (1908) earlier demarcation. Due to steep environmental gradients, the KMPP has disparate floristic elements in relatively close proximity to each other, as noted by many previous studies (Levyns, 1938, 1964; Taylor, 1979).

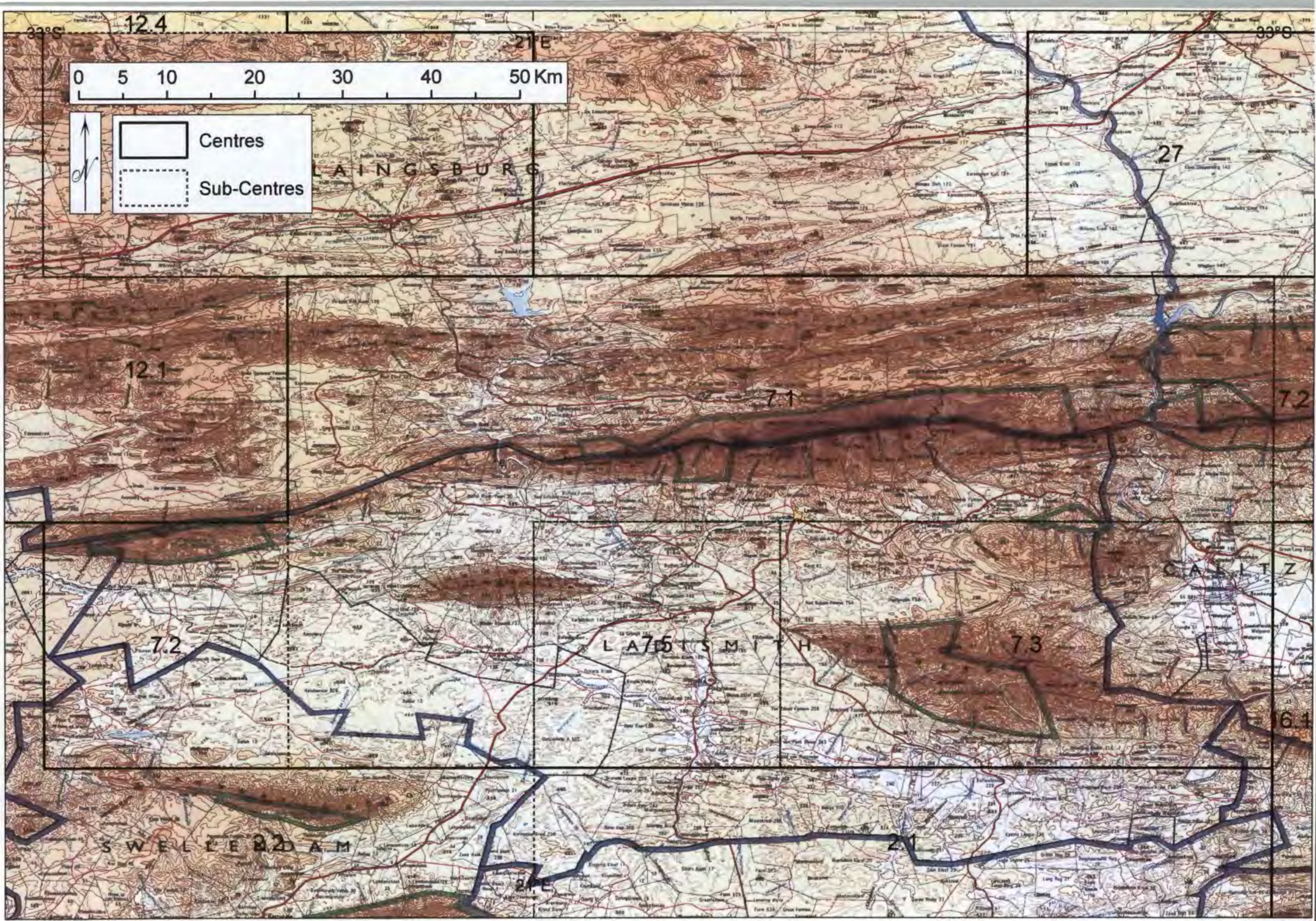


Figure 39: Position of the Karoo Mountain Phytogeographical Province and Centre (PC 7 western portion)

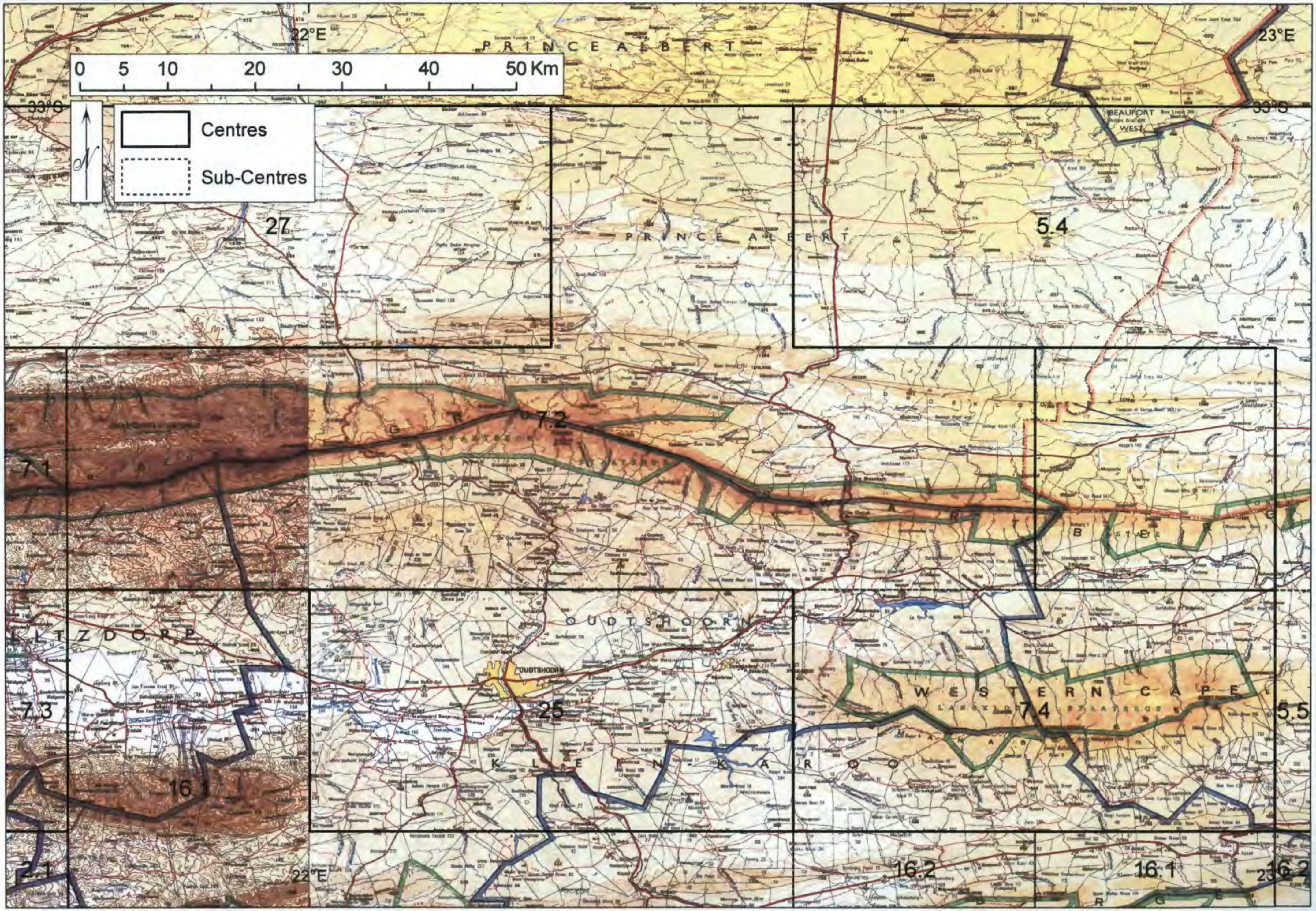


Figure 40: Position of the Karoo Mountain Phytogeographical Province and Centre (PC 7 eastern portion)

The KMPP identified here consists of a single PC, the Karoo Mountain Centre (PC 7), although it may be quite rightly argued that the Greater Witteberg Centre (PC 12) or parts thereof may or should form part of the KM phytogeographical province. The Greater Witteberg Centre (PC 12) shows greater affinities to the NWPP in my study. In all the hierarchical analyses included here (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), the Greater Witteberg (PC 12) is indicated as basal to the NWPP. This is similar to the phytogeographical boundaries of Weimarck, whose Northwest Phytogeographical Centre includes the two southerly PSCs (12.1 and 12.3) of my Greater Witteberg Centre (PC 12). However, the clustering of my Greater Witteberg with the NWPP rather than with the KMPP is less congruent with the divisions of Goldblatt and Manning (2000). The bias of my dataset to montane "fynbos" taxa may have contributed to the stronger affinities of the Greater Witteberg (PC 12) to the NWPP, rather than the KMPP. These affinities are likely to be restricted to the higher lying areas of the Greater Witteberg, with the lower lying areas containing a more arid Succulent Karoo flora. A more representative or comprehensive dataset may strengthen the affinities of the Greater Witteberg to the KMPP. In my Combined Dataset, part of the western Little Karoo around the Waboomsberge (northern parts of PSC 2.2) showed stronger affinities to the Greater Langeberg Mountains than the KMPP.

Aside from the Witteberg, there is much congruence between the phytogeographical boundaries of this study and those of Goldblatt and Manning (2000), and Weimarck, but there are also notable differences. My study indicates that the area approximately east of Snykloof (including the Slypsteenberg) and the Kammanassieberg is better placed in the SEPP, while both Weimarck, and Goldblatt and Manning (2000) include the area in the KMPP. The main PC is divided into a number of PSCs, centred on mountains. The Karoo Mountain Centre (PC 7) contains the Klein Swartberg (PSC 7.1), the Groot Swartberg (PSC 7.2), Rooiberg (PSC 7.3) and Kammanassieberg (PSC 7.4).

In Asteraceae, Fabaceae, Polygalaceae (*Muraltia*) and Rosaceae (*Cliffortia*) the KMPP region is well developed. While Fabaceae is ubiquitous globally and Asteraceae is usually the best represented family in arid to semi-arid regions (Goldblatt and Manning, 2000), it is notable that the KMPP of *Muraltia* and *Cliffortia* are also strongly developed.

Except for the Combined Dataset and Asteraceae, which extend the KMPP westward, there is usually a decrease in the extent of continuous geographical area incorporated into the KMPP, particularly at the western and eastern ends. This is either from a lack of floristic development in these areas, or because neighbouring PCs have extended beyond their traditional phytogeographical boundaries (Goldblatt and Manning, 2000; Weimarck, 1941). In many of these cases, congruence between the adjacent PC sub-centre boundaries and the traditional phytogeographical boundaries can be observed.

The more mesic Bruniaceae and Orchidaceae show the least phytogeographical development in the KMPP. Neither have any endemics, merely containing outliers from neighbouring PCs, usually the SEPP. Poaceae also shows weak KMPP PC development, containing one, possibly two PC endemic taxa.

#### 2.4.2.1.1.5.1 The Karoo Mountains PC (PC 7)

There is clear differentiation of the Swartberg Mountain Range into the Klein (PSC 7.1) and Groot Swartberg (PSC 7.2). This boundary occurs in QDS 3321BC, through the middle of which runs Die Poort, where the Gamka-Gouritz River cuts through the Swartberg Range. A more accurate geographical analysis may thus increase the number of Groot Swartberg endemics, if the mountains east of Die Poort are included with the Groot Swartberg.

The East Touwsberg Sub-Centre (PSC 7.5) produces the same number of endemics (4) when combined with the Karoo Mountain Centre (PC 7), or the Greater Langeberg Centre (PC 2). No analysis combined this QDS (3321CA) with the Langeberg Centre (PC 2), but PAE (Analysis 2) and MInt (Analysis 5) combined it with parts of the Klein Swartberg Sub-Centre (PSC 7.1). This may indicate antagonistic affinities of taxa in this QDS to the LBPP and KMPP.

Considerable areas of the eastern KMPP, to the east of the Groot Swartberg and Kammanassie Mountains, are combined with the Southeast Centre (PSC 5.4 and 5.5). These sub-centres are poorly supported by taxa. The East Little Karoo PC (PC 25) and the South Groot Karoo PC (PC 27) are geographically close to the KMPP, but appear quite distant from the core CFR and are nested between the Southern and Northern Succulent Karoo OGUs (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26).

There are numerous examples of succulent taxa from Aizoaceae and *Crassula* that occur in the arid band that stretches along the entire eastern (Hartmann, 1993) and northern interior winter rainfall boundary of the CFR. These occur on the rain-shadowed inland slopes of mountains, such as the Rooiberg in the KMPP (Taylor, 1979), and presumably also the NWPP and the other CFR phytogeographical provinces. Some of these taxa link the NWPP and KMPP (and even the SEPP), or Succulent Karoo, or they may overlap into both CFR and Succulent Karoo floristic regions in this area. An analysis of a combined dataset of all Cape and Succulent Karoo taxa at the QDS scale may not necessarily provide increased resolution of where the exact boundaries and affinities lie, due to interdigitisation at this scale, and the antagonistic ecological affinities of these different clades. Lombard et al., (1999) reported a 40% difference on the correspondence of hotspots of richness between succulents and Red Data List taxa.

Greater understanding may instead be gained by analysing the clades independently. As succulents are fairly well represented in this area, this lack of congruence could account for some floristic irregularities. CFR taxa would likely combine the NWPP and KMPP to the SWPP and rest of the CFR, while Succulent Karoo elements may combine the NWPP and KMPP to the Succulent Karoo.

### 2.4.2.1.1.5.1.1 Klein and Groot Swartberg (PSC 7.1 and 7.2 respectively)

The Klein and Groot Swartberg are geographically central in the KMPP, and usually form a single floristic unit (for example, in the Combined Dataset, *Erica,* Fabaceae, Geophytes, Polygalaceae, Proteaceae, Rosaceae and Rutaceae). In the Combined Dataset, Fabaceae, Polygalaceae, Rosaceae and Rutaceae, there is further floristic differentiation into Klein and Groot Swartberg Sub-Centres at lower floristic hierarchical levels.

In Asteraceae, the RDL Taxa, and the Restionaceae, the Klein and Groot Swartberg occur in different PCs, although in Restionaceae they may still combine into a single larger cluster. In Asteraceae, the Klein Swartberg shows higher affinities to the Western KMPP rather than the Groot Swartberg. In the RDL Taxa, the Groot Swartberg and Kammanassieberge combine with the Western SEPP, rather than the Klein Swartberg. In both cases, sub-centre boundaries are congruent with the traditional phytogeographical boundaries.

An interesting pattern that emerged was the extension of the Swartberg PC along the Gouritsrivier, in *Erica* and Geophytes. In *Erica,* it includes more of the Rooiberg and surrounding Little Karoo QDSs.

### 2.4.2.1.1.5.1.2 Rooiberg (PSC 7.3)

The phytogeography of the Rooiberg has been studied before (Taylor, 1979). The Rooiberg is fairly well defined in my study, forming a distinct floristic unit in the Combined Dataset, Asteraceae, Fabaceae, the RDL Taxa and Rosaceae.

Within the KMPP, the Rooiberg seems most closely affiliated with the Swartberg (my Combined Dataset, *Erica,* Fabaceae, Geophytes) and specifically to the Klein Swartberg by Proteaceae and the RDL Taxa, or the Groot Swartberg by Asteraceae. In Polygalaceae, the Rooiberg is disjunct with the Klein Swartberg west of the Buffelsrivier and the Touwsberg.

Datasets that show the Rooiberg having affinities to areas outside the KMPP include Restionaceae, where it is part of the LBPP. Rutaceae suggests Rooiberg affinities to the Western Outeniqua Mountains.

### 2.4.2.1.1.5.1.3 Kammanassieberg (PSC 7.4)

The Kammanassie Mountain is situated close to the boundary between the KMPP and SEPP, and appears to be a transitional area. Goldblatt and Manning (2000) included it in their KMPP, while Weimarck left it in his Knysna Interval. Its conflicting affinities are also apparent in my study. There is distinct Kammanassieberg phytogeographical development in the Combined Dataset, Asteraceae, the RDL Taxa and Restionaceae.

In my study, the Kammanassie is often included in an enlarged PC that includes eastern portions of the KMPP and western and/or northern portions of the SEPP. Examples include Geophytes and the RDL Taxa, in which there are some levels of sub-centre development; and Proteaceae, which has no sub-centre development. Geophytes include the Kammanassie in the western SEPP (Outeniqua PC), while the RDL Taxa indicate stronger KMPP affinities. In *Erica*, the Kammanassieberge form a PC with the Kougaberge of the SEPP, with almost no apparent KMPP affinities.

Datasets where the Kammanassieberge show more distinct KMPP affinities include the Combined Dataset; Rosaceae, where affinities are more specifically with the Swartberg; and Asteraceae and Rutaceae, where relationships to the Groot Swartberg are apparent.

### **2.4.2.1.1.6 Agulhas Plains Province (APPP; PCs 4, 21, 24)**

My Agulhas Plains Province is more extensive than the APPP delimited by Goldblatt and Manning (2000), reaching east of Mossel Bay and further inland. Weimarck identified a Bredasdorp sub-centre in his South-Western Centre (Figure 11), but it included the whole area between the Riviersondereinde and the coast, which I sub-divide between my Riviersondereinde (PSC 10), the Hottentots Holland (PSC 1.1 and 1.2) as well as the Agulhas (PSC 4.1) PC in the Combined Dataset. Although he listed some limestone and calcareous endemics in his Bredasdorp Sub-Centre, he did not recognise an independent Agulhas Plains Centre as did Goldblatt and Manning (2000). Analysis of the hierarchical relationships of the PC using different weightings (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26) revealed that there is a close relationship between the Southwest Centre (SWPP) and the Agulhas Plains (PC 4). In two of five weighting techniques, the Agulhas Plains (PC 4) were found to be more closely affiliated with the SWPP than with the rest of the APPP PC (PC 21 and 24). The boundary between the SWPP and APPP probably interdigitates repeatedly, with numerous outcrops of TMS surrounded by other substrate types such as shale, limestone and littoral sand deposits (Figure 18; Table 12). Thus, taxa occurring in the SWPP, in both the SWPP and NWPP (Weimarck's Western Endemics) and in the LBPP, may have scattered occurrences in the APPP. This results in the affinities of the Agulhas Plains (PC 4) to these PCs, which may obscure the distinctiveness of the APPP.

The Agulhas Plain Centre (PC 4) corresponds to Kruger's (1979) Southern Coastal Fynbos, and Acock's (1988) Southern Coastal Fynbos and Coastal Renosterveld. Cowling and Holmes (1992) also identified this area as having high species diversity and endemism. In a PAE study of Restionaceae, Linder (2001) also identified this area as phytogeographically distinct.

In the hierarchical analyses, the Agulhas Centre (PC 4) shows the least stability of all the phytogeographical provinces discussed thus far and proved the most difficult to classify, due to conflict between the different analyses. The lack of geographical accuracy could result in a "cascade" effect, where numerically superior neighbouring TMS PCs could overrun the boundaries of the smaller Limestone, or lowland PCs, reducing their size. Thus, results need to be interpreted cautiously, until more accurate spatial data can pinpoint taxonomic distributions and ultimately PC boundaries. The literature reflects this conflict in the relationships of this phytogeographical area and at various times, the different results found were recorded (*cf.* Goldblatt and Manning and Weimarck).

The results of the Bell, MInt and Unsmoothed PC Frequency Weighting Technique Hierarchical Analysis (Figure 23, Figure 24 and Figure 25) group the entire southern coastal plain from Gansbaai in the west to Mossel Bay in the east (PC 4, 21, 24) into a distinct, independent phytogeographical unit, much like Goldblatt and Manning (2000) (Figure 2), and place it as sister to the ((SEPP, KMPP), LBPP) floristic unit. By contrast, in the Unweighted (Figure 22) and Smoothed PC Frequency Weighted Analyses (Figure 26), the Agulhas Plains (PC 4) is classified as a sister group to the rest of the SWPP. This bears similarities to the studies of Weimarck and Oliver et al., (1983) (Figure 12), and may include non-littoral elements.

Further investigations revealed the following: combining the Agulhas Plains Centre (PC 4) with the core SWPP produces a further 174 endemic taxa, while combining the Agulhas Plains Centre (PC 4) to the remaining eastern APPPs only produces 18 extra endemics. Thus, in terms of sheer numbers of endemics, combining the Agulhas Plains Centre (PC 4) to the SWPP is more favourable. However, combining the Agulhas Plains Centre (PC 4) with the core SWPP increases endemism in the SWPP by 22.08%, while combining the Agulhas Plains Centre (PC 4) to the remaining eastern APPPs increases endemism there by 112.5%. Furthermore, the average distributional range of endemic species is smaller when the Agulhas Plains Centre (PC 4) is combined with the APPP rather than the SWPP, namely, four QDSs versus eight QDSs respectively. Thus, there are more range-restricted species shared amongst the APPP PCs (PCs 4, 21, and 24), than between the Agulhas Plains PC (PC 4) and the SWPP-NWPP phytogeographical provinces. This is further substantiated by the fact that the APPP PCs (PCs

4, 21, and 24) form a cluster in the Species Area Weighting Technique (MInt, Figure 24), which emphasises range-restricted taxa. Thus, there are a few conflicting scenarios.

The most perplexing aspect about this APPP conundrum is why the East Agulhas Plains (PC 21) and Far East Agulhas Plains (PC 24) do not cluster with the Agulhas Plains Centre (PC 4) in the SWPP, in the Unweighted and Smoothed PC Frequency Weighted Analyses (Figure 22 and Figure 26). This may indicate that the taxa shared between the SWPP and APPP do not extend far into the APPP, or, at least, do not reach its eastern regions.

Despite the fact that there are many variations in phytogeographical patterns in the APPP, these variations appear to centre on three main phytogeographical units or areas on the APPP. These are the West Agulhas Plains, the Potberg and the East Agulhas Plains.

In the majority of the datasets I analysed in which the APPP and SWPP were retrieved, the APPP either forms continuous PCs, or it is not combined with the SWPP (for example, Asteraceae, Ericaceae, Fabaceae, Geophytes, Poaceae, Polygalaceae, Proteaceae, RDL Taxa, Restionaceae, Rosaceae and Rutaceae). Only in Bruniaceae and Orchidaceae are portions of the APPP merged with the SWPP. However, it is important to bear in mind that I mostly utilised Species Area Weighting Techniques (Bell and Integration Weighting) in these analyses and produced the same results as the Hierarchical PC Analysis, using a similar weighting technique that emphasised range-restricted taxa.

The East Agulhas Plains (PC 21) and the Far East Agulhas Plains (PC 24) form a nested clade in all five analyses, and its position relative to the other clusters is identical, namely as sister to the ((SEPP, KMPP), LBPP) floristic unit. Its affinities to this area are presumably due to the large contact boundary between the APPP and LBPP. The grouping of three PCs forming the APPP (PC 4, 21, 24) are upheld, and recorded in the summary table (Table 14). Finer spatial analyses may reduce much of the conflict.

###### 2.4.2.2.1.6.1 The West Agulhas Plains (PSC 4.1)

The West Agulhas Plains display at least some distinct Agulhas Plains PC development in almost all the groups I analysed, even if it was, in some instances, only a single QDS, as in Bruniaceae. The only exception is Orchidaceae. The Combined Dataset is assumed to depict the most common, or the average size of a West Agulhas Plains PC and corresponds satisfactorily with Goldblatt and Manning's (2000) Phytogeographical Boundaries. Mention will be made where the APPP extends northwards beyond these boundaries, which is similar to the patterns displayed by Weimarck's Bredasdorp Sub-Centre.

Figure 41: Position of the West Agulhas Plains Phytogeographical Centre (PC 4)

The results of my study reveal that the West Agulhas Plains most commonly form an independent PC. In *Erica* and Geophytes, this PC corresponds adequately to the northern boundaries of the PC in the Combined Dataset. In Rosaceae, the PC is even more reduced, due to other fragmented PCs. In Polygalaceae, Proteaceae and the RDL Taxa, there is an independent West Agulhas Plains PC, but it extends northwards into the western Overberg Rûens area.

Another relatively common pattern is for the West Agulhas Plains to be affiliated with the Potberg PC (for example, the Combined Dataset, Bruniaceae and Rutaceae). The two areas are usually sub-divided into independent sub-centres in the same PC, except in Bruniaceae. In Bruniaceae, the SWPP extends southwards, while in Rutaceae, the APPP extends northwards into the SWPP and LBPP, and includes most of the Overberg Rûens area.

In Asteraceae, Fabaceae, Poaceae and Restionaceae, nearly the entire APPP area forms a single PC. In Poaceae, it is reduced in size in the west, as the SWPP expands southwards. In Restionaceae the PC corresponds sufficiently to the Combined Dataset, although there is only a single sub-centre, which is split between the West Agulhas Plains and the Potberg. In Asteraceae and Fabaceae, the West Agulhas Plains PC is expanded into the SWPP and the eastern LBPP. Both have adequately defined sub-centres that correspond to the three main APPP PCs, namely the West Agulhas Plains, the Potberg and the East Agulhas Plains.

There is no notable APPP PC development in Orchidaceae and there are no limestone endemic orchids (Table 45). Instead, in Orchidaceae, the SWPP extends to Cape Agulhas, via overlap in QDS ranges of TMS biotic elements littoral sand elements.

### 2.4.2.1.1.6.2 The Potberg (PSC 4.2)

The Potberg is a TMS hill (611 m) on the Agulhas Plains, with limestone to the south and shale to the north. As a result, diverse edaphic endemics were identified in the various datasets that I analysed. There appear to be two dominant patterns, namely, either the Potberg is affiliated with the West Agulhas Plains (for example, the Combined Dataset, Bruniaceae, Restionaceae or Rutaceae), or it is part of a nearly entire APPP (for example, Asteraceae, *Erica,* Fabaceae (with stronger eastern affinities) and Poaceae). In both cases, the Potberg frequently forms a distinct, independent sub-centre. The Potberg does not constitute an independent sub-centre in Bruniaceae, Restionaceae, *Erica* and Poaceae.

The Potberg forms an independent sub-centre within a larger East Agulhas Plains PC in the RDL Taxa; while in Geophytes and Rosaceae, the Potberg forms a totally independent PC.

Figure 42: Position of the East Agulhas Plains and Far East Agulhas Plains Phytogeographical Centre (PC 21 and 24 respectively)

An unusual pattern is observed in Polygalaceae and Proteaceae. In Polygalaceae, the Potberg forms a sub-centre that has close affinities to the Central Langeberg Mountains, while in Proteaceae it forms a PC with a QDS in the Bree River Valley-Robertson Karoo area, between the RZE and the West Langeberg.

As with the West Agulhas Plains, there is no independent PC development in the Potberg area for Orchidaceae. Furthermore, surrounding PCs do not even incorporate QDSs from the Potberg vicinity.

#### 2.4.2.1.1.6.3 East Agulhas Plains (PC 21 and 24)

This area is usually the most underdeveloped of all PC APPP areas, both in terms of diversity and numbers of endemics. This is possibly due to an eastward shift out of the true winter rainfall area, combined with the absence of nearby mountains.

Consequently, in most datasets, there is no independent East Agulhas Plains PC development. In Bruniaceae and Rosaceae, no QDSs in this area are assigned to a PC, while in Geophytes, Orchidaceae and Polygalaceae, only a single QDS is assigned to a LBPP PC. In Proteaceae, all of the East Agulhas Plains combined with the East LBPP and the West SEPP.

The next most frequently observed pattern is for the East Agulhas Plains to form part of an enlarged APPP. In Asteraceae, it forms an independent sub-centre within the larger PC, while in Poaceae and Restionaceae, there is less clear differentiation. In *Erica*, Fabaceae and the RDL Taxa, it combines with the Potberg, forming a separate and distinct sub-centre in the latter. In the Combined Dataset and Rutaceae, the East Agulhas Plains form an independent PC, with sub-centre development in the latter.

#### 2.4.2.1.1.7 A Problematic Core CFR PC

#### 2.4.2.1.1.7.1 Bree River Valley (Worcester-Bonnievale Valley)

One of the more contentious areas of assigning QDSs to PCs in the CFR lies on the boundary between the NWPP and SWPP in the Bree River Valley. Mountainous regions of both the SWPP and NWPP are represented in many of these QDSs, resulting in conflict in assigning these QDSs to maximise endemism. Additionally, there is a strongly developed Succulent Karoo flora here, forming what van Wyk and Smith (2001) refer to as the Worcester-Robertson Karoo Centre. Usually one PC benefits at the cost of another (potential cascade effects). It is highly likely that more accurate taxon distributional data in this region will result in higher overall levels of endemism in many of datasets analysed here, as has been demonstrated in the Geophytes Dataset (Appendix I: Chapter 9).

Datasets that maintain the traditional NWPP-SWPP boundaries in this area are the Combined Dataset, Asteraceae, Bruniaceae, *Erica* and Restionaceae. This may be due to the dominance of "fynbos" taxa in these datasets, with their TMS montane affinities. In Proteaceae, the SWPP is slightly more dominant, while in Polygalaceae and Rosaceae, the NWPP appears to be slightly more dominant. The SWPP extends even further north in Poaceae, including the Ceres and Elandsberg QDS with the SWPP; while in Orchidaceae, the NWPP is more dominant, including substantial parts of the SWPP. The pattern in Rutaceae is a little more complex. Most of the PCs follow the traditional NWPP-SWPP boundary, except for a single PC that straddles the Berg-Bree River Valleys, the Central Southwestern-S Northwestern Mountains (PC 3). The sub-centres to some extent are centred in the traditional phytogeographical provinces, except for one (PSC 3.1) that extends into the SWPP from the NWPP. However, this may be due to a cascade effect of adding sequential QDSs to a PC and needs to be confirmed at a finer geographical scale.

In the Fabaceae, Geophytes and RDL Taxa Datasets, there is distinct independent PC development centred on the Bree River Valley area. In the Geophytes Dataset, this pattern is continued further north, into the Little Berg River Valley. The hierarchical affinities of these PCs have not been fully investigated, as these datasets are incomplete. The endemic taxa of this PC indicate mixed floristic affinities. In the Geophytes Dataset, the two dominant substrates of endemic taxa are clay and sandstone (Table 42). This indicates a TMS fynbos element and a Renosterveld and/or Karoo element, which is confirmed by the vegetation units in which the endemic taxa are most frequently found (Table 42 (Geophytes) and Table 39 (Fabaceae)). These different elements are likely to be in conflict, with the clay elements trying to consolidate the lower lying clay areas, while the TMS elements would try and group the higher lying TMS areas together.

#### 2.4.2.1.2 Remaining Winter Rainfall Phytogeographical Centres

The Namaqualand Centres form the sister group to the CFR centres, largely corroborating the results of Born et al., (2006), who grouped these additional areas into two "regions": the Hantam-Tanqua-Roggeveld Region and a Namaqualand Region. In my datasets the Hantam-Tanqua-Roggeveld Region shows very little development, due to my dataset bias to CFR (fynbos) taxa. Poaceae seems to be the exception to this rule, with its Namaqualand PC having disjunct outliers in the Roggeveld and NWPP.

Certain parts of Namaqualand that contain sufficient numbers of Cape Clade elements (Appendix II) have fairly well developed PCs (PC 11, 15, 17, 20 and 22). With the exception of the Bell (Figure 23) and Smoothed Centre Frequency Weighting Analysis (Figure 26), this cluster is retrieved as a single group, sister to the core CFR (Figure 22, Figure 24 and Figure 25).

###### 2.4.2.1.2.1 Hantam-Roggeveld Region

The Hantam-Roggeveld Region is centred on the Southwest Escarpment and is antipodal to the Northeast Escarpment PC (PC 18) both geographically and in terms of moisture seasonality and availability, being far more arid. Weimarck identified the Hantam-Roggeveld area as a sub-centre of his Northwest Centre, although he questioned its validity as a Cape Sub-Centre due to its weak floristic links to the CFR, based on the Cape elements that he analysed. More recent studies, focusing on geophytes (Manning, Goldblatt and Snijman, 2002), and succulents (van Wyk and Smith, 2001), have designated an independent Hantam-Roggeveld Centre. Weimarck restricted his sub-centre to smaller areas of higher altitude on the western escarpment, where Cape Clades (Linder 2003) were likely to occur. However, the Hantam-Roggeveld Centres of the latter authors were considerably more enlarged, being inclusive of other floras. Manning et al., (2002) included the Tankwa Karoo Basin (to the west) in the Centre, while van Wyk and Smith (2001) extended their Centre east to include the Nuweveldberg Mountains. van Wyk and Smith (2001) commented on its exceptional geophyte diversity and endemism, particularly Iridaceae, which was recorded by Manning et al., (2002), although diversity and endemism was still shown to be low compared to core CFR PCs. Nordenstam (1969) found the Hantam-Roggeveld, together with the Nuweveldberg Mountains, to be a fairly important centre of diversity and endemism in *Euryops*, and stated that it had strong CFR links. All this again serves to emphasise the significance of data bias, pattern retrieval depends largely on the floristic elements being analysed. The Hantam-Roggeveld areas should at least form a centre in their own right, as proposed by van Wyk and Smith (2001), and Goldblatt and Manning (2002).

In my present study, a distinct, independent, consolidated Hantam-Roggeveld floristic unit was not identified. I found greater PC development in the more southerly Roggeveld/Klein-Roggeveld area. In many of my datasets, PC northerly development stopped on Karookop (PSC 12.4 in the Combined Dataset). This is a small mountain (1516 metres), is located immediately to the south of the Klein Roggeveld, and was usually floristically associated with the Greater Witteberg Centre (PC 12) in my analyses. However, there are no mesic Cape Clade elements endemic to it (Appendix II). The current study indicates that the Klein-Roggeveldberge (PSC 12.4) has stronger affinities to the NWPP in the core CFR, through its inclusion in the Greater

Witteberg Centre (PC 12) (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). Its position may change with the addition of floral elements from outside the CFR, notably, the Succulent Karoo. It is possible that Weimarck identified this sub-centre shortly after his revision of *Cliffortia* (Weimarck, 1934). In the Rosaceae Dataset, the Arid Interior PC (PC 9), which is centred on the Great Escarpment and occurs disjunctly in the Hantam-Roggeveld Sub-Centre of Weimarck (1941), and in the Cedarberg where he found affinities of the Hantam to lie. It may be that at the time of Weimarck's (1941) phytogeographical study, the taxa of his study were under-collected across their ranges, giving them the impression of being more range-restricted and thus endemic to the Hantam-Roggeveld Sub-Centre and the NWPP area.

PC development in the Hantam-Roggeveld and its affinities to the CFR are fairly weak in my datasets. In this study, a few groups (for example, Bruniaceae, *Erica* and Rutaceae) showed no PC development in the Hantam-Roggeveld. Other groups (for example, Proteaceae and Restionaceae) PCs only just reach the south of Karookop. These represent some of the most characteristic Cape Clades (Linder, 2003), or clades that define fynbos. It must also be noted that the RDL Taxa Dataset and the Geophytes Dataset were largely biased to taxa within the predefined geographical confines of the CFR. There are also a number of endemic geophytes there (van Wyk and Smith, 2001; Manning et al., 2002).

The Hantam-Roggeveld displays affinities to the NWPP in Orchidaceae and Poaceae, the latter being only a single disjunct QDS Namaqualand outlier.

The Hantam displays affinities to the NWPP in Asteraceae and the RDL Taxa, and possibly in *Erica*. In Asteraceae, the relationship is also fairly general, but the QDS in the Hantamsberg forms a distinct sub-centre. Interestingly, the Klein-Roggeveld affinities of Asteraceae seem to be to the KMPP. In the RDL Taxa, the relationship is more geographically-specific, with the Hantam being associated with the area to the southeast of the Gifberg and Nieuwoudtville Escarpment, while the Klein-Roggeveld/Karookop area of the RDL Dataset indicates Witteberg affinities. There are similar disparate affinities in the Combined Dataset, where the Hantamsberg is grouped with the Vanrhynsdorp PC, while the Klein-Roggeveld/Karookop seems to group with the Greater Witteberg and ultimately the NWPP. The affinities of the Klein-Roggeveld-Karookop Area are possibly to the KMPP in Fabaceae, Geophytes and Proteaceae.

The conflicting affinity of the Hantam-Roggeveld in my various datasets reflects the least dual affinities of the floral elements here, in relation to both the NWPP and KMPP. However, this area may be floristically important enough to be elevated to a higher floristic level, as suggested by Manning et al., (2002) and van Wyk and Smith (2001). Determining this may be of greater importance than determining its affinities to the NWPP or KMPP. Additionally, if proper floristic boundaries can be established for the Hantam-Roggeveld, the subsequent determination of its affinities would be far simpler.

### 2.4.2.1.2.2 The Southern Suuculent Karoo Cluster (Southern Namaqualand)

In my Combined Dataset, there is well-developed PC formation from the Vanrhynsdorp Centre (PC 17) and Nieuwoudtville Escarpment (PC 11) southwards. This represents the northern-most extent of the RDL Taxa Dataset, which explains the retrieval of these areas. North of this, the only area with significant PC development is the Kamiesberg, due to the presence of high altitude Cape Clade elements (Appendix II). The Gifberg PC (PC 15) and Nieuwoudtville Escarpment PC (PC 11) contain scattered Cape Clade elements, and are grouped together as a northern extension of the NWPP (nNWPP) and form part of the South Succulent Karoo (sSK), with the Vanrhynsdorp PC. The West Coast (PC 22) and Saldanha Peninsula (PC 19) centres form a cluster within the sSK, rather than the core CFR.

#### 2.4.2.1.2.2.1 Southern Succulent Karoo (Namaqualand)

The Gifberg PC (PC 15), Nieuwoudtville Escarpment PC (PC 11) and the Vanrhynsdorp PC (PC 17), consistently formed a united cluster, which I name the Southern Succulent Karoo (sSK, Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). All three PCs were found to occur outside the core CFR cluster. This grouping is most likely due to the dominance of geophyte taxa on the Nieuwoudtville Escarpment (PC 11), and succulent taxa around Vanrhynsdorp (PC 17). Analysis of the endemic taxa (Appendix II) reveals that the Gifberg PC (PC 15) contains a mere seven Cape Clade endemics (Appendix II) and the Nieuwoudtville Escarpment PC (PC 11) contains a paltry four endemic taxa from Cape Clades (Appendix II). These endemics are restricted to the higher lying mesic areas and are overwhelmed by geophytic and xerophytic taxa, which accounts for their placement outside the core CFR and being grouped in the Succulent Karoo cluster. This sSK cluster, which includes Cape Clade elements, is marked as the "northern NWPP" (nNWPP, Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), as it represents a northern floristic archipelago, or extension of the NWPP. Thus, overall, these QDSs/PCs show greater affinities to the Succulent Karoo, but within this area are geographically small, high altitude archipelagos of the CFR. These areas contain CFR taxa that are grouped into and referred to as the nNWPP. This is a geographically restricted part of the sSK, ecologically restricted to higher TMS areas in the sSK. When analysing exclusively Cape Clade datasets, these QDSs are invariably grouped with the CFR, due to clade bias. Similar situations occur east of the CFR, for example, in the Suurberg and Grahamstown areas and within the CFR, especially where there is a steep gradient between montane and low altitude taxa, as in the KMPP.

The Vanrhynsdorp PC (PC 17) is a low altitude PC, containing no endemic mesic montane ("fynbos") Cape Clades (Appendix II). Its affinity to the Gifberg PC (PC 15) and Nieuwoudtville Escarpment PC (PC 11) is exclusively due to non-montane Cape Clades, and thus shows the most distant relationship to the CFR. The placement of these three PCs outside the core CFR is closer to the classification of Weimarck than that of Goldblatt and Manning (2000), who focused more on the geographical concept of the CFR, making the CFR a spatially continuous entity. There is distinct taxonomic (floristic) turnover in this area, associated with changes in altitude, soil, and moisture availability. The lower altitude arid areas are referred to as the Knersvlakte (van Wyk and Smith, 2001).

#### 2.4.2.1.2.2.1.1 The Gifberg and Nieuwoudtville Escarpment

In the Combined Dataset, the Gifberg and Nieuwoudtville Escarpment show very strong affinities to each other (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), even though there is distinct PC development in each area. In the Geophyte Dataset, they combine into a single large northern Northwest PC, relatively independent of the rest of the NWPP. However, both the Gifberg and Nieuwoudtville Escarpment are floristically distinct enough to be placed in different sub-centres. In the Fabaceae and Restionaceae Datasets, they combine into a single, smaller PC, with distinct, disjunct sub-centres in the Gifberg and Nieuwoudtville Escarpment areas. The Gifberg and Nieuwoudtville Escarpment show distinct independent PC development in the Combined Dataset and Bruniaceae.

Most commonly, in my datasets, the Gifberg and Nieuwoudtville Escarpment form independent sub-centres of a larger NWPP. This occurs in Asteraceae, *Erica* (only Gifberg) and Orchidaceae (only Nieuwoudtville Escarpment). In Proteaceae, the Gifberg and Nieuwoudtville Escarpment combine into a single sub-centre, within a larger central and northern NWPP. In Polygalaceae, the Gifberg shows minor phytogeographical development with a single QDS sub-centre, as does the Nieuwoudtville Escarpment, which contributes a single QDS to form a sub-centre with the Kamiesberg. In Rutaceae, the NWPP extends to the Gifberg and Nieuwoudtville Escarpment, but there is no independent sub-centre development on the Nieuwoudtville Escarpment, and only minor development on the Gifberg, associated with the Pakhuis floristic area. This is a little surprising, considering that diversity and endemism in Diosmeae is best developed in the NWPP, but may indicate that it is restricted to and concentrated in the south, in the Cedarberg Mountain Range.

Poaceae share characteristics with Polygalaceae, in that the Nieuwoudtville Escarpment shows strong affinities to the Kamiesberg, but differs in that this larger phytogeographical unit is centred in the Succulent Karoo, rather than the NWPP, as in Polygalaceae.

There is no independent floristic development in the northern NWPP in Rosaceae and floristic development here is usually associated with disjunct satellite PC QDSs.

In conclusion, although many Cape Clades have endemics in the Gifberg and on the Nieuwoudtville Escarpment, Cape Clade endemics are not very numerous in these areas. The majority of endemics here are not from mesic Cape Clades (Appendix II) and it is likely that only small, high altitude portions of the QDSs from these regions should be included in the CFR.

###### 2.4.2.1.2.2.1.2 The Vanrhynsdorp Centre

Although in very close proximity to the northern boundary of the CFR, the Vanrhynsdorp PC has no endemic mesic montane Cape Clade representatives (Appendix II). In the majority of groups analysed here (for example, Asteraceae, Bruniaceae, *Erica,* Orchidaceae, Polygalaceae, Proteaceae, Restionaceae, Rosaceae and Rutaceae) there is no independent PC development in this area. Fabaceae is represented by a single disjunct QDS in the Vanrhynsdorp PC, and is an outlier of the Nieuwoudtville-South Gifberg (PC 10) PC and does not represent an independent Vanrhynsdorp PC.

Only in datasets that do not contain exclusive montane Cape Clades is there some Vanrhynsdorp PC development. The Geophyte Dataset contains a Vanrhynsdorp sub-centre that forms part of the extreme northern NWPP, in a similar pattern to Fabaceae, but in this case, phytogeographical development is sufficient to form a discreet sub-centre. In Poaceae, the Vanrhynsdorp area forms part of a large southern Namaqualand PC.

Independent Vanrhynsdorp PCs are found only in the RDL Taxa and the Combined Dataset, principally as both contain significant numbers of non-fynbos endemics (non-CFR TMS montane taxa), especially succulents and geophytes (Appendix II).

In conclusion, my results do not support the inclusion of the Vanrhynsdorp Centre in the core CFR.

###### 2.4.2.1.2.2.2 The southern West Coast (PC 20, 22)

My Combined Dataset's SWPP Sandveld (PSC 6.2) and Saldanha Peninsula (PC 20) floristic units are situated in Weimarck's Malmesbury Flats Sub-Centre, which formed part of his SWPP. By contrast, I found that the Saldanha Peninsula (PC 20) was not nested in the SWPP (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), or even in the core CFR. Instead, it forms a coastal cluster, with the West Coast PC (PC 22), which I name the west Coast Cluster (wCoast). Interestingly, the wCoast unit is disjunct across two QDS of the Piketberg-Swartland-Sandveld Centre (PC 14). This bears remarkable resemblance to the vegetation map of Acocks (1953) and White (1986). This cluster is then sister to the south Succulent Karoo Clade (Figure 22,

Figure 23, Figure 24, Figure 25 and Figure 26). Born et al., (2006) did not recognise this, as they used Goldblatt and Manning's (2000) phytogeographical areas, which included the southern half of this region in the NWPP. These affinities are probably largely due to the dominance of endemic geophytes in the Saldanha PC, although two genuine fynbos elements are present (Appendix II). The West Coast Centre (PC 22) has a QDS conflict with the Piketberg-Swartland-Sandveld Centre (PC 14). The QDS 3218AB can be placed in either of these PCs and adds 5 endemic taxa to both. The West Coast Centre (PC 22) has no endemic fynbos elements (Appendix II).

#### 2.4.2.1.2.2.2.1 Saldanha Peninsula

The formation of a phytogeographically distinct Saldanha Peninsula PC (PC 20) is most strongly developed in the Geophytes Dataset and to a lesser extent, the RDL Taxa and Combined Datasets. The Asteraceae, Fabaceae and Polygalaceae Datasets each contribute only a single endemic, although in Polygalaceae, the northern area seems to be more closely associated with an enlarged NWPP Sandveld Centre. There is no independent PC development in *Erica,* Orchidaceae, Restionaceae and Rutaceae. This is hardly surprising, as most Combined Dataset endemics in this area are either granite or limestone endemics (Table 12), while there are no TMS endemics. Instead, in those clades dominated by TMS endemics, neighbouring PCs, particularly the Sandveld PC, extend into this area. This is usually only as far as the Langebaan Lagoon, but occasionally further, as in Rutaceae. Groups where there was no PC development in this area include Bruniaceae, Poaceae, Proteaceae and Rosaceae.

#### 2.4.2.1.2.2.2.2 The West Coast Centre

The affinities of the northern West Coast Region are contradictory in my different datasets, largely due to a lack of sufficient data.

In Asteraceae and the Geophyte Datasets, affinities of the West Coast area are divided, partly to the NWPP, but both also show some independent PC development. In Proteaceae, the NWPP Sandveld extends to the West Coast region. In Polygalaceae, the general NWPP extends to the West Coast region, while in Fabaceae, it is specifically the Gifberg portion of the NWPP that makes the linkage.

In the RDL Taxa and Rutaceae, the situation is a little more complex, and the West Coast shows some affinities to the NWPP Sandveld, but also to the Saldanha Peninsula in the SWPP, especially in the RDL Taxa. In Orchidaceae and Restionaceae, the NWPP West Coast includes QDSs which show disjunct SWPP affinities. There is no West Coast PC development in Bruniaceae, Poaceae and Rosaceae.

### 2.4.2.1.2.2.3 The Central and Northern Succulent Karoo (Namaqualand)

Apart from the Kamiesberg, the area north of the sSK cluster is very poorly represented by taxa from my datasets. The PCs in this area usually cluster together to form an isolated group (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26) distant to the core CFR, or the southern Succulent Karoo cluster. I name this cluster the northern Succulent Karoo (nSK), which corresponds to the central and northern Namaqualand areas. Only in the Smoothed PC Frequency Weighting is the sSK more closely related to nSK rather than the core CFR (Figure 26). These relationships are mostly based on the Cape elements included in this study and may not be pertinent classifications based on taxa that are numerically dominant in the area.

The central Namaqualand area can be divided into two clusters: the first comprises the Kamiesberg (PC 19) and the Bitterfontein-Garies (PC 31) Centres, which are largely associated with the escarpment and Kamiesberg uplands. The second comprises the lower lying Garies-Kotzesrus (PC 44) and the Moedverloorberg (PC 47) Centres.

The northern Namaqualand area comprises the Buffelsbank-Kommaggas (PC 36), McDougall's Bay (PC 45) and Koingnass (PC 51) PCs in South Africa, which show affinities to the Southern Namibian PCs, such as the Southern Namibia (PC 43), and the Swartkop (PC 46) Centres. This is a curious pattern, as the Southern Namibia PC is disjunct across the Orange River, a potentially significant barrier. In addition, the South African PCs are lowland, while the Southern Namibia PC (PC 43) is at higher altitude.

Since only the Kamiesberg PC contained large numbers of endemics and is the only PC with appreciable Cape Clade representatives, it is the only PC that I will discuss in more detail. The remaining PCs contain mostly asterid, or grass endemics (Appendix II).

#### 2.4.2.1.2.2.3.1 The Kamiesberg (PC 19)

My Kamiesberg Centre (PC 19) includes the whole escarpment from Bitterfontein to Springbok, though it is centred on the Kamiesberg. The Kamiesberg Sub-Centre (PSC 19.1) has a number of Cape elements represented and endemic to it (Appendix II). This PC comprises a disjunct island of mesic Cape elements at high altitude, where there is sufficient precipitation to support the montane Cape elements. This was recognized by Marloth (1908) and Weimarck, and described in detail by Adamson (1938). The low-lying areas receive considerably less rainfall and the xerophytic floristic elements of the Succulent Karoo are dominant. This is readily apparent when one views the hierarchical relationships of the PCs identified in this study. The Kamiesberg PC (PC 19), despite having a few CFR endemics, is consistently classified as part of the Northern Succulent Karoo OGU (Figure 22, Figure 23, Figure 24, Figure 25 and Figure

26). It is the most important PC with floristic links (Cape Clade elements) to the CFR in the Northern Succulent Karoo cluster. van Wyk and Smith (2001) stated that although succulent diversity is high, endemism is surprisingly low and grouped the Kamiesberg with the CFR at a regional level. Although the Kamiesberg does have CFR elements as well as endemic taxa, caution should be exercised in interpreting the extent of the Kamiesberg's floristic links to the CFR. Most of the CFR elements are restricted to fairly high altitude areas in the Kamiesberg, although some, for example, *Aspalathus angustifolia robusta* occur in the attitudinally/climatically transitional Renosterveld.

Drége (1843) recognised the floristic distinctness of the Kamiesberg and collected Cape elements from it, although Marloth (1908) was the first to link the Kamiesberg floristically to the CFR. Weimarck identified the area as a sub-centre of his Northwest Centre, to which it has affinities. Goldblatt and Manning (2000) do not depict the Kamiesberg as part of the CFR in their phytogeographical map. Acocks (1988) noted the presence of fynbos vegetation on the higher peaks, while he described the vegetation of the lower mountainous areas as Mountain Renosterveld, which is in turn was surrounded by Namaqualand Brokenveld. Low and Rebelo (1996) use very similar vegetation types to Acocks (1988).

*Erica*, Orchidaceae, RDL Taxa, Restionaceae and Rutaceae each have a single endemic recorded from the Kamiesberg. Asteraceae, Fabaceae and Restionaceae each have two endemics occurring there. Only in Polygalaceae and Rosaceae are direct floristic relationships to the NWPP displayed by PCs. In the former, it is shown to be a near distinct sub-centre, while in the latter, it is a disjunct QDS of a much more southerly NWPP PC. In the Combined Dataset, Geophytes and Poaceae, the Kamiesberg forms a sub-centre within a larger Namaqualand/Succulent Karoo PC. There is no PC development on the Kamiesberg in Bruniaceae.

In conclusion, although there are definite high altitude floristic links between the Kamiesberg and CFR, the area of concern in the Kamiesberg is very small and the floristic links are very tenuous. The vast majority of the Kamiesberg area has much stronger links to the Succulent Karoo.

#### 2.4.2.1.2.3 The Karoo Cluster

There is a minor Karoo cluster, comprising the East Little Karoo (PC 25) and/or South Groot Karoo (PC 27), that is sister to the combined cCFR and sSK cluster. The small number of taxa, of arguable CFR affinities (Appendix II) contributes to the instability of its formation and placement (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). The absence of adequate data precludes further discussion.

#### 2.4.2.2 The Summer Rainfall OGUs

The Summer Rainfall Cluster comprises the major remaining cluster and forms a neat sister cluster to the Winter Rainfall cluster (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). However, this is somewhat artificial and simplistic, due to the lack of data for the summer rainfall region in my analysis. Data for these eastern summer rainfall areas are not equally represented in the different datasets, making regional taxonomic comparisons unreasonable.

Four major floristic areas of significance to Cape clades are identified here. I refer to the area immediately east of the core CFR as the Eastern Cape Flora Archipelagos (eArchipelagos) or Albany Centre. There are scattered representatives of Cape Clades here. The current dataset lacks xerophytic and thicket taxa, which characterise large areas of this region. The PCs identified for this area usually cluster together (Figure 23, Figure 24, Figure 25 and Figure 26), except in the Unweighted Hierarchical Analysis (Figure 22).

Further to the northeast are two significant, closely related montane PCs, the Greater Drakensberg PC (13), and the more distant North-eastern Escarpment PC (18). Although these regions share taxa, they have different climatic and geological characteristics. The Drakensberg is more temperate and comprises mostly basalt, while the North-eastern Escarpment PC (18) is more tropical, and the geology is considerably more complex and varied (van Wyk and Smith, 2001). I discuss these two PCs together, due to their close affinities in my study (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26).

The last significant PC in the summer rainfall cluster is the Natal Coast Centre (PC 23). This is a simplistic demarcation, due to the paucity of data gained for this area in my study. My Natal Coast Centre (PC 23) consists almost exclusively of Orchid endemics, although it does contain a single *Erica* endemic. This PC is situated on the lower lying areas east of the Eastern Escarpment. Despite forming an outgroup to the Greater Drakensberg PC (13) and the North-eastern Escarpment PC (18), I treat it separately due to data inadequacies, which may indicate a stronger relationship than is actually the case, due to my dataset biases to montane taxa. In addition, environmental conditions in this lower topographic area are different from the previous two largely montane PCs.

#### 2.4.2.2.1 The Eastern Cape Flora Archipelagos (eArchipelagos) and Albany Centre

East of the core CFR PC, there are scattered, disjunct areas containing elements of Cape Clades. The closest elements form a phytogeographic cluster, here referred to as the Eastern Archipelagos (eArchipelagos), representing the mountains north (PC 26, 29) and east (PC 28) of Grahamstown, and the mountains of the East Suurberg PC (PC 28). These PCs form a cluster in all Hierarchical Analyses (Figure 22, Figure 23, Figure 24 and Figure 25), except the Smoothed Centre Frequency Weighting Analysis (Figure 26), where the East London PC (PC 35) is also included. The three core PCs (26, 28, 29) occur within the geographical area of Weimarck's Zuurberg Sub-Centre. Weimarck noted the impoverished nature of the Cape Flora in this area and that many previous authors (Bolus, 1886, 1905; Marloth, 1908) considered his adjacent more westerly Cockscomb Sub-Centre as the most easterly extent of the purely Cape Flora. This broadly corresponds to the eastern boundaries of my core CFR, which does not extend east beyond the Sundays River. The Sundays River eastern boundary of the CFR is largely congruent to the eastern CFR boundary of Goldblatt and Manning (2000) and the eastern boundary of the core CFR in my study. East of this, CFR elements are restricted to higher altitude sites and analysing the flora as a whole would result in these Cape elements being overwhelmed by thicket and sub-tropical elements; which would probably result in the retrieval of the Albany Phytogeographical area. Conversely, concentrating specifically on Cape Clades would result in these areas being incorporated into the CFR, as in my clade/group datasets.

Further east are two minor PCs with distinctly Cape Clade elements, namely the inland Katberg Centre (PC 32) and the coastal Kiwane Centre (PC 41) (Appendix II). There are other PCs in the area with endemic taxa that may be nested in Cape Clades. However, it would require phylogenies in order to test for monophyly. These include *Borbartia gracilis* (1) in the East London PC (35), *Euryops ciliatus* (2) in the Tarkastad-SADA PC, and *Helichrysum isolepsis* (2) in the Willowvale PC. A more exhaustive study of the flora of this region would likely retrieve additional Cape elements that are not included in my study in this area.

In my study, these eArchipelago PCs (26, 28 and 29,) usually form a larger cluster with other PCs (32, 35 and 41) (Figure 23, Figure 24, Figure 25 and Figure 26), except in the Unweighted Hierarchical Analysis (Figure 22), where it was not retrieved, and they are loosely referred to as the Albany Centre. I employ this name loosely due to its geographic location, rather than its floristic composition. The Zuurberg Sub-Centre of Weimarck appears to overlap with the Albany Centre (van Wyk and Smith, 2001; Croizat, 1965). Part of this dichotomy may be due to the focus on different plant groups or elements, such as CFR elements (Weimarck) and *Euphorbia* (Croizat, 1965).

There are additional endemic CFR elements further east, in the Pondoland Centre (van Wyk and Smith, 2001), which were not included in my study, such as *Raspalia trigyna* in Bruniaceae and *Leucodendron pondoense* in Proteaceae (van Wyk, 1990). These CFR elements may indicate historical relationships between these floristic areas.

#### 2.4.2.2.2 The Eastern Escarpment (eEscarpment)

The Eastern Escarpment of South Africa has long been proposed as a high altitude temperate corridor, along which temperate elements may have migrated (Levyns, 1962, 1964; Linder, 1992, 1994; Galley et al., 2006; Galley and Linder, 2006), and penetrated further north into the East Africa Uplands. Two principal montane PCs were identified in my study: the Greater Drakensberg Centre (PC 13) and the North-eastern Escarpment Centres (PC 18), which cluster together in all four hierarchical analyses (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). Each of these PCs has a few endemic Cape elements (Appendix II). There are a number of peripheral, single QDS centres with single endemics surrounding the more developed PCs in these areas. With additional sampling, these smaller PCs may merge with the larger PCs.

##### 2.4.2.2.2.1 The Greater Drakensberg Centre (PC 13)

The phytogeographical significance of the Drakensberg has long been recognised (Phillips, 1917; Hilliard and Burtt, 1987; van Wyk and Smith, 2001; Carbutt and Edwards, 2002; Carbutt and Edwards, 2006). The Drakensberg is grouped with the Stormsberge in the Greater Drakensberg Centre and contains endemic taxa belonging to Cape Clades (Linder, 2003). Curiously, the Cape Taxa in the Greater Drakensberg Centre have much larger distribution areas than their relatives in the core CFR. Although the diversity of some taxa (for example, *Erica,* Orchidaceae, Poaceae and Rosaceae) is low, the endemism is high, due to the large geographic areas of the PC. The Cape element does not form a dominant component of the endemic flora of the Drakensberg, but the relationships are of phytogeographical and potential historical interest.

The Greater Drakensberg Centre forms part of the Eastern Escarpment Cluster, which in turn is nested in the Summer Rainfall cluster (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26).

##### 2.4.2.3.2.2 The North-eastern Escarpment Centre (PC 18)

The North-eastern Escarpment, situated to the northeast of the Drakensberg, is closely associated floristically and environmentally with the Drakensberg Centre (PC 13). It is further removed from the core CFR than the Drakensberg and contains fewer endemics with CFR affinities (Appendix II). The Pilgrim's Rest Sub-Centre (18.1) near Graskop is the only sub-centre to contain non-orchid endemics, namely *Erica atherstonei* (5) and *Merxmuelleria davyi* (2), which may indicate historical CFR affinities. The North-eastern Escarpment Centre (PC 18), as defined here, is equivalent to the Mpumalanga Highlands Centre that Goldblatt and Manning (1999) noted for *Gladiolus*. It is essentially an amalgamation of floristically closely related areas, which have also been treated as centres in their own right (van Wyk and Smith, 2001). The sub-centres identified here are comparable to the Barberton, Wolkberg and Soutpansberg Centres of van Wyk and Smith (2001). Scattered around the three primary sub-centres, Pilgrim's Rest (PSC 18.1), Barberton (PSC 18.2) and the Wolkberg-Soutpansberg Sub-Centres (PSC 18.3), are a number of isolated QDSs, with a single taxon endemic to them, which show no affiliations to surrounding PCs. These smaller PCs (and PSCs) should in all likelihood be merged into their larger neighbours, which may occur with additional taxon sampling.

As with the Greater Drakensberg Centre, the bias to Cape Clade taxa with potential CFR affinities and the exclusion of floristic elements that are more dominant or characteristic of the region, has hampered the identification of finer phytogeographical boundaries. The identification of PCs in spite of this bias serves to highlight the significance of the area for endemic taxa, as well as potential historical relationships with the core CFR. Interestingly, despite having only half as many endemics as the Drakensberg PC, it occupies just over a quarter of the geographical area, further emphasising the floristic and conservation importance of the North-eastern Escarpment Centre.

#### 2.4.2.2.3 The Natal Coast Centre (PC 23)

The Natal Coast Centre (PC 23) is an elongated PC, situated mostly in the coastal areas, extending from about the Buffalo River in East London in the South, to the South Africa-Mozambique border in the north. It is centred in the Maputo-Tongaland Centre of van Wyk and Smith (2001). It is sister to the Eastern Escarpment PC in all analyses (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), although this is principally due to Orchidaceae. In my study, it contains relatively few Cape Clade taxa. No members of the Disinae are endemic here. *Erica aspalatifolia* (12) is endemic, but is a fairly widespread taxon. The absence of significant numbers of Cape elements is likely due to the greater sub-tropical affinities of the area.

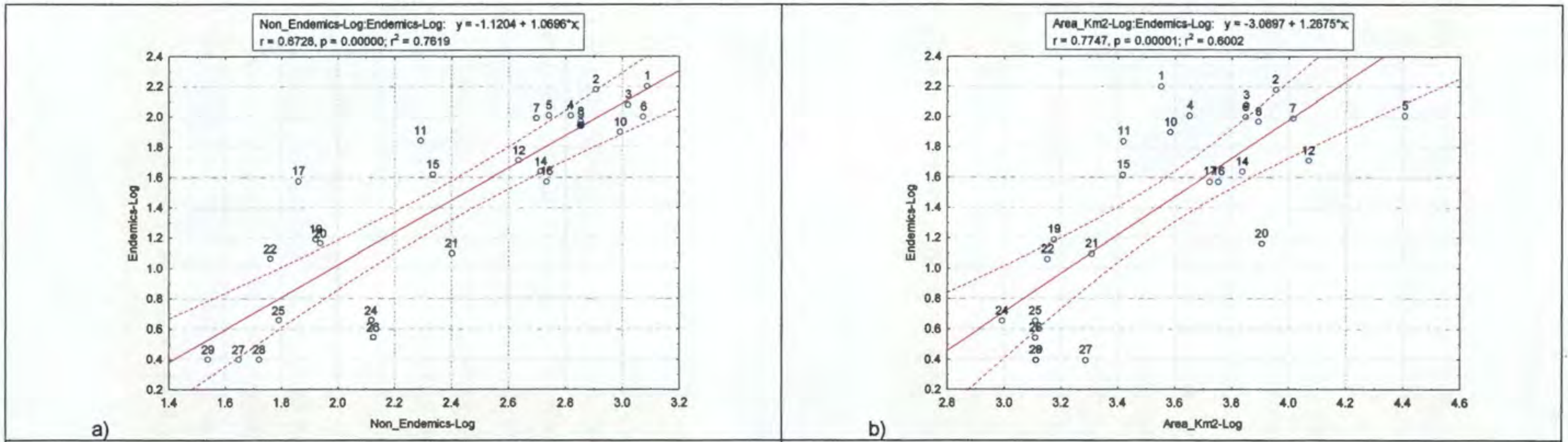
### 2.4.3 The Relationship between Endemism, diversity and PC Area

Here I compare the relationship between endemism, diversity, and PC area in the Combined Dataset PCs, and how they compare to endemism, diversity, and PC area in my clade/guild datasets.

In my Combined Dataset, a highly significant relationship ($r^2 = 0.76$, $P<0.001$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 43a). Furthermore, a significant relationship ($r^2 = 0.60$, $p<0.001$) was also found between the number of endemic taxa and PC area (Figure 43b), and between the numbers of non-endemic taxa and the PC area ($r^2 = 0.45$, $p<0.001$). I removed the larger summer rainfall PCs (13, 18 and 23), due to their undue effects on the area regressions. I also excluded all PCs with a single endemic taxon, essentially leaving me with winter rainfall PCs. Even so, a stronger correlation was obtained with the exclusion of the Cape Peninsula, which constituted an outlier, due to its exceptional numbers of endemic and non-endemic PC taxon numbers in proportion to its small area. I found that the size of a PC gives a good indication of the number of endemics contained therein, as has been observed by other authors (Exell and Gonçalves, 1974; Major, 1988; Anderson, 1994; Harté and Kinzig, 1997). However, from my regression, it is clearly not the only predictor variable, and further analysis would be beneficial (see Chapter 4). Generally, as PC area increases, the number of endemics increase faster than the number of non-endemics.

#### 2.4.3.1 Comparison of Regression Results between Datasets

All the regression analyses yielded statistically significant results, except the Bruniaceae PC area regressions (Table 10). Further, all regression analyses indicated a positive relationship between PC endemic taxa, non-endemic PC taxa, and PC area (Table 10). Generally, there was a strong correlation between PC endemism and PC non-endemic taxa. In Poaceae, the relationship is weak, while in Proteaceae it is very weak. In Proteaceae, the Stellenbosch-Bainskloof centre has low endemism, but high diversity. Similarly, regression of PC endemism against PC area was usually strong, with weak correlations only being recorded for Proteaceae and the RDL Taxa. Proteaceae and the RDL Taxa have very small PCs with many endemics, but large PCs with few endemics, which prevent a consistent trend. The regression of non-endemic taxa was generally weak in most datasets. In some cases this has a biological basis, as many CFR taxa have large numbers of range restricted taxa (Ericaceae, Proteaceae,



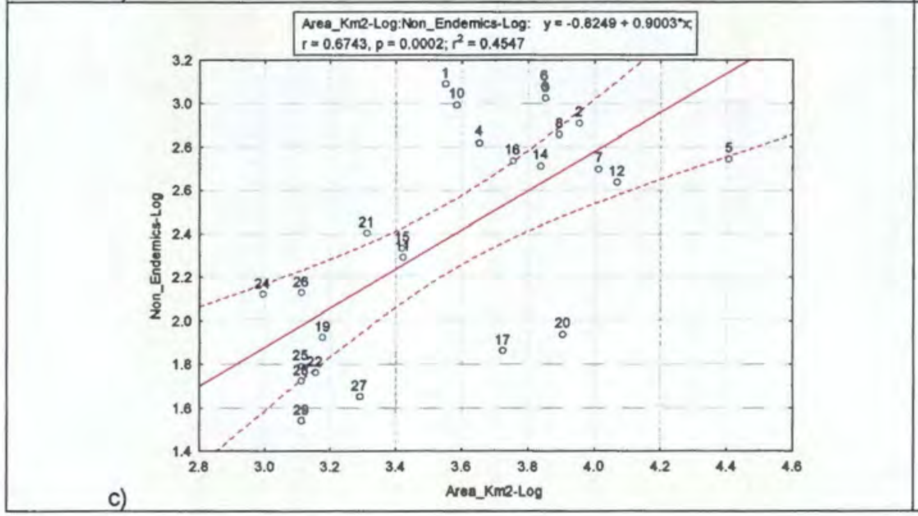


Figure 43a-c: The correlation between Endemism, diversity and area in the Combined Dataset.
The numbers on the graph correspond to the Combined Dataset PC table above (Table 9) and the PC Maps (Figure 18 and Figure 19).

Rutaceae etc.). However, this result also reflects bias in dataset assembly, where range restricted taxa were specifically targeted (Asteraceae, RDL Taxa). Rosaceae's poor performance is perplexing, considering its taxa are relatively widespread in the CFR; thismight indicate under-collection.

Table 10: Summary of the Correlation Coefficients and significance values for the regression analyses conducted on my datasets. $r^2 < 0.5$ and p values > 0.05 emboldened.

| | $r^2$ | | | p | | |
|---|---|---|---|---|---|---|
| | End-Non End | End-PC Area | Non-end-PC Area | End-Non End | End-PC Area | Non-end-PC Area |
| Combined Dataset | 0.76 | 0.60 | **0.45** | 0.001 | 0.001 | 0.001 |
| Asteraceae | 0.80 | 0.67 | **0.49** | 0.001 | 0.001 | 0.001 |
| Bruniaceae | 0.63 | 0.75 | 0.69 | 0.033 | **0.054** | **0.088** |
| Ericaceae | 0.72 | 0.63 | **0.40** | 0.001 | 0.001 | 0.009 |
| Fabaceae | 0.68 | 0.78 | 0.61 | 0.001 | 0.001 | 0.001 |
| Geophytes | 0.74 | 0.71 | 0.77 | 0.001 | 0.001 | 0.001 |
| Orchidaceae | 0.63 | 0.79 | 0.64 | 0.001 | 0.001 | 0.001 |
| Poaceae | **0.49** | 0.68 | 0.56 | 0.005 | 0.005 | 0.005 |
| Polygalaceae | 0.68 | 0.58 | **0.41** | 0.0005 | 0.002 | 0.020 |
| Proteaceae | **0.29** | **0.31** | **0.28** | 0.033 | 0.020 | 0.028 |
| RDL Taxa | 0.86 | **0.39** | **0.20** | 0.001 | 0.001 | 0.001 |
| Restionaceae | 0.61 | 0.82 | 0.78 | 0.001 | 0.001 | 0.001 |
| Rosaceae | 0.51 | 0.66 | **0.38** | 0.014 | 0.0023 | 0.042 |
| Rutaceae | 0.54 | 0.69 | **0.48** | 0.001 | 0.001 | 0.001 |
| Average | 0.64 | 0.65 | 0.51 | 0.0068 | 0.0066 | 0.0143 |

### 2.4.3.2 Phytogeographical aspects of the relationships between Endemic PC taxa, Non-endemic PC taxa, and PC endemism

Generally, in my analysis, CFR PCs, particularly in the extreme Southwest, were over-represented with respect to diversity and endemism, which often, but not always resulted in a steeper gradient. In particular, the Peninsula frequently constituted an outlier, and was often excluded. Occasionally, some of the geographically small southwest PCs had very large numbers of taxa and endemics and constituted extreme outliers, which had a negative effect on the correlation coefficient. Conversely, summer rainfall PCs contained fewer taxa, and occupied larger geographic areas, decreasing the gradient.

Geographic incongruence between the PCs in my different datasets makes exact comparisons difficult, but I will attempt to discuss the general patterns. In the clade or guild datasets, the PCs of the NWPP and SWPP often merge into larger PCs, but this is not always consistent, making comparisons difficult. Conversely, in the Combined Dataset, the eastern PCs (LBPP, KMPP and SEPP) form largely continuous PCs, but they are more fragmented in the clade or guild datasets. PCs in the east with less fynbos taxa are more variable with regards to merging phytogeographical areas. Where merging of phytogeographical areas occurs, PCs are discussed starting in the southwest to northeast, which is usually congruent with the levels of endemism and diversity. Furthermore, comparisons can only be made where PCs are well-defined. I regard PCs of small taxonomic and geographic size (one or two QDSs, or one or two endemic or non-endemic taxa) too marginal to discuss. Datasets favouring range restricted or endemic taxa (Asteraceae, Geophytes and RDL Taxa) will generally have slightly higher ratios of endemic taxa than the more inclusive or monophyletic clade datasets.

#### 2.4.3.2.1 The Western CFR Phytogeographical Centres

##### 2.4.3.2.1.1 SWPP

From all my datasets, I recognise four major PCs (or floristic areas) in the SWPP, the Hottentots Holland-Kleinrivierberge Centre, the Cape Peninsula Centre, the Stellenbosch Mountains/Sandveld Centre (which may be further divided into higher and lower altitude areas), and the Riviersonderend Centre. The SWPP forms a consolidated PC in Orchidaceae, Poaceae and Restionaceae to varying degrees. In my Combined Dataset, and in general, diversity and endemism of the SWPP is centred on Hottentots Holland-Kleinrivierberge, and there is usually very little differentiation into smaller PCs in my clade/guild datasets.

Total numbers of endemic taxa and non-endemic taxa are highest in the Hottentots-Kleinrivier Centre (PC 1) of the Combined Dataset (Figure 43a-c), which is remarkable considering the geographic size of the PC at 8 QDSs (Table 9). Because numbers of both endemic taxa and non-endemic taxa are higher than predicted by PC area (Figure 43b and c), levels of endemic taxa do not exceed that predicted by numbers of non-endemic taxa (Figure 43a). This is very similar to the floristic patterns in the Geophytes, Polygalaceae, RDL Taxa, and Rosaceae datasets. However, in many of my datasets, including Asteraceae, Ericaceae Orchidaceae, Poaceae, and Proteaceae, the SWPP/Hottentots-Holland PC has higher than predicted levels of endemic and non-endemic taxa compared to PC area, and higher than predicted numbers of endemic taxa than predicted by non-endemic PC taxa. In the Restionaceae dataset, endemism is higher than predicted by numbers of non-endemic taxa and PC area. The SWPP performs as predicted in the Bruniaceae dataset. The SWPP does not feature very much in the Rutaceae dataset regression, due to the small and fragmented nature of the SWPP PC in my Rutaceae dataset. As an exception, in Fabaceae, the Hottentots-Holland PC is only overrepresented by non-endemic taxa.

In the Combined Dataset, the Cape Peninsula Centre (PC 9) displays identical patterns to the Hottentots-Holland Centre (PC 1), because both endemic (Figure 43b) and non-endemic taxa (Figure 43c) are much higher than predicted by PC area, but not in relation to each other (Figure 43a). This pattern is repeated in nearly all my datasets where the Peninsula forms an essentially independent PC, including Asteraceae, Ericaceae, Fabaceae, and the RDL Taxa Datasets. In my Proteaceae Dataset, Peninsula PC endemism is further highlighted by also exceeding the value predicted by non-endemic PC taxa. The extremely high endemism and diversity of the Peninsula necessitated to its exclusion from regression in the Combined Dataset, and other analyses, including Ericaceae, Proteaceae, and the RDL Taxa dataset. These exceptional levels of diversity and endemism have been well documented previously (Cowling, MacDonald and Simmons, 1995; Simmons and Cowling, 1996; Trinder-Smith, Cowling, Linder, 1996; Helme and Trinder-Smith, 2006). In the Rosaceae and Rutaceae Datasets, the Peninsula has slightly more non-endemic taxa than predicted by PC area.

In the Stellenbosch Mountains/Sandveld Centre (PC 6) of the Combined Dataset, there is good congruence between the numbers of endemic and non-endemic taxa, although endemism is slightly lower than predicted (Figure 43a), while numbers of non-endemic taxa (Figure 43c) are higher than predicted by PC area. Numbers of PC endemics (Figure 43b) fall close to the 95% confidence line, and are comparatively lower when compared to numbers of non-endemic taxa. This pattern of high diversity but relatively low endemism, is not unusual in my datasets where the Stellenbosch Mountains/Sandveld area form a distinct PC. Fabaceae, Proteaceae, and RDL Taxa Datasets display similar patterns, although in the latter, the mountains and plains are in different PC, but both PCs display similar patterns. This may indicate that the Stellenbosch Mountains/Sandveld Centre is an area of phytogeographical overlap, boosting diversity, but not endemism, or that my phytogeographical boundaries may require further modification to increase endemism.

In my Combined Dataset, the Riviersonderend (RZE) Centre (10) has fewer endemic taxa than predicted by non-endemic taxa (Figure 43a), but higher than expected levels of endemic (Figure 43b) and non-endemic taxa (Figure 43c) relative to PC area, and thus displays similar floristic patterns as the Stellenbosch Mountains/Sandveld Centre (6). It is perhaps significant that both PCs occur on the boundary between the NWPP and SWPP, and may be areas of overlap for floras from these phytogeographical provinces. Similarly, in the Proteaceae Dataset, the RZE contains expected levels of endemic versus non-endemic taxa and PC area, and marginally elevated levels of endemism than predicted by PC area. However, the RZE PC of Proteaceae has the highest numbers non-endemic taxa of all Proteaceae PC (marginally higher than the Hottentots Kleinrivier PC), and far exceeds that predicted by PC area. In most of my other datasets, the RZE PC is not very well-defined, or does not form a distinct independent PC.

#### 2.4.3.2.1.2 NWPP

From my various datasets, I recognise four to sometimes seven PCs in the NWPP, namely the Groot Winterhoek-West Langeberg Centre, the Cedarberg Centre, the Sandveld and Piketberg (occasionally these are further divided into higher and lower altitude areas in my different datasets), and the Gifberg (15) and Nieuwoudtville Escarpment (11), which again may form a single or two separate PCs. Additionally, hierarchical analysis of the Combined Dataset PCs places the Greater Witteberg (PC 12) in the NWPP. However, in many of my individual clade/group datasets, parts of the Witteberg cluster with the KMPP, and are discussed there.

The NWPP forms a more consolidated PC in Asteraceae, Bruniaceae, Ericaceae, Orchidaceae and Polygalaceae, but to varying degrees. In Asteraceae, endemism is higher than predicted by non-endemism, but both fall within levels predicted by PC area. In the Bruniaceae, Ericaceae (with a Witteberg outlier), Orchidaceae and Polygalaceae Datasets, the NWPP falls mostly within expected ranges, except in Orchidaceae (where endemism is slightly lower than predicted by non-endemic taxa) and Polygalaceae (where endemism is slightly higher than predicted by non-endemic taxa).

In the Combined Dataset NWPP, diversity and endemism are highest in the Groot Winterhoek-West Langeberg Centre (PC 3), which is ranked third in endemism and diversity of all PCs in the Combined Dataset of my study (Table 9). Levels of both endemism and diversity are higher than expected from PC area (Figure 43b and Figure 43c respectively), but are in the expected range for each other (Figure 43a). In Rosaceae, the Groot Winterhoek-West Langeberg Centre has more endemics that predicted by non-endemic taxa or PC area, but expected non-endemic taxa predicted by PC area. In Rutaceae, the Groot Winterhoek-Hexrivier-West Langeberg Centre is generally over-represented by non-endemic taxa, with levels of endemism performing poorly, while in Proteaceae, it generally performs as predicted.

In the Cedarberg PC of the Combined Dataset, endemism values are as predicted by non-endemic taxa (Figure 43a) and PC area (Figure 43b), while non-endemic taxa are as predicted by PC area (Figure 43c). In the Geophytes Dataset, the Cedarberg Centre has significantly higher levels of endemic and non-endemic taxa than predicted by PC area, but not relative to each other. Where there is distinct independent PC development in my remaining datasets in the Cedarberg, the datasets usually combine the Cedarberg with surrounding phytogeographical areas, such as the Gifberg and/or Nieuwoudtville, or Groot Winterhoek and/or the Hexrivier Mountains. In Proteaceae and Rutaceae, the Gifberg and Nieuwoudtville combine with the Cedarberg. In Proteaceae, levels of endemism are higher than predicted by either non-endemic taxa or PC area. However in Rutaceae, endemism is only over-represented relative to numbers of non-endemic taxa. Poaceae occupies an intermediate geographic position, as the Cedarberg PC includes the northerly Gifberg and southerly Groot Wintershoek, with numbers of endemic and non-endemic taxa both higher than predicted by PC area, and with endemic taxa marginally higher than predicted by non-endemic taxa. In the Fabaceae, RDL Taxa and Restionaceae (and Witteberg in Restionaceae) Datasets, the Cedarberg extends southwards to incorporate the Groot Winterhoek and Hexrivier areas. In the Restionaceae and RDL Taxa datasets, this area has expected levels of endemic and non-endemic taxa. In Fabaceae, there are more endemic taxa than predicted by either non-endemic taxa, or PC area.

In the Combined Dataset, the NPWC Sandveld and Piketberg form a single distinct independent PC (14). There are marginally fewer endemic taxa than predicted by both non-endemic taxa and by the PC area (Figure 43a and Figure 43b). On the other hand, there are marginally more non-endemic taxa than predicted by PC area (Figure 43c). In the Proteaceae Dataset, the Piketberg-Sandveld PC has less than expected levels of endemism, although non-endemic taxa fall within the expected margin predicted by PC area. In Fabaceae the Piketberg-Sandveld area has expected levels of endemic and non-endemic taxa. In Orchidaceae, the small geographic size of the PC results in a low ratio of endemic taxa, but it has a high number of non-endemic taxa compared to PC area.

In my Combined Dataset, a taxonomically impoverished PC is centred on the Greater Witteberg (PC 12) and extends to the northwest to the Swartruggensberge. Levels of endemic taxa do not deviate from expected (Figure 43a and Figure 43b). However, numbers of PC non-endemic taxa are lower than predicted from PC area (Figure 43c). Independent PC development on the Witteberg occurs in a number of my datasets, although, even in datasets with independent PC development, conflicting affinities to the NWPP or KMPP are apparent (for example, *Erica*). The RDL Taxa Witteberg PC has higher levels of endemic taxa than predicted by non-endemic taxa, although numbers of endemic and non-endemic taxa are lower than predicted by PC area, due to the arid and peripheral position of the PC. In the Poaceae Dataset, the Witteberg combined with the Hexrivierberge to the west, and has higher than expected numbers of non-endemic taxa, with relatively low endemism. In the Geophyte dataset, the Witteberg has higher endemism than predicted by non-endemic numbers, while numbers of endemic and non-endemic taxa are as predicted by PC area. There is poor taxonomic Witteberg PC development in Proteaceae, Erica, and Rosaceae, with the latter two PCs consisting of a single QDS.

In the Combined Dataset and the RDL Taxa Dataset, the Gifberg (15) and Nieuwoudtville Escarpment (11) form distinct independent PCs. In both Combined Dataset PCs (11, 15), endemism is higher than predicted by either non-endemic taxa or PC area (Figure 43a and Figure 43b), while numbers of non-endemic taxa are within predicted limits. In the RDL Taxa Dataset, the Nieuwoudtville Escarpment has more endemic taxa than predicted by non-endemic PC taxa and PC area, but also has more non-endemic PC taxa than predicted by PC area, as it is relatively small. The Gifberg PC is larger in the RDL Taxa Dataset, facilitating relatively high ratio of endemic taxa, but both endemic and non-endemic taxa fall within expected limits predicted by PC area. In Restionaceae, due to the relatively small size of the Gifberg- Nieuwoudtville Escarpment PC, and its peripheral and more arid nature of the PC in the relatively mesic Restionaceae, endemism is lower than predicted by both numbers of non-endemic taxa and PC area. In Fabaceae the Gifberg and Nieuwoudtville Escarpment form a single PC, which has expected levels of endemic and non-endemic taxa.

#### 2.4.3.2.1.3 APPP

The APPP can be generally divided up into three phytogeographical areas, the Western APPP, the Potberg in the central position geographically and the Eastern APPP, with various clustering permutations of these three areas among my different datasets. In the Combined Dataset, the Western APPP merges with the Potberg and has higher numbers of endemic and non-endemic taxa than predicted by PC area (Figure 43b and Figure 43c), while the numbers of endemic and non-endemic taxa correlate well with each other (Figure 43a). In Rutaceae, the Western APPP also merges with the Potberg, with an overrepresentation of endemism, while numbers of non-endemic taxa are as predicted by PC area. The Western APPP also merges with the Potberg in Bruniaceae and Poaceae, although in both, numbers of endemic and non-endemic taxa are nearly as predicted.

In the Asteraceae, Fabaceae and Restionaceae Datasets, the Western, Potberg, and Eastern APPP combined into a single consolidated PC. In Asteraceae and Fabaceae, levels of endemism and non-endemic taxa are nearly as predicted, although there is a slight elevation in endemism, while in Restionaceae, numbers of endemic and non-endemic are as predicted.

The Western APPP forms a distinct independent PC in Ericaceae, Geophytes (marginal), Polygalaceae, Proteaceae and Rosaceae. In Proteaceae and Polygalaceae, levels of endemic and non-endemic taxa as expected. In Ericaceae, PC endemic and non-endemic taxa are higher than predicted but PC area, but not with regards to each other. In all the remainder (Geophytes and Rosaceae), endemism is generally lower than predicted by either non-endemic taxa.

The Potberg forms an independent PC in the Proteaceae, Rosaceae and the Geophyte Datasets. In Proteaceae and Rosaceae, numbers of endemic and non-endemic taxa are as expected, while in geophytes, endemism is less than predicted by numbers of non-endemic taxa, while numbers of non-endemic taxa are higher than predicted by PC area. In the Ericaceae and Rosaceae datasets, the Potberg merges with the Eastern APPP, and in both datasets, levels of endemic and non-endemic taxa are generally as expected, although in *Erica*, numbers of endemic taxa are lower than predicted by non-endemic taxa.

The Eastern APPP forms an independent PC in the Combined Dataset, Polygalaceae and Rutaceae Datasets. Levels of endemism are poor in the Combined Dataset and Polygalaceae, but as predicted by non-endemic taxa in Rutaceae (Figure 43a and Figure 43b for the Combined Dataset), while levels of non-endemic taxa are more or less as predicted by PC area (Figure 43c for the Combined Dataset).

### 2.4.3.2.2 The Eastern CFR Phytogeographical Provinces

In some of my datasets, the eastern phytogeographical provinces (LB, KM, and SE) merge into larger phytogeographical units. This occurs either because there are relatively fewer range restricted taxa than widespread taxa in these areas, particularly in montane fynbos datasets (Bruniaceae and Orchidaceae), or because datasets contain taxa in many different habitats which link QDSs together (RDL Taxa). Taxa may be under-collected, and PCs maybe be disjunct and fragmented, leading to PCs with artificially low geographical areas. Endemicity and diversity of montane fynbos clades are lower in the eastern CFR, but families like Orchidaceae, which have summer rainfall clades are reasonably well represented, although orchid endemicity in the eastern CFR is still lower than in the western CFR.

In Bruniaceae, the KMPP and SEPP merge into a single PC, which has less than predicted numbers of endemic taxa in relation to non-endemic taxa and PC area, but non-endemic taxa are as predicted by PC area. In the Geophytes Dataset, the KMPP, eastern LBPP and western to central SEPP cluster into a single PC. This PC has higher levels of endemicity in relation to numbers of non-endemic taxa, but numbers of endemic taxa are as predicted by PC area, while non-endemic taxa are less than predicted by PC area. In the Orchidaceae Dataset, the KPMC, LBPP, and SEPP merge into a single PC, with predicted numbers of endemic and non-endemic PC taxa.

#### 2.4.3.2.2.1 LBPP

As generally occurs in eastern phytogeographical provinces in the CFR of my Combined Dataset, the Langeberg forms a single consolidated PC. In the clade or guild datasets, the LBPP frequently merges with the more easterly phytogeographical provinces, such as the KMPP and SEPP, as in Bruniaceae, Orchidaceae and Poaceae. In the Combined Dataset, the Greater Langeberg PC (2) has the second highest levels of endemism (Figure 43a and Figure 43b), but only has the fifth highest level of diversity, representing a very high ratio of endemic taxa (16 %) (Table 9), in the Combined Dataset (Figure 43a and Figure 43b). In the Asteraceae, Rutaceae and the RDL Taxa Datasets, endemism is higher than predicted by either non-endemic taxa, or PC area, although only marginally so in the RDL Taxa Dataset. In most of the remaining datasets, including Bruniaceae, Fabaceae, Geophytes (including part of the Witteberg), Proteaceae, Restionaceae and Rosaceae, the Langeberg has expected levels of endemic and non-endemic taxa. In Ericaceae, the Langeberg has higher than expected non-endemic taxa than predicted by area, while endemism does not deviate from predicted values. LBPP PC development in Poaceae is poor, the mountains having expected levels of diversity and endemism, while the plains have high levels of non-endemic taxa. Although LBPP PC development in Polygalaceae is better than in the Poaceae

Dataset, there are still expected levels of endemism, while numbers of non-endemic taxa are slightly higher than predicted by PC area.

### 2.4.3.2.2.2 KMPP

From my various datasets, I recognise four significant phytogeographical areas in the KMPP. These include the Klein Swartberg, Groot Swartberg, the Rooiberg and the Kammanassie Mountains. However, there are very little consistent phytogeographical groupings of phytogeographical areas in the KMPP between datasets, largely due to a paucity of CFR taxa in the region. For this reason, my KMPP discussion vacillates between phytogeographical areas and clade/guild datasets rather than focussing on phytogeographical areas exclusively

In the Combined Dataset, the KMPP comprises a single phytogeographical centre. The Karoo Mountain Centre (PC 7) consists of the Klein and Groot Swartberg, Rooiberg and the Kammanassie Mountains. In the KMPP, fynbos is generally restricted to high altitude archipelagos, with lower diversity and abundance of fynbos taxa, relative to the western CFR. The result is that clustering combinations between these archipelagos vary between my datasets. This makes exact comparisons difficult. In the Combined Dataset, the Karoo Mountain Centre (PC 7) contains more endemic taxa than predicted by non-endemic taxa (Figure 43a), although endemic and non-endemic taxa fall within the expected range considering the area of the PC (Figure 43b and Figure 43c respectively).

The Fabaceae and Polygalaceae KMPP PC consolidate a number of KMPP mountain ranges, including the Witteberg, Rooiberg, Klein and Groot Swartberg, but not the Kammanassie Mountains. Both Fabaceae and Polygalaceae have more endemic taxa than expected from non-endemic taxa. PC area is generally a good predictor of endemic and non-endemic taxon numbers for both Fabaceae and Polygalaceae in the KMPP. The Rosaceae Dataset combined the Klein and Groot Swartberg and Kammanassieberg (but not the Rooiberg or the Witteberg), and has higher levels of endemism than predicted by non-endemic taxa, while again, PC area is a good predictor of the numbers of endemic and non-endemic taxa.

The Ericaceae and Proteaceae Datasets combine the Klein Swartberg, Groot Swartberg and Rooiberg into a single PC, which have expected levels of endemic and non-endemic taxa. The Rutaceae Dataset combined the Witteberg, and Klein and Groot Swartberg into a single PC, while PC development is progressively poorer in the Restionaceae and Poaceae Datasets, and is restricted to the Swartberg. In Rutaceae, endemic and non-endemic taxa are as expected, except where endemic taxa are less than predicted by PC area. In the Restionaceae and Poaceae Datasets, the small size of KMPP PC results in a lower than predicted ratio of endemic taxa, with a marginal overrepresentation of non-endemic taxa.

In the Asteraceae and the RDL Taxa Datasets, the Klein and Groot Swartberg are placed in different PCs. In Asteraceae, the Klein Swartberg is combined with the Greater Witteberg, and endemic taxa are slightly higher than predicted by non-endemic taxa, while PC area is a good predictor of both endemic and non-endemic taxon number. The Asteraceae Groot Swartberg PC contains expected levels of endemic and non-endemic taxa. In the RDL Taxa Dataset, the Witteberg and Klein Swartberg-Rooiberg form distinct independent PCs, while the Groot Swartberg-Kammanassieberg combines with the western SEPP. The RDL Taxa Klein Swartberg-Rooiberg PC has predicted numbers of endemic and non-endemic taxa. The RDL Taxa Groot Swartberg-Kammanassieberg-W SEPP PC has higher levels of endemic taxa than predicted by non-endemic taxa due to its large PC area; however, the numbers of endemic and non-endemic taxa are lower than predicted by the PC area.

The Restionaceae Dataset has two small PCs on the Kammanassieberg, with nearly predicted levels of endemic and non-endemic taxa. In the Ericaceae Dataset, the Kammanassie Mountains merge with the Kouga Mountains, with predicted numbers of endemic and non-endemic taxa.

#### 2.4.3.2.2.3 SEPP

Three major phytogeographical areas may be identified from all my datasets in the SEPP, the Western, Central (Tsitsikamma) and Eastern (Cockscomb) SEPP PCs. However, in the Combined Dataset the eastern two PCs merge into a single PC (Figure 18: PC 5 of the Combined Dataset). Geographically, I define the Far Eastern SEPP as that area east of the Sundays River.

As in the KMPP, fynbos (especially the endemic component) is generally restricted to higher altitude archipelagos in the SEPP, but overall there is lower diversity and abundance of fynbos taxa here. This makes the clustering less robust, and combinations between these archipelagos vary between my datasets, thus making exact comparisons difficult. As there are very few consistent phytogeographical groupings of areas in the SEPP, between datasets, my discussion vacillates between phytogeographical areas and clade/guild datasets, rather than on phytogeographical areas exclusively. The most common clustering of PCs includes: the Western SEPP with parts of the LBPP, or the Western and Central SEPP, or the Central and Eastern SEPP.

##### 2.4.3.2.2.3.1 The Western SEPP

In the Combined Dataset, Rutaceae and Polygalaceae Datasets, the Western SEPP forms a distinct and independent PC. Endemism is generally under-represented in the Combined Dataset (PC 16) (Figure 43a and Figure 43b), and more so in the Polygalaceae and Rutaceae Datasets. In the Asteraceae, Ericaceae, Fabaceae and Restionaceae Datasets, the Western SEPP is combined with the Central SEPP. In the Asteraceae and Ericaceae Datasets, endemic and non-endemic taxa are nearly as predicted, expect in the Asteraceae Dataset where endemic taxa are higher than predicted by non-endemic taxa. In the Fabaceae Dataset, endemic and non-endemic taxa are lower than PC area would predict, but correlate well with each other. In the Restionaceae Dataset, levels of endemism are lower than predicted.

In the Proteaceae dataset, the Western SEPP combines with parts of the LBPP, with expected levels of endemic and non-endemic taxa. In the RDL Taxa Dataset, the Western SEPP forms a PC with the eastern KMPP, and has higher levels of endemic taxa than predicted by non-endemic taxa due to its large PC area, although numbers of endemic and non-endemic taxa are lower than predicted by PC area.

###### 2.4.3.2.2.3.2 Central SEPP

The Central SEPP has quite poorly developed PCs in most datasets. It is best developed as an independent PC in the RDL Taxa Dataset, where endemic and non-endemic taxa are fewer than predicted by area. In Polygalaceae and Rutaceae, PC development is very poor, but is distinct and independent of surrounding phytogeographical areas. In Polygalaceae endemism in general is underrepresented, while in Rutaceae, the ratio of endemic to non-endemic taxa is low.

In the Combined Dataset, Proteaceae and Rosaceae Datasets, the Central SEPP is combined with the Eastern SEPP. In the Combined Dataset (Figure 43b) and Proteaceae Datasets, there are higher levels of endemic taxa than predicted by non-endemic taxa, but in the Combined Dataset the numbers of endemic and non-endemic taxa are lower than predicted by PC area. Conversely, in Rosaceae, numbers of endemic taxa are less than predicted by either non-endemic taxa or PC area.

###### 2.4.3.2.2.3.3 Eastern SEPP

Many of my datasets show some PC development in the Eastern SEPP, although fynbos clades generally taper off in diversity and endemism by this longitude. In the Combined Dataset, this area is merged with the central SEPP (discussed in Section 2.4.3.2.2.3.2). The Asteraceae, Fabaceae and Rutaceae Datasets show distinct independent PC development in the Eastern SEPP, albeit relatively limited. While Fabaceae shows expected levels of diversity and endemism, endemism is generally lower than predicted in Asteraceae and Rutaceae. Furthermore, two of the three Rutaceae PCs here have lower than predicted non-endemic taxa. Although this floristic pattern in Diosmeae is real, sample bias in Fabaceae (*Aspalathus*) and Asteraceae (endemic CFR genera) is the predominant cause for the underrepresentation of these groups in this area.

###### 2.4.3.2.2.3.4 Far Eastern SEPP

Where there is PC development east of the Sundays River in the Far Eastern SEPP, it is usually very fragmented and often restricted to PCs with few, or a single endemic taxon, as in the Combined Dataset, Asteraceae, Ericaceae, Fabaceae, Poaceae, Polygalaceae, the RDL Taxa and Rutaceae Datasets. Usually there are expected levels of endemism as predicted by non-endemic taxa. However, where PC are large (Asteraceae, Fabaceae, Polygalaceae, RDL Taxa and Rutaceae Datasets), numbers of endemic and non-endemic PC taxa are usually less than predicted by PC area.

#### 2.4.3.2.3 Non-Core CFR PCs

As the Cape Flora (Linder, 2003) is represented outside of the core CFR, and some of my natural datasets included taxa distant from the CFR, I was able to retrieve non-CFR PCs. Typically, better represented PCs occurred on mountains in the arid region to the north of the CFR (Namaqualand/Succulent Karoo), and on the Great Escarpment, including the Drakensberg and North-eastern Escarpment. Cape taxa outside the CFR generally occupy larger ranges, and are by definition, less abundant, especially when compared to PCs in the core CFR. This often results in PC outliers that skew the regression graphs using PC area. Where these points had an undue influence on the regression, or caused insignificant correlations, they were excluded. PCs excluded from regression analysis are listed in Table 11.

Table 11: PCs excluded from regression analyses to obtain a significant correlation.

| Dataset | Excluded PC |
|---|---|
| Combined Dataset | Peninsula, Drakensberg, Northeastern Escarpment, Natal Coast, all PC with only a single endemic taxon |
| Asteraceae | - |
| Bruniaceae | - |
| Ericaceae | Peninsula, Eastern Escarpment |
| Fabaceae | Saldanha Peninsula |
| Geophytes | Natal Midlands, East London, Northern Namaqualand lowlands |
| Orchidaceae | - |
| Poaceae | Western North Transvaal |
| Polygalaceae | - |
| Proteaceae | Peninsula, for Kamiesberg End:Non-End only |
| RDL Taxa | Peninsula, Zuurberg |
| Restionaceae | Drakensberg |
| Rosaceae | Eastern Escarpment, Arid Interior, South-eastern Mountains |
| Rutaceae | Kamiesberg |

Orchidaceae is an exception, as my dataset included all orchid taxa in Southern Africa. As Orchidaceae includes summer rainfall tropical clades, summer rainfall PCs were well represented, and did not have unduly lower than expected numbers of endemic or non-endemic taxa, as did some of the other datasets I analysed, and thus were not excluded (Table 11).

In the Combined Dataset, peripheral winter rainfall PCs, including the Vanrhynsdorp PC (17) and the Kamiesberg PC (19), have higher than predicted numbers of endemic taxa than predicted by non-endemic taxa (Figure 43a), substantially higher in the Vanrhynsdorp PC; however, numbers of endemic taxa are as predicted by PC area (Figure 43b). The

Vanrhynsdorp PC (17) has substantially lower non-endemic than predicted by PC area (Figure 43c) indicating data collection bias to range restricted RDL Taxa.

Surprisingly for an arid area, the Northern Namaqualand PC of Orchidaceae has expected levels of endemism and diversity; while in Poaceae, the Namaqualand and Southern Namibia PC have expected levels of endemism, but numbers of non-endemic taxa are lower than predicted by PC area.

#### 2.4.3.2.4 Summary

Most of my datasets that represent montane fynbos clades display Levyns' (1964) characteristic pattern of having their highest levels of endemism and diversity in the southwest of the CFR, with numbers gradually tapering off to the north and east. My Geophytes Dataset does not follow Levyns' (1964) pattern, having high numbers of taxa on the Nieuwoudtville Escarpment. Similarly, the RDL Taxa Dataset also does not follow Levyns' (1964) pattern either, as it comprises relatively high numbers of non-fynbos taxa, for example, succulents and geophytes; however, I have demonstrated that fynbos taxa within the RDL Taxa do indeed follow Levyns' (1964) classic pattern (Chapter 14, Section 14.1.4). Nevertheless, I found that both my Fabaceae and Rutaceae datasets, containing two substantial fynbos clades (*Aspalathus* and Diosmeae respectively), have higher diversity and endemism in the NWPP rather than the SWPP, and do not strictly follow Levyns' (1964) pattern.

My fynbos clade datasets generally have higher levels of endemism in the Hottentots-Kleinrivier Mountains and Peninsula than predicted by both non-endemic taxa and PC size, while non-endemic taxa are well correlated with PC area. The Peninsula frequently had much higher levels of endemic and non-endemic taxa than predicted by PC area, and often constituted an extreme outlier. In these cases, it was necessary to exclude the Peninsula (Table 11), as it is probable that factors other than area are strongly involved in facilitating the extraordinary endemism and diversity observed on the Peninsula. In the Stellenbosch Mountains/Sandveld, and where I retrieved a distinct RZE PC, endemism is generally higher than predicted by PC area, but as predicted by the numbers of non-endemic taxa. This may indicate overlap form neighbouring phytogeographical provinces (NWPP, APPP). This is particularly apparent in the Stellenbosch Mountains/Sandveld PC, which frequently had high diversity, but low endemism (Combined Dataset, Fabaceae, and Proteaceae).

Where the NWPP consolidates into a single PC, I mostly found higher than predicted levels of endemism (Asteraceae, Erica, Fabaceae and Proteaceae), or predicted numbers of endemics (Orchidaceae; Polygalaceae and Restionaceae). Where the Groot Winterhoek forms a distinct PC, the numbers of endemic and non-endemic taxa are as expected in Proteaceae, while in the geographically smaller Rutaceae Groot Winterhoek PC, non-endemic taxa are higher than predicted. Because the Groot Winterhoek PC is enlarged in the Combined Dataset to include the Hexrivier West Langeberg Mountains, endemic and non-endemic taxa are higher than predicted by PC area.

The Cedarberg mostly had either higher than predicted levels of endemism, in my Combined Dataset and RDL Taxa Dataset, or slightly higher numbers of endemic and non-endemic taxa than predicted by PC area in Geophytes and Poaceae. Endemism is either as predicted, or less than predicted in the Sandveld and Piketberg PC. The Rutaceae dataset merged the Cedarberg and Piketberg/Sandveld areas into a single PC, which had higher than predicted levels of endemism. Where a Gifberg-Nieuwoudtville Escarpment PC is retrieved, endemism is usually under-represented for fynbos datasets, but higher than predicted in the Combined Dataset and RDL Taxa Datasets, which contain a higher proportion of succulents and geophytes. In my Geophyte Dataset, NWPP (Southern Namaqualand PC) endemism is much higher than predicted by either non-endemic taxa or PC area.

The APPP and LBPP PCs mostly have predicted, or less than predicted, levels of endemism, except in the Rutaceae Dataset and Combined Datasets where endemism is higher than predicted.

In the KMPP PC, endemism is mostly as expected in relation to PC area, but higher than predicted by non-endemic taxa especially in geographically larger PCs, as larger PCs are more inclusive of taxon ranges; otherwise levels of endemism are as expected.

The SEPP PCs generally have predicted to less than predicted numbers of endemic and non-endemic taxa, although there is the occasional exception, such as RDL Taxa, which includes the highest proportions of range restricted non-fynbos taxa of my datasets.

Due to the relatively large geographic size and low taxonomic diversity of summer rainfall PCs, numbers of endemics correlate well with numbers of non-endemic taxa. However, the large geographic size of PCs resulted in numbers of endemic and non-endemic taxa usually being less than predicted by PC area. This is often to the extent that these data points have to be excluded from my regression analyses (Table 11).

Where diversity and endemism deviate from values predicted by PC area, alternative explanations need to be invoked, such as more favourable contemporary environmental conditions (investigated in Chapter 4), or historical processes like speciation, persistence, and extinction.

Table 12: Habitat Data for the Combined Dataset for PCs that have Habitat Data.

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Conglomerate | Loam | Limestone/Calcareous | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliffs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats | Other | Unknown |
| 1 | Hottentots-Kleinrivier | 22 | 8 | 26 | 19 | 13 | 3 | 1 | | 45 | 4 | 2 | 1 | | 1 | 2 | | 1 | 96 | 4 | 1 | 17 | 43 | 7 | 2 | 34 | 9 | 6 | 1 | | | | | 3 | | |
| 2 | Greater Langeberg | 12 | 8 | 21 | 12 | 12 | 9 | 2 | | 42 | 4 | 8 | 1 | | 3 | | 1 | 7 | 87 | 3 | 2 | 2 | 11 | 1 | 4 | 32 | 3 | 10 | 7 | 1 | 2 | 4 | | | | |
| 3 | Groot Winterhoek-West Langeberg | | | | 9 | 11 | 16 | 9 | | 33 | 5 | 4 | 1 | | | | | 7 | 56 | 10 | | 11 | 6 | 6 | 1 | 28 | 7 | 20 | 6 | | | | | | | |
| 4 | Agulhas Plains | 7 | | | 7 | | | | | 11 | 1 | 1 | | 1 | 1 | 36 | 2 | 2 | 8 | 2 | 20 | 23 | 4 | | | 10 | 16 | 7 | 4 | | | | | 25 | | |
| 5 | Southeastern Centre | 8 | 4 | 9 | 7 | 5 | 4 | | | 16 | | | | 1 | | 3 | | 3 | 36 | 5 | 3 | 8 | 1 | 3 | 6 | 22 | 4 | 8 | 1 | 1 | 6 | 4 | | 5 | | |
| 6 | Stellenbosch-Bainskloof Mtns & Sandveld | 8 | 6 | 10 | 7 | 6 | 5 | 2 | | 13 | 1 | 2 | 10 | | | | 1 | 3 | 33 | 5 | 10 | 28 | 11 | 2 | | 30 | 26 | 3 | 5 | 1 | | | | 4 | 1 | |
| *6.1* | *Stellenbosch-Bainskloof Mtns* | *3* | *4* | *9* | *1* | *2* | *2* | *1* | | *8* | | *1* | *3* | | | | | *2* | *21* | *3* | *5* | *1* | *6* | *2* | | *13* | *3* | | | *1* | | | | | | |
| *6.2* | *Sandveld* | *1* | | | *4* | | | | | | | *1* | *3* | | | | | | *1* | | *5* | *11* | | | | *5* | *12* | *2* | *4* | | | | | *2* | | |
| 7 | Karoo Mtn Centre | 3 | 3 | 28 | 1 | 6 | 11 | 8 | 2 | 31 | 3 | | | | | | 1 | 6 | 51 | 2 | 3 | 2 | 6 | 1 | 5 | 30 | 2 | 8 | 2 | | | | | | | |
| 8 | Cedarberg | 3 | 1 | 17 | 2 | 7 | 10 | 3 | | 38 | 4 | | | | 1 | | | 7 | 49 | 5 | | 2 | 2 | 3 | 6 | 28 | 5 | 7 | 1 | | 1 | | | | | |
| 9 | Peninsula | | | | 11 | 8 | 2 | | | 24 | | 3 | 1 | | | 1 | | 3 | 42 | 9 | 1 | 11 | 16 | 2 | 2 | 27 | 7 | 3 | | 1 | | | | 2 | | |
| 10 | RZE | 7 | 5 | 13 | 4 | 8 | 7 | 1 | | 29 | 1 | 4 | | | | | 1 | 1 | 53 | 7 | 1 | 3 | 7 | 2 | 2 | 15 | 5 | 2 | 4 | | 1 | | | | | |
| 11 | Nieuwoudtville Plateau | 1 | | | | 6 | 1 | | | 12 | | 11 | | | | | 1 | 3 | 7 | 2 | | 6 | 2 | 1 | | 10 | 5 | 7 | 6 | | 1 | | | | | |
| 12 | Greater Witteberg | | | 1 | | 1 | 2 | 1 | 1 | 11 | | | | | | | 2 | 1 | 14 | 1 | | | | | 3 | 5 | 2 | 2 | | | 2 | | | | | |
| 13 | Drakensberg | | | | | | 4 | 8 | 12 | 2 | | | | | | | 2 | 3 | 3 | 6 | | | 6 | | 1 | 6 | | | | 2 | | 11 | | | | |
| 14 | Piketberg-Swartberg-Sandveld | 3 | | 2 | 3 | 3 | 1 | | | 14 | | 2 | | | | | 1 | | 24 | | | 4 | | | 1 | 11 | 5 | 6 | 1 | 1 | 1 | | | | 1 | |
| 15 | Gifberg | 1 | | | 1 | 4 | | | | 13 | | 1 | | | | | | | 18 | | | 4 | 2 | 1 | 1 | 14 | 3 | 1 | | | 2 | | | | | |
| 16 | West Southeastern Centre | 3 | 5 | 5 | 2 | 4 | | | | 8 | | | | | | | | | 16 | 2 | | 2 | 6 | | 1 | 1 | 7 | 2 | | 1 | | | | | | |
| 17 | Vanrhynsdorp | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 18 | Northeastern Escarpment | | | 1 | | | 4 | 1 | 2 | | | | | | | | | | 2 | 4 | 1 | 1 | 2 | | 2 | 7 | | | | | | 6 | 1 | | | |
| 19 | Kamiesberg | | | 1 | 1 | | | | | | | | 1 | | | | | | | | | | 1 | | | | | 1 | 1 | | | | | | | |
| 20 | Saldanha Peninsula | | | | 1 | | | | | | | 1 | 7 | | | 4 | 1 | | 2 | 4 | 2 | 1 | | | | 6 | 3 | | | | | | | 2 | | |
| 21 | East Agulhas Plain | 1 | | | 1 | | | | | 1 | | | | | | 7 | | 1 | | 1 | 4 | 1 | | | | 1 | 2 | 1 | | | | | | 2 | | |
| 22 | West Coast | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | 3 | | | | | | | 3 | | |
| 23 | Natal Coast | | | | 4 | 4 | 2 | 1 | | | | | | | | | | 1 | | 1 | 1 | | 4 | | | 1 | 1 | | | 2 | | 2 | | 2 | | |
| 24 | Far East Agulhas Plain | | | | | | | | | | | | | | | | | | | | | 1 | | | | 1 | 1 | | 2 | | | 1 | 1 | 1 | | |
| 25 | East Little Karoo | | | | | | | | | | | | | 1 | | | | | 1 | | 1 | | | | | 1 | 1 | | | | 1 | | | | | |
| 26 | South Grahamstown | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 27 | South Groot Karoo | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 28 | East Suurberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 29 | North Grahamstown | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 30 | Transkei | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 31 | Bitterfontein-Garies | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 32 | Katberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 33 | West Transvaal | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 34 | North Natal2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 35 | East London | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 36 | Buffelsbank-Komaggas | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 37 | East Soutpansberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| 38 | N Barberton | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | |
| 39 | Tarkastad-SADA | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 40 | Willowvale | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 41 | Kiwane | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 42 | NE Wolkeberg | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | | | | | | |
| 43 | South Namibia | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 44 | Garies-Kotzesrus | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 45 | McDougall's Bay | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 46 | Swartkop | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 47 | Moedverloorberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 48 | South Drakensberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 49 | Brandvlei | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 50 | Windhoek | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 51 | Koingnaas | | | | | | | | | | | | | | | | | | | | | | 1 | | | | 1 | | | | | | | | | |
| 52 | Lebombo | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 53 | Joubertsberge | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 54 | Mbazwana | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| 55 | SE Barberton | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 56 | N Botswana-Okavango | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 57 | East Tanzania | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 58 | West Tanzania | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Totals | 83 | 44 | 143 | 97 | 100 | 83 | 38 | 17 | 351 | 23 | 41 | 28 | 3 | 6 | 53 | 13 | 51 | 621 | 77 | 60 | 139 | 137 | 32 | 37 | 342 | 133 | 96 | 45 | 13 | 17 | 32 | 2 | 51 | 3 | 0 |

### 2.4.4 Habitat Table Comparisons

#### 2.4.4.1 General

What is immediately apparent when inspecting the habitat tables of the Combined Dataset (Table 12) and the Individual Datasets, is that endemic taxa are not restricted to one particular habitat type. Even though habitat data for taxa are not treated equally in the literature, allowing only a cursory investigation, it is fairly obvious that the most frequently occurring environmental variables of PC endemic taxa are a stony/rocky sandstone substrate and sloping ground, between altitudes of 0 - 1500 metres. These variables are all closely related and likely to be largely spatially congruent. Most of the CFR mountains are sandstone, with sloping ground between 0-1500 metres, which is usually rocky. Cowling and Proches (2005) reported that 70% of taxa occur in mountain fynbos, so the expectation would be that similarly high ratios of endemics would occur in these habitats, as this is where most of the CFR taxa occur. As I have stated already, I could not conduct rigorous statistical analyses of the endemic versus non-endemic taxa, due to their unequal treatment in the literature. Thus, I repeat Linder's (2005) call for systematic documentation of the ecology of Cape plants.

#### 2.4.4.2 Altitude

I make use of qualitative (low, medium, and high) and quantitative (500 metre intervals) altitude categories, as both are utilised by Goldblatt and Manning (2000). Qualitative data is generally more subjective and relative, being dependent on geographic area. Most clade researchers in Goldblatt and Manning (2000) make use of quantitative altitude data. The one significant exception to the use of quantitative data for altitude is Ericaceae (Oliver and Oliver, 2000), which contributes a disproportionately large number of records in the qualitative altitude category.

Inspection of quantitative altitude categories (Table 12) reveal that the numbers of Geophyte and RDL Taxa endemics drop off rapidly above 1000 metres and are very poorly represented above 1500 metres. Fabaceae has many endemic taxa below 1000 metres, while the majority of Restionaceae endemics occur between 500 and 2000 metres. Orchidaceae endemics occur at comparatively high altitude, usually starting at 1000 metres, and often exceeding 2000 metres, due to high numbers of endemics on the Eastern and Northeastern Escarpment (Table 45).

#### 2.4.4.3 Rock type

As sandstone is the most frequent (almost regarded as a default) rock type in the CFR, many authors in Goldblatt and Manning (2000) do not always state categorically whether a taxon occurs on sandstone, but rather seem only to specify a rock type if it is not sandstone, hence the high frequency of poorly recorded data (Strikethrough text in Table 12) in Bruniaceae, Fabaceae, Orchidaceae and Restionaceae, indicating a lack of data records. Asteraceae, Polygalaceae and Proteaceae have comparatively high numbers of their PC endemics on sandstone. Ericaceae, Poaceae and Rutaceae have relatively few clay endemics, while Asteraceae, Ericaceae and Restionaceae have comparatively few granite endemics. Conversely, the Geophyte Dataset has very high numbers of both clay and granite endemics. Although numbers of Ericaceae endemics on sandstone could not be assessed, the very low numbers on other substrates indicate that Ericaceae endemics have a high preference for sandstone substrates.

Table 13: Comparison of Habitat frequencies between the different Datasets I analysed.
Figures in bold are higher than the average, while those in italics in a grey cell are much less than the average.
Figures that have strike through formatting represent Dataset categories with insufficient data.

| | | Combined Data | Asteraceae | Bruniaceae | Ericaceae | Fabaceae | Geophytes | Orchidaceae | Poaceae | Polygalaceae | Proteaceae | RDL Taxa | Restionaceae | Rosaceae | Rutaceae | Category % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Altitude | Low | 2.7 | | | **11.3** | 3.6 | 1.2 | 0.3 | **5.3** | 2.1 | 0.5 | 2.9 | 0.8 | **7.0** | 1.7 | 3.1 |
| | Middle | 1.5 | | | **7.6** | | 0.2 | | | | | 1.2 | 0.3 | 1.0 | 2.2 | 1.6 |
| | High | 4.8 | | | **14.5** | 0.8 | 0.7 | 1.0 | **9.2** | 0.7 | 3.6 | 3.5 | 3.0 | **15.0** | **7.6** | 4.7 |
| Altitude | 0-500 | 3.3 | 2.4 | | | **19.1** | 3.2 | 2.3 | | | | 2.6 | 3.8 | | | 3.0 |
| | 500-1000 | 3.4 | 2.1 | | | **18.9** | 2.4 | 4.0 | | | | 2.7 | **5.7** | | | 3.1 |
| | 1000-1500 | 2.7 | **3.4** | | | **7.8** | 1.4 | **7.0** | | | 1.3 | 1.5 | **9.7** | | 0.2 | 2.6 |
| | 1500-2000 | 1.3 | 1.9 | | | 2.8 | *0.4* | **6.3** | | | 1.3 | *0.3* | **4.6** | | | 1.2 |
| | >2000 | 0.6 | 0.2 | | | | | **7.0** | | | | 0.7 | 0.8 | | | 0.5 |
| Rock Type | Sandstone | 11.6 | **21.5** | ~~3.6~~ | | ~~1.3~~ | 13.3 | ~~6.6~~ | 11.5 | **21.1** | **21.5** | 13.5 | ~~1.3~~ | 15.0 | 16.5 | 11.8 |
| | Shale | 0.8 | 1.1 | | | 0.5 | 0.4 | 0.3 | 1.5 | | 2.5 | 1.0 | 1.8 | | 2.2 | 0.8 |
| | Clay | 1.4 | 1.0 | | *0.1* | | **8.5** | 1.3 | *0.8* | 1.5 | 1.3 | 2.6 | | | *0.5* | 1.6 |
| | Granite | 0.9 | *0.3* | | *0.1* | | **2.8** | 0.7 | 0.8 | 0.7 | 1.5 | 1.3 | *0.3* | | 0.5 | 0.9 |
| | Conglomerate | 1.0 | 2.4 | 1.8 | 0.6 | 1.6 | 1.2 | | 2.3 | 2.8 | 0.5 | 2.4 | 1.9 | 1.0 | 5.6 | 1.2 |
| | Loam | 0.2 | | | | | 0.2 | | | | | 0.1 | 0.3 | | | 0.1 |
| | Limestone/Calcareous | **1.8** | | | | | 0.4 | | | | 1.3 | 0.3 | | | | 0.7 |
| | Other | 0.4 | | | 0.1 | | 0.2 | | **3.5** | | 0.5 | 0.7 | 0.5 | | 1.2 | 0.4 |
| Topography | Summits/Ridges/Plateaus | 1.7 | 2.4 | ~~1.0~~ | **8.9** | ~~0.5~~ | | **3.6** | **3.5** | | **5.6** | 1.4 | 1.6 | 1.0 | 1.7 | 2.3 |
| | Slopes | 20.6 | 26.2 | 22.5 | 23.5 | ~~4.1~~ | 15.4 | *9.6* | 19.8 | **34.0** | 26.2 | *2.6* | 17.3 | **37.0** | 23.2 | 20.4 |
| | Outcrops/Clifs/Crevices | 2.6 | 0.9 | **12.6** | 2.3 | ~~0.3~~ | 3.2 | 4.3 | 4.6 | | 1.3 | 2.3 | 1.9 | 1.0 | 2.2 | 2.4 |
| | Hills | 2.0 | 1.8 | | **3.6** | 0.3 | 1.4 | *0.7* | | **4.9** | *0.5* | 1.6 | *0.8* | 1.0 | **2.7** | 1.8 |
| | Flats | 4.7 | 3.7 | ~~1.8~~ | 4.3 | ~~1.3~~ | **7.7** | *2.6* | 3.8 | 4.2 | **7.7** | 4.4 | 2.7 | 3.0 | 3.4 | 4.3 |
| Habitat | Moist Habitats | 4.6 | 3.0 | **7.3** | 5.6 | ~~0.5~~ | 4.8 | **9.9** | 4.6 | *0.7* | 5.1 | 3.5 | *1.5* | 4.0 | 4.8 | 4.6 |
| | Riverine | 1.6 | 1.1 | 1.8 | *0.5* | 0.5 | 1.1 | 1.7 | **2.3** | | 1.3 | 1.2 | **2.2** | **2.0** | 0.7 | 1.0 |
| | Dry | 1.2 | *0.6* | | *0.6* | | 2.2 | 3.6 | **7.6** | **3.5** | **3.6** | 1.4 | **3.2** | | 1.9 | 1.5 |
| | Stony/Rocky/Gravelly | 11.3 | 9.3 | **17.1** | 7.8 | ~~0.3~~ | 11.1 | 6.3 | 8.4 | **23.2** | 6.2 | 12.7 | 9.2 | ~~1.0~~ | 8.7 | 10.3 |
| | Sandy | 4.4 | *1.6* | | 5.2 | ~~0.5~~ | 4.8 | *2.0* | 4.6 | *0.7* | **7.2** | 4.4 | 3.8 | | **6.5** | 4.0 |
| Vegetation | Fynbos | 3.2 | 1.0 | | ~~0.1~~ | 2.2 | 3.2 | ~~0.7~~ | ~~0.8~~ | | | 3.5 | | | ~~0.2~~ | 3.0 |
| | Renosterveld | 1.5 | *0.2* | | | **7.2** | **5.6** | 1.0 | | | | 2.6 | | | ~~0.2~~ | 1.6 |
| | Forest | 0.4 | | | | **2.6** | 0.2 | **3.0** | | | 0.5 | 0.2 | 0.3 | 1.0 | | 0.5 |
| | Karooid | 0.6 | *0.2* | | | **4.7** | 1.1 | | | | | **1.5** | | | | 0.7 |
| | Grassy Vegetation | 1.6 | *0.3* | | | *0.5* | *0.4* | **11.6** | **3.5** | | | *0.3* | *0.3* | | *0.5* | 1.0 |
| | Bushveld | **0.7** | | | | **0.5** | | 0.3 | | | | 0.1 | | | 0.2 | 0.1 |
| | Coastal Habitats | 1.7 | 2.1 | | *0.9* | *0.3* | 2.2 | 2.6 | **3.5** | *0.7* | 1.3 | 2.4 | **3.5** | 1.0 | **4.8** | 1.9 |
| | Other | 1.0 | 0.3 | 1.0 | | 0.3 | | 0.7 | | | | | | | | 0.1 |
| | Unknown | | ~~9.9~~ | ~~2.7~~ | ~~4.4~~ | ~~0.5~~ | | | | | | | | | | 1.2 |
| Dataset Totals | | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100.0 |

## 2.4.4.4 Topography/Terrain

Differentiation of topography into summits/ridges/plateaus, slopes, and outcrops/cliffs/crevices, may have been a little ambitious, as not all sources describe such level of detail, for example, in Polygalaceae, Bruniaceae and Fabaceae (Goldblatt and Manning, 2000). Although Orchidaceae is well represented by many widespread taxa on slopes, hills and flats, not many are range-restricted endemics, accounting for the poor representation of Orchidaceae in these environments (Table 12). However, Orchidaceae is relatively well represented by endemics on summits/ridges/plateaus (Table 12). RDL Taxa are also relatively poorly represented on slopes. Proteaceae and Restionaceae also have few endemics on hills, which are mostly shale in the CFR. Conversely, Ericaceae, Polygalaceae and Rutaceae have many endemics on hills. Taxa that have large numbers of endemics on summits/ridges/plateaus include Ericaceae, Proteaceae, Orchidaceae and Poaceae, while Bruniaceae has a high number of taxa on outcrops/cliffs/crevices. While it is expected that Geophytes would have many endemics on the flats, it is surprising that Proteaceae, typically considered as a montane fynbos clade, has such a high number of endemics on flats (Table 12).

#### 2.4.4.5 Habitats

Both Bruniaceae and Orchidaceae have a strong representation of endemics in moist habitats, while Polygalaceae and Restionaceae are under-represented in moist habitats, but have many endemics in arid habitats. However, Restionaceae is also over-represented in Riverine Habitats. Ericaceae has few endemics in Riverine or Dry habitats, as most Ericaceae endemics prefer higher altitude habitats which receive higher levels of moisture, but which may be too high for distinct riverine channel development. Asteraceae has relatively few endemics recorded from arid habitats. This is surprising as Asteraceae is usually one of the better-represented families in arid areas. However, my Asteraceae Dataset is biased towards CFR endemics. Furthermore, asterid taxa in arid environments may not be as range-restricted as their fynbos counterparts, particularly those asterid taxa that overlap from the more arid Karoo into the CFR. Polygalaceae, Asteraceae and Orchidaceae have relatively few endemics in sand habitats, while Proteaceae and Rutaceae have high numbers of endemic taxa in sandy habitats.

#### 2.4.4.6 Vegetation

As nearly 70% of CFR taxa occur in fynbos (Cowling and Proches, 2005), it is often treated as the default vegetation type in Goldblatt and Manning (2000), thus vegetation types are more frequently mentioned if taxa are not in fynbos. This results in an under-representation of endemics in fynbos in my tables (inadequate data is represented by strikethrough text in Table 12, for example, Ericaceae, Orchidaceae, Poaceae and Rutaceae).

I record few Asteraceae endemics in the Renosterveld. This is somewhat surprising as Goldblatt and Manning (2000) note that microphyllous Asteraceae are common in this vegetation type. However, the bias of my Asteraceae dataset to CFR endemic genera may at least partially explain this. Conversely, Fabaceae and Geophytes have high numbers of endemics in the Renosterveld vegetation category. This should be investigated further phytogeographically.

Forest taxon diversity is fairly poor in the CFR, with forest endemism being even poorer. Aside from the Knysna Interval (Weimarck, 1941), forest habitats are largely restricted to disjunct populations in ravines and moister south facing slopes on mountains. The relatively high numbers of Orchidaceae endemics in Forest habitats are due to epiphytic orchids in the Orchidaceae Dataset Natal Coast PCs (Table 45). However, the slightly elevated numbers of Fabaceae endemics in Forest habitats are not as easily explained.

Numbers of endemic taxa in Karoo vegetation are generally quite low in my analysis, due to data bias focusing on fynbos taxa (see Combined Dataset). My Asteraceae Dataset has particularly few endemics in Karoo type vegetation, while my RDL Taxa Dataset and especially my Fabaceae Dataset, have a relatively high proportion of endemics in Karoo vegetation. The RDL Taxa Dataset has high numbers of geophytes and succulents, accounting for its high representation in the Karoo vegetation category. The high representation of Fabaceae in Karoo may be due to its tolerance, or preference (of certain of the Fabaceae taxa) for the nutrient richer shale derived soils that support Renosterveld and Karoo vegetation types.

Most of my datasets contain very few endemic taxa in grassy vegetation, for example, Asteraceae, Fabaceae, Geophytes, RDL Taxa, Restionaceae and the Rutaceae Datasets. However, Orchidaceae has many endemic taxa in grassy vegetation, predominantly due to Orchid PC development on the Eastern (Drakensberg) and North-eastern Escarpment. Poaceae itself displays a propensity towards endemism in grassy vegetation.

Coastal vegetation types have relatively low proportions of Ericaceae, Fabaceae and Polygalaceae endemics, but contain high proportions of Rutaceae, Restionaceae and Poaceae endemics.

Table 14: Summary of PC identified in this Study.

Centres in the literature refer to the phytogeographical divisions of Goldblatt and Manning (2000), unless followed by a *, which indicates phytogeographical divisions of Weimarck. nSK-Other Total and Summer-Other-Total are the combined totals for the minor PC in those areas, which only have a single endemic.

| Hierarchical OGU | PC | Centres in the Literature | Ericaceae | Asteraceae | Rutaceae | Iridaceae | Fabaceae | Proteaceae | Restionaceae | Orchidaceae | Aizoaceae | Poaceae | Rhamnaceae | Polygalaceae | Rosaceae | Amaryllidaceae | Asphodelaceae | Campanulaceae | Hyacinthaceae | Scrophulariaceae | Apocynaceae | Bruniaceae | Oxalidaceae | Crassulaceae | Euphorbiaceae | Eriospermaceae | Lobeliaceae | Geraniaceae | Brassicaceae | Penaeceae | Cyperaceae | Malvaceae | Boraginaceae | Colchicaceae | Gymnosperms | Sterculiaceae | Thymelaeaceae | Apiaceae | Hypoxidaceae | Penaeaceae | Rubiaceae | Santalaceae | Anthericaceae | Araceae | Droseraceae | Geissolomataceae | Grammitidaceae | Liliaceae | Plumbaginaceae | Sapindaceae | Tecophilaeaceae | Zygophyllaceae | Grand Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SWPP-Total | | | 112 | 69 | 22 | 30 | 16 | 45 | 32 | 8 | 11 | 2 | 9 | 12 | 11 | 2 | | 7 | 5 | 4 | 2 | 9 | 3 | 1 | | | 1 | 1 | 4 | 5 | 2 | | 2 | | | 1 | 1 | | | 1 | | 2 | | | 1 | | 1 | | | | | | 434 |
| SWPP | Hottentots-Kleinrivier (1) | SWPP | 56 | 23 | 8 | 4 | 4 | 23 | 14 | 4 | 1 | 1 | 2 | 7 | 3 | 1 | | 1 | 1 | | | 4 | | 1 | | | 1 | | | 4 | | | 2 | | | | | | | | | 1 | | | | | 1 | | | | | | 167 |
| SWPP | Stellenbosch-Bainskloof Mtns and Sandveld (6) | SWPP | 12 | 17 | 8 | 13 | 5 | 7 | 6 | 2 | 5 | | 2 | | 7 | 1 | | | 2 | 4 | | 2 | 3 | | | | | | 1 | | | | | | | | | | | 1 | | 1 | | | 1 | | | | | | | | 100 |
| SWPP | Peninsula (9) | SWPP | 25 | 10 | | 7 | 3 | 10 | 7 | 2 | 3 | 1 | 1 | 5 | 1 | | | 4 | 1 | | 2 | 1 | | | | | | | 2 | | 2 | | | | | 1 | | | | | | | | | | | | | | | | | 88 |
| SWPP | RZE (10) | SWPP | 19 | 19 | 6 | 6 | 4 | 5 | 5 | | 2 | | 4 | | | | | 2 | 1 | | | 2 | | | | | | 1 | 1 | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | 79 |
| NWPP-Total | | | 33 | 45 | 36 | 35 | 40 | 12 | 2 | 11 | 13 | 6 | 12 | 2 | 3 | 8 | 5 | 4 | 5 | 5 | 5 | 3 | 0 | 5 | 5 | 1 | 2 | 4 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 314 |
| NWPP | Groot Winterhoek-West Langeberg (3) | NWPP | 23 | 15 | 9 | 10 | 22 | 6 | 6 | | 5 | 4 | 3 | 2 | 2 | 1 | 1 | | 1 | | 1 | 5 | 2 | 1 | | | 1 | 1 | 1 | | | | | | | | | | | 1 | | | | | | | | | | | | | 123 |
| NWPP | Cedarberg (8) | NWPP | 7 | 14 | 20 | 12 | 8 | 4 | 2 | 1 | | 1 | 8 | | | 2 | 1 | 3 | 2 | | | | 1 | 2 | 1 | | 1 | | 1 | | | | | 1 | | | | | 1 | | | | 1 | | | | | | | | | | 94 |
| NWPP | Piketberg-Swartberg-Sandveld (14) | NWPP | 2 | 7 | 4 | 7 | 6 | 1 | | 1 | 3 | 1 | | | | | | 5 | 1 | 2 | 1 | | | | | | | | | | | | | | | 2 | | | | | | | | | | | | | | | | | 43 |
| NWPP | Greater Witteberg (12) | NW*/KM | 1 | 9 | 3 | 6 | 4 | 1 | 3 | | 5 | | 1 | | 1 | 3 | 2 | | 1 | 3 | 3 | | | 2 | | 1 | | 1 | | | | 1 | | | | | | | | | 1 | | | | | | | | | | | | 52 |
| LBPP | Greater Langeberg (2) | LBPP | 24 | 23 | 18 | 9 | 13 | 9 | 13 | 6 | 6 | 2 | 2 | 2 | 3 | 1 | 2 | 1 | 2 | 1 | 1 | 4 | 1 | 1 | | | 3 | | | 2 | 1 | 1 | 1 | 1 | | | | | | | | | | | | 1 | | | | | | | 154 |
| KMPP | Karoo Mtn Centre (7) | KMPP | 17 | 18 | 4 | 9 | 10 | 7 | 7 | | 2 | 1 | 2 | 4 | 6 | | 1 | | | 2 | 3 | | 1 | 1 | | 2 | | | 1 | | | 1 | | | | | | | | | | | | | | | | | | | | | 99 |
| SEPP-Total | | | 23 | 17 | 14 | 4 | 11 | 11 | 2 | 4 | 5 | 3 | | 1 | 1 | 4 | 8 | 1 | | 1 | 6 | | 2 | 2 | 7 | 2 | 3 | 1 | | | 1 | 1 | | | 3 | | 1 | | | | | | | | | | | | | 1 | | | 140 |
| SEPP | Southeastern Centre (5) | SEPP | 14 | 16 | 9 | 4 | 9 | 4 | 1 | 1 | 5 | 1 | | 1 | 1 | 4 | 8 | | | | 6 | | 1 | 1 | 7 | 2 | 1 | 1 | | | | | | | 3 | | 1 | | | | | | | | | | | | | 1 | | | 102 |
| SEPP | West Southeastern Centre (16) | SEPP | 9 | 1 | 5 | | 2 | 7 | 1 | 3 | | 2 | | | | | | 1 | | 1 | | | 1 | 1 | | | 2 | | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | 38 |
| APPP-Total | | | 21 | 14 | 30 | 2 | 9 | 7 | 5 | | 3 | | 6 | 5 | 3 | 1 | 2 | 4 | 2 | | 1 | 1 | | | 2 | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | 119 |
| APPP | Agulhas Plains (4) | APPP | 21 | 9 | 26 | 2 | 7 | 7 | 5 | | 3 | | 5 | 5 | 3 | 1 | | 4 | 2 | | 1 | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | 103 |
| APPP | East Agulhas Plain (21) | APPP | | 5 | 3 | | 2 | | | | | | 1 | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 12 |
| APPP | Far East Agulhas Plain (24) | APPP | | | 1 | | | | | | | | | | | | 2 | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 4 |
| sSK-Total | | | 1 | 20 | 1 | 27 | 8 | 4 | | 1 | 9 | 1 | 1 | 1 | | 10 | 9 | 2 | 5 | 6 | 1 | 1 | 9 | 4 | 4 | 9 | 1 | 3 | | | | | | 1 | | | 1 | 2 | | | | | | 1 | | | | 1 | 1 | | 1 | 1 | 147 |
| sSK | Vanrhynsdorp (17) | | | 6 | | 4 | | | | | 7 | | | | | 2 | 4 | | 2 | | | | 1 | 2 | 1 | 5 | | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | | 1 | 37 |
| sSK/nNWPP | Nieuwoudtville Plateau (11) | NWPP | | 9 | | 18 | 6 | 2 | | 1 | 2 | 1 | 1 | | | 4 | 3 | | 3 | 4 | | 1 | 3 | 2 | 2 | 2 | | | | | | | | | | | 1 | 1 | | | | | | 1 | | | | 1 | | | 1 | | 69 |
| sSK/nNWPP | Gifberg (15) | NWPP | 1 | 5 | 1 | 5 | 2 | 2 | | | | | | 1 | | 4 | 2 | 2 | | 2 | 1 | | 5 | | 1 | 2 | 1 | 2 | | | | | | 1 | | | | 1 | | | | | | | | | | | | | | | 41 |
| nSK/nNWPP | Kamiesberg (19) | NWPP* | 1 | 4 | 1 | | 1 | 2 | 1 | 1 | | 2 | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 15 |
| eArchipelagos-Total | | | 1 | 2 | 1 | | 1 | | | | | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 7 |
| eArchipelagos | South Grahamstown (26) | SEPP* | 1 | 1 | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| eArchipelagos | East Suurberg (28) | SEPP* | | | | | | | | | | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 |
| eArchipelagos | North Grahamstown (29) | SEPP** | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 |
| wCoast-Total | | | | 3 | | 8 | 2 | | | | | | 1 | | | | | 3 | 2 | 1 | 1 | | 1 | 1 | | | | 1 | | | | | | | | | | | 1 | | | | | | | | | | | | | | 25 |
| wCoast | Saldanha Peninsula (20) | SWPP | | 1 | | 7 | 1 | | | | | | 1 | | | | | | 2 | | | | 1 | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | 14 |
| wCoast | West Coast (22) | NWPP | | 2 | | 1 | 1 | | | | | | | | | | | 3 | | 1 | 1 | | | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 11 |
| Karoo-Total | | | | | | 1 | | | | | | | | | | | | | 2 | 1 | | | | | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 6 |
| Karoo | East Little Karoo (25) | KMPP | | | | | | | | | | | | | | | | | 2 | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 4 |
| Karoo | South Groot Karoo (27) | KMPP | | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 |
| eEscarpment-Total | | | 20 | 1 | | | | | 1 | 32 | | 13 | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 68 |
| eEscarpment | Greater Drakensberg (13) | Drakensberg | 16 | 1 | | | | | 1 | 19 | | 11 | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 49 |
| eEscarpment | Northeastern Escarpment (18) | | 4 | | | | | | | 13 | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 19 |
| Maputa-Pondo | Natal Coast (23) | | 1 | | | | | | | 10 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 11 |
| nSK-Total | | | | 4 | | 1 | | | | | | 2 | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 8 |
| Summer-Total | | | 1 | 3 | 1 | 1 | 2 | | 1 | 8 | | 3 | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 21 |
| Totals | | | 255 | 223 | 128 | 126 | 113 | 97 | 73 | 72 | 49 | 36 | 33 | 28 | 28 | 27 | 26 | 26 | 21 | 20 | 20 | 20 | 20 | 16 | 14 | 14 | 10 | 8 | 7 | 7 | 4 | 4 | 3 | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1560 |

## 2.5 SUMMARY OF PHYTOGEOGRAPHICAL PATTERNS

Relatively large numbers of QDSs were assigned to PCs, thus indicating that endemism is common throughout the CFR. However, endemism is concentrated in the west, particularly the southwest and is congruent with high levels of winter rainfall. Hierarchical analysis of the Combined Dataset revealed similar patterns to the two most significant and comprehensive previous phytogeographical studies by Goldblatt and Manning, (2000) and Weimarck (1941). PCs were found to cluster in the six traditional phytogeographical provinces (phytogeographical centres, sensu Goldblatt and Manning, 2000), the SWPP, NWPP, LBPP, APPP, KMPP and SEPP. Generally, within these phytogeographical provinces, PCs are strongly associated with particular TMS mountain ranges, indicating the importance of substrate and topography within the CFR for PC formation, and the numeric dominance of montane 'fynbos' taxa. However, there was also PC development on the lower lying areas neighbouring the mountains, notably the APPP and the Swartland and Rûens areas. It was found that although there is noticeable congruence between many of my different phylogenetic datasets, and to previously described floristic patterns (Goldblatt and Manning, 2000; Weimarck, 1941), there are also notable differences. Floristic patterns are determined by the dominance of particular floristic/biotic elements within each dataset.

Evidence of a SWPP is recovered in most datasets and its northern boundary is generally congruent with the Berg-Bree River systems. In montane TMS CFR clades, it typically contains the highest levels of endemism and diversity phytogeographical provinces in the CFR. Diversity and endemism are sometimes as much as double the next richest phytogeographical province (which is usually the NWPP), as in Bruniaceae, *Erica*, Orchidaceae, Polygalaceae, Proteaceae and Restionaceae. In Asteraceae, Poaceae and Rosaceae, the SWPP and NWPP contain nearly equal numbers of endemic taxa, although the SWPP usually contains slightly more, but this is not very significant. Floristic patterns in Rosaceae are ambiguous, as one of its major PCs straddles the NWPP and SWPP.

Another significant and unexpected result is that the Saldanha PC (PC 20) forms a nested cluster with the West Coast PC (PC 23), which clusters outside the core CFR and has closer affinities to the Southern Succulent Karoo cluster (Figure 22, Figure 24, Figure 25 and Figure 26), rather than the SWPP in my Hierarchical Analysis of PCs. This needs to be investigated further. The Saldanha Peninsula is most strongly developed in the Geophytes Dataset.

Geographically, the NWPP is defined by the Berg River system to the south and its termination to the north and east seems to coincide with the 200-250mm rainfall isohyte. The boundary between the NWPP and KMPP is less distinct, with the Swartruggens, Bontberg and Witteberg areas showing dual affinities to the NWPP and KMPP. In the Fabaceae, Geophytes, the RDL Taxa and Rutaceae Datasets, the NWPP contained more endemic taxa than the SWPP. In the Rutaceae Dataset, this is nearly double.

The core of the KMPP is situated on the Swartberg Range. In the Combined Dataset the Western KMPP (Witteberg to Swartruggens) has affinities to the NWPP, although lower lying areas might have greater affinities to the KMPP. This is an area of contention, and may be why Weimarck (1941) and Goldblatt and Manning (2000) treated them differently. The clade/group subset datasets usually include the Swartruggens as part of the NWPP and the Witteberg in the KMPP.

This study has identified the presence of distinct phytogeographical units on the Agulhas Plains, although the hierarchical placement of some of the areas is still contentious. Reasons for this conflict may be why Weimarck (1941) and Goldblatt and Manning (2000) treated them differently. Apart from having affinities to each other, the Western Agulhas Plains show strong affinities to the SWPP, while the more easterly Agulhas PCs show affinities to the LBPP-KMPP. The APPP is particularly well developed in Rutaceae.

LBPP forms a distinct PP, comprising a single PC in the Combined Dataset, but is not independent in all the clade/group datasets, often combining with the SEPP, as in Bruniaceae and Orchidaceae.

In many of the subset datasets analysed here, the Southeast Centre (Goldblatt and Manning, 2000; Weimarck, 1941) is poorly developed. Generally CFR clades decrease in diversity and levels of endemism as one proceeds further east, correlating with the decreasing winter rainfall and increasing summer rainfall regimes. In Bruniaceae, Geophytes and Orchidaceae, the SEPP, LBPP and KMPP form a single phytogeographical unit, to varying degrees. My Hierarchical Analysis of PCs also supports this, showing the following relationship: ((SEPP, LBPP), KMPP). As with other winter arid phytogeographical provinces analysed here, PC development is best in montane areas, with major river systems congruent with floristic boundaries.

Areas to the north of the CFR, in the winter rainfall region, in Namaqualand/Succulent Karoo (Kamiesberg), and areas to the east, in the summer rainfall parts of Southern Africa (Drakensberg, Barberton, Pilgrims Rest, Wolkberg) showed some PC development for Cape Clades. The PCs of Cape Clades (Linder, 2003) in the Drakensberg usually occupy a much larger geographic area when compared to Cape Clade PCs in the CFR and winter rainfall areas (Kamiesberg). Here there are very few narrow endemics (relative to Cape endemic range sizes in the CFR) and they have a lower diversity than CFR PCs, but have relatively high Cape Clade endemism, due to the larger geographic area of these PCs.

## 2.6 CONCLUSIONS

1. There is relatively good congruence between this study and previous studies, indicating a robust common pattern. Datasets showed robustness to different weightings and different analyses, indicating real patterns, not merely statistical artefacts.
2. There is relatively good congruence between the phytogeographical patterns of this study and previous studies, indicating robust common phytogeographical patterns. Further, there is fairly good congruence between the different Cape (especially fynbos) taxonomic groups analysed within this study, indicating repeated patterns and possibly shared histories. Congruence is not exact and differences are due to different edaphic and topographic preferences of biotic elements.
3. Endemism is widespread in the CFR, but is concentrated in definite areas and habitats. The greatest number of endemics and taxa occur in the western winter rainfall CFR, which usually has the greatest phytogeographical development. Endemism and richness is concentrated on sandstone slopes, supported by analysis of habitat preferences of endemic fynbos taxa, and an investigation into the environmental correlates of richness. Differences in the frequencies of richness of the individual datasets in different phytogeographical areas may be explained by different ratios of biotic elements. Further, different biotic elements have different barriers to gene flow.
4. Numbers of taxa endemic to phytogeographical centres are strongly correlated with both the taxon richness and geographic size of the phytogeographical centres.
5. Outliers of Cape Clades are represented outside the core CFR area and are endemic to higher altitude mesic sites in the succulent Karoo, or high altitude cool sites in the summer rainfall areas. However, the patterns identified here do not necessarily coincide with contemporary floristic patterns of the succulent Karoo or Drakensberg floras, which are under-represented in this analysis, but possibly only to the montane TMS fynbos flora, which are the most representative in this dataset.
6. Analysing individual clades prevents a more numerous clade for example, *Erica*, from dominating others (clade bias), and obscuring the smaller clades' unique floristic patterns, where these patterns are different from numerically dominant clades.
7. Although there is not exact congruence between any dataset, certain datasets can be grouped together, based on their levels of congruence. Bruniaceae, *Erica,* Proteaceae (Proteeae) and Restionaceae seem to have high levels of congruence. They display the greatest affinities to montane Mediterranean environments on TMS and are essentially restricted to the CFR. Ericaceae (*Erica*) shows similarities, but possibly to a lesser extent. Orchidaceae (Diseeae), Poaceae (Danthonieae) and possibly Rosaceae (*Cliffortia*), also show a higher preference for cooler montane environments, but are less restricted to the CFR, being fairly well represented on the Eastern and Northeastern Escarpment as well. Fabaceae (*Aspalathus*), Geophytes and

Rutaceae (Diosmeae) are unusual in that the NWPP contains the greatest numbers of endemic taxa. There is also evidence that these three datasets have significant lower altitude PC formation, which may be related to a lower moisture regime adaptation, or adaptation to non-TMS substrates. Low altitude PC formation is also significant in Asteraceae, Polygalaceae (*Muraltia*) and the RDL Taxa.

8. Phytogeographical boundaries depend on the environmental preferences of the taxa analysed. For example, different biotic elements have different barriers to gene flow. The valley created by the Gouritsrivier would likely pose a significant barrier to montane taxa; while the abrupt habitat change caused by the near closed canopy continuous forest (Weimarck's Knysna Interval) would be a significant barrier to the dispersal of lower altitude taxa. Thus the relative dominance of biotic elements needs to be taken into account during analysis and interpretation of phytogeographical patterns.

Potential Areas of Further Research

1. Datasets that deviate from fynbos datasets, such as Geophytes, and even Fabaceae and Rutaceae, should be investigated further floristically, at a finer geographic scale. Additional investigation of Geophyte phytogeographical patterns with a more complete dataset would prove most interesting.
2. Clades of the Succulent Karoo Flora should be critically analysed to show centres of succulent endemism. This would also make the analysis more representative in the different geographical areas and shed more information on the Greater Cape Floristic Region.

# 2.5. GLOSSARY AND ABBREVIATIONS

**APPP** Agulhas Plains Phytogeographical Province is a new floristic area designated by Goldblatt and Manning (2000), and is geographically congruent with the Bredasdorp Sub-Centre of Weimarck (1941). It is situated on the lower altitude coastal belt around Cape Agulhas, and it the most southerly floristic unit in Africa

**Bell** Bell Weighting was previously proposed (Linder, 2001) as a weighting technique for characters (taxa) in the identification of PCs

**Cape Clade** a concept defined by numerous authors using different terminology (also Cape element), referring to taxa that have their centres of diversity, or centres of endemism within the CFR. Often these taxa are not restricted to the CFR, and have PCs along the eastern escarpment (especially in the Drakensberg) in South Africa. Cape clades/elements also occur in the east African highlands, and in Europe. There is a gradual tapering off in diversity and abundance to the east and north.

**Cape Element** see Cape Clade

**CFR** Cape Floristic Region, a higher level botanical area defined by the distribution and endemism (floristics) of characteristic taxa. The CFR is closely congruent with the fynbos biome.

**PC** Phytogeographical Centre; in this study, PC denotes a smaller floristic unit nested within a phytogeographical province (PP), defined by endemic taxa. Although hierarchical, PCs – like traditional taxonomic levels (genera and families) – may not necessarily be equivalent or comparable

**Fynbos** Literally "fine bush", one of the two major vegetation components of the fynbos biome, consists mostly of microphyllous or sclerophyllous leaved taxa, usually on nutrient poor coarse grained TMS soils in montane environments

**Fynbos Biome** The fynbos biome is a vegetation unit consisting of two sub-ordinate vegetation types, fynbos and Renosterveld. The fynbos biome is closely congruent with the Cape Floristic Region

**GIS** Geographic Information Systems are computer based software used for exploration, display, and analysis of spatial data

**Int** Integration Weighting was used to weight characters (taxa) used in identifying PCs

**KMPP** Karoo Mountain Phytogeographical Province is slightly more complex to define at a finer geographical scale. Situated to the north of the Langeberg and up to the Klein and Groot Swartberg Mountain Ranges, east of the NWPP, and west of the SEPP (though the boundaries between the latter two PPs are variable between different taxa). Most Cape Clade elements are restricted to the more mesic higher lying areas.

**LBPP** Langeberg Phytogeographical Province occurs on the Langeberg Mountains (which consist of a prominent east-west watershed), and associated lowland areas to the south (generally situated between the Bree and Gouritz Rivers).

**MInt** Modified Integration Weighting is an adaptation of the Integration Weighting Technique used in the weighting of characters (taxa) for the identification of PCs

**NWPP** Northwest Phytogeographical Province is the northern extension of the CFR (north of the SWPP), largely restricted to the winter rainfall area, though more arid than the SWPP, becoming more arid along a northerly gradient. The northern boundary is relatively sharply defined, though there are outliers, notably at high altitude in the Kamiesberg.

**OGU** Operational Geographic Unit, equivalent to and used interchangeably with floristic unit, a non-hierarchical area defined by the endemic taxa it contains

**PAE** Parsimony Analysis of Endemism is an established clustering technique used in identifying areas of endemism (Rosen, 1988; Morrone, 1994; Morrone, 1995)

**PP** Phytogeographical Province, in this study refers to the hierarchical sub-division below the Region but above my PC level, which have been designated phytogeographical centres by previous authors (Weimarck, 1941; Goldblatt and Manning, 2000). There are generally six such PPs in the CFR, the SWPP, NWPP, APPP, LBPP, KMPP, and the SEPP

**Renosterveld** One of the two major vegetation components of the fynbos biome, containing mostly sclerophyllous taxa on higher nutrient fine grained shale derived soils at lower altitude

**SAHN** Sequential Agglomerative Hierarchal Nesting is a clustering algorithm used to cluster entities based on a similarity value

**PSC** Phytogeographical Sub-Centre; PSCs are small floristic units nested within PCs

**SEPP** Southeast Phytogeographical Province represents the eastern most continuous PP of the CFR, though Cape elements extend beyond its eastern boundary, either in readily identifiable fynbos islands at high altitude, or as scattered individuals in other floristic areas

**SWPP** Southwest Phytogeographical Province is centred in the heart of the CFR, situated between the Berg and Bree Rivers; it receives the highest winter rainfall, and usually contains the highest levels of diversity and endemism

**UPGMA** Unweighted Pair-Grouping Method, Arithmetic Average is a weighting technique used by the SAHN clustering algorithm

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# Chapter 3: An Assessment of the Methods employed in the Numerical Phytogeographical Analysis of the Cape Floristic Region

## 3.1 ABSTRACT

Aim: To compare the optimality of several approaches in the establishment of choria in the CFR, to determine whether one approach offers substantially better performance than the others, or whether a multiple analysis approach is more beneficial. Finally, to investigate the usefulness of GIS in chorological analysis.

Methods: These approaches include: existing techniques such as unweighted UPGMA; Bell-Shaped Curve Weighted Parsimony Analysis of Endemism (PAE), a new approach using Bell-Shaped Curve Weighting and UPGMA; and newly introduced Integration weighting. Results of the different techniques were combined, and supplemented with GIS analysis. Analyses are undertaken on a combined representative dataset of CFR taxa, and taxonomic/functional derivatives thereof.

Results: Differences between various weighting and clustering algorithms were less than anticipated. However, weighting is substantially better than not weighting. Although the differences between weighting techniques were not great, Bell-Shaped Curve Weighting, using UPGMA, consistently produced the most optimal results. Further, GIS interrogation of candidate phytogeographical centres substantially enhanced their endemic composition and size, and is thus recommended. Post clustering GIS analyses may offset any marginal benefits of a single approach. However, a multiple clustering approach was found to highlight areas of conflict, where floristic/biotic elements overlapped. The large dataset that was analysed, with comprehensive statistical analyses using modern techniques, allowing for the recovery of additional phytogeographical detail not previously described in the CFR. I uncovered substantial congruence with previous studies. Phytogeographical conflict and differences within my study, between derivative datasets, and with previous studies, alluded to differences in floristic/taxonomic composition (different frequencies of biotic elements) of datasets that were analysed.

Conclusions: Differences in weighting techniques are less than expected. Substantial improvement of chorial delimitation is facilitated by GIS analysis, while multiple weighting and/or clustering approaches help to highlight potential areas of conflict/biotic element overlap.

**Keywords:** Phytogeographical Centre(s) (PC); Chorology; Parsimony Analysis of Endemism (PAE); Cape Floristic Region (CFR); Geographical Information Systems (GIS); biogeography; phytogeography; floristic patterns

## 3.2 INTRODUCTION

The establishment of floristic units is a fundamental starting point in many fields of biogeography. This reduction or summary of data allows for phytogeographical mapping, historical interpretation (Major, 1988; Rosen, 1988), and conservation planning (Platnick, 1992; Myers, Mittermeier, Mittermeier, da Fonseca and Kent, 2000). van Wyk and Smith (2001) stated that in relation to ecological biogeography, research in both floristic (chorological) and historical biogeography has been neglected in southern Africa. Techniques used to retrieve either biogeographical centres or candidate areas/centres of endemism are not mutually exclusive, and face similar problems. Both approaches seek to unite predefined areas based on shared taxa, while avoiding the "noise" generated by widespread less informative taxa. Floristic and historical biogeographies differ with regards to their input data, and how the data are further interpreted. Floristic studies typically include large datasets representative of the area under investigation, and determine floristic area patterns, which generally infer untested historical processes. Historical studies focus on individual taxa, and whilst also constructing floristic area patterns, these areas are further used in conjunction with phylogenies to facilitate historical interpretation for that particular taxon (Garzón-Orduña, Miranda-Esquivel and Donato, 2008). My study focuses on the former floristic biogeographic approach.

Intuitive delimitation of phytogeographical centres (PCs) (Weimarck, 1941; White, 1993; Takhtajan, 1986; Jurgens, 1997; van Wyk and Smith, 2001) allows for easy down-weighing of taxa with little biogeographical information, but is not analytically rigorous. Numerical methods, which cluster predefined areas or Operational Geographic Units (OGUs) (Crovello, 1981) into biogeographical centres, based on shared taxa (Stehli and Wells, 1971; Oliver et al., 1983; Rosen, 1988; Williams, 1992; Morrone, 1994; Morrone and Crisci, 1995; Linder, 2001; Szumik et al., 2002; Szumik and Goloboff, 2004; Mast and Nyffeler, 2003; Giokas and Sfenthourakis, 2008) are objective, but do not automatically down-weigh uninformative taxa. An example of uninformative taxa would be widespread taxa, which contain little or no information on the delimitation of biogeographical centres (Raup and Crick, 1979; Nelson and Platnick, 1981), as these occur in all areas. Furthermore, widespread taxa are rarely sampled uniformly throughout their distributional ranges, resulting in false absences and artificial disjunctions. Null models have previously been employed to generate an "index of similarity" (Raup and Crick, 1979; McCoy, Bell and Walters, 1986); to identify biotic elements (Hausdorf and Hennig, 2003); and to filter out conflicting taxa (Mast and Nyffeler, 2003; Giokas and Sfenthourakis, 2008). Randomisation models have also been used to determine pre-identified areas that have higher numbers of range-restricted taxa (potential endemics) than predicted from their diversity (Jetz, Rahbek and Colwell, 2004). Specialised programmes have also been developed to identify centres of endemism (CoEs) (Szumik, Cuezzo, Goloboff and Chalup, 2002; Szumik and Goloboff, 2004). Alternatively, to maximise the contributions of informative range-restricted taxa, and to minimise noise from widespread taxa, various weighting techniques have been proposed, including inverse weighting (Williams, 1992) and Bell-Shaped Weighting (Linder, 2001). These can be considered analogous to successive weighting techniques, used in cladistic analyses, but are *a priori* rather than *a posteriori* methods. Inverse weighting is excellent for highlighting taxa that are restricted to single OGUs, but is of less use in weighting for clustering, due to the very steep drop-off in weighting values with increasing range sizes. Bell-Shaped Weighting corrects this problem, but it is difficult and potentially time consuming to optimise the two controlling variables. There is a need for a weighting scheme that is quicker and easier to implement, but still achieves a similar weighting function as Bell-Shaped Weighting. I used weighting techniques due to the large size of my dataset, which exceeded current randomisation (Monte Carlo) programme limits, precluding further comparisons of methods.

I tested the efficacy of weighting techniques in the Cape Floristic Region (CFR). At last count, the CFR contained 9087 species of vascular plants in an area of 90 000 km$^2$ (Goldblatt, Manning and Snijman, 2008), of which nearly 69% were endemic (Goldblatt and Manning, 2000; Cowling et al., 1992; Gentry, 1986; Cody, 1986; Takhtajan, 1986; Myers, 2000). The CFR is characterised by high beta and gamma diversity (Kruger and Taylor, 1979; Cowling, 1983; Cowling, 1990; Cowling et al., 1992; Simmons and Cowling, 1996), indicating a high turnover rate in the flora. The CFR thus provides a large number of potentially structured distribution ranges with which to undertake phytogeographical analysis. The floristic uniqueness of the CFR has long been recognised (Bolus, 1886; Marloth, 1908; Levyns, 1938, 1962, 1964; Good, 1974; Goldblatt, 1978; Takhtajan, 1986; Linder, 2003), and the region has a rich history of biogeographical analyses using various techniques (Drége, 1843; Rehman, 1880; Engler, 1882; Bolus, 1886; Bolus, 1905; Marloth, 1908; Weimarck, 1941; Oliver et al., 1983; Goldblatt and Manning, 2000). The biogeographical subdivision of the CFR that is currently being used (Goldblatt and Manning 2000) is rather coarse, thus missing much of the rich detail and concentrations of endemics in the Cape Flora (Linder, 2003; Moline and Linder, 2005).

Here I sought ways to improve the numerical methods for defining biogeographical centres. In particular, I explored different weighting systems and clustering approaches. I presented a new weighting system that was sensitive to the peculiarities of individual clades/datasets without subjective user-defined variables, although still retaining the effectiveness of the Bell-Shaped Curve Weighting Technique. In addition, I also explored the use of GIS to refine the delimitation of the phytogeographical centres and also endemism. I demonstrated my method using the Cape Flora, and presented a new and finer phytogeographical classification of the flora. I then compared my new classification to previous phytogeographical classifications of the CFR.

## 3.3 METHODS

### 3.3.1 Database assembly and subdivision for analysis

The development and assembly of the dataset are detailed elsewhere (Chapter 2, Section 2.3.1.1). A total of 4 414 taxa (including 304 infra-specific taxa; mostly subspecies and varieties, and a few forms), in 412 genera, in 69 families were used in this study. Approximately 91.7% of these species were present in the CFR, thus approximately 41.9% of all CFR species were analysed. Greater attention was given to collecting distributional data for taxa that were concentrated in the CFR. However, to avoid geographic circularity in determining the boundaries of PCs or the CFR, no fixed geographical boundary was observed.

Datasets differed in their method of compilation. The Protea Atlas Project Dataset was compiled from a very thorough sampling regime, as both widespread and rare species were most likely to have been recorded from all the QDSs in which they might occur. Herbarium-specimen based datasets (for example, Orchidaceae, Poaceae, and Restionaceae) and my datasets assembled from taxonomic revisions (Rutaceae), were more likely to under-represent widespread species. Finally, the remaining datasets (Asteraceae, Geophytes, and RDL Datasets) were biased, only including range-restricted species, thus excluding more widespread species, especially in the RDL Dataset.

My Combined Dataset can be regarded as a sufficiently representative floristic sample of the entire flora of the CFR. The data were also partitioned taxonomically, functionally (geophytes) and by rarity (Red Data List) (Chapter 2, Section 2.3.1.1), to assess whether the patterns obtained from the combined data were repeated in the different partitions.

### 3.3.2 Operational Geographic Units (OGUs)

I scored distributions as presence data per QDS grid square. Alternative OGUs available for the CFR are the Broad Habitat Units (established by Cowling and Heijnis, 2001; and also by Moline and Linder, 2005), and vegetation units, defined by Mucina and Rutherford (2006). However, both these require point locality data for the distributions, to enable each record to be assigned to its OGUs. As yet, there are few datasets georeferenced with the required degree of accuracy. OGU size is important, because in larger OGUs an increasingly large proportion of taxa become endemic and so are uninformative for clustering purposes. When OGUs are defined too narrowly, the number of false absences increases. Due to the long use of QDSs in the Cape Flora, collectors have often attempted to complete the sampling at QDS level.

### 3.3.3 Weighting

Widespread taxa do not contribute to the delimitation of PCs and can provide confusing or conflicting information (Nelson and Platnick, 1981). In order to reduce the impact of these widespread taxa, I used three weighting approaches (Bell, Int and MInt) to develop derivative matrices for each of my datasets (Chapter 2, Section 2.3.2), in addition to an unweighted matrix. Weighting values or contributions of the taxa were adjusted to range from a minimum of zero, to a maximum of nine in PAUP4.0b10Win (Swofford, 1998), and one to nine in the UPGMA analyses. I defined the weighted contribution as the number of taxa multiplied by their weighting score, which was unique to each derivative matrix.

In Bell-Weighting (Linder 2001), the weight of each character (taxa) is determined by the equation $y=e^{-ax^p}$, where $y$ is the weighting value of the taxon and $x$ the taxon range in the QDS (or relevant OGU). There are two variables: $a$ is an area modifier which affects the horizontal axis for weighting, while $p$ affects the steepness of the slope, essentially the vertical axis component of weighting. Linder (2001) evaluated the effects of various $a$ and $p$ values on Restionaceae, and found that $a = -0.005$, and $p = 3$ produce the greatest number of PCs, but not the greatest numbers of endemic taxa; whereas using $a = -0.005$, and $p = 2$, resulted in higher numbers of endemics, but fewer PCs. The variables $a$ and $p$ in the equation $y=e^{-ax^p}$ should be adjusted to better fit particular datasets. Restionaceae showed similar distributional properties to other Cape Clades (Levyns, 1964; Linder, 2003), and consequently I used the $a$ and $p$ values optimised for Restionaceae for all of my datasets.

I exploited the relationship between taxon range and the frequency of taxa in these range size categories to develop a novel weighting system, which I called **<u>Int</u>egration Weighting (Int)**. The relationship between taxon area and the frequencies of taxa with that area can be used to plot a line of best fit, and the equation of the graph can be integrated. The area under the curve can then be divided into a pre-selected number of equal area portions, and taxa with ranges in these portions can be weighted accordingly, with the highest weighting for those taxa closest to the origin. This weighting technique may more adaptable to individual datasets *a priori*, and thus require less *a posteriori* assessment than Bell-Shaped Curve Weighting, one of the shortcomings noted by Szumik et al., (2002). Thus, my method took into account the relative distributional sizes of taxa as a proportion of the entire clade or dataset, as well as the relative frequencies of the taxa in each distribution category, by integrating the relationship between these two properties. Although the number of subdivisions was arbitrary, I divided the area under the curve into nine equal area portions, to make it comparable to the PAE and Bell analyses. In all datasets, except Orchidaceae, the equation that best described the data was that of an exponential curve. A list of the Integration formulas and their Goodness of fit ($r^2$) are provided (Table 15).

In the RDL Datasets that contained high proportions of range-restricted taxa, the Y-axis curve of the graph was relatively steep, with the result that not all weighting categories contained taxa. In these cases, taxa occupying the lowest meaningful range for clustering (two QDSs) were advanced to a weighting of nine, often leaving a gap between it and the next utilised weighting category. This is similar to Inverse Weighting (Williams, 1992), where weighting categories 8, 7, and 5 are not utilised, and to Bell-Shaped Curve Weighting, (p=3; a=0.005), where weighting categories 8, 6, and 4 are not utilised (Table 16). In order to establish whether these gaps had an adverse effect on the performance of the Integration Weighting Technique (Int), I modified the parameters of Int to better utilise all the weighting categories, and called it the **Modified Integration Technique (MInt)**. Here the area under the curve was integrated between two QDSs (x-axis) and the maximum area range value, as only characters that occurred in two or more OGUs (QDSs) were useful in clustering. It proved adequate in most cases to utilise all, or nearly all weighting categories. In instances where it did not prove adequate to weight all taxa sequentially, the weighting values for the various areas were further subjectively adjusted to make full use of all weighting values between one and nine, by inspection, although in most cases (except the RDL Taxa Dataset, Table 16) this was relatively minor as indicated by the similar average weighting values employed (Table 16).

Table 15: Equations and Goodness of Fit Values for graphs used in Integration Weighting, listed in order of descending $r^2$ values.

| Rank | Dataset | Equation | $r^2$ Correlation Coefficient | # Taxa in Study |
|---|---|---|---|---|
| 1 | Combined Data: | $y = 4959.1x^{-1.814}$ | ($r^2 = 0.9204$) | 4 414 |
| 2 | Ericaceae: | $y = 450.3x^{-1.4593}$ | ($r^2 = 0.9017$) | 816 |
| 3 | RDL Taxa: | $y = 2428.3x^{-2.3951}$ | ($r^2 = 0.8831$) | 1 549 |
| 4 | Orchidaceae_Pwr:<br>(Exp) | $y = 34.753e^{-0.0791x}$<br>($y = 179.93x^{-1.207}$) | ($r^2 = 0.8755$)<br>($r^2 = 0.8554$) | 469 |
| 5 | Fabaceae: | $y = 118.67x^{-1.2582}$ | ($r^2 = 0.8712$) | 334 |
| 6 | Asteraceae: | $y = 176.67x^{-1.562}$ | ($r^2 = 0.8441$) | 432 |
| 7 | Geophytes: | $y = 122.85x^{-1.3483}$ | ($r^2 = 0.8319$) | 407 |
| 8 | Rutaceae: | $y = 83.503x^{-1.1787}$ | ($r^2 = 0.8278$) | 253 |
| 9 | Proteaceae: | $y = 99.747x^{-1.0608}$ | ($r^2 = 0.8037$) | 403 |
| 10 | Restionaceae: | $y = 98.664x^{-1.096}$ | ($r^2 = 0.7830$) | 348 |
| 11 | Poaceae: | $y = 15.167x^{-0.6355}$ | ($r^2 = 0.7616$) | 142 |
| 12 | Polygalaceae: | $y = 26.292x^{-0.9}$ | ($r^2 = 0.7474$) | 121 |
| 13 | Rosaceae: | $y = 15.928x^{-0.6982}$ | ($r^2 = 0.6986$) | 121 |
| 14 | Bruniaceae: | $y = 11.658x^{-0.6843}$ | ($r^2 = 0.5544$) | 80 |

Table 16: Weighting Values assigned to taxon distribution range sizes.
Displayed are Inverse Weighting and various parameters of Bell Shaped Curve Weighting. Also recorded are average Int Weighting and MInt Weighting for all datasets, and the extreme examples of high weighting in Poaceae (for a strong right graph tail), and low weighting in the RDL Taxa (for a strong left graph tail).

| Range Size (# QDS) | Inverse Weighting | Bell (p=3; a=-0.005) | Bell (p=2; a=-0.005) | Bell (p=3; a=-0.001) | Average | | Poaceae | | RDL Taxa | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Int | MInt | Int | MInt | Int | MInt |
| 1 | - | - | - | - | - | - | - | - | - | - |
| 2 | 9 | 9 | 9 | 9 | 9.0 | 9.0 | 9 | 9 | 9 | 9 |
| 3 | 6 | 9 | 9 | 9 | 6.1 | 8.1 | 8 | 9 | 2 | 8 |
| 4 | 4 | 7 | 9 | 9 | 5.5 | 7.4 | 8 | 9 | 2 | 7 |
| 5 | 3 | 5 | 9 | 9 | 5.1 | 6.6 | 8 | 8 | 1 | 6 |
| 6 | 2 | 3 | 8 | 8 | 4.7 | 6.1 | 8 | 8 | 1 | 5 |
| 7 | 2 | 2 | 8 | 7 | 4.6 | 5.6 | 8 | 8 | 1 | 4 |
| 8 | 2 | 1 | 7 | 6 | 4.3 | 5.1 | 7 | 8 | 1 | 3 |
| 9 | 1 | 1 | 7 | 5 | 4.1 | 4.8 | 7 | 8 | 1 | 2 |
| 10 | 1 | 1 | 6 | 4 | 3.9 | 4.5 | 7 | 7 | 1 | 1 |
| 11 | 1 | 1 | 5 | 3 | 3.8 | 4.4 | 7 | 7 | 1 | 1 |
| 12 | 1 | 1 | 5 | 2 | 3.6 | 4.2 | 7 | 7 | 1 | 1 |
| 13 | 1 | 1 | 4 | 1 | 3.6 | 4.1 | 7 | 7 | 1 | 1 |
| 14 | 1 | 1 | 4 | 1 | 3.4 | 3.7 | 7 | 7 | 1 | 1 |
| 15 | 1 | 1 | 3 | 1 | 3.2 | 3.6 | 6 | 7 | 1 | 1 |

### 3.3.4 Computerised Clustering Algorithms Employed

Six analyses were performed to cluster the QDSs into PCs and to avoid erroneous artefacts that could result from a single analysis. The first five clustering analyses were performed on the QDS input raw data, the performances of which are listed in Table 17. The sixth analysis was performed on the consensus results of analyses one to five to cluster the PCs and PSCs to determine the hierarchial relationships between them. Although clustering techniques based on shared taxa are unable to make use of taxa restricted to single OGUs, subsequent analysis in GIS would identify these taxa and areas, so this was not considered a serious impediment to the clustering approach undertaken.

Techniques utilised in this study were chosen due to their time efficiency and long established track record of utilisation and success in establishing phytogeographical patterns in biogeography. The clustering algorithms used included parsimony (Rosen, 1988; Morrone, 1994; Morrone and Crisci, 1995; Linder, 2001; Cavieres et al., 2002; Rovito et al., 2004; Tribsch, 2004; Ramdhani et al., 2008), implemented in PAUP4.0b10Win (Swofford, 1998) and UPGMA, using the Jaccard similarity co-efficient (Conran, 1995; de Mera et al., 1997; Borchsenius, 1997; Garcia-Barros et al., 2002; Tribsch, 2005; Hunter, 2005; Ramdhani et al., 2008), implemented in NTSyspc v 2.02i (Rohlf, 1998). Neither of these approaches take shared absences into account, which is important considering the range restricted nature of the taxa analysed. As the Jaccard similarity coefficient is sensitive to large differences in species richness between OGUs (Born et al., 2006), I avoided implementing a generalised phenon-line to identify clusters (see below). PAE is very computing intensive, and was consequently only undertaken on the Bell-Weighted data, using the optimised variables identified by Linder (2001), which he found to be more effective than unweighted PAE, and the other weighting methods he employed. Conversely, as UPGMA is much more time efficient, it was implemented on all the weighting techniques that I employed. Further, both PAE and UPGMA techniques have proven success in the CFR (Linder and Mann, 1998; Linder, 2001), providing further support for their utilisation in this study, which focuses on CFR taxa.

PAE has received much criticism as a historical biogeographical technique (Brooks and Veller, 2003; Santos, 2005). In this study, the use of PAE is restricted to pattern retrieval, and does not include historical interpretation, for which phylogenies are required (Santos, 2005). Another criticism of PAE is the use of a hypothetical all-zero outgroup, which precludes a dispersalistic model (Santos, 2005). Due to the relatively short dispersal distances in fynbos (Linder, 1985; Slingsby and Bond, 1985) reducing dispersal, and the regularity of fire as a potential vicariance mechanism (Linder, 1985), this criticism may prove less of a theoretical hinderance in the fynbos biome.

Although promising, techniques like NDM (Szumik et al., 2002; Szumik and Goloboff, 2004) have not enjoyed widespread utilisation, and require a unique reference grid identification system. Matrix size limits of modern null model approaches (Mast and Nyffeler, 2003; Giokas and Sfenthourakis,

2008) discounted them from this study. Other avenues for analysis, particularly on larger datasets could include Primer (Clarke and Gorley, 2006) with Bray-Curtiss similarity.

Other novel techniques that have been used to uncover centres of endemism that have not enjoyed widespread usage include corrected weighted endemism (Crisp et al., 2001) and spatial autocorrelation analysis (Getis and Ord, 1996). However, as these techniques do not necessarily delimit "hard geographic boundaries" between centres, lists of strict endemics cannot be generated. Thus, these methods were not utilised.

The choice of clustering technique may not be as critical if the approach is to obtain a consensus from a number of different techniques or analyses, rather than relying on a single analysis.

### 3.3.5 Constructing PC: Identification of Dendogram clusters to Mapped PC

Potential PCs from each of the five analyses, for each dataset, were identified on the dendograms (Chapter 2, Section 2.3.4). In PAE, each clade defined was treated as a potential PC. In the UPGMA, previous studies have made use of a cut-off phenon-line to identify clusters (Rosen, 1988, Linder and Mann, 1998; Linder, 2001). I did not use a phenon line, but instead used clusters that were identified based on geographic continuity, with an initial minimum cluster size of at least three QDSs. More QDS branches were added until a large cluster was encountered. As a result, clusters were based on their individual merits, not as an average of the entire dendogram, and consequently clusters with weaker representations of range-restricted taxa were retained. This approach prevented the loss of clusters with lower densities, which have weaker similarity values, a problem noted by Born et al., (2006). I initially started with small rather than large clusters, as these were easier to enlarge in subsequent GIS interrogation, if the addition of more OGUs would result in an increase in PC endemism. This approach maximises the number of 'complete' clusters, without arbitrarily discounting basal QDSs on the dendogram. An alternative approach may be to use a cut-off phenon-line for clusters, and migrate down the tree adding single OGU branches (or two OGU branches, or whatever minimum is set), until one encounters a neighbouring cluster that exceeds this value, or until one encounters the next cluster defined by the phenon-line cut-off. Subsequent GIS interrogation was also able to recover any potential PCs that were omitted by cluster analysis. I also investigated the effects of cluster size demarcation using my unweighted dataset. Cluster size was deliberately reduced in Unweighted_Narrow (Unw_N) and increased in Unweighted_Wide (Unw_W).

The QDSs from these five analyses (Table 17) were then plotted as areas on maps in the GIS for each dataset. These potential PC clusters were further refined by: 1) removing potential PC clusters that had no endemic taxa; and 2) pruning from the PC clusters those QDSs that did not include any of the endemic taxa of the PC.

### 3.3.6 GIS Interrogation: Establishing Consensus amongst Analyses and Refinment of PCs

Congruency for the refined core PC areas from the five analyses was initially determined by visual interrogation in the GIS, using ArcView3.x (ESRI, 2000) and ArcMap9.x (ESRI, 2005) GIS, and consensus centres/sub-centres were established. Ultimately, the boundaries of PCs and PSCs were determined by the distributions and concentrations of the endemic taxa themselves, which was summarised in the refined core PCs. A robust floristic pattern was indicated by consistent retrieval and spatial congruence in the different analyses, and was demarcated as a PC. A potential PC, which was not consistently retrieved in all analyses, but which was nested within potential PCs of one or more of the other analyses, was identified as a PSC. Where there was substantial overlap (>50%) of the refined PCs from the different analyses, showing a lack of spatial congruence, the consensus PC was enlarged to include the area of all relevant input PCs, with subsequent investigation of the distributions of endemic taxa for potential PSC demarcation.

Where there was marginal overlap (one or a few QDSs) between refined input PCs from the different analyses, the effects of the addition or subtraction of the QDS from the refined input PCs were assessed. The QDS was then assigned to the PC that provided the highest overall endemicity for the dataset. If the net endemicity value was equal for the QDS in either of the PCs, then the endemic taxon with the smallest distribution of conflicting taxa was favoured. If this was also indecisive, the relative increase in PC endemicity (i.e. the percentage increase in number of endemics in a PC) was also considered in some cases. Finally, after consensus was established, additional spatial analyses were undertaken in the GIS to determine if there were any further taxa or QDSs that could be added to the PC to increase levels on endemism.

Consensus PCs and PSCs where mapped (Figure 18, Figure 19) and floristic and geographic properties tabulated (Table 9, Table 18) for each of my derivative datasets (Chapter 2, Section 2.3.1.3).

### 3.3.7 Assessment of Weighting Techniques and Clustering Algorithms Employed

The performance of the consensus PCs and each of the five individual analyses were assessed by summing the relevant values of the individual datasets (Table 17). Although summarising multiple datasets added additional levels of complexity to my comparison, it provided more comprehensive evidence of a technique's performance in a number of diverse "real world" datasets, and was thus preferred over a single test or hypothetical dataset.

I also searched for a pre-clustering measure to predict the success of the weighting technique. At present, there is no accepted method or measure of determining the most optimal configuration for centres of endemism (CoEs), or chorological units. Thus, comparisons of the analyses (Analyses 1 to 5) were undertaken at various stages in the analyses. I summed the results from each individual dataset (combined dataset, taxonomic datasets, growth form, and threat) to compare the totals for each analysis (Table 17). In PCs, area, endemism and diversity were positively correlated (Exell and Gonçalves, 1974; Major, 1988; Anderson, 1994; Chapter 2; Section 2.4.3), and these were all values that were negatively correlated to the number of PCs. The greater the number of PCs that were delimited, the smaller they were on average and consequently fewer taxa were found to be endemic to each PC. This was also apparent in Linder (2001). The relationships among these variables were not necessarily linear.

It is difficult to determine the optimal size of a PC or the appropriate demarcation for it. It is likely that this optimal area may be different at different biogeographical/evolutionary/ecological scales for different taxa/clades (families/genera) (Nehei, 2008). I found it to be different for the same clade in different biogeographic areas (for example, core CFR PCs versus the Drakensberg PC size, Table 18).

I compared the performance of the various weighting techniques that I employed using two further calculations (measures). Assessing the performances of the weighting techniques, using these two measures should not override the previous floristic and geographic measures of performance, such as the number of PCs, the number of PC endemics, PC richness, and the number of QDSs in the PCs. However, they are better used in conjunction with them (Table 17), to assess the analytical performance of the techniques.

*Measure 1 (Linear):* *(Σtaxa endemic to PC/ΣPC diversity)/(Σ#PC/((Σ#QDS in PC))*

*Measure 2 (Log):* *(Σtaxa endemic to PC/ΣPC diversity)/(Σ#PC/(Log(Σ#QDS in PC))*

The Log Measure of endemism counters the tendency of the area of the PC to dominate the measure, by logging the areas of the PC, arguably representing a more realistic measure.

## 3.4 RESULTS

### 3.4.1 Properties of the Integration Weighting Equations

Relatively high $r^2$ values, mostly above 0.7 (Table 15), were obtained for the relationship between taxon range size and the frequency of taxa in each range size. The completeness of the clade did not seem to significantly affect the goodness of fit ($r^2$), with incomplete datasets (for example, Asteraceae) and artificial groups (for example, RDL Taxa) having stronger correlation coefficients than Proteeae (Proteaceae), Danthioideae (Poaceae), *Cliffortia* (Rosaceae) and Bruniaceae. The goodness of fit ($r^2$) of the relationship between taxon range size and frequency was strongly affected by the dataset size.

## 3.4.2 Performance of the Different Methods

### 3.4.2.1 Analytical Effects of the different weighting approaches on character generation

The three weighting methods generated similar numbers of characters (35 000 to 48 000), compared to the 10 000 unweighted characters (Table 17). MInt produced the greatest number of weighted characters (Table 17), due to its more gradual decrease in weighting of the distribution ranges (Table 16, Figure 44), while the steeper differential in weighting for the other analyses (Table 16) produced slightly fewer weighted characters. The marginally lower numbers of characters generated by Bell: UPGMA compared to Bell: PAE (Table 17) were due to the differences in data preparation in splitting the datasets into eastern and western portions for the PAE analyses (Ericaceae, Orchidaceae), although identical weighting was undertaken in both analyses.

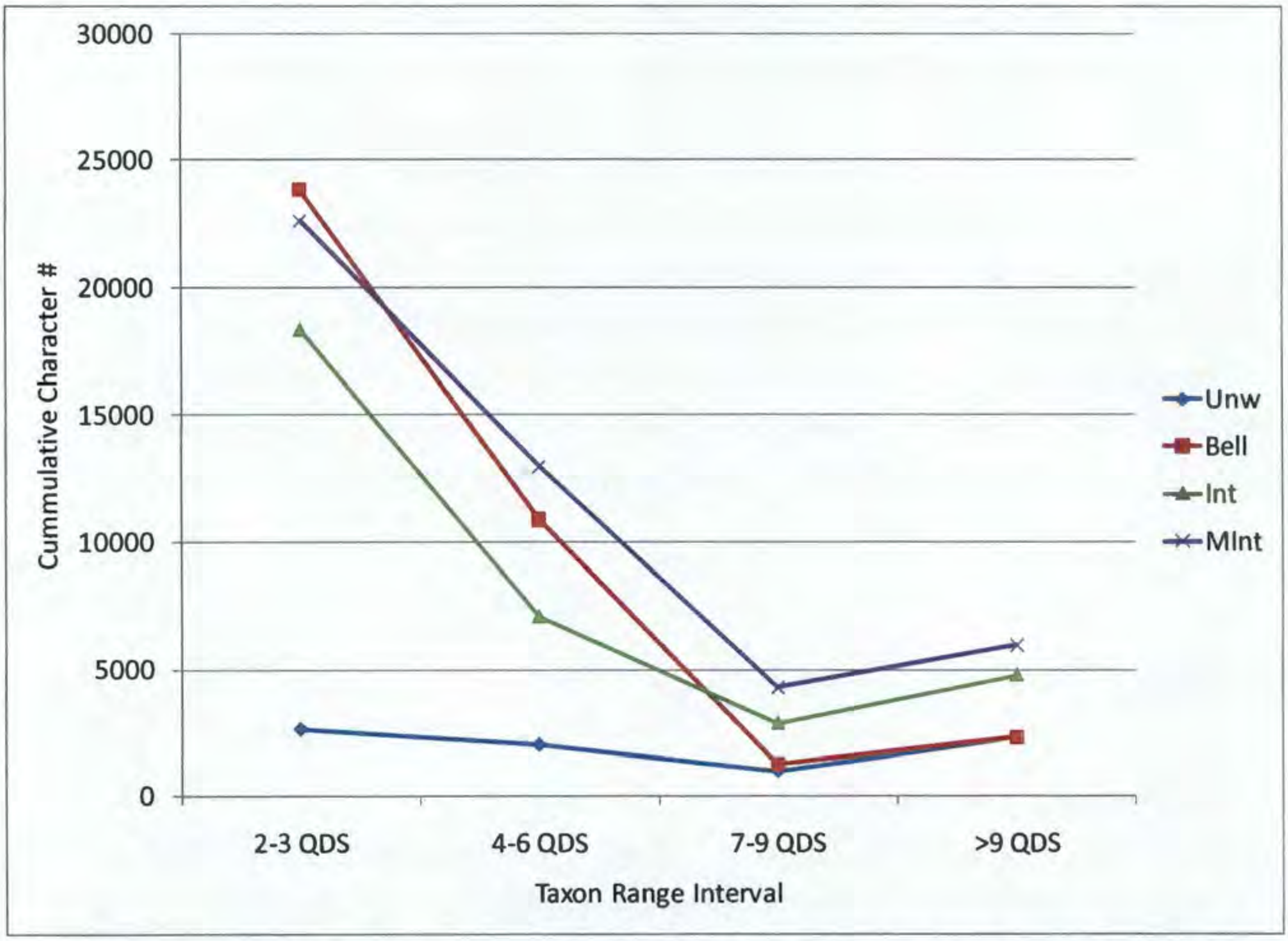

Figure 44: Cumulative weighted effective character contributions of taxa from my different analyses within designated range sizes. The upward trend after 7-9 QDSs is due to the combining of all taxa with ranges greater than nine QDSs, and is thus a statistical artefact. The steeper weighting of the Bell shaped curve weighting is clearly seen by its crossing of the MInt and Int lines.

A breakdown of the weighting into different taxon range sizes (Figure 44) revealed that Bell-Shaped Curve Weighting produced the highest number of characters in the smallest taxon range category, followed closely by MInt. The steepness of successive weighting dropped off as follows: Bell, Int and MInt (Table 16; Figure 44).

The Unweighted analyses, with the fewest input characters, produced the greatest number of dendograms, possibly indicating less resolution of the dendogram structure than for the weighted analyses. Although Bell: UPGMA generated a weighted contribution of characters between Int and MInt (Table 17), it produced nearly double the number of dendograms than either of the integration techniques (Table 17). The number of trees from Bell: PAE (Analysis 2) were not comparable to the number of dendograms of Jaccard analyses, and excluded (Table 17).

Table 17: Statistical summary assessment of the different analytical techniques I employed. A breakdown of the performance of each derivative dataset is tabulated in Appendix C3.

| | Analysis 1 | | Analysis 2 | Analysis 3 | Analysis 4 | Analysis 5 | |
|---|---|---|---|---|---|---|---|
| | Unw_N | Unw_W | Bell:PAE | Bell:UPGMA | Int | MInt | Consensus |
| Clustering | UPGMA | UPGMA | PAE | UPGMA | UPGMA | UPGMA | - |
| # of Effective Characters | 9941 | 9941 | 40385 | 40223 | 35034 | 47683 | - |
| # Dendograms | 83227 | 83227 | - | 61451 | 30345 | 32425 | - |
| # clusters | 668 | 567 | 532 | 616 | 613 | 593 | - |
| # PC endemics | 2787 | 3012 | 2914 | 3248 | 3097 | 3053 | 4197 |
| # PC Taxa | 9290 | 9308 | 9439 | 9531 | 9514 | 9461 | 9815 |
| # PCs | 332 | 299 | 404 | 366 | 357 | 356 | 317 |
| # QDS in PCs | 975 | 1085 | 1301 | 1416 | 1264 | 1307 | 2554 |
| Linear Measure | 1.30 | 1.17 | 1.27 | 1.17 | 1.24 | 1.16 | 0.85 |
| Log Measure | 21.13 | 20.88 | 27.35 | 27.15 | 25.53 | 25.28 | 29.59 |

### 3.4.3.2 Phytogeographic performance of the five analyses

The four phytogeographic characteristics of the PCs (Table 17), and the Linear and Log Measures of Endemism (Table 17) were used to assess the PC of the different weighting techniques that I employed and were discussed together. They should be viewed as a single composite result.

A comparison of the PAE and UPGMA clustering algorithms revealed a slightly different emphasis in the retrieval of PC properties. I found that the Bell: UPGMA retrieved 11% more endemics, while the Bell: PAE retrieved 10% more PCs (Table 17), accounting for their similar Log Measures of endemism (Table 17).

Of the individual analyses, the Unweighted analyses (Unw_N and Unw_W) generally performed most poorly in all phytogeographical properties of PCs that I investigated (Table 17), except in two cases: Bell: PAE had fewer endemics than Unw_W, and Unw_N produced more PCs than the Combined PC results. Using larger, but fewer clusters (Unw_W) resulted in an 8% increase in endemism (Table 17), but 9.9% fewer PCs (Table 17) when compared to the Unw_N cluster delimitation. As PC diversity (Table 17) and area (Table 17) were positively correlated with PC endemism values (Table 17), the effects of cluster size can had a noticeable effect on the results of the weighting technique employed.

In the remaining individual weighted analyses (Bell: PAE, Bell: UPGMA, Int, MInt), endemism, diversity, and area values were relatively similar (Table 17). Bell: UPGMA usually had the highest scores of these three PC properties, followed closely by the Int analysis. There was only a 6.4% difference between PC endemism numbers between MInt and Bell: UPGMA, and a 4.9% difference between Int and Bell: UPGMA (Table 17). Bell: PAE produced a large number of PCs, but had the lowest endemism and diversity of these three weighting analyses. MInt has comparable endemism, PC number, and PC area, but low diversity. By contrast, in the Consensus approach with GIS analysis, there was a 22.6% increase in the number of PC endemics, a 2.9% increase in PC diversity, both brought about principally by increasing the area of PCs through assigning 44.6% more QDSs to the PCs. Conflict between the PCs from the individual analyses caused these PCs to merge into larger PCs, but also resulted in a concomitant drop in PC numbers (Table 17) by 13.4% for the Consensus analysis compared to Bell: UPGMA.

The Unw_N and Bell: PAE weighting techniques performed best in the Linear Measure of endemism (Table 17), due to the lower number of QDSs incorporated into the PCs (see formula). Furthermore, most of the other floristic and geographic properties of the Unw_N analyses were low, and compensated for each other, thus the ratios between the values in the Linear Measure were not found to be as marked for the Unw_N analysis. The Consensus datasets performed poorly in the Linear Measure, due to its large unlogged area.

Bell: PAE had the highest Log Measure of Endemism (Table 17). Ranked second was the Consensus Dataset, closely followed by Bell: UPGMA. Int and MInt also had similar scores, and slotted into fourth and fifth place respectively (Table 17). Finally, the Unweighted Analysis, both using Narrow and Wide clustering demarcation also had similar values, and performed the poorest in the Log Measure of endemism (Table 17).

### 3.4.3 Phytogeographic Results for the CFR

The spatial locations of the PCs I retrieved were mapped together with a comparison to those of Weimarck (1941) (Figure 45) and Goldblatt and Manning (2000) (Figure 46). Taxonomic properties are summarised in Table 18, while comparisons of areal overlap are provided in the appendix (Appendix C3, Table 21).

Table 18: Taxonomic properties of the major Centres identified for the dataset Combined Dataset (labels correspond to PC/PSC labels in Figures 2 and 3).

| Label | Centres<br>Sub-Centres | Area | Family # | Genus # | Diversity | Spp >=0.5 | Endemics | Weimarck | GandM | Comments |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Hottentots-Kleinrivier | 8 | 37 | 172 | 1381 | 439 | 158 | Hottentots Holand/ Bredasdorp | SWPC | |
| 1.1 | Hottentots-West Kleinrivier | 5 | 36 | 168 | 1313 | 364 | 131 | Hottentots Holand/ Bredasdorp | SWPC | |
| 1.2 | East Kleinrivier | 3 | 21 | 87 | 439 | 22 | 6 | Bedasdorp | SWPC | |
| 2 | Greater Langeberg | 14 | 41 | 173 | 958 | 257 | 152 | Langeberg | LBPC | |
| 2.1 | East Langeberg | 5 | 30 | 122 | 574 | 90 | 46 | Langeberg | LBPC | |
| 2.2 | Central Langeberg | 5 | 31 | 122 | 543 | 86 | 38 | Langeberg | LBPC | |
| 2.3 | West Langeberg Plains | 2 | 26 | 85 | 269 | 27 | 12 | Langeberg | LBPC | |
| 2.4 | Central Langeberg Plains | 2 | 26 | 71 | 283 | 14 | 7 | Langeberg | LBPC | |
| 3 | Groot Winterhoek-West Langeberg | 11 | 39 | 187 | 1167 | 276 | 117 | Groot Wintershoek | NWPC | |
| 3.1 | Hexriver-West Langeberg | 6 | 34 | 155 | 873 | 131 | 54 | Groot Wintershoek | NWPC | |
| 3.2 | Groot Winterhoek | 4 | 29 | 135 | 768 | 92 | 43 | Groot Wintershoek | NWPC | |
| 3.3 | Riebeek-Kasteel | 1 | 15 | 31 | 87 | 1 | 1 | Malmesbury Flats | SWPC | |
| 4 | Agulhas Plains | 11 | 33 | 130 | 759 | 224 | 101 | Bredasdorp | APPC | |
| 4.1 | West Agulhas Plain | 8 | 27 | 115 | 642 | 147 | 58 | Bredasdorp | APPC | |
| 4.2 | Potberg | 3 | 27 | 88 | 331 | 45 | 25 | Bredasdorp/Langeberg | APPC | |
| 5 | Southeastern Centre | 46 | 39 | 147 | 655 | 206 | 102 | South-Eastern PC | SEPC | |
| 5.1 | Grootwinterhoek-Vanstadens | 12 | 30 | 105 | 386 | 64 | 33 | Cockscomb | SEPC | |
| 5.2 | Springbokvlakte | 6 | 20 | 41 | 80 | 18 | 13 | Zuurberg/ outside | Outside | |
| 5.3 | Tsitsikamma | 5 | 17 | 71 | 337 | 12 | 10 | Zitzikamma | SEPC | |
| 5.4 | Slypsteenberg-Antoniesberg | 6 | 22 | 47 | 114 | 14 | 7 | Outside/ Karoo Mountains | Outside/ KMPC | |
| 5.5 | Kouga | 4 | 20 | 62 | 228 | 18 | 5 | Zitzikamma/ Knysna | KMPC | |
| 5.6 | Baviaanskloofberge | 3 | 18 | 51 | 152 | 6 | 4 | Zitzikamma | KMPC | |
| 5.7 | NW Baviaanskloofberge | 1 | 10 | 12 | 21 | 1 | 1 | Karoo Mountains | KMPC | |
| 5.8 | Grootrivierberge | 1 | 9 | 12 | 15 | 1 | 1 | outside | Outside | |
| 5.9 | Remainder | 8 | 14 | 64 | 210 | 2 | 0 | outside | Outside | |
| 6 | Stellenbosch-Bainskloof Mtns/Sandveld | 13 | 36 | 184 | 1288 | 295 | 100 | South-Western PC | SWPC | |
| 6.1 | Stellenbosch-Bainskloof Mtns | 4 | 31 | 152 | 1073 | 153 | 50 | French Hoek | SWPC | |
| 6.2 | Sandveld | 9 | 29 | 114 | 539 | 106 | 36 | Malmesbury Flats | SWPC | |
| 7 | Karoo Mtn Centre | 16 | 35 | 136 | 597 | 191 | 98 | Karoo Mountains | KMPC | |
| 7.1 | Klein Swartberg-West Touwsberg | 5 | 29 | 94 | 339 | 57 | 30 | Karoo Mountains | KMPC | |
| 7.2 | Groot Swartberg-Anysberg | 6 | 26 | 94 | 358 | 53 | 26 | Karoo Mountains | KMPC | |
| 7.3 | Rooiberg | 2 | 24 | 56 | 168 | 21 | 13 | Karoo Mountains | KMPC | |
| 7.4 | Kamanassie | 2 | 19 | 51 | 168 | 12 | 10 | Knysna Interval | LBPC | |
| 7.5 | East Touwsberg | 1 | 14 | 21 | 40 | 4 | 3 | Knysna Interval | LBPC | |
| 8 | Cedarberg | 12 | 39 | 151 | 808 | 224 | 93 | Cedarberg | NWPC | |
| 8.1 | Cedarberg Core | 6 | 37 | 138 | 736 | 174 | 58 | Cedarberg | NWPC | |
| 8.2 | S Koebeeberge-Boegoeberge | 2 | 18 | 33 | 61 | 7 | 6 | outside | NWPC/ outside | |
| 8.3 | Southeast Cedarberg-Skurweberge | 2 | 18 | 75 | 335 | 18 | 5 | Cedarberg/ Groot Wintershoek | NWPC | |
| 8.4 | Remainder | 2 | 3 | 3 | 3 | 0 | 0 | outside | Outside | |
| 9 | Peninsula | 3 | 29 | 145 | 801 | 162 | 87 | Peninsula | Outside | |
| 10 | RZE | 6 | 29 | 148 | 1061 | 199 | 79 | Frenchhoek | SWPC | |
| 11 | Nieuwoudtville Plateau | 4 | 34 | 102 | 264 | 98 | 69 | outside | NWPC | |
| 12 | Greater Witteberg | 18 | 34 | 137 | 483 | 106 | 51 | Groot Wintershoek/ outside | KMPC/ NWPC | |
| 12.1 | Witteberg Core | 5 | 25 | 76 | 242 | 29 | 12 | Groot Wintershoek/ Karoo Mountains | KMPC | |
| 12.2 | Southwest Karoo | 2 | 24 | 49 | 96 | 18 | 11 | outside | Outside | |
| 12.3 | SE Cold Bokkeveld-North Waboomsberg | 4 | 27 | 83 | 293 | 22 | 9 | Groot Wintershoek | KMPC/ NWPC | |
| 12.4 | Karookop-Klein-Roggeveldberge | 2 | 7 | 8 | 8 | 3 | 3 | outside | Outside | |
| 12.5 | Swart Ruggens | 2 | 18 | 38 | 87 | 6 | 2 | Groot Winterhoek/ Cedarberg | NWPC | |
| 12.6 | Inverdoorn | 1 | 6 | 8 | 8 | 2 | 2 | outside | Outside | |
| 12.7 | Droekloof | 1 | 7 | 7 | 7 | 3 | 1 | outside | Outside | |
| 12.8 | North Tankwa Karoo | 1 | 6 | 7 | 7 | 1 | 1 | outside | Outside | |
| 13 | Drakensberg | 94 | 8 | 36 | 229 | 101 | 48 | Drakensberg | Outside | |
| 14 | Piketberg-Swartberg-Sandveld | 11 | 37 | 141 | 558 | 112 | 43 | North-Western | NWPC | |
| 14.1 | Piketberg | 4 | 22 | 90 | 379 | 53 | 24 | Outside | NWPC | |
| 14.2 | Swartberg-Sandveld | 4 | 34 | 107 | 324 | 40 | 9 | Outside | NWPC | |
| 14.3 | Graafwater | 1 | 14 | 28 | 60 | 2 | 2 | Outside | NWPC | |
| 14.4 | West Piketberg Sandveld | 1 | 14 | 21 | 42 | 1 | 1 | North-Western | NWPC | |
| 14.5 | Remainder | 1 | 13 | 18 | 28 | 0 | 0 | | NWPC | |

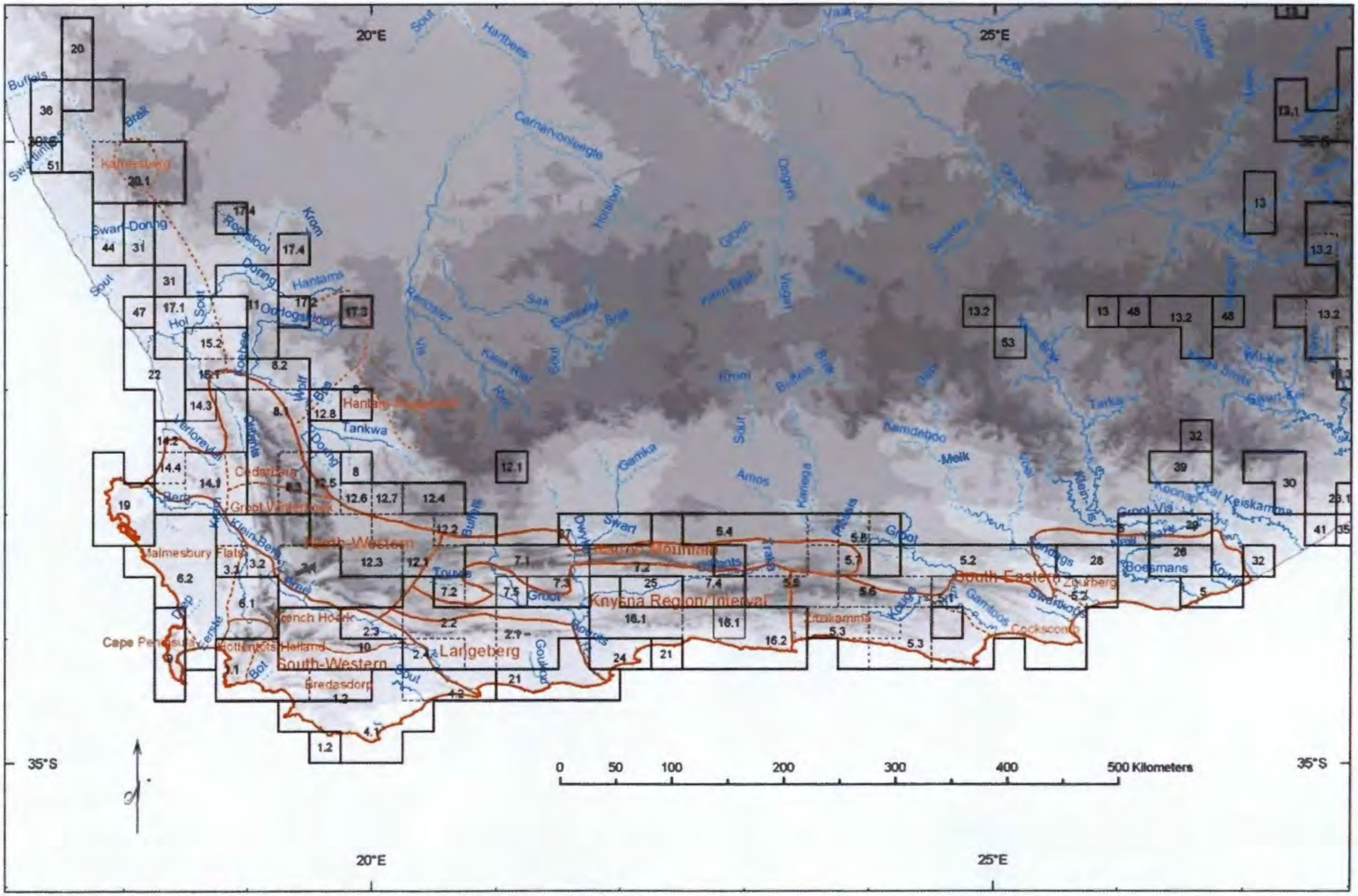

Figure 45: The similarities between my Combined Dataset and the Centres of Weimarck (1941).

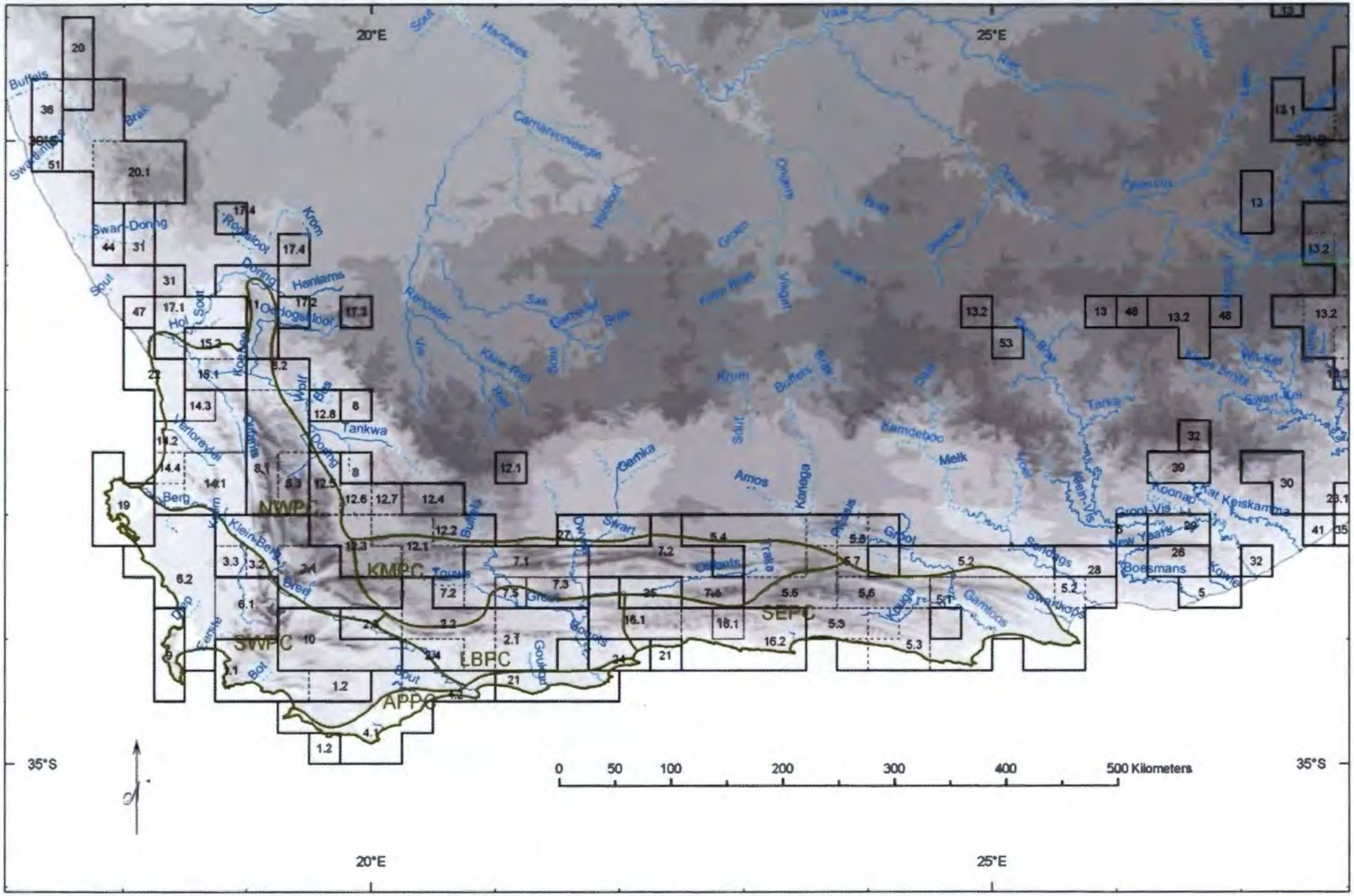

Figure 46: The similarities between my Combined Dataset and the Phytogeographical Centres of Goldblatt and Manning (2000).

## 3.5 DISCUSSION

I found that preferentially weighting my data enabled the retrieval of more optimal and efficient PCs, reducing the interference of widespread taxa (Raup and Crick, 1979; Nelson and Platnick, 1981; McCoy et al., 1986). Surprisingly, even though Linder (2001) demonstrated the benefits of weighting a few years ago, with logical theoretical and empirical arguments, no phytogeographic studies have made use of this approach. Weighting may be less critical in studies that analyse broad continental or trans-oceanic areas (Stehli and Wells, 1971), or island type areas (Trejo-Torres and Ackerman, 2001; Aguilar-Aguilar et al., 2003; Vargus et al., 2008), where OGUs are often geographically broad or taxonomically unique enough to preclude serious conflict in area relationships (Raup and Crick, 1979).

Mast and Nyffeler (2003) reported a dramatic reduction in the number of dendograms generated after using a null-model to filter out taxa that did not co-occur significantly. Caution needs to be exercised here between the benefits of improved analytical time and improved floristic patterns. In my study, although MInt weighting generated the greatest number of total characters, and nearly half the number of dendograms than the Bell: UPGMA technique, Bell: UPGMA still produced slightly more optimal choria (Table 17, Table 19, Appendix C3: Table 20). Thus, although analytical complexity and time may be reduced, this may not lead to more optimal PCs. Giokas and Sfenthourakis (2008) found that the null-model technique also resulted in fewer and smaller candidate areas of endemism. While this may be desirable for historical biogeographic analyses, it is less beneficial in chorological delimitation, requiring additional GIS refinement. However, these smaller candidate areas may be beneficial as core chorological areas, or PSCs. Practically, collector effort may also affect the levels of co-occurrence. Theoretically, null-models struggle to differentiate between closely occurring disparate biotic elements, particularly in coarse QDSs, or even larger degree squares, but may favour the numerically dominant biotic elements instead. In fynbos, this could lead to the complete dominance of TMS fynbos clade patterns over other less well-represented edaphic biotic elements (shale, granite, limestone and littoral). Thus null models may benefit most from using OGUs that reflect the habitat properties of the biotic elements (Moline and Linder, 2005), as this will reduce ecological spatial conflict among the biotic elements being analysed. This may also help identify where vicariance barriers could be shared between different edaphic/biotic elements. Whether a null model will be able to differentiate between historical or contemporary processes, shaping distributional patterns is debatable. As with PAE and other clustering techniques, historical interpretation of patterns should only be undertaken with a phylogeny, or alternative analytical techniques of proven success in interpreting/retrieving historical processes (Brookes and van Veller, 2003; Nehei, 2007; Garzón-Orduńa, Miranda-Esquivel and Donato, 2008). Without weighting, null models could still be biased to favour widespread taxa (Raup and Crick, 1979), as these are more likely to co-occur purely because their larger ranges increase the probability of overlap.

The calculation of a co-occurrence index (Mast and Nyffeler, 2003; Giokas and Sfenthourakis, 2008) was not unlike Linder's (2001) congruence index. The principle difference being that the null model co-occurrence index was taxon-based and *a priori*, and filtered out taxa that did not co-occur more than expected. While the congruence index (Linder, 2001) was *a posteriori* and chorion-based, it served to assess the amount of geographic overlap between taxa endemic within an OGU. Co-occurrence indexes were originally conceived (Raup and Crick, 1979; McCoy, Bell and Walters, 1986) as phytogeographic groupings and were based on taxon similarity between demarcated areas. My approach used taxon endemism optimality. Endemic taxa are more likely to reflect historical and current ecological properties of flora in PCs. Even PCs with a single endemic may provide interesting phytogeographic interpretation, and were thus retained by me.

I found very little difference between the relative numerical performances of the different weighting techniques that I employed (Table 17 and Table 20). My assessment of the different weighting techniques indicated that Bell: UPGMA performed slightly more optimally overall for my individual analyses, although this was not universal for every dataset in every category that I investigated (Table 19). However, this is not to say that the different analyses produced similar phytogeographical results. Inspection of the results of the Bruniaceae dataset included as an example (Figure 13, Figure 14, Figure 15, Figure 16, and Figure 17) clearly indicate phytogeographical differences between analyses. Exploring these differences in a GIS and finding consensus optimised the number of endemics in the PCs and geographic size of the PCs noticeably (Table 17 and Table 20). This is easier to do in a GIS, particularly for large datasets such as analysed here, rather than by inspection, as was undetaken by Tribsch (2004). For this reason, I would recommend an integrative approach, using multiple analyses, rather than a single analysis which maybe only marginally more optimal, or an approach whereby a single consensus tree is computed without inspection in a GIS.

Table 19: The frequencies of datasets recording the highest values in each analysis for the various optimality criterions I identified. .

| | Ranking | | | | | | |
|---|---|---|---|---|---|---|---|
| | Unw_N | Unw_W | Bell: PAE | Bell: UPGMA | Int | MInt | Combined |
| PC Endemics | - | 1 | 1 | 10 | 2 | | 13 |
| PC Richness | - | 1 | 1 | 8 | 3 | 2 | 14 |
| Number of PC s | - | - | 6 | 6 | 4 | 2 | 2 |
| PC Area | - | 1 | 3 | 7 | 1 | 3 | 14 |
| Linear Measure | 6 | 2 | 4 | - | 3 | 2 | - |
| Log Measure | - | - | 5 | 5 | 3 | 2 | 7 |
| Sum | 6 | 5 | 20 | 36 | 16 | 11 | 50 |

Although Bell-Shaped Curve Weighting has been criticised for *a posteriori* modification of its variables (Szumik et al., 2002), I found that amongst phytogeographically similar taxa, the variables only had to be "calibrated" once for highly optimal results, as was done by Linder (2001) for Restionaceae. The Int weighting technique performed slightly less optimally than the Bell: UPGMA. MInt helped compensate for the graph asymmetry (handedness) of Int using an exponential curve in skewed "unnatural" datasets like the RDL Taxa. Slight improvements to the Integration technique may be affected if more complex curves are used, such as the Fisher-Tippett distribution or the Weibull distribution. However I do not anticipate that this would alter floristic properties of the PCs significantly.

Variability between the relative numeric performances of my different techniques was less than the difference in performance in demarcating narrow or wide clusters for candidate PCs (Table 17). As I did not consider the results of the clustering techniques to be significantly different, especially when complemented by GIS refinement, the selection of a particular clustering algorithm(s) may be one of personal choice. UPGMA is more time efficient, but PAE produces more easily definable candidate PCs. Alternative clustering programmes such as Primer (Bray-Curtis Similarity) may also prove equally beneficial, and has the further advantage of accommodating far larger datasets. There were far greater gains to my optimality criteria in the assignment of OGUs to chorological units using an integrative approach with GIS analysis (Table 17). In addition, by combining the results in the GIS, it provided a spatial framework from which to investigate and pinpoint geographically conflicting data, and also aided with the retrieval of patterns in the multiple analyses, thus giving confidence that the patterns were authentic and robust. Running a single analysis would preclude this. Integrative PC retrieval may be further enhanced with other weightings such as Inverse weighting, or other novel techniques such as NDM (Szumik et al., 2002; Szumik and Goloboff, 2004), or using null-models (Raup and Crick, 1979; McCoy, Bell and Walters, 1986; Mast and Nyffeler, 2003; Giokas and Sfenthourakis, 2008). Currently, modern software generating null-models are limited to matrices of 300 by 800 (Gortelli and Entsminger, 2006) considerably smaller than many of my individual datasets, precluding its inclusion for comparison.

### 3.5.1 Phytogeographic implications for the CFR

There was good congruence in the floristic patterns retrieved from my individual analyses, facilitating the construction of consensus PCs, no doubt facilitated by the high levels of beta and gamma diversity in the CFR (Latimer, Silander and Cowling, 2005; Cowling et al., 1992; Cowling, 1990; Simmons and Cowling, 1996). My results also showed strong congruence to earlier floristic studies on the Cape Flora (Figure 45 and Figure 46; Appendix C3: Table 21), which used either intuitive (Goldblatt and Manning, 2000; Weimarck, 1941) or other computing techniques (Oliver et al., 1983). My study helped interpret differences between these earlier classifications. Thus, I am confident that my methods were appropriate, and that the floristic patterns retrieved were authentic and robust. Levels of congruence are summarised (Table 9 and Table 21) and discussed briefly. More comprehensive taxon sampling, and more intensive analytical techniques, enabled me to retrieve additional phytogeographical details than previous analyses (Goldblatt and Manning, 2000; Oliver et al., 1983; Weimarck, 1941), especially in the Langeberg and Karoo Mountain PCs. Analyses of taxonomic and functional subdivisions of my data (Appendix I: Chapters 5 to 17) helped explain differences between earlier studies. Levels of diversity and endemism largely conformed to the characteristic patterns of Levyns (1964), having their highest levels of endemism and diversity in the southwest of the CFR, with numbers gradually tapering off to the north and east.

Weimarck (1941) and Marloth (1908) analysed taxonomic datasets biased to TMS Clades, while Goldblatt and Manning (2000) used a geographic rather than a taxonomic approach. This affected boundary delimitation. Weimarck (1941) recognised areas outside a contiguous core CFR with Cape elements, which Goldblatt and Manning (2000) excluded in their study. These included areas from east of the Sundays River in the Zuurberg Sub-Centre of Weimarck (1941) (my PCs: 26, 28 and 29). Born et al., (2006) noted higher levels of endemism including these Zuurberg Sub-Centre areas with the CFR. A taxonomic approach (Marloth, 1908; Weimarck, 1941) may have enlarged the area of the CFR, and also allowed for the recognition of disjunct or satellite PCs, perhaps at the cost of neighbouring choria, while the strict geographic boundaries of Goldblatt and Manning (2000) did not. For example, Weimarck (1941) was able to identify CFR affinities in the Kamiesberg (PC 20), Hantam-Roggeveld, and Drakensberg (PC 13), while these areas were excluded from Goldblatt and Manning (2000). I found that the Nieuwoudtville Escarpment (11) and the Gifberg (15) had stronger affinities to the succulent Karoo than the core CFR (Chapter 2, Section 2.4.1.1), which was closer to the classification of Weimarck (1941), than that of Goldblatt and Manning (2000) (Table 21), although the Nieuwoudtville Escarpment (11) and the Gifberg (15) had CFR affinities, restricted to high altitude mesic sites on TMS. Further, I found that the Saldanha Peninsula showed stronger affinities to the succulent Karoo than the core CFR (Table 21, and see Chapter 2, Section 2.4.1.1), which was in agreement with the classifications of Acocks (1953) and White (1986), but conflicted with both Weimarck (1941) and Goldblatt and Manning (2000).

Differences between the taxonomic approach (Marloth, 1908; Weimarck, 1941) and the geographic approach (Goldblatt and Manning, 2000) also helped explain differences in internal CFR boundaries. Thus, for example, Weimarck (1941) grouped the Witteberg into his Northwest Centre based on TMS elements, while Goldblatt and Manning included it in their KMPC due to geophytic and succulent taxa (see Table 21). While the Cape elements are confined to mesic high altitude TMS sites, the succulent Karoo and certain geophytic elements occur in lower xeric areas, usually on richer soils. Although Weimarck (1941) identified limestone and calcareous elements in his Bredasdorp Sub-Centre, he did not designate an exclusive Agulhas Plains PC, as retrieved by Goldblatt and Manning (2000) and by myself (Table 9 and Table 21). The floristic importance of the limestone elements has only recently become apparent (Cowling, 1990; Cowling and Holmes, 1992). The use of habitat defined OGUs (Moline and Linder, 2005) may help reduce conflict in the Witteberg (12) and on the Agulhas Plains (4, 21, and 24).

The absence of sufficient data in the study of Weimarck (1941) accounted for the general lack of phytogeographical detail from the LBPC and KMPC, which I found to have numerous phytogeographical sub-units, and this may also have explained his failure to retrieve the Piketberg/ Northern Sandveld (14) phytogeographic unit. Weimarck's (1941) Knysna Interval is curious, and may partly reflect his recognition of the low altitude xeric succulent Karoo Flora and mesic forest flora in his Knysna Interval. However, my Western Southeast PC (16) had a very strong endemic Cape element, possibly indicating the lack of data available to Weimarck at the time of his map construction for this area as well. I found the Western Southeast PC (16) to have its strongest affinities to the SEPC, congruent with Goldblatt and Manning (2000) (Table 21).

### 3.5.2 Conservation Implications

The electronic list of taxa endemic to PCs that I identified can serve as an important starting point in regional conservation planning, highlighting taxa most in need of special species consideration. The list of endemics can also be used by habitat unit mappers to draw attention to the whereabouts of these special species when planners utilise habitat units for systematic conservation planning.

### 3.5.3 Conclusions

The large dataset that I analysed, with comprehensive statistical analyses, using modern chorological techniques, allowed for the recovery of additional phytogeographical detail not previously described in the CFR. I uncovered substantial congruence with previous studies. Phytogeographical conflict and differences within my study, between derivative datasets, and with previous studies, alluded to the differences in floristic/taxonomic composition (biotic elements) of the datasets analysed.

Although weighting of taxa produced substantially better phytogeographical centres, ultimately there was not very much difference between the different weighting methods that I investigated. However, Bell-Shaped Curve Weighting ($a = -0.005$, and $p = 3$) most consistently produced the best results, even if the advantages were slight. Despite possible criticism for using *a posterioiri* "calibration", I found that once calibrated ($a = -0.005$, and $p = 3$), Bell-Shaped Curve Weighting performed slightly more optimally on similar floristic taxa. In my study, Bell-Shaped Curve Weighting with the UPGMA clustering produced slightly more optimal centres than PAE, with the same weighting. However, PAE produced more easily definable candidate centres, and may be preferred from that perspective. Ultimately, there is still no objective way to define cluster sizes or candidate centres on dendograms, which can either be larger undivided clusters from PAE; or variably sized clusters from UPGMA, as there is still no objective way to determine the position of phenon-lines or cut-off values in UPGMA (nevertheless, UPGMA still performed better here). This is significant, as I found that the delimitation of narrow or wide candidate centres had a greater impact on centre optimality than the weighting technique employed. A more direct interface between clustering algorithms and a GIS may be required to resolve this.

Sizes of PCs and numbers of endemics can be substantially enhanced with further GIS interrogation, which has been largely neglected in the past. This may have more benefit for chorological studies than for candidate centres of endemism used in cladistic biogeographic analyses. The gains of GIS interrogation could offset any differences in optimality of weighting technique. However, importantly, I found that conducting multiple clustering analyses was beneficial, highlighting areas of congruence and conflict, which could then be interrogated and resolved in a GIS. Ultimately, I recommend undertaking diverse or multiple clustering analyses, the choice of which would be of personal preference, but that clustering should be supplemented by GIS interrogation.

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## 3.7 APPENDIX: Chapter 3

Table 20: Statistical summary assessment of the derivative dataset score for the different analytical techniques employed

| Dataset | # Characters | | | | | # Dendograms | | | | | # Clusters | | | | | | # Endemics | | | | | | | Diversity | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Unweighted | Bell: PAE | Bell: UPGMA | Int | MInt | Unweighted | Bell: PAE | Bell: UPGMA | Int | MInt | Unw_N | Unw_W | Bell: PAE | Bell: UPGMA | Int | MInt | Unw_N | Unw_W | Bell: PAE | Bell: UPGMA | Int | MInt | Combined | Unw_N | Unw_W | Bell: PAE | Bell: UPGMA | Int | MInt | Combined |
| Combined Data | 421 | 2265 | 2206 | 1606 | 2196 | 9999 | | 2 | 4 | 2 | 76 | 76 | 85 | 92 | 92 | 100 | 1231 | 1231 | 1165 | 1179 | 1165 | 1122 | 1567 | 4258 | 4258 | 4248 | 4270 | 4279 | 4239 | 4384 |
| Asteraceae | 80 | 397 | 385 | 515 | 553 | 840 | | 3 | 24 | 4 | 36 | 29 | 39 | 14 | 14 | 12 | 138 | 209 | 170 | 281 | 259 | 217 | 279 | 392 | 392 | 395 | 416 | 415 | 406 | 432 |
| Bruniaceae | 812 | 3054 | 3017 | 3014 | 3758 | 6144 | | 32 | 1 | 2 | 21 | 6 | 12 | 6 | 14 | 6 | 15 | 28 | 15 | 31 | 30 | 29 | 40 | 74 | 76 | 73 | 75 | 75 | 76 | 79 |
| Erica | 328 | 1490 | 1469 | 1414 | 1704 | 1872 | | 6 | 1 | 2 | 58 | 34 | 41 | 33 | 26 | 27 | 189 | 295 | 205 | 277 | 274 | 269 | 347 | 787 | 784 | 792 | 790 | 789 | 786 | 809 |
| Fabaceae | 407 | 1826 | 1826 | 1647 | 1929 | 9999 | | 9999 | 9999 | 9999 | 37 | 28 | 45 | 27 | 26 | 25 | 77 | 87 | 105 | 124 | 119 | 121 | 159 | 297 | 298 | 320 | 320 | 318 | 325 | 329 |
| Geophytes | 455 | 1502 | 1390 | 1750 | 2012 | 3200 | | 1040 | 8 | 192 | 51 | 51 | 55 | 65 | 63 | 65 | 179 | 179 | 202 | 222 | 226 | 221 | 289 | 366 | 366 | 384 | 398 | 400 | 395 | 407 |
| Orchidaceae | 139 | 362 | 349 | 814 | 839 | 9999 | | 9999 | 2 | 4 | 50 | 50 | 56 | 51 | 51 | 49 | 25 | 25 | 38 | 41 | 43 | 33 | 113 | 307 | 307 | 364 | 352 | 370 | 350 | 419 |
| Poaceae | 121 | 545 | 545 | 679 | 752 | 9999 | | 9999 | 9999 | 9999 | 51 | 51 | 21 | 59 | 40 | 39 | 14 | 14 | 20 | 27 | 24 | 24 | 63 | 105 | 105 | 118 | 125 | 120 | 120 | 138 |
| Polygalaceae | 403 | 1250 | 1281 | 2083 | 2351 | 24 | | 12 | 4 | 4 | 40 | 40 | 29 | 44 | 43 | 44 | 22 | 22 | 42 | 37 | 36 | 33 | 61 | 97 | 97 | 116 | 111 | 109 | 109 | 121 |
| Proteaceae | 1549 | 7532 | 7532 | 4582 | 7721 | 9999 | | 9999 | 9999 | 9999 | 50 | 27 | 24 | 36 | 44 | 33 | 71 | 78 | 80 | 84 | 78 | 78 | 100 | 384 | 395 | 395 | 397 | 396 | 396 | 400 |
| RDL Taxa | 348 | 1066 | 1066 | 1448 | 1709 | 1152 | | 9999 | 27 | 54 | 61 | 61 | 52 | 56 | 62 | 64 | 665 | 665 | 700 | 737 | 664 | 723 | 837 | 1522 | 1522 | 1528 | 1543 | 1531 | 1541 | 1549 |
| Restionaceae | 121 | 347 | 337 | 703 | 740 | 9999 | | 9999 | 270 | 2160 | 52 | 41 | 21 | 46 | 46 | 47 | 57 | 62 | 52 | 69 | 60 | 62 | 136 | 335 | 338 | 335 | 342 | 334 | 338 | 348 |
| Rosaceae | 279 | 1096 | 1170 | 1303 | 1521 | 9999 | | 360 | 6 | 3 | 40 | 40 | 17 | 42 | 44 | 39 | 22 | 22 | 21 | 29 | 22 | 21 | 46 | 107 | 107 | 110 | 117 | 113 | 110 | 121 |
| Rutaceae | 4478 | 17653 | 17650 | 13476 | 19898 | 2 | | 2 | 1 | 1 | 45 | 33 | 35 | 45 | 48 | 43 | 82 | 95 | 99 | 110 | 97 | 100 | 160 | 259 | 263 | 261 | 275 | 265 | 270 | 279 |
| Totals | 9941 | 40385 | 40223 | 35034 | 47683 | 83227 | | 61451 | 30345 | 32425 | 668 | 567 | 532 | 616 | 613 | 593 | 2787 | 3012 | 2914 | 3248 | 3097 | 3053 | 4197 | 9290 | 9308 | 9439 | 9531 | 9514 | 9461 | 9815 |
| Ranks | 5 | 3 | 2 | 4 | 1 | 4 | | 3 | 1 | 2 | 6 | 2 | 1 | 5 | 4 | 3 | 7 | 5 | 6 | 2 | 3 | 4 | 1 | 7 | 6 | 5 | 2 | 3 | 4 | 1 |

| Dataset | # PCs | | | | | | | # QDS in PCs | | | | | | | Linear Meassure | | | | | | | Log Meassure | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Unw_N | Unw_W | Bell: PAE | Bell: UPGMA | Int | MInt | Combined | Un_N | Unw_W | Bell: PAE | Bell: UPGMA | Int | MInt | Combined | Unw_N | Unw_W | Bell: PAE | Bell: UPGMA | Int | MInt | Combined | Unw_N | Unw_W | Bell: PAE | Bell: UPGMA | Int | MInt | Combined |
| Combined Data | 62 | 62 | 72 | 79 | 82 | 83 | 58 | 226 | 226 | 230 | 246 | 239 | 230 | 432 | 0.079 | 0.079 | 0.086 | 0.089 | 0.093 | 0.096 | 0.048 | 3.480 | 3.480 | 3.828 | 4.205 | 4.315 | 4.260 | 3.817 |
| Asteraceae | 31 | 24 | 41 | 14 | 13 | 12 | 33 | 78 | 92 | 117 | 130 | 124 | 119 | 174 | 0.140 | 0.139 | 0.151 | 0.073 | 0.065 | 0.054 | 0.122 | 2.328 | 2.688 | 3.628 | 1.926 | 1.659 | 1.317 | 4.232 |
| Bruniaceae | 8 | 4 | 9 | 4 | 5 | 5 | 7 | 25 | 44 | 30 | 41 | 41 | 48 | 62 | 0.065 | 0.033 | 0.062 | 0.040 | 0.049 | 0.040 | 0.057 | 0.387 | 0.332 | 0.433 | 0.375 | 0.454 | 0.426 | 0.772 |
| Erica | 23 | 14 | 28 | 18 | 17 | 15 | 18 | 78 | 97 | 122 | 99 | 94 | 124 | 264 | 0.071 | 0.054 | 0.059 | 0.064 | 0.063 | 0.041 | 0.029 | 1.178 | 1.101 | 1.484 | 1.317 | 1.238 | 1.050 | 1.480 |
| Fabaceae | 23 | 17 | 31 | 21 | 19 | 22 | 20 | 63 | 69 | 104 | 114 | 95 | 114 | 154 | 0.095 | 0.072 | 0.098 | 0.071 | 0.075 | 0.072 | 0.063 | 1.298 | 1.071 | 2.113 | 1.677 | 1.489 | 1.688 | 1.940 |
| Geophytes | 29 | 29 | 45 | 47 | 48 | 46 | 32 | 92 | 92 | 134 | 144 | 143 | 137 | 205 | 0.154 | 0.154 | 0.177 | 0.182 | 0.190 | 0.188 | 0.111 | 2.980 | 2.980 | 4.808 | 5.292 | 5.477 | 5.218 | 4.449 |
| Orchidaceae | 13 | 13 | 22 | 15 | 14 | 13 | 16 | 29 | 29 | 52 | 54 | 60 | 46 | 207 | 0.037 | 0.037 | 0.044 | 0.032 | 0.027 | 0.027 | 0.021 | 0.249 | 0.249 | 0.509 | 0.386 | 0.356 | 0.275 | 0.844 |
| Poaceae | 11 | 11 | 15 | 17 | 14 | 14 | 21 | 16 | 16 | 43 | 41 | 33 | 33 | 229 | 0.092 | 0.092 | 0.059 | 0.090 | 0.085 | 0.085 | 0.042 | 0.367 | 0.367 | 0.574 | 0.833 | 0.649 | 0.649 | 1.859 |
| Polygalaceae | 11 | 11 | 18 | 19 | 19 | 15 | 12 | 22 | 22 | 58 | 55 | 45 | 41 | 100 | 0.113 | 0.113 | 0.112 | 0.115 | 0.139 | 0.111 | 0.060 | 0.603 | 0.603 | 1.429 | 1.396 | 1.410 | 1.030 | 1.261 |
| Proteaceae | 17 | 17 | 20 | 19 | 20 | 20 | 20 | 55 | 87 | 77 | 85 | 72 | 72 | 130 | 0.057 | 0.039 | 0.053 | 0.047 | 0.055 | 0.055 | 0.038 | 0.693 | 0.709 | 0.865 | 0.851 | 0.847 | 0.847 | 1.018 |
| RDL Taxa | 56 | 56 | 52 | 52 | 50 | 57 | 31 | 157 | 157 | 178 | 192 | 157 | 176 | 205 | 0.156 | 0.156 | 0.134 | 0.129 | 0.138 | 0.152 | 0.082 | 4.902 | 4.902 | 4.721 | 4.890 | 4.344 | 5.305 | 3.280 |
| Restionaceae | 15 | 14 | 16 | 18 | 17 | 16 | 14 | 38 | 48 | 47 | 64 | 46 | 48 | 106 | 0.067 | 0.054 | 0.053 | 0.057 | 0.066 | 0.061 | 0.052 | 0.583 | 0.574 | 0.556 | 0.789 | 0.685 | 0.656 | 1.135 |
| Rosaceae | 9 | 9 | 12 | 13 | 13 | 12 | 14 | 32 | 32 | 36 | 49 | 35 | 32 | 140 | 0.058 | 0.058 | 0.064 | 0.066 | 0.072 | 0.072 | 0.038 | 0.430 | 0.430 | 0.526 | 0.718 | 0.583 | 0.533 | 1.077 |
| Rutaceae | 24 | 18 | 23 | 30 | 26 | 26 | 21 | 64 | 74 | 73 | 102 | 80 | 87 | 146 | 0.119 | 0.088 | 0.120 | 0.118 | 0.119 | 0.111 | 0.082 | 1.651 | 1.394 | 1.872 | 2.498 | 2.025 | 2.034 | 2.428 |
| Totals | 332 | 299 | 404 | 366 | 357 | 356 | 317 | 975 | 1085 | 1301 | 1416 | 1264 | 1307 | 2554 | 1.30 | 1.17 | 1.27 | 1.17 | 1.24 | 1.16 | 0.85 | 21.13 | 20.88 | 27.35 | 27.15 | 25.53 | 25.28 | 29.59 |
| Ranks | 5 | 7 | 1 | 2 | 3 | 4 | 6 | 1 | 2 | 4 | 6 | 3 | 5 | 7 | 1 | 5 | 2 | 4 | 3 | 6 | 7 | 6 | 7 | 2 | 3 | 4 | 5 | 1 |

Table 21: % Area overlap between the PCs identified in my study, and those of Weimarck (1941), and Goldblatt and Manning (2000).

| | | Weimarck (1941) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Row Labels** | **South-Western** | **North-Western** | **Langeberg** | **Karroo Mountain** | | **Knysna Interval** | **South-Eastern** | **Outside** | **Total $Km^2$** |
| SWPP | Hottentots-Kleinrivier | 100.0 | | | | | | | | 3556.2 |
| | Peninsula | 100.0 | | | | | | | | 546.1 |
| | Stellenbosch-Bainskloof Mtns and Sandveld | 100.0 | | | | | | | | 7058.1 |
| | RZE | 99.9 | 0.1 | | | | | | | 3841 |
| APPP | Agulhas Plains | 87.2 | | 12.8 | | | | | | 4486 |
| | East Agulhas Plain | | | 82.1 | | | 17.9 | | | 2039.2 |
| | Far East Agulhas Plain | | | 0.1 | | | 99.9 | | | 983.6 |
| NWPP | Groot Winterhoek-West Langeberg | 27.8 | 71.7 | | | | 0.5 | | | 7093.8 |
| | Cedarberg | | 56.8 | | | | | | 43.2 | 7826.7 |
| | Piketberg-Swartberg-Sandveld | 10.8 | 64.7 | | | | | | 24.5 | 6856.9 |
| | Greater Witteberg | | 42.8 | | 9.7 | | 0.1 | | 47.3 | 11009.2 |
| | Greater Langeberg | 15.8 | 3.1 | 57.1 | 2.4 | | 21.7 | | | 8972.2 |
| | Karoo Mtn Centre | | | | 48.0 | | 45.1 | | 6.9 | 10310.1 |
| SE | West Southeastern Centre | | | | | | 93.8 | 6.2 | | 5657.3 |
| | Southeastern Centre | | | | 9.1 | | 4.7 | 51.3 | 34.9 | 25526.4 |
| gK | East Little Karoo | | | | | | 100.0 | | | 1286.5 |
| | South Groot Karoo | | | | 4.9 | | | | 95.1 | 1940.5 |
| wC | Saldanha Peninsula | 99.3 | 0.7 | | | | | | | 1499.4 |
| | West Coast | | | | | | | | 100.0 | 1421.1 |
| sSK | Gifberg | | 17.2 | | | | | | 82.8 | 2626.5 |
| | Nieuwoudtville Plateau | | | | | | | | 100.0 | 2638.6 |
| | Vanrhynsdorp | | | | | | | | 100.0 | 2635.1 |
| SR | East Suurberg | | | | | | | 100.0 | | 1290.1 |
| | South Grahamstown | | | | | | | 100.0 | | 1290.1 |
| | North Grahamstown | | | | | | | 30.8 | 69.2 | 1293.8 |
| | Grand Total ($Km^2$) | 24534.9 | 19456.7 | 7366.6 | 9723.5 | | 15908.5 | 20434.9 | 31505.3 | 128930.4 |

| | | Goldblatt and Manning (2000) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Row Labels** | **Southwest** | **Northwest** | **Langeberg** | **Karoo Mountain** | **Agulhas Plain** | | **Southeast** | **Outside** | **Total $Km^2$** |
| SWPP | Hottentots-Kleinrivier | 99.3 | | | | 0.7 | | | | 3556.3 |
| | Peninsula | 100.0 | | | | | | | | 546.1 |
| | Stellenbosch-Bainskloof Mtns and Sandveld | 99.8 | 0.2 | | | | | | | 7058.1 |
| | RZE | 97.8 | 2.2 | | | | | | | 3840.9 |
| APPP | Agulhas Plains | 46.5 | | 6.5 | | 47.0 | | | | 4486.1 |
| | East Agulhas Plain | | | 34.0 | | 59.3 | | 6.7 | | 2039.1 |
| | Far East Agulhas Plain | | | 73.2 | | 15.7 | | 11.1 | | 983.6 |
| NWPP | Groot Winterhoek-West Langeberg | 21.7 | 68.0 | | 10.3 | | | | | 7093.7 |
| | Cedarberg | | 67.3 | | | | | | 32.7 | 7826.7 |
| | Piketberg-Swartberg-Sandveld | 4.2 | 95.8 | | | | | | | 6857 |
| | Greater Witteberg | | 18.9 | | 27.3 | | | | 53.8 | 11009.2 |
| | Greater Langeberg | 11.8 | 3.7 | 66.0 | 18.5 | | | | | 8972.2 |
| | Karoo Mtn Centre | | | 9.7 | 84.0 | | | 2.1 | 4.2 | 10309.9 |
| SE | West South-eastern Centre | | | 17.9 | 6.6 | | | 75.4 | | 5657.2 |
| | South-eastern Centre | | | | 9.6 | | | 48.2 | 42.2 | 25526.5 |
| gK | East Little Karoo | | | 3.7 | 57.9 | | | 38.4 | | 1286.5 |
| | South Groot Karoo | | | | 20.1 | | | | 79.9 | 1940.6 |
| wC | Saldanha Peninsula | 92.9 | 7.1 | | | | | | | 1499.4 |
| | West Coast | | 84.6 | | | | | | 15.4 | 1421.1 |
| sSK | Gifberg | | 70.0 | | | | | | 30.0 | 2626.5 |
| | Nieuwoudtville Plateau | | 48.7 | | | | | | 51.3 | 2638.5 |
| | Vanrhynsdorp | | 19.0 | | | | | | 81.0 | 2635.2 |
| SR | South Grahamstown | | | | | | | | 100.0 | 1290.1 |
| | East Suurberg | | | | | | | | 100.0 | 1290.1 |
| | North Grahamstown | | | | | | | | 100.0 | 1293.7 |
| | Grand Total ($Km^2$) | 21247.1 | 24164.4 | 9692.7 | 18922.3 | 3497.1 | | 18214.9 | 29605 | 125343.5 |

Abbreviations: PP Phytogeographical Province; SW Southwest; NW Northwest; SE Southeast; gK Great Karoo; wC west Coast; sSK south Succulent Karoo; SR Summer Rainfall

# Chapter 4: Environmental Correlates of Richness in the Cape Floristic Region

## 4.1 ABSTRACT

Aim: The primary aim of this study was to test the energy-water or habitat heterogeneity hypotheses as explanations of patterns of plant species richness in the Cape Floristic Region (CFR). Secondly, I evaluated the effects of different types of input data (random units versus non-random chorial units), and floristic datasets. Thirdly, I investigated which analytical method (GWR or OLS) performed best. Non-stationarity and spatial auto-correlation were also investigated.
Location: The Cape Floristic Region, southwestern South Africa.
Methods: Patterns of taxon and endemism richness where analysed using Geographically Weighted Regression (GWR), a spatially sensitive regression technique, and were compared to the results of "global" ordinary least squares (OLS). To assess how different geographic input units and floristic differences would affect the model, two types of geographic input units, and four derivative floristic datasets were analysed. Climatic and habitat heterogeneity parameters used in previous correlation studies were supplemented by additional variables. Spatial non-stationarity was investigated and depicted on maps using pseudo-t values. Spatial auto-correlation was quantified for input variables and model residuals, and displayed in spatial correlograms with progressive Bonferroni correction.
Results: Variables of the energy-water hypothesis (Potential evapo-transpiration – negative correlation with richness; length of uninterrupted growth season – positive; rainfall concentration – positive and negative; average altitude (equivalent to mean annual minimum temperature) – negative) and habitat heterogeneity hypothesis (altitudinal variance – positive correlation; slope – positive; topographic diversity index – positive; length of rainfall gradient – positive; July temperature range – positive; number of vegetation units – positive; area of fynbos area – positive, and area of TMS/Witteberg substrate – positive) performed as expected from the literature, but displayed considerable spatial non-stationarity. It was found that using different input units with the same data, or analysing floristic derivatives of a dataset invoked different models. GWR Models showed high adjusted $r^2$ values (78.3-91.2%), indicating good explanatory power, and performed better than OLS models. GWR successfully annulled the effects of spatial auto-correlation of model residuals.
Main Conclusions: Both the energy-water hypothesis as well as the habitat heterogeneity hypothesis in the CFR, are important as they help explain richness in the CFR. Potential evapo-transpiration and various measures of topographic heterogeneity provided much explanatory power. The use of GWR facilitated the correlation of richness with growth season length (GRS) for the first time in the CFR, which has its strongest influence in the winter rainfall portion of the CFR, and which contain high numbers of annuals and geophytes. Caution should be exercised in comparing different studies, using different input units, and analysing different floristic/structural/functional components of flora, as different models may be invoked. The effects of spatial non-stationarity should also result in caution when selecting dependent variables and study areas that are too heterogeneous for global regression models, as complex functions may be required to explain seemingly anomalous richness patterns, from differentially adapted taxa (for example, combining succulent and tree taxa).

Keywords: Geographically Weighted Regression (GWR); Cape Floristic Region (CFR); fynbos, habitat heterogeneity hypothesis; species-energy hypothesis.

## 4.2 INTRODUCTION

Attempting to explain the apparent patterns of taxon richness in different areas of the globe has been one of the great preoccupations of many eminent biologists, for example, Alexander von Humboldt (1769-1859) and Alfred Russel Wallace (1823-1913) (for a review, see Gaston, 2000). However, although progress has been made, nearly two centuries of research has not resulted in a universally accepted hypothesis (Gaston, 2000).

The complexity and uniqueness of individual areas and the scale of analyses are confounding problems (Gaston, 2000). At the global scale, richness is generally negatively correlated with latitude, primarily due the amount of solar energy available, with adjustments for continentality (for a review see Gaston, 2000; Currie et al., 2004; Kreft and Jetz, 2007). The generality of the equator to poles richness gradient has been closely scrutinised (Stevens, 1989; Currie, 1991; Currie et al., 1999), and there are notable deviations, particularly in Mediterranean areas, such as the CFR (Gentry, 1986; Cody, 1986; Major, 1988). Local climate and terrestrial surface morphology further modify this gross latitudinal gradient, contributing to form distinct floristic regions with unique histories, with various hierarchical subdivisions of biotas, from global (for example, the Holarctic) to regional scales (Good, 1974; Takhtajan, 1986). The great variability in species richness between these regions is one of the notable discrepancies in the distribution of taxon richness (Currie, 1991). A number of attempts have been made to determine which environmental parameters determine these patterns (for reviews see Gaston, 2000; Currie et al., 1999; Kreft and Jetz, 2007).

A synopsis of these competing hypotheses is provided by Currie (1991) and Gaston (2000), and contextualised for South African plants by Cowling et al., (1997), so this will not be repeated in detail here. Briefly, environmental explanatory variables for taxon richness are derived from climate, abiotic (physical environment, topography) and biotic (vegetation unit frequency, vegetation structure, competition, predation) properties. Theoretically, environmental explanatory variables fall into the following paradigms or hypotheses: 1) Heterogeneity (spatial, scale dependant); 2) Energy-Water (light, temperature and rainfall, affecting photosynthesis and productivity); 3) Favourableness (predictability of temporal heterogeneity, environmental harshness) which could be a subset of the energy-water hypothesis; and 4) History (geological time scales; Cowling et al., 2008). It is generally accepted that one variable can be classified in several different hypotheses (Currie, 1991; Cowling et al., 1997; Gaston, 2000; Thuiller et al., 2006). Due to this, and to the causal and/or collinear (whether statistical or theoretical) relationship between these variables, it is perhaps not as important to over interpret the importance of individual variables, but to rather understand the general hypothesis, which the variable advocates.

Early models for interpreting richness in southern Africa were relatively simple, limited by the analytical techniques available, computational ability, and the resolution and availability of environmental data. Linder (1991), using a uniformly sized grid (ca. 650 km$^2$), found that the primary determinant of diversity, in a relatively restricted area in the Southwest Phytogeographical Province (SWPP) of the Cape Floristic Region (CFR), was mean annual precipitation (MAP). However, by sub-dividing the dataset along taxonomic lines, Linder (1991) found altitude to be the best explanatory variable for Ericaceae, and that the number of substrate types was only significant in Restionaceae. Linder (1991), using a crude map by Moll et al., (1984), found that the number of vegetation types did not produce any significant correlation with richness. Hoffman et al., (1994) analysed the effects of mean annual precipitation (MAP) and potential evapo-transpiration (PET) and terrestrial area (henceforth referred to as "area") among 1260 sites of physiographically homogenous units across South Africa, ranging in size from ca. 1000 km$^2$ to 70000 km$^2$. Hoffman et al., (1994) found PET to have twice the explanatory power of MAP, while area alone was not a significant correlate. Cowling et al., (1997) undertook an analysis of plant richness data, from 63 sites across South Africa. This was undertaken against a comprehensive suite of 12 variables, including various climatic variables, topographic diversity index, and area. Regional richness data were analysed across South Africa, as a whole, and in individual biomes, resulting in the identification of biome-specific explanatory variables. Cowling et al., (1997) found the strongest multiple regression correlations for fynbos diversity with rainfall concentration, and rainfall coefficient of variation for the wettest three months of the year. Additionally, they found that area, and the heterogeneity variables: topographic diversity index, rainfall range, and July temperature range, were important in explaining plant diversity in fynbos, in their simple regressions. Thuiller et al., (2006) used Boosted Tree Regression (BTR) to analyse how nine explanatory variables explained patterns of QDS taxon richness across South Africa, and within geographical subsets defined by biomes. As with Cowling et al., (1997), the suite and contributions of explanatory variables varied between biomes. Although Thuiller et al., (2006) found that the altitudinal heterogeneity index was the most important variable nationally, in the Fynbos Biome, the three most important variables were (in decreasing order of influence): 1) mean annual precipitation (accounting for 31% of variation in richness), 2) net primary productivity (23%), and 3) their altitudinal heterogeneity index (20%). O'Brien's (1993) approach was slightly different, by selecting a single guild, trees/shrubs, to analyse richness patterns in southern Africa. She invoked a negative parabolic relationship to PET and a positive linear relationship to mean annual precipitation. O'Brien et al., (2000) later refined the model by adding topographic range to account for under prediction of their model in areas of high relief, and over prediction in areas of low relief.

Although PET has proved a useful explanatory variable at a globally level (Kreft and Jetz, 2007); and in both North America (Currie, 1991) and southern Africa (O'Brien et al., 1993; O'Brien et al., 2000), its relationship differs fundamentally in these latter two areas (Hoffman et al., 1994; Hawkins et al., 2003a). In North America, positive relationships have been observed (Currie, 1991; Hawkins et al., 2003a), while in southern Africa negative relationships have been seen (O'Brien et al., 1993; Hoffman et al., 1994; Cowling et al., 1997; Hawkins et al., 2003a). This is generally due to different factors limiting production (biomass accumulation). In North America, low temperatures have an inhibiting effect on production, and lower PET; while in southern Africa, temperatures are usually higher, but production is rather limited by water availability (Hawkins et al., 2003a). Thus, in many studies in southern Africa, measures of water abundance or availability (Linder, 1991; O'Brien et al., 1993; Cowling et al., 1997; Thuiller et al., 2006) are often incorporated into models. Thus, MAP is not only a variable of favourableness, but also indirectly of usable or convertible energy in southern Africa. Globally, PET is positively correlated with richness (Kreft and Jetz, 2007), highlighting the importance of the extent of the study area.

As science and technology advance, analytical techniques are becoming increasingly complex (see Dormann et al., 2007), and are better able to deal with potential pitfalls such as collinearity and spatial auto-correlation among the burgeoning array of independent variables (Legendre, 1993; Lennon, 2000; Dormann et al., 2007) and within models (Diniz-Filho et al., 2003; Dormann et al., 2007; Kreft and Jetz, 2007). A relatively recent technique is Geographically Weighted Regression (GWR) (Fotheringham et al., 2002). GWR was developed to explore and account for the spatial non-stationarity of the influence of independent explanatory variables across a study area. Non-stationarity means that the influence of the values of an explanatory (independent) variable, on the dependent variable (richness), varies in different geographic locations of the study area, and is thus spatially sensitive. For example, a 500 metre change in altitude on a coastal mountain has a different affect on richness than a 500 metre altitude, hundreds of kilometres inland. GWR takes this into account by differentially decreasing the contribution of data points to the regression the more distant they are from data point under consideration. Ultimately, distant data points could contribute nothing to the regression at a particular point, depending on the distance, referred to as the bandwidth, and determined by the GWR programme (Fotheringham, 2002). Thus, GWR represents a local, rather than global fitting regression. The geographic specificity of the regression coefficients did not allow for prediction outside the study area (Dormann et al., 2007), but my intention was not to devise a general/global predictive model (*sensu* O'Brien et al., 1993; O'Brien et al., 2000), but rather to seek to understand which environmental variables and hypotheses might explain richness patterns within the remarkably diverse and endemic rich CFR.

The primary aim of this study was to determine which environmental parameters best explained diversity and endemism richness, of both total taxa and fynbos taxa in the CFR. Thus, I divided the dataset into floristic sub-sets, to assess whether these different floristic components required different suites of explanatory variables. Subsidiary objectives were to determine whether the GWR offered improvement over previous analyses, whether there were notable patterns of non-stationarity in variable influence, and whether GWR offered additional insights (or invoked different variables) to explain the exceptionally high diversity and endemism in the CFR (Goldblatt, 1978; Goldblatt and Manning, 2000, 2002; Kreft and Jetz, 2007), which was mostly equivalent to the fynbos biome (Cowling et al., 1992; Cowling et al., 1997). The impacts of spatial auto-correlation have been somewhat neglected in southern Africa, while non-stationarity has not been considered before, and was explored here for the first time in the CFR. Further, I analysed the effects of the input data, using random, essentially uniformly sized grid cells (QDS), and irregular, floristically non-random input data.

The CFR is an ideal area to study the relationship between richness and explanatory variables because it is relatively well known and explored botanically (Goldblatt, 1978; Goldblatt and Manning, 2000, 2002), with well sampled grids. Previous correlation research has been undertaken here, which allows for a comparison of numerous independent global regression techniques (Linder, 1991; Hofmann et al., 1994; Cowling et al., 1997). In addition, there are high levels of diversity and endemism with high turn-over (Cowling et al., 1992; Cowling et al., 1997; Kreft and Jetz, 2007) along steep gradients (Goldblatt and Manning, 2000, 2002; Cowling et al., 2008), resulting in abrupt changes in richness.

## 4.3 METHODS

### 4.3.1 Datasets

The dataset that was recently used to identify PCs in the CFR (Section 2.3.1.1) was used in the present study to identify environmental variables that could explain diversity richness and endemism richness in the CFR. The data were derived from a variety of sources (outlined in Section 2.3.1.3), including previous biogeographical studies (such as Oliver et al., 1983), taxon specialists, the South African Plant Red Data List (RDL) and the Protea Atlas Project, taxonomic monographs and herbaria. The CFR contains 9087 species (Goldblatt, Manning and Snijman, 2008). This study focused on taxa in the core CFR, and included 4053 taxa (31966 records) in the QDS analyses, and 4051 taxa (31740 records) in the Phytogeographical Sub-Centre (PSC) analysis. Raw data were captured and analysed at the QDS scale of resolution (Edwards and Leistner, 1971). The dependant floristic variables (Table 1) were fourth root transformed to decrease heteroscedasticity of the residuals (Sokal and Rohlf, 1995).

I did not exclude unequally sized coastal grids, as have others (O'Brien et al., 1993; O'Brien et al., 2000; Van Rensburg et al., 2002; Van Rensburg et al., 2004), as many of the highest diversity QDSs and PSCs in the CFR occur along the coast, for example, in the Hottentots-Holland, Kogelberg and Cape Peninsula. As has been well established, diversity and endemism are usually positively correlated with area globally (Exell and Gonçlaves, 1974; Harte and Kinzig, 1997) as well as in the CFR (Chapter 2, Section 2.4.3), terrestrial area was incorporated as an explanatory variable in the analysis. Area is usually interpreted as a surrogate for heterogeneity (Rosenweig, 1995; Cowling et al., 1997), and is thus conceptually similar to my vegetation count variable (Table 23). Further, habitat specific area measures were also included, such as the fynbos biome area, and the TMS/Witteberg substrate area.

I divided the original dataset into four floristic derivatives: 1) Total Diversity, 2) Total Endemism, 3) Fynbos Diversity, and 4) Fynbos Endemism. This was done in order to investigate whether these floristic differences could be explained by different explanatory variables. The derivative datasets are summarised in Table 1. Shrub or shrub-like genera (excluding succulents) with at least 50% of their taxa endemic to the CFR were assigned to the Fynbos datasets. Although not exhaustive in the classification of taxa to the Fynbos datasets, fynbos specific patterns should nevertheless emerge if significantly different.

I undertook the analysis using two types of input data, or Operational Geographic Units (OGUs) (Crovello, 1981) (Table 1): firstly, using QDSs, and secondly, using the PSCs that were identified earlier (Chapter 2). I chose to use the PSCs rather than PCs to increase habitat uniformity (for example, separating the Stellenbosch Mountains from the Southern Sandveld), and to reduce the geographic extent of certain PCs (the Southeast PC) to make them more comparable to other PCs. Whereas QDSs represented random OGUs (Crovello, 1981), PSCs represented non-random clustering of QDSs based on floristic similarity. PSC are conceptually similar to the global floristic units of Kreft and Jetz (2007), but at a sub-regional scale. I thus investigated the strength of the relationship between diversity and endemism at these different spatial scales, and whether different environmental parameters were required to explain these different dataset derivatives. The biotic and abiotic properties of 214 QDSs where analysed, with an average size of 560.2 km$^2$, and a standard deviation of 177.0 km$^2$. The PSC analysis consisted of 56 OGUs, with an average size of 2034.5 km$^2$, and a standard deviation of 1213.2 km$^2$. Due to the differences in size between the QDSs and PSCs that I used, aspects of scale may have also influenced the composition of the models. However, this was not investigated formally here.

Table 22: Derivative floristic datasets and sizes analysed in the different geographic input types.

| Floristic Dataset Derivative | QDS | Phytogeographic Sub-Centres (PSC) |
|---|---|---|
| Total Diversity | Summed frequency of all taxa occurring in a QDS (4053 taxa) | Summed frequency of all taxa in a PSC (4051 taxa) |
| Total Endemism | Summed frequency of CFR endemics occurring in a QDS (3613 taxa) | Summed frequency of all taxa endemic to a PSC (1196 taxa) |
| Fynbos Diversity | Summed frequency of fynbos taxa occurring in a QDS (3096 taxa) | Summed frequency of fynbos taxa occurring in a PSC (3095 taxa) |
| Fynbos Endemism | Summed frequency of fynbos CFR endemics occurring in a QDS (2774 taxa) | Summed frequency of fynbos taxa endemic to a PSC (775 taxa) |

Mapped OGU richness values of the different floristic dataset derivatives are provided in Appendix C4 (Figure 52), for comparative purposes, and to help with regression interpretation.

### 4.3.2 Choice of Technique (GWR)

Considerations of non-stationarity (Brunsdon et al., 1998; Fotheringham et al., 2002) and spatial auto-correlation (Legendre, 1993; Lennon, 2000; Diniz-Filho et al., 2003; Jetz et al., 2005) led me to select Geographically Weighted Regression (GWR) as an appropriate analytical technique (Osborne et al., 2007, Bickford and Laffan, 2006, Wang et al., 2005, Foody, 2004, Fotheringham et al., 2002) to explore the relationship between diversity and endemism richness and environmental explanatory variables. GWR is a spatially sensitive local regression analysis, as opposed to global regression, which allows for non-stationarity of variables. Non-stationarity means that the influence of the explanatory variables may vary geographically across the study area. GWR has also been shown to sufficiently account for the effects of spatial auto-correlation (Fotheringham et al., 2002, Brunsdon et al., 2002, Wang et al., 2005, Osborne et al., 2007, Cassemiro et al., 2007, Propastin et al., 2006, Propastin et al., 2007, Zhang et al., 2008). However, some concerns have been raised with this statistical component of GWR (Leung et al., 2000, Jetz, 2005, Austin, 2007). Thus, spatial autocorrelation was measured in the explanatory variables utilised, and for the model residuals, using Moran's *I* coefficient, and displayed in spatial correlograms (Legendre and Legendre, 1998), using Spatial Analysis in Macroecology software (SAM v3.0) (Rangel et al., 2006). The significance tests of Moran's *I* coefficient were calculated using Monte Carlo permutation tests (1000 randomisations), and adjusted using progressive Bonferroni corrections (Legendre and Legendre, 1998).

The theoretical and mathematical implications of GWR have been extensively covered in the literature (Fotheringham et al., 2002; Foody, 2004; Foody, 2005; Osborne et al., 2007; Wimberly et al., 2008), and will not be discussed in detail here.

For my GWR analysis, I made use of a Gaussian model, with bi-square adaptive kernel, with bandwidth determined by AIC minimisation. I invoked the adaptive kernel to ameliorate edge effects on the boundary of the study area, to account for any spatial gaps in the data, and to maintain equal sample size in the PSC analyses where data points where not uniformly spaced. GWR analysis was undertaken using the GWR 3.0 software available at http://ncg.nuim.ie/ncg/GWR/software.htm (Fotheringham et al., 2002).

Table 23: List of Environmental Explanatory variables considered for model construction, listed according to the hypothesis they support.

| Hypothesis Variable | Abbreviation | Derivation | Unit of Measure | Derivation and/or source [examples of SA richness studies using similar variables] |
|---|---|---|---|---|
| **Heterogeneity Hypothesis** | | | | |
| Average Altitude | Alt_Ave | Averaged for all grid point | m | Kerr et al., 2001 |
| Topographic Diversity | TD1 | Coefficient of variation of all the grid altitude values | % | (van Rensburg et al., 2002). Cowling[a] et al., 1997- [(van Rensburg et al., 2004, Richardson et al., 2005)] |
| Length of altitude gradient | Alt_R | Difference between the highest and lowest SRTM90 (Jarvis et al., 2006) grid point | m | Linder, 1991; O'Brien et al., 2000 |
| Average Slope | Slope | Ave. Slope values computed from SRTM90 using Spatial Analyst in ArcView 3.3 (ESRI, 2000) | | |
| Topographic Heterogeneity | Alt_Var | Topographic variance in a 7 QDS square roving window in IDRISI | | DEAT, 2008, unpublished |
| Length of Rainfall gradient | RAR | Difference between the highest and lowest MAR grid points | mm | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 |
| Length of Temp gradient | RWT | Difference between the highest and lowest July min day temperature | °C | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 – [(van Rensburg et al., 2002, Thuiller et al., 2006)] |
| Vegetation Count | Veg_C | Count of Vegetation Units (from Mucina and Rutherford, 2006) | | Mucina and Rutherford, 2006 – [(van Rensburg et al., 2002, Botes et al., 2007)] |
| Vegetation Evenness | Veg_E | Shannon-Weinner Evenness applied to veg. area | | van Rensburg[a] et al., 2002 |
| Geology Count | Geol_C | Count of ENPAT substrate (STRATPARNA) types | | |
| Geology Evenness | Geol_E | Shannon-Weinner Evenness applied to ENPAT substrate (STRATPARNA) area | | |
| Terrestrial OGU Area | T_Area | Terrestrial extent of OGU Area | Km$^2$ | Cowling[a] et al., 1997 |
| Fynbos Area | Fynbos Area | Fynbos Biome Area in OGU | Km$^2$ | |
| TMS-Witteberg Area | TMS_Witte_A | TMS-Witteberg substrate area in OGU | Km$^2$ | |
| **Energy-Water/Productivity/Favourableness Hypothesis** | | | | |
| Mean Annual Precipitation | MAP | Ave for all grid points | mm | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 – [(van Rensburg et al., 2002, O'Brien, 1993)] |
| Potential Evaporation | PEV | Yearly average from gridded A-pan values | mm | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 – [(Richardson et al., 2005)] |
| Potential Evapo-transpiration | PET | FAO Penman - Montheith (1992) Method | mm | |
| Growing Season duration | GRS | Number of consecutive days where daily mean rainfall exceeds daily PEV | days | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 |
| Primary Production | PRM_PRD | Computed as the generic (i.e. non-biome specific) net above-ground primary production based on Rosenweig's (1968) equation and determined for a July-June season over a 30-100 year period | t.ha$^{-1}$.yr$^{-1}$ | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 –[(Thuiller et al., 2006)] |
| July Water Soil Stress | H2O_Stress | July Soil Water Stress Percent Days Under Stress | % | Schulze,1997b – [(Thuiller et al., 2006)] |
| Solar Radiation | SRAD | Mean annual solar radiation | MJ.m$^{-2}$.yr$^{-1}$ | Schulze, 1997a, 1997b – [(van Rensburg et al., 2002)] |
| Rainfall Reliability | PCV | Coefficient of variation of annual Precipitation | % | Schulze, 1997a, 1997b – [(Thuiller et al., 2006)] |
| Rainfall Concentration | RCO | Markham's (1970) concentration index, based on the vector representation of mean monthly rainfall totals, where magnitude is the amount of rain and direction is the month of the year. Summed monthly values are divided by MAR, yielding values ranging from 0% (zero seasonality) to 100% (all rainfall in a single month) | | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 |
| Annual temperature range | RAS | Range between January's mean of daily maximum and July's mean of daily minimum averaged for all grids | °C | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 |
| Aveage annual minimum temperature | MIN | Absolute mean monthly minimum temperatures averaged for the year | °C | Schulze, 1997a, 1997b – [(van Rensburg et al., 2002, Richardson et al., 2005, Botes et al., 2007)] |
| Average annual maximum temperature | MAX | Absolute mean monthly maximum temperatures averaged for the year | °C | Schulze, 1997a, 1997b –[(van Rensburg et al., 2002) |
| Summer temperature regime | MST | Mean of January daily maximum temperatures averaged for all grid points | °C | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 – [(van Rensburg et al., 2002, Richardson et al., 2005, Botes et al., 2007)] |
| Winter temperature regime | MWT | Mean of July daily minimum temperatures averaged for all grid points | °C | Schulze, 1997a, 1997b, Cowling[a] et al., 1997 – [(Richardson et al., 2005)] |

### 4.3.3 Selection of Explanatory Variables

A comprehensive list of explanatory variables was compiled from previous studies in southern Africa (Linder, 1991; O'Brien et al., 1993; Hoffman, et al., 1994; Cowling et al., 1997; O'Brien et al., 2000; Cumming, 2002, van Rensburg et al., 2002, van Rensburg et al., 2004) and elsewhere (Currie, 1991, Gaston, 2000, Kerr et al., 2001, Hawkins et al., 2003a, Rodríguez et al., 2005). Details of all the explanatory variables that were considered and their sources are listed in Table 23. The effects of latitude are likely to be less influential than the variables I investigated, due to the relatively restricted latitudinal range of the CFR (31°S to 35°S), and were thus not incorporated in my study. Latitude has previously been excluded as an explanatory variable in the CFR (Linder, 1991), as it was in studies across South Africa (Hoffman et al., 1994; Cowling et al., 1997; Thuiller et al., 2006). However, its exclusion from countrywide studies is more contentious.

Initially, simple regression was undertaken between dependent and independent variables, using linear and non-linear functions to identify strong global correlations. All variables were tested for collinearity (Pearson's $r^2$), to ensure that collinear variables ($r^2$>=0.65) were not co-selected in the multiple regression GWR models, which may cause erroneous results (Quinn and Keough, 2003). Results of the collinearity test are recorded in the Appendix C4 (Table 31). Due to the large number of explanatory variables and the number of potential permutations of these variables, I did not adopt an exhaustive approach as conducted by Wang, Ni and Tenhunen (2005). Instead, I used an iterative forward stepwise selection approach (Quinn and Keough, 2003). Thus, against the selected floristic richness value, all explanatory variables were regressed, and the AIC values of the most optimal models recorded. The best model was then selected and the remaining explanatory variables were then added one at a time, to see if the model could be significantly improved (by lowering the AIC value by least 3 points (Fotheringham et al., 2002)) by adding additional explanatory variables. This was repeated until the addition of one of the remaining variables no longer improved the AIC values. Occasionally, in cases where different variables resulted in similar AIC values, all possible optimisation routes were explored with iterative forward stepwise inclusion of additional explanatory variables, recognizing that different combinations of variables could have a disproportionate effect on lowering the AIC score (Wang et al., 2005). All models were cross-checked against all floristic datasets, to ensure that the most optimal model was selected. The AIC results of these cross checked models are recorded in Appendix C4 (Table 29 and Table 30).

A potential disadvantage of using many parameters is that the optimal combination of multiple parameters may not always be achieved. However, the consequence of using fewer parameters is that the best parameters might not even be considered, even if the optimal configuration of considered parameters is achieved. Furthermore, by using fewer parameters, expert opinion is introduced *a priori* to select parameters, but when many parameters are used, expert opinion is required *a posteriori* to interpret parameter selection by the model. However, individual variables may not be as important as the broader hypotheses, which they invoke.

Previous GWR analyses (Shi et al., 2006; Wimberly et al., 2008) have reported anomalies (negative instead of positive and visa versa) in the influence of parameters over geographically limited areas. Generally, the low pseudo-t values indicate that these values did not deviate significantly from zero (Mennis, 2006; Wimberly et al., 2008). Therefore, where low pseudo-t values occur in this study, the parameter influences are not discussed. In the cases where the pseudo-t's are high (and perhaps significant), they are ecologically difficult to interpret (Shi et al., 2006), and may be a statistical artefact.

## 4.4 RESULTS

### 4.4.1 Model Selection

In the QDS analysis, Model QDS_M1 produced the lowest AIC values in three of the four floristic datasets, while Model QDS_M2 produced the lowest AIC values for the Fynbos endemics dataset (Table 24). Even though the Fynbos endemics dataset was explained more optimally by QDS_M2, QDS_M1 was only slightly less optimal (see Appendix C4, Table 30).

I found more variability in model selection for the PSC analyses than for the QDS level analyses. Here, three different models were required to explain richness patterns. Model PSC_M1 most optimally explained both Total diversity and Fynbos diversity; while PSC_M2 most optimally explained Total PSC endemism richness, and PSC_M3 best explained Fynbos PSC endemism richness (Table 24).

I found much stronger correlations between the different floristic datasets in my study at the QDS scale than at the PSC scale (Table 25). This greater uniformity between the floristic QDS datasets explained why the same model (QDS_M1) was optimal for three of four floristic datasets in the QDS analyses, while in the PSC analyses, three models were required, one to explain diversity (PSC_M1), one to explain Total PSC endemism (PSC_M2), and another to explain Fynbos PSC endemism (PSC_M3).

### 4.4.2 Variables of Models

Parameters of the habitat heterogeneity hypothesis were represented in all Models, while the energy-water hypothesis parameters occurred in seven of the eight models (Table 24), indicating equal representivity of both hypotheses in explaining richness in the CFR. This further corroborates the importance of more inclusive models, incorporating heterogeneity and energy-water hypotheses, together explaining richness (Gaston, 2000; Kreft and Jetz, 2007).

Table 24: Model Variables (var.) selected for the most optimal models with the lowest AIC scores. GRS = duration of growth season; RAR = rainfall range; Veg_C = vegetation count; PET = potential evapotranspiration; RWT = July minimum temperature range; RCO = rainfall concentration; Alt_Var = altitudinal variation; RAS = Annual temperature range; Alt_Ave = average altitude of input unit; slope = topographic slope; TDI = topographic diversity index; Fynbos_Area = area of OGU covered in Fynbos vegetation; TMS-Witteberg = area of OGU covered by TMS and Witteberg substrate types.

| | | Derivative floristic Dataset | Model | Var1 | Var2 | Var3 | Var4 | Var5 | AIC | # of Hetero vars | # of Energy vars |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Analysis | QDS | Total_Div | QDS_M1 | GRS | RAR | Veg_C | PET | RWT | 200.3 | 4 | 3 |
| | | Total_End | QDS_M1 | GRS | RAR | Veg_C | PET | RWT | 184.2 | 4 | 3 |
| | | Fynbos_Div | QDS_M1 | GRS | RAR | Veg_C | PET | RWT | 186.5 | 4 | 3 |
| | | Fynbos_End | QDS_M2 | GRS | RAR | Alt_var | RAS | RCO | 170.0 | 3 | 4 |
| | PSC | Total_Div | PSC_M1 | Fynbos_Area | Alt_Ave | Slope | PET | | 63.7 | 2 | 2 |
| | | Total_End | PSC_M2 | Veg_C | TDI | | | | 26.1 | 2 | - |
| | | Fynbos_Div | PSC_M1 | Fynbos_Area | Alt_Ave | Slope | PET | | 65.7 | 2 | 2 |
| | | Fynbos_End | PSC_M3 | TMS-Witteberg | TDI | RCO | PET | | 33.8 | 2 | 2 |

Table 25: Correlations between the derivative floristic datasets for the random and non-random OGUs investigated in this study.

| | | PSC | | | |
|---|---|---|---|---|---|
| | | Total Div | Total End | Fynbos Div | Fynbos End |
| QDS | Total Div | | 0.7243 | 0.9886 | 0.8184 |
| | Total End | 0.9585 | | 0.6487 | 0.8836 |
| | Fynbos Div | 0.9825 | 0.9302 | | 0.7809 |
| | Fynbos End | 0.9561 | 0.9783 | 0.9624 | |

#### 4.4.2.1 Energy-Water Hypothesis

PET was the most frequently retrieved parameter, in six of the eight models (Table 24). In my QDS analyses, the negative effects of PET on richness were highest in the central and especially central interior CFR (Swartberg, Langeberg and Witteberg), corresponding to the xeric Little Karoo, with its effects tapering off to the west and east (Figure 47). In the QDS analyses, PET had less effect on richness in the western CFR. The patterns of the PET slopes were similar in the Total Diversity and Fynbos diversity PSC analyses to that in the QDS level analyses, but displaced slightly to the west (Figure 47 and Figure 48). In the PSC diversity analysis, the strongest correlation was found between the Agulhas Plains and the

Witteberg/Klein Roggeveld, tapering off to the northwest and east. However, in the model of Fynbos PSC endemics, the effects of PET were more significant in the western CFR (Figure 49). In the Fynbos PSC endemics dataset, the removal of the endemic geophyte and succulent taxa may have been the cause of a much steeper gradient along the western seaboard, the gradient of which tapered off to the more mountainous interior, where there were fewer of these growth forms relative to fynbos taxa (loss of 20-30% endemic richness in the mountains, but higher in the northern Gifberg PSC and Nieuwoudtville Escarpment; and between 50 to >80% loss in endemic richness in the lower lying areas west of the mountains).

In the QDS analyses, uninterrupted growing season duration (GRS) was mostly positive throughout the CFR, but had its strongest influence on richness in the western CFR (Figure 47). This corresponds to the concentrated winter rainfall portion of the CFR, and both the influence of GRS and the amount of winter rainfall decrease from west to east in the CFR. The influence of GRS is strong where potential evapo-transpiration (PET) showed a weaker influence on richness.

Rainfall concentration (RCO) was retrieved in both the QDS and PSC analyses for Fynbos endemic taxa, and generally had a positive effect on richness. In the PSC analysis, RCO had its strongest influence in the NWPP, and decreased slightly in influence in the SWPP, where the Hottentots Holland-Kogelberg area also receives appreciable amounts of summer rainfall (Figure 49). Generally, RCO tapered off in influence from the west to the east, with a slight drop in influence (low pseudo-t values indicate that the influence here is insignificant) in the west central CFR, where there were no consistent trends. The effects of RCO in the QDS analysis showed inconsistent regional trends. Broadly, in the western CFR, there was a weak but positive correlation between increasing RCO and richness, increasing to the northwest CFR. As one travelled east, two local patterns emerged. The RCO continued to drop, until an inversion point was reached with richness in the Little Karoo, resulting in a negative relationship. Further, the eastern inland areas of low Fynbos richness received increasingly concentrated summer rainfall, further increasing the negative relationship between RCO and richness here. The use of GWR identified a further anomaly between RCO and richness. The relationship between fynbos endemism richness and RCO was negative in the extreme southwest of the SWPP. This was due firstly to the high RCO, but low endemism richness of Fynbos endemic taxa on the Saldanha Peninsula, and secondly due to the relatively lower RCO on the Peninsula and Kogelberg, but extremely high endemism richness.

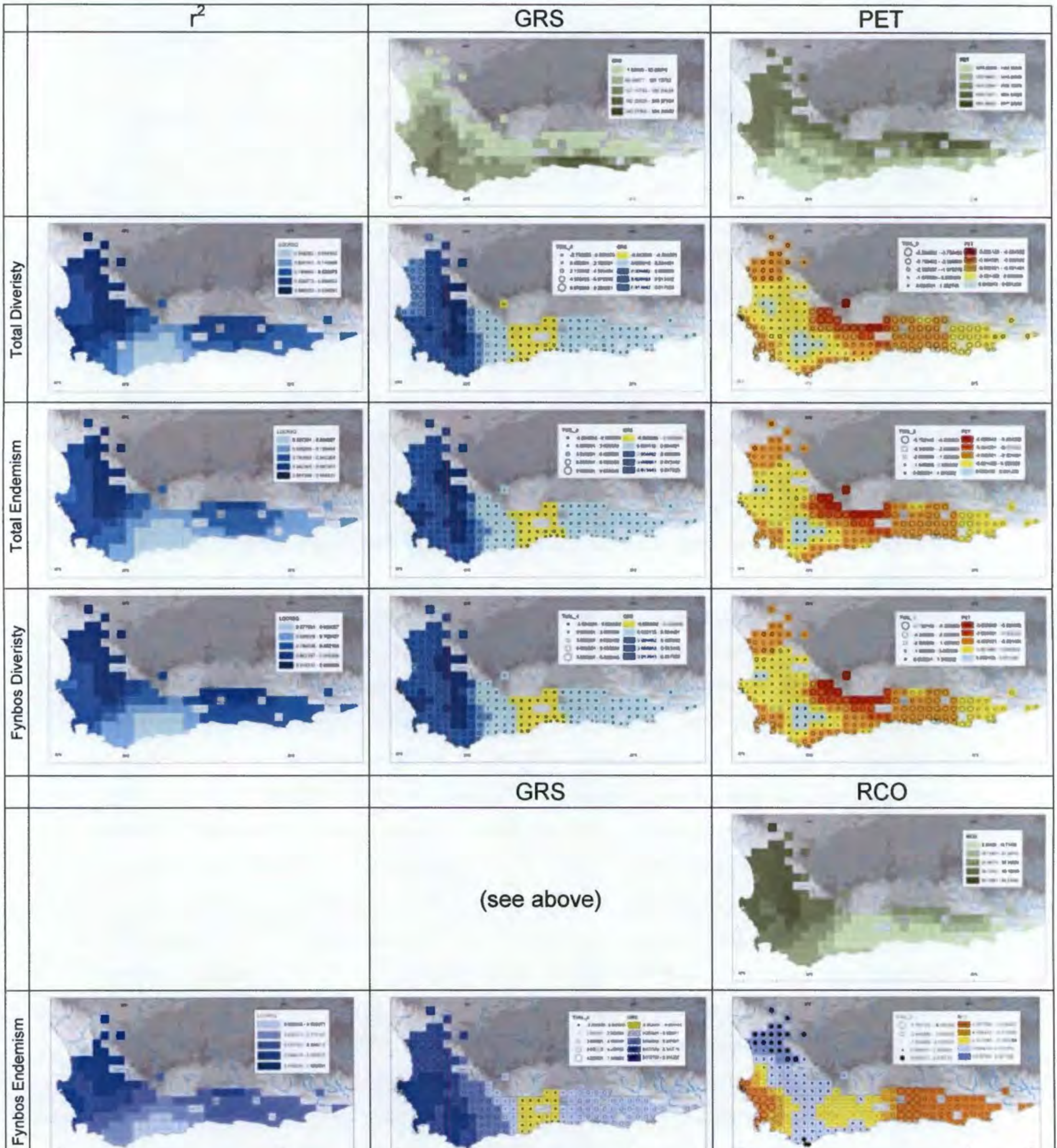


Figure 47: GWR Maps for the QDS Analysis (1 of 2).

Increasing magnitude of slope of parameters indicated by increasing darkness of colour, positive by blue, negative by red. Similarly, increasing magnitude of pseudo-t's indicated by size of circles, with direction of influence indicated by hollow/solid circles, depending on most dominant/widespread influence.

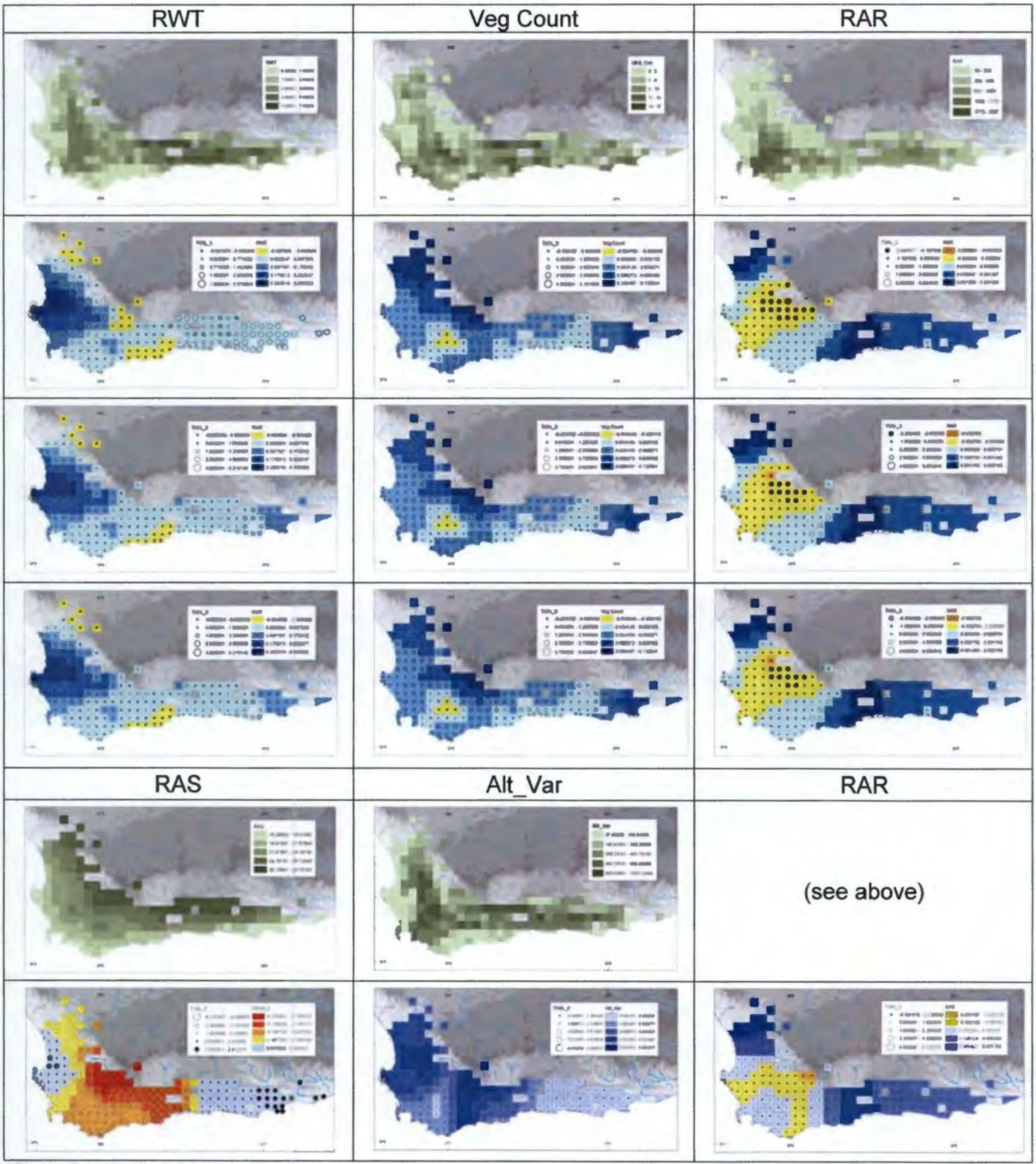


Figure (cont'd): GWR Maps for the QDS Analysis (2 of 2)

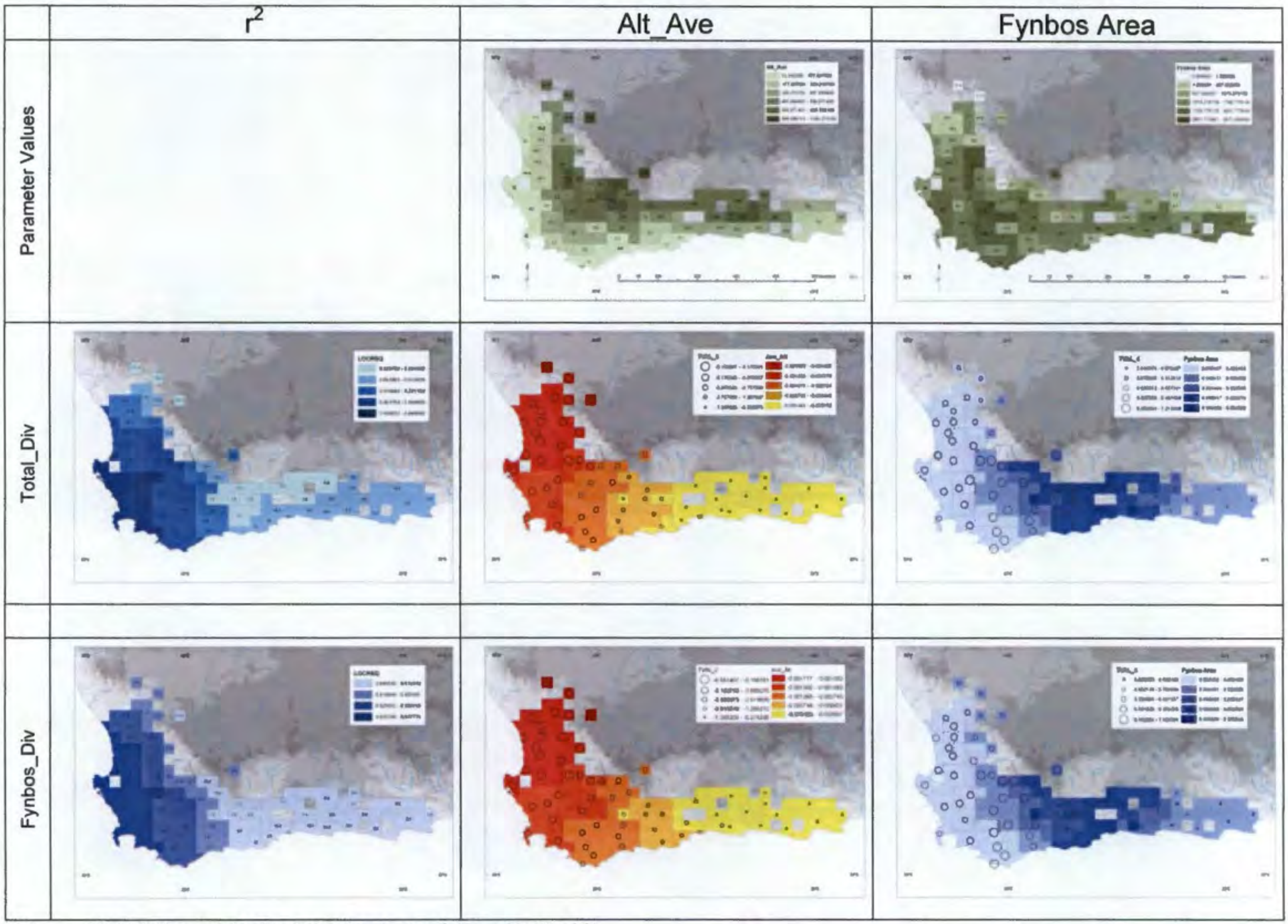


Figure 48: GWR maps for the PSC Analysis of diversity (1 of 2)
Increasing magnitude of slope of parameters indicated by increasing darkness of colour, positive by blue, negative by red. Similarly, increasing magnitude of pseudo-t's indicated by size of circles, with direction of influence indicated by hollow/solid circles, depending on most dominant/widespread influence.

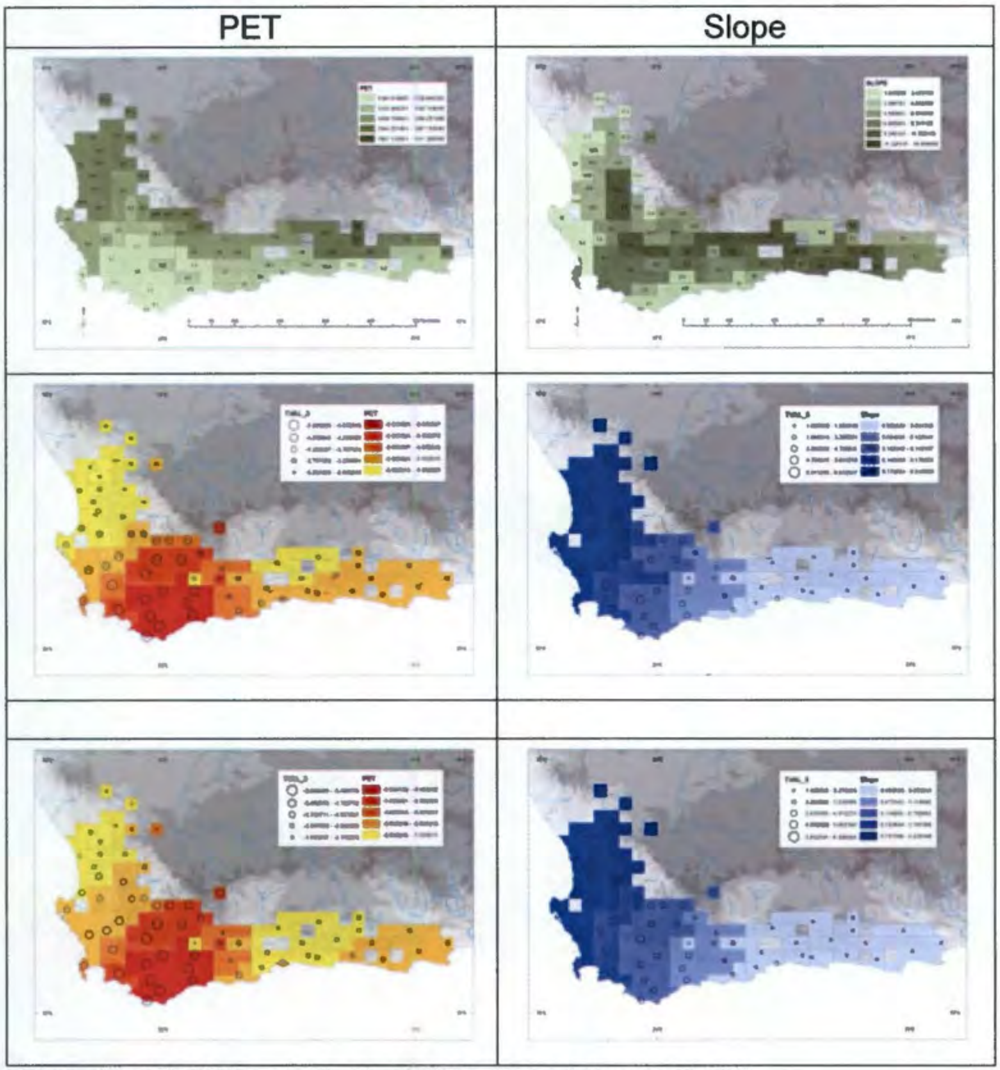


Figure (cont'd): GWR maps for the PSC Analysis of diversity (2 of 2)

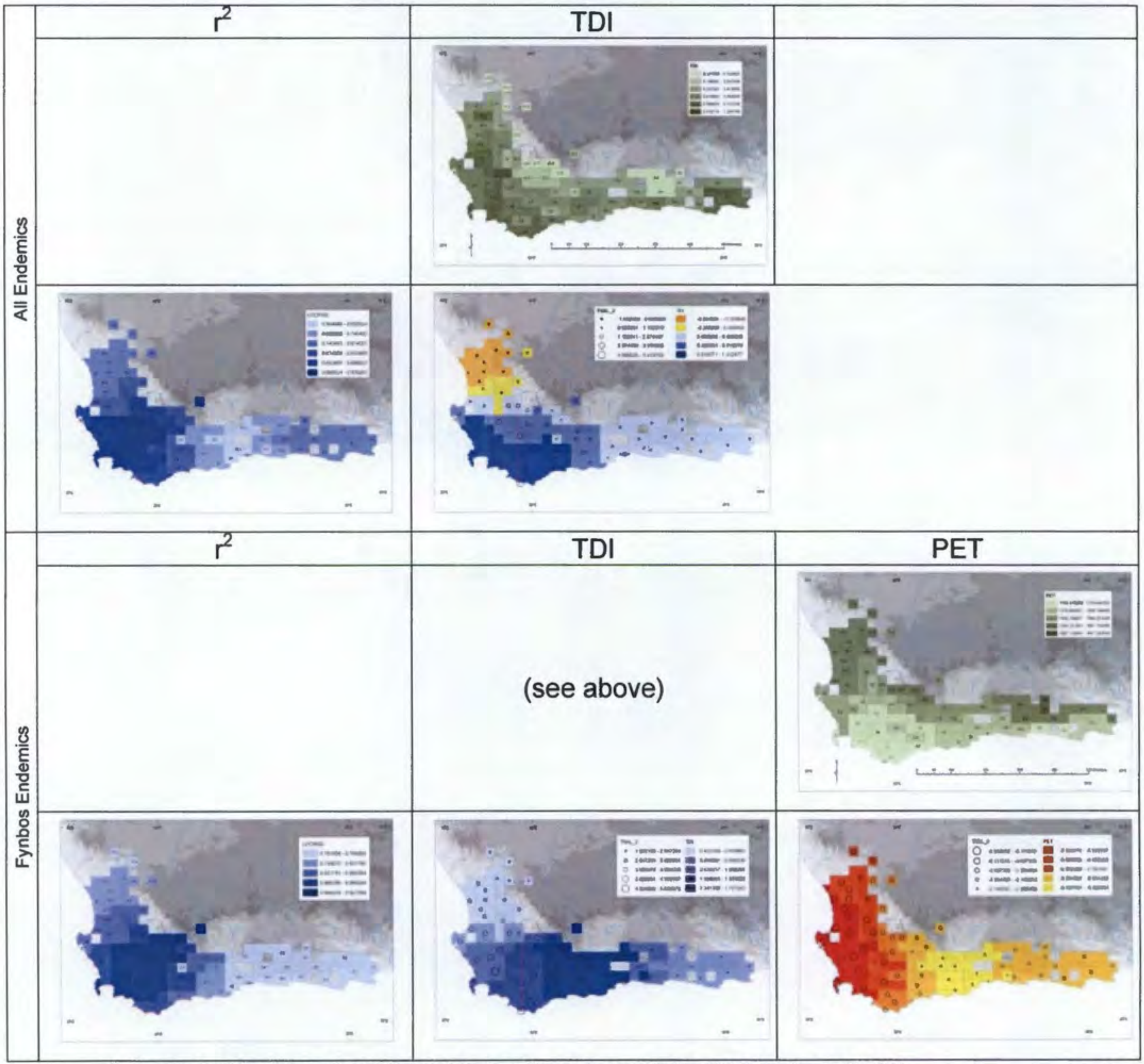


Figure 49: GWR maps for the Total and Fynbos Endemic taxa in the PSC Analyses (1 of 2)
Increasing magnitude of slope of parameters indicated by increasing darkness of colour, positive by blue, negative by red. Similarly, increasing magnitude of pseudo-t's indicated by size of circles, with direction of influence indicated by hollow/solid circles, depending on most dominant/widespread influence.

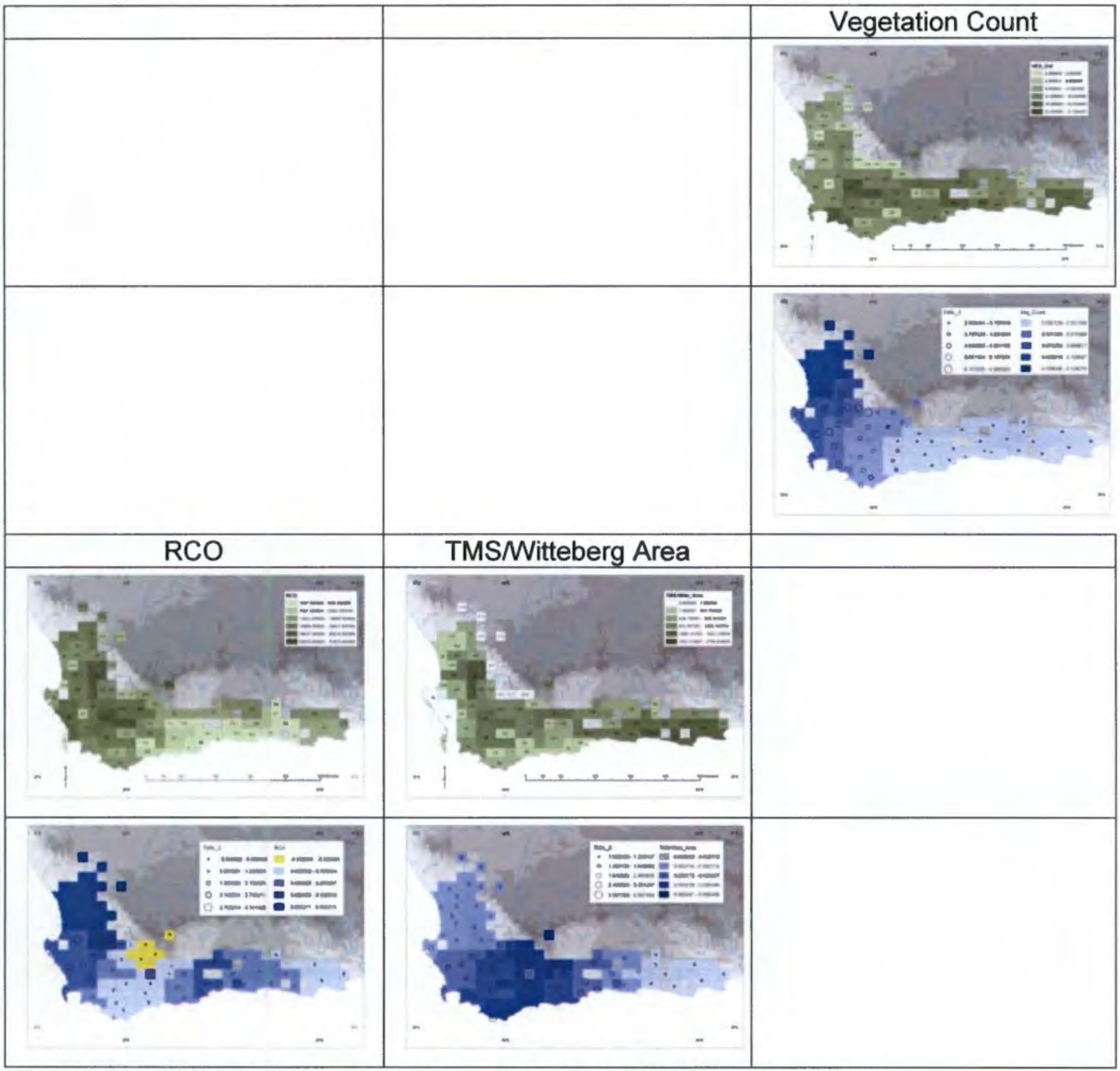


Figure (cont'd): GWR maps for the Total and Fynbos Endemic taxa in the PSC Analyses (2 of 2)

In the PSC diversity models, average altitude was found to be negatively correlated with richness, and had its strongest influence in the western CFR (Figure 48). The highest diversity values were found in the relatively low altitudinal coastal mountains of the Hottentots-Holland/Kogelberg, Riviersonderend and Stellenbosch Mountains, which were mostly below 1000 metres in height (Figure 52, and Chapter 2, Section 2.4.4, Table 19). There were also appreciable levels of diversity on the Cape Peninsula, and the relatively flat West Agulhas Plains, and southern Sandveld/Malmesbury areas (Figure 52).

#### 4.4.2.2 Heterogeneity Hypothesis

Direct measures of topographic heterogeneity (altitudinal variance, slope and the topographic diversity index (TDI)) were invoked in six of my eight models (Table 24). I found that slope was incorporated in the model of PSC diversity (Figure 48), the TDI for PSC endemism (Figure 49), and altitudinal variance for Fynbos QDS endemics (Figure 47). While slope/TDI/altitudinal variance may be linked conceptually to average altitude, the relationship is not necessarily spatially congruent (O'Brien et al., 2000). Slope was positively correlated with PSC diversity in the west and northern CFR, tapering off in influence to the south and east (Figure 48). For Total PSC endemics, the affects of the TDI were strongest in the southwest CFR (Figure 49). Even though there were steep slope and high TDI values in the eastern PSC, there were no strong consistent relationships with richness at the QDS scale, allowing for a strong correlation or consistent trend (Figure 47 and Figure 48). The effects of the TDI were more extensive and widespread for the Fynbos PSC endemics than for the Total PSC endemics dataset, indicating the importance of a slope habitat for Fynbos endemics throughout the CFR (Figure 49; and see Chapter 2, Section 2.4.4). Mountain slopes are less important for succulent and geophyte endemics, which have high richness in the northwest of the CFR (around Vanrhynsdorp).

In the QDS analysis, the annual rainfall range (RAR) had a strong influence on richness, where the growth season duration (GRS) and July minimum temperature range (RWT) had weak explanatory power in the central and eastern CFR (Figure 47). This corresponded to the aseasonal rainfall area (Schulze, 1997) of the CFR. Further, the values of RAR and PET appeared antagonistic. Generally, where RAR was strongly positive, PET was strongly negative, notably in the Little Karoo, including the Swartberg and Langeberg Mountain Ranges (Figure 47). In the central and east CFR, RAR emerged as a stronger explanatory variable of richness than GRS. However, this is not to say that RAR has no influence in the western CFR, or GRS in the eastern CFR, but that RAR has greater explanatory power in the central CFR.

In the QDS analyses, vegetation count was found to have a positive effect on richness, almost throughout the CFR (Figure 47). Low vegetation count values were found to correlate strongly with the lower richness in the peripheral, more arid northern and northeast parts of the CFR, and the extreme eastern CFR for QDS diversity. GWR detected a correlation gradient of increasing richness and vegetation count from the Witteberg/Klein Roggeveld to the Gifberg and Nieuwoudtville escarpment. In these peripheral parts of the CFR (Witteberg/Klein Roggeveld), where the number of vegetation types are less numerous (relative to numbers within the CFR), the relatively low richness values correlate with low vegetation type numbers. Vegetation count was also found to be a good explanatory variable for richness in the Total PSC endemism analysis (Figure 49). The relationship was strongest in the north, tapering off to the south (where topographic diversity became more influential) and tapering off more so to the east. In my PSC analysis of diversity (Figure 48), there was a positive correlation between richness and fynbos area (a habitat specific area measure of heterogeneity) throughout the CFR, but the pattern was strongest in the central CFR, decreasing to the west where average altitude and slope were better predictors of richness (Figure 48).

In the QDS models, range of minimum July (winter) temperatures (RWT) featured most strongly over a limited geographical area in the central western CFR, although it was generally positive throughout the CFR, and had a greater effect on diversity than endemism (Figure 47). There was a particularly strong correlation RWT and richness between the lower lying coastal flats around Elandsbaai/Lambert's Bay to the Groot Winterhoek and Cedarberg. Annual temperature range (RAS) was only incorporated once, in the QDS Fynbos endemics model (Figure 47). RAS had its greatest effect on the escarpment, and moderated towards the coast, and was similar to the average altitude (QDS correlation of 0.52). Thus, it was not too surprising to observe a negative relationship with richness, from the Hottentots-Holland-Kogelberg to the Witteberg. As with rainfall concentration for QDS Fynbos endemics (Figure 47), there were two localised contrary patterns, on the Saldanha Peninsula and the PE/Cape Padrone areas inland. Both were associated with low richness coastal areas of low seasonal temperature difference (low RAS), with neighbouring areas of higher richness and less moderate temperature differences. However, as RAS increased towards the escarpment, and richness also decreased, a negative relationship was observed.

### 4.4.3 GWR Model Results

GWR performed better than OLS for both the QDS (Table 26) and the PSC input data (Table 27), with lower AIC values and higher $r^2$ values (following Fotheringham et al., 2002; Foody, 2004; Wang et al., 2005; Zhang et al., 2008). In the QDS analyses, OLS results were poorer than those conducted in the PSC analyses. Furthermore, the improvement of GWR over OLS was relatively greater in the QDS analyses than in the PSC analyses.

Table 26: Statistical comparison between the results of GWR and OLS models for the QDS Analysis

| | Total_Div (M1) | | Total_Ends (M1) | | Fynbos_Div (M1) | | Fynbos_Ends (M2) | |
|---|---|---|---|---|---|---|---|---|
| | OLS | GWR | OLS | GWR | OLS | GWR | OLS | GWR |
| AIC | 363.18 | 200.30 | 410.18 | 184.16 | 373.13 | 186.49 | 392.10 | 170.01 |
| $r^2$ | 0.6505 | 0.8934 | 0.5838 | 0.9043 | 0.6733 | 0.9150 | 0.6554 | 0.9069 |
| Adjusted $r^2$ | 0.6404 | 0.8678 | 0.5718 | 0.8820 | 0.6638 | 0.8926 | 0.6454 | 0.8917 |
| Df | 6 | 41.182 | 6 | 40.365 | 6 | 44.404 | 6 | 23.88 |
| Bandwidth | | 56 | | 57 | | 52 | | 70 |
| F | | 11.186 | | 16.928 | | 12.551 | | 20.838 |

Table 27: Statistical comparison between the results of GWR and OLS models for the PSC Analysis

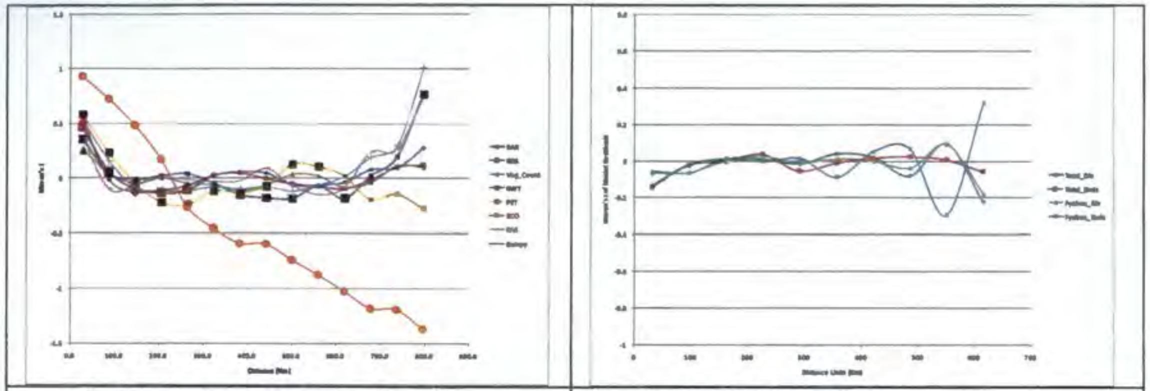
| | Total_Div (M1) | | Total_Ends (M2) | | Fynbos_Div (M1) | | Fynbos_Ends (M3) | |
|---|---|---|---|---|---|---|---|---|
| | OLS | GWR | OLS | GWR | OLS | GWR | OLS | GWR |
| AIC | 79.26 | 63.73 | 48.262 | 26.064 | 81.68 | 65.74 | 41.399 | 33.833 |
| $r^2$ | 0.8566 | 0.9259 | 0.6641 | 0.8588 | 0.8668 | 0.9317 | 0.7608 | 0.8618 |
| Adjusted $r^2$ | 0.8422 | 0.9049 | 0.6448 | 0.8189 | 0.8535 | 0.9124 | 0.7369 | 0.8207 |
| Df | 5 | 7.23 | 3 | 9.13 | 5 | 7.23 | 5 | 7.62 |
| Bandwidth | | 42 | | 27 | | 42 | | 40 |
| F | | 5.743 | | 6.6263 | | 5.8323 | | 4.1596 |

### 4.4.4 Assessment of Explanatory Variables for Non-Stationarity

Parameter estimates of the QDS analysis displayed much higher levels of non-stationarity than those used in the PSC analysis (Table 28). This may be on account of the thinning out of data points (see Lennon, 2000). Only non-stationarity values for parameters that were actually incorporated (Table 24) in the models are displayed (Table 28), not the entire suite of parameters considered for selection (Table 23). OGU original variable values invoked in models were mapped above the parameter influence value maps (Figure 47, Figure 48 and Figure 49) to aid in the interpretation of the GWR analyses.

Table 28: p significance values for the Monte Carlo Test for Stationarity of predictor variables selected in the QDS and PSC models. Underlined values are nearly significant (nearly display non-stationarity), while those in grey are more stationary.

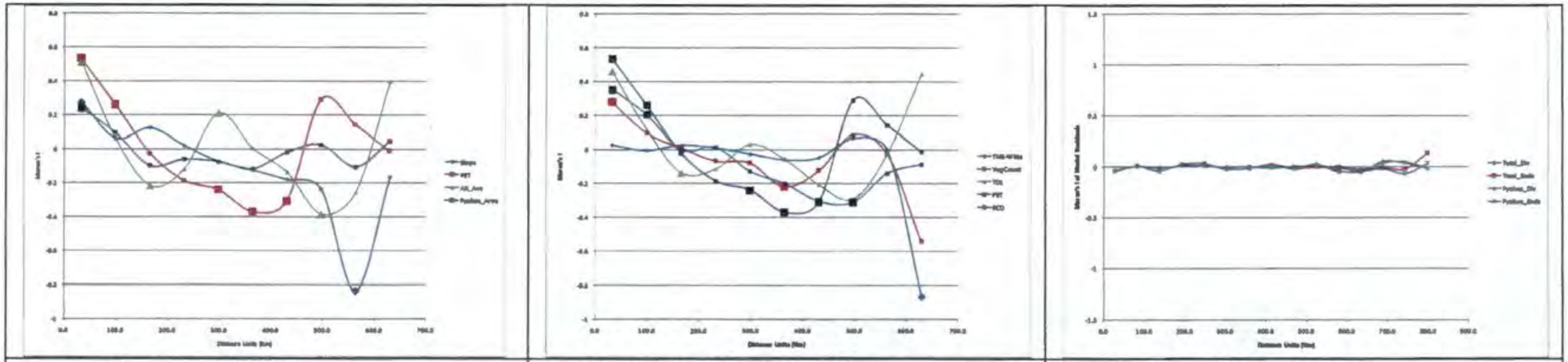
| | QDS | | | | PSC | | | |
|---|---|---|---|---|---|---|---|---|
| | Total Div | Total Ends | Fynbos Div | Fynbos Ends | Total Div | Total Ends | Fynbos Div | Fynbos Ends |
| GRS | 0.000 | 0.000 | 0.000 | 0.000 | - | - | - | - |
| RWT | 0.010 | 0.010 | 0.010 | 0.000 | - | - | - | - |
| RAS | 0.010 | 0.000 | 0.010 | 0.000 | - | - | - | - |
| Alt_Var | 0.020 | 0.020 | 0.010 | 0.020 | - | - | - | - |
| RAR | 0.000 | 0.050 | 0.010 | 0.030 | 0.460 | 0.860 | 0.450 | 0.940 |
| PET | 0.000 | 0.000 | 0.000 | 0.000 | 0.020 | 0.130 | 0.020 | 0.050 |
| Veg_C | 0.000 | 0.000 | 0.000 | 0.000 | 0.040 | 0.000 | 0.070 | 0.070 |
| RCO | 0.010 | 0.000 | 0.000 | 0.000 | 0.470 | 0.700 | 0.550 | 0.530 |
| Fynbos_Area | - | - | - | - | 0.820 | 0.650 | 0.880 | 0.690 |
| TMS-Witteberg | - | - | - | - | 0.070 | 0.110 | 0.080 | 0.070 |
| Alt_Ave | - | - | - | - | 0.490 | 0.780 | 0.480 | 0.460 |
| TD1 | - | - | - | - | 0.340 | 0.450 | 0.370 | 0.190 |
| Slope | - | - | - | - | 0.030 | 0.060 | 0.010 | 0.060 |



a) Diversity and endemism variables

b) Model Residuals

Figure 50: Moran's *I* values for environmental Variables (a) used in the CFR QDS analysis (with Bonferroni correction).
All variables exhibit positive auto-correlation up to about 200 km. The lower values of the Moran's *I* Residuals of the models (b) for the various floristic datasets analysed indicates that the model removed the affects of spatial auto-correlation (Diniz-Filho et al., 2003).



a) Diversity Variables

b) Endemism Variables

c) Model Residuals

Figure 51: Moran's *I* values for environmental Variables used in the CFR PSC Diversity (a) and endemism (b) analysis (with Bonferroni correction).
The lower values of the Moran's *I* Residuals of the models (c) for the various floristic datasets analysed indicates that the model removed the affects of spatial auto-correlation (Diniz-Filho et al., 2003).

### 4.4.5 Assessment of Spatial Auto-Correlation

Moran's *I* tests indicated that there was significant positive spatial auto-correlation between environmental explanatory variables up to about 200 km (Figure 50 and Figure 51). Moran's *I* analyses of model residuals with Bonferroni correction indicated no significant spatial auto-correlation in the model residuals (after Diniz-Filho et al., 2003).

## 4.5 DISCUSSION

### 4.5.1 Hypotheses Invoked

A review by Hawkins et al., (2003a) indicated that energy, water, or water-energy best explained richness in 82 of 85 cases. However, Hawkins et al., (2003a: 3106-3107) focused on gradients extending over 800 km, which they considered "minimally sufficient to encompass a range of climates." At smaller scales, other abiotic and even biotic variables may become increasingly important (O'Brien, 1993; Hawkins et al., 2003a). Few studies in the northern hemisphere have described species richness primarily as a function of the habitat heterogeneity hypothesis – an exception is Kerr et al., (2001). Apart from scale, habitat heterogeneity variables are usually less well represented in studies, typically only being represented by variance of topography, while climatic variables are usually more numerous, complex, and derived. Globally, Mediterranean areas, and the CFR in particular constituted an outlier to decreasing richness and endemism with latitude (Cowling et al., 1996; Linder, 2003; Kier et al., 2005; Kreft and Jetz, 2007). This may have encouraged biogeographers to investigate additional variables and hypotheses to explain the exceptional richness in the CFR. As with Cowling et al., (1997) and Thuiller et al., (2006), my models nearly equally incorporated variables from both the energy-water hypothesis and the environmental heterogeneity hypothesis for the CFR (Table 24), suggesting that both hypotheses contribute to explaining richness in this specific region. The advantages of an inclusive synergistic approach have recently been demonstrated in an analysis of richness patterns in global floristic regions (Kreft and Jetz, 2007).

#### 4.5.1.1 The Energy-Water Hypotheses

Variables of the energy-water hypothesis have been frequently invoked to explain species richness patterns, internationally (Hawkins et al., 2003a; Rodríguez et al., 2005; Bickford and

Laffan, 2006; Kreft and Jetz, 2007), in southern Africa (Linder, 1991; O'Brien et al., 1993; Hoffman, et al., 1994; Cowling et al., 1997; Thuiller et al., 2006), and in the CFR (Linder, 1991; Cowling et al., 1997; Thuiller et al., 2006). I found parameters incorporating aspects of the energy-water hypothesis to be well represented, occurring in seven of my eight models (Table 23 and Table 24). Although the particular variables may vary, the repeated retrieval of these related variables (potential evapo-transpiration, growth season duration, and potentially indirect rainfall gradient, rainfall concentration and average altitude) emphasised the importance of the species energy hypothesis in explaining richness in the CFR. The utilisation of GWR helped to identify the area specific importance (or non-stationarity) of these variables.

Potential evapo-transpiration (PET) is a frequently considered variable of the energy-water hypothesis, both internationally (Currie, 1991; Hawkins et al., 2003a, Rodriguez et al., 2005; Bickford and Laffan, 2006; Kreft and Jetz, 2007), and in southern Africa (O'Brien, 1993, 2000; Hoffman et al., 1994; Thuiller et al., 2006). However, Cowling et al., (1997) did not consider species-energy theory (principally PET) to be a good explanatory variable in Southern Africa. They insightfully counter that relatively high richness occurs in environments where productivity is limited by nutrients and moisture availability (fynbos and Karoo). Similarly, PET had little explanatory power in the study of Thuiller et al., (2006). However, my study strongly supported PET as an explanatory variable of richness in the CFR, and PET was incorporated into six of my eight models, making it the most frequently retrieved individual variable in my study. As with Hoffman et al., (1994), I found a negative correlation between PET and richness in all models where it was included. In arid southern Africa, water is a more significant inhibitor of production rather than temperature (Hoffman et al., 1994; Hawkins et al., 2003a). The effects of temperature are more significant in the more temperate northern hemisphere, where low temperatures may lower metabolism, and water availability (ice), thus resulting in a positive relationship between PET and richness (Currie, 1991; Hawkins et al., 2003a). While the energy-water hypothesis may explain absolute levels of richness, history may explain which specific taxa (lineages) could best take advantage of, or diversify in the nutrient poor conditions, accounting for the explosive radiation in a few selected taxa in the CFR (Richardson et al., 2001; Linder, 2003). The energy-water hypothesis alone cannot directly explain why certain taxa are under-represented in certain areas, for example, *Oxalis* in the Agulhas Plains PP of the CFR; or why *Erica* may have twice the number of taxa in a given area than Restionaceae or Proteaceae. However, in conjunction with historical constraints, a greater understanding of richness patterns could be achieved.

Uninterrupted growing season duration (GRS) has generally not been considered as a variable outside of southern Africa. GRS is invoked in South Africa due to the strong seasonal concentration of rain in certain parts of South Africa. Cowling et al., (1997) found GRS to be a significant explanatory variable in the Grassland and Savannah Biomes, but not in the Fynbos Biome. This is the first study to identify GRS as an important explanatory variable of richness in the CFR, no doubt facilitated by the local (GWR) rather than a global regression approach. In my QDS analyses, GRS was found to have a strong positive influence on richness in the western CFR, which was strongly congruent with the concentrated winter rainfall portion of southern Africa (Schulze, 1997a; Schulze, 1997b). The importance of GRS could be interpreted as follows: if rainfall is seasonal and all else is hypothetically equal, the longer the growing season, the greater the water availability, which would have a positive effect on productivity. Thus, it follows that there was a positive correlation between GRS and MAR; both at the QDS level (0.70) and the PSC level (0.76) in the CFR (Appendix C4). Thuiller et al., (2006) found that mean annual rainfall accounted for 31% of variation in richness in the fynbos biome, while mean annual rainfall was Linder's (1991) most important explanatory variable of richness in the Southwest PP of the CFR. A longer growing season may also allow a type of temporal heterogeneity or niche differentiation. Essentially, there could be early and late flowering taxa that could make use of a different suite of pollinators, which in turn may support a greater richness of taxa (temporal rather than spatial niche differentiation). A longer growing season would also allow plants longer periods to accumulate resources for less favourable seasons, lowering mortality, and ultimately extinction risk. I propose that over evolutionary time, areas with larger GRS may be more resilient to change, also lowering extinction risk, and possibly act as refugia (*cf.* Meadows and Baxter, 1999; Cowling and Lombard, 2002). Further, the region where GRS was the most influential coincides with the two phytogeographical provinces/centres with the highest number of annuals and geophytes in the CFR, as listed in Goldblatt and Manning (2000). Although dependent and independent variables were averaged annually in this study, which may not be entirely appropriate for seasonal geophytes or annuals, or areas such as the CFR, which have concentrated seasonal growing seasons. This may have prompted Cowling et al., (1997) to restrict variables like rainfall coefficient of variation to the wettest consecutive three months. Nevertheless, longer GRS, results in increased winter rainfall (and higher annual rainfall), which is particularly important for these life forms, potentially facilitating their persistence, and also their diversification (Proches, Cowling, and du Preez, 2005). Length of growth season (GRS) may be a hidden explanatory variable of richness in other Mediterranean ecosystems, particularly for explaining geophyte and annual growth form richness. GRS was not retrieved in the PSC analyses. However, rainfall concentration (RCO) was retrieved as an explanatory variable for Fynbos endemics, for both the QDS and PSC level analyses. RCO, in isolation, was difficult to interpret. Cowling et al., (1997) interpreted it at the regional scale (west CFR versus east CFR) as a measure of seasonality, which was shown to be highest in the western, winter rainfall portion of the CFR. Thus, RCO could be indirectly related to GRS, which was highly influential in the western CFR in my QDS level analyses. Patterns of RCO influence behaved as expected in the Fynbos PSC endemics analysis. However, it appeared as if local (QDS) patterns of RCO had more complex local patterns than at the PSC or regional geographic level in the QDS Fynbos Endemics dataset. The mapped model Fynbos PSC endemic analysis RCO parameters seem to have provided input units that resulted in a more gradual decrease in endemism richness (and RCO), possibly by averaging the results over a larger input area (see Lennon, 2000).

Average altitude was found to be negatively correlated with richness in the PSC diversity models, and had its strongest influence in the western CFR. Given that fynbos richness is generally associated with mountains, the negative correlation of richness with average altitude may at first seem counter intuitive. However, fynbos richness was more strongly associated with slope/mountainous areas (habitat heterogeneity) rather than average altitude (which better translated into the energy-water hypothesis) (Chapter 2, Section 2.4.4). Average altitude was strongly affected by the atmospheric lapse rate (-6.5°C/km asl; O'Brien, 1993), hence its strong correlation with annual minimum monthly temperature (MIN). A preliminary correlation analysis indicated an $r^2$ of 0.96 at the PSC level, and 0.92 at the QDS level between average altitude and MIN (see Appendix C4, Table 31). Models computed with average altitude replaced by MIN showed only slightly poorer AIC values (Total PSC diversity: AIC = 67.98; Fynbos PSC diversity: AIC = 68.84; Table 29 and Table 30, Appendix C4). Closer proximity to the escarpment and increasing altitude and continentality may also lead to increasing aridity, due to the decreased penetration of the moisture bearing cold fronts. Further, with higher average altitude, and/or lower MIN, the prevalence of frost increases, and winter energy decreases, lowering productivity in winter, the growing season of fynbos. Thus, average altitude forms part of the energy hypothesis. Due to the pervasive influence of average altitude on other variables, the possibility that it is a surrogate for other parameters should not be discounted.

#### 4.5.1.2 The Habitat Heterogeneity Hypotheses

Apart from a few studies (Kerr and Packer, 1997; Kerr et al., 2001; Kreft and Jetz, 2007), the habitat heterogeneity hypothesis has received less international attention than the energy-water hypothesis (Kerr et al., 2001; Hawkins et al., 2003a). When considered, it is usually only represented by one, or at best a few variables (Currie, 1991; Kerr and Packer, 1997; Guégan et al., 1998; Kerr et al., 2001; Hawkins et al., 2003a; Rodriguez et al., 2005; Wang et al., 2005). Initially, O'Brien et al., (1993) exclusively advocated the energy-water theory as a primary determinant of richness for trees in southern Africa, but later refined their model further (O'Brien et al., 2000) by incorporating topographic heterogeneity to explain residuals in areas of high and low altitude. Conversely, Cowling et al., (1997) found measures of environmental heterogeneity (area, topographic diversity, annual rainfall gradient, and July minimum temperature range) to have the highest correlation with richness in the fynbos biome, using simple regression. A recent study in southern Africa criticized the energy-water hypothesis as a primary or "first order" explanation in favour of a habitat/topographic heterogeneity hypothesis (Thuiller et al., 2006). However, focusing exclusively on the Fynbos Biome, Thuiller et al., (2006) found that although topographic heterogeneity was important, it ranked third after mean annual precipitation and net primary production. I found that energy-water hypothesis variables occurred in seven of the eight models, and that habitat heterogeneity variables were found in all eight models, indicating nearly equal representation of both hypotheses in the models.

In this study, various direct measures of topographic diversity (topographic diversity index, slope, altitudinal variance) were incorporated into five of the eight models. The high levels of beta and gamma diversity in the CFR (Latimer, Silander and Cowling, 2005; Cowling et al., 1992; Cowling, 1990; Simmons and Cowling, 1996) over relatively short geographic distances may also increase the importance of habitat heterogeneity based variables. This is in agreement with Kerr et al., (2001) who interpreted habitat heterogeneity to be indicative of beta diversity. The high importance of topographic heterogeneity in the CFR, when compared to studies in the northern hemisphere, may also have an historical basis, due to different bottlenecks experienced by taxa in these different regions. In the northern hemisphere, the recent glaciations (Maslin et al., 1998) may have rendered the mountains too cold to harbour many species or to act as refugia. Conversely, the gradual desiccation of Africa since the Tertiary (Axelrod and Raven, 1978; Hendey, 1982; Cowling et al., 2008) may have increased the importance of mountains as refugia due to orographic processes.

The climatic variables retrieved here that are indicative of environmental or topographic heterogeneity include annual rainfall range (RAR) (Cowling et al., 1997), influenced by orographic processes, and the July minimum temperature range (RWT) (Cowling et al., 1997), due to atmospheric lapse rate (-6.5°C/km asl; O'Brien, 1993). Cowling et al., (1997) found that RAR was a significant correlate of richness in the CFR. The retrieval of rainfall range supports the notion of high levels of species turnover (beta diversity) in the CFR (Cowling et al., 1992). However, RAR subtly (indirectly) also incorporates aspects of the energy-water hypothesis, as it is moderately correlated (0.57-PSC, 0.39-QDS) with mean annual rainfall (MAR). This heterogeneity interpretation from RAR correlated with richness is in agreement with Thuiller et al., (2006), who measured habitat heterogeneity by topographic variability alone. While modern GIS technology (Satellite Radar topography mission (SRTM) and Light Detection and Ranging (LIDAR)) may make topography the easiest of these variables to quantify accurately, advocating topographic variability alone, or without adequate interpretation of its influence on other variables, implies that in isolation it is the most important variable. Thus caution needs to be exercised in the interpretation of variables.

Vegetation count, another measure of habitat heterogeneity (Linder, 1991; van Rensburg et al., 2002, 2004; Kreft and Jetz, 2007), was found to have a positive effect on richness, almost throughout the CFR in the QDS analyses. Vegetation count is similar to the vegetation type count of Linder (1991), and conceptually similar to the vegetation land cover diversity of Kerr et al., (2001), both of which indicate a positive relationship between habitat heterogeneity and richness. Kerr et al., (2001) found vegetation land cover diversity to be the most important correlate of butterfly richness in Canada. In this study, low vegetation count values were found to correlate strongly with the lower richness in the peripheral, more arid northern and northeastern parts of the CFR, and the extreme eastern CFR for QDS diversity.

Terrestrial area (of input units) has also been interpreted as a surrogate for environmental heterogeneity, with the probability that larger areas, potentially including more habitat types by chance alone (Rosenweig, 1995; Cowling et al., 1997). Terrestrial area, although having a strong positive correlation with endemic and diversity richness (Chapter 2, Section 2.4.3), was not incorporated as an optimal explanatory variable in any of my models. However, in my PSC analyses of diversity, there was a positive correlation between richness and fynbos area (a habitat specific area measure of heterogeneity) throughout the CFR, but the pattern was strongest in the central CFR, where there were appreciable areas of Succulent Karoo vegetation, thus making fynbos area more limiting and important. Furthermore, within the fynbos biome itself, the central CFR is likely to have higher proportions of mountain fynbos (mountain fynbos may correlate more directly with richness) relative to other fynbos types (Cowling and Proches, 2005), relative to the western CFR, which has large areas of lower richness lowland Sandveld and shale Renosterveld. If I had used a variable like the area of mountain fynbos, it may have yielded stronger habitat area correlations in the west, rather than the more general Fynbos biome area, which included areas of lower richness low altitude vegetation.

Interestingly, fynbos area was not included as an optimal explanatory variable in the PSC endemism models. However, the TMS/Witteberg substrate area (another habitat specific measure of heterogeneity) was positively correlated with richness for the Fynbos PSC endemics, with its greatest influence in the southwestern and central CFR. This may indicate that a relatively high proportion of Fynbos endemics are associated specifically with TMS/Witteberg substrate, rather than with other fynbos substrates (shale, limestone, granite and quaternary) in the CFR. This was supported by a preliminary analysis of endemic habitat frequencies (Chapter 2, Section 2.4.4), but requires more rigorous analysis. TMS/Witteberg is mostly a montane substrate, perhaps further supporting a montane fynbos area based variable. In conclusion, in areas where richness is concentrated in particular habitats, area specific measures of habitat should be considered. This is perhaps the spatial equivalent of Cowling et al.'s (1997) temporally specific rainfall coefficient of variation, with calculations restricted to the wettest three months of the year.

### 4.5.2 The impact of different geographic input units, and derivative floristic datasets on GWR Models

Most GWR studies that have investigated the effects of scale, have altered bandwidth size (Foody, 2004; Bickford and Laffan, 2006), and thus effective sample size, rather than the size or type of input units *per se*. This study clearly demonstrated that different parameters are invoked for different types of geographic input data, specifically QDS (random, uniform) and PSC (non-random, irregular). Analyses of differentially sized random input units were not undertaken, but may also invoke different parameters for optimisation.

Different floristic components of the data (total richness versus endemic, especially fynbos, richness), were explained by different models even with identical geographic input data. Differences between the floristic datasets, principally diversity and endemism, were higher in the PSC level analyses, reflected by an additional model required to explain richness patterns (Table 24). Overall, CFR endemism is nearly 70% (Goldblatt et al., 2005). However, in this study, slightly more than 89% of both Total Diversity and Fynbos Diversity were shown to be endemic to the CFR (Table 22). Therefore, the majority of the species were endemic in the QDS analyses, and contributed towards the QDS endemism richness score. PSC endemic representivity was much lower than PSC diversity, and proportionately less than CFR endemism in the QDS analyses (Table 22). This was clearly demonstrated by the similarity between the floristic datasets at the QDS and PSC levels, using a simple correlation (Table 25). The Fynbos endemics datasets (QDS and PSC) showed a large departure from other floristic datasets, with different models being slightly more optimal in the QDS and PSC analyses for the Fynbos Endemics (Table 24). However, even though specific model explanatory variables may differ, the two principle hypotheses of energy-water and habitat heterogeneity were apparent in nearly all my models. Only one of my eight models invoked a single hypothesis, namely the habitat heterogeneity hypothesis, for PSC total endemic taxa (Table 24). It would be interesting to compare models of fynbos and non-fynbos taxa, with a more comprehensive non-fynbos dataset.

As I have demonstrated, using different input units or derivative floristic datasets can invoke different models; care should therefore be taken when making comparisons between studies (Cowling et al., 1997; Thuiller et al., 2006) that are conducted at different geographic scales, that make use of different input units, and that analyse different floristic, taxonomic or ecological sub-sets of data, and that occur over or within different ecological or biogeographical units, for example, biomes or floristic regions. All these factors may have an effect on the explanatory variables selected, and may affect the non-stationarity of the variables.

### 4.5.3 Mapping of GWR Parameter influences

Generally, the explanatory variables in my study performed similarly to previous studies conducted in the region (Linder, 1991; Hoffman et al., 1994; Cowling et al., 1997; Thuiller et al., 2006). However, over geographically limited areas, explanatory variables that generally had a positive influence on richness were negative, for example, in the QDS analyses (Figure 47). Variables that mostly had a positive effect on richness were: growth season length; rainfall gradient; July minimum temperature gradient; and vegetation count), while potential evapo-transpiration was mostly negative, but when positive it was mostly not significant, due to the low pseudo-t values (Mennis, 2006; Wimberly et al., 2008). This phenomenon was less frequent in the PSC level analyses, possibly due to the averaging of localised dependent and independent variables over larger geographic areas. Whether these patterns reflected genuine or artificial anomalies in the data, they were likely to weaken the global regression analyses, while the GWR was better able to cope with them, with higher $r^2$ values (Table 26 and Table 27).

### 4.5.4 Analytical Considerations

Adjusted $r^2$ values in my study varied between 78.3-91.2% (Table 26 and Table 27), and were mostly higher than the $r^2$ values from many previous studies in the Fynbos Biome such as Linder (1991), Cowling et al., (1997) and Thuiller et al., (2006). However, higher values have been recorded (Kruger and Taylor, 1979; Cowling et al., 1992). The strong performance of

GWR was due to its ability to incorporate non-stationarity into the analyses, thus offering improvement over OLS (Wang et al., 2005; Propastin et al., 2007a; Propastin et al., 2007b; Zhang et al., 2008). Being local, GWR computed a regression value for each point, therefore it avoided complex non-linear fitting, to force fit a global formula (Hawkins et al., 2003a). However, across geographic gradients, the effects of GWR may be non-linear (for example, rainfall concentration and annual temperature range in the Fynbos QDS endemics).

Apart from the analytical techniques used (list in Dormann et al., 2007), at least three dataset specific factors may have influenced the model parameter selection: 1) size of input units; 2) geographic extent of study area; and 3) floristic/taxonomic/functional/growth form attributes of the datasets. I will discuss each factor below.

The use of different input units had a dramatic effect on model variable selection. QDSs were essentially geographically random and of uniform size, while PSCs were floristically non-random, and of irregular size. With PSCs, area based measures of heterogeneity were incorporated (Fynbos area for PSC diversity; and TMS/Witteberg Area for Fynbos PSC Endemics). The floristic grouping of OGUs, based on taxon similarity, seemed to have grouped the QDSs together in a non-random way, bringing these area-based variables (fynbos vegetation area, TMS/Witteberg substrate area) to the fore. The grouping together of QDS units with similar floras may also have resulted in the grouping together QDSs of similar environmental variables, resulting in more abrupt changes in the values of the independent variables of the OGUs, thus lowering spatial auto-correlation, and perhaps non-stationarity (Table 28). However, the effects of thinning out data points cannot be ignored (Lennon, 2000). Differences between QDS and PSC models raised warning flags about making comparisons between studies using different input units, although comparisons of differentially sized random OGUs was not explicitly tested in this study. For example, O'Brien (1993) used grid blocks of 20 000 $km^2$ (ca. 137 × 137 km), while Thuiller et al., used QDSs (ca. 25 × 25 km, = 650 $km^2$). Thus, the analyses of Thuiller et al., (2006) were 29-30 times finer by area than the analyses of O'Brien (1993).

The geographic extent of the study area may also influence parameter selection (Hawkins et al., 2003b), and the influence of the parameters in GWR (Wang et al., 2005). Both the studies of Cowling et al., (1997) and Thuiller et al., (2006) demonstrated quite clearly that at the national level, and within the different biomes of South Africa, different parameters are invoked, which vary in their magnitude to explain richness. The more geographically restricted the study area is, the greater the chance that the independent variables will have a uniform (stationary) relationship with richness. For example, Linder's (1991) study was geographically restricted to the exclusively winter rainfall region in the SWPP of the CFR, largely removing the effects of rainfall seasonality. Further, in such restricted geographic areas, there may be a greater chance of collinearity. Linder (1991) found collinearity between rainfall and altitude, but the inclusion of areas from the Karoo Mountain Phytogeographical Province may have reduced this collinearity, or at least increased non-stationarity of the parameters. As biomes are largely congruent with sub-continental climatic phenomena (Rutherford and Westfall, 1986; Mucina and Rutherford, 2006), it is no surprise that climatic explanatory variables differ in these different areas, and that taxa (richness) within particular biomes have adapted to "local" biome characteristics (Hawkins et al., 2003a). Thus, confining analyses to biomes or chorological units (as suggested by Cowling et al., 1997) may help keep some parameters more constant or stationary. Further, regression may be influenced by large areas with a particular character, which contribute a relatively high proportion of the sample size, for example, the Nama Karoo. This may create biases in a global regression model. Subdivision into more uniform areas, such as biomes (Cowling et al., 1997; Thuiller et al., 2006), or local regression techniques like GWR may help overcome these biases, and help identify local to regional level specific patterns.

Apart from sub-dividing datasets geographically (biomes, regions) and analysing these individually, sub-dividing datasets into taxonomic groups, floristic units, or ecological guilds, may yield a further understanding of taxon or biotic element specific responses to environmental variables (see Currie, 1991; Linder, 1991; Currie et al., 1999; Hawkins et al., 2003a), and enable grouping of datasets displaying similar responses. For example, analysing a particular floristic (CFR versus Succulent Karoo) or taxonomic group (Aizoaceae versus Orchidaceae), or a structural or life history group (for example trees (O'Brien, 1993; O'Brien et al., 2000), succulents, or epiphytes). This keeps the biotic adaptations or limitations of taxa more constrained, and shows how the richness of the selected group responds to explanatory variables (Currie et al., 1991; Linder, 1991). This approach may invoke different explanatory variables for the different groups, as there are trade-offs to adaptation. My relatively simplistic division into different floristic groups had a marked effect of parameter selection in my PSC analyses between diversity and endemism, even though there was a relatively strong correlation between diversity and endemism (and area) (Chapter 2, Section 2.4.3). Currie (1991) and to a lesser extent Linder (1991) selected different variables to explain richness patterns in different taxonomic groups. This may have important effects on biodiversity prediction for conservation in non-GWR studies.

### 4.5.5 Conclusions

Using GWR, environmental variables can explain much (78.3-91.2%) of the patterns in richness in the CFR. I also found that different models were required to optimally explain richness in the different types of input data (QDS versus PSC), and between diversity and endemism richness in the CFR. Only in the PSC analyses were habitat specific measures of areal habitat heterogeneity retrieved. However, although the specific variables selected may be different, they almost always highlighted the importance of both the energy-water hypothesis (potential evapo-transpiration (negative); growth season duration (positive); rainfall concentration (pos/neg); average altitude (equivalent to annual minimum temperature (neg)) and the habitat heterogeneity hypothesis (altitudinal variance (pos); slope (pos); topographic diversity (pos); rainfall range (pos); July minimum temperature range (pos); vegetation count (positive); fynbos area (pos), and TMS/Witteberg area (pos)). In only a one model was a single hypothesis invoked, namely the habitat heterogeneity hypothesis. The retrieval of both hypotheses in nearly all analyses indicated the importance of both hypotheses for modelling richness in the CFR.

In all cases, GWR displayed greater explanatory power than OLS. Although general terrestrial area was not selected, habitat specific area measures were, for example, area of fynbos, and area of TMS/Witteberg substrate. The use of GWR facilitated the retrieval of uninterrupted growing season (GRS) for the first time in the CFR, which had its strongest influence in areas with high numbers of annuals and geophytes, and may be important in other Mediterranean Ecosystems, particularly where annuals or geophytes are well represented. GWR was shown to remove the statistical significance of spatial auto-correlation.

Although southern Africa may be an ideal template to analyse the response of richness to environmental variables (O'Brien et al., 1993; Thuiller et al., 2006), results could be confounded by incorporating dependent or independent variables that are too diverse and/or over too broad a study area, due to notable levels of spatial non-stationarity. Conversely, smaller more uniform geographic areas could increase the collinearity of variables. Although seeking uniformity in either the dependent variable (O'Brien et al., 1993) or independent variables, through geographically or climatically more uniform areas (Cowling et al., 1997; Thuiller et al., 2006) may result in the selection of different variables, either approach could prove useful to understanding patterns of richness. This study, and that of Thuiller et al., (2006), indicated that to understand richness in the CFR, both energy-water and habitat heterogeneity hypotheses should be considered, with the realisation that more inclusive models may yield better results (Gaston, 2000; Kreft and Jetz, 2007).

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## 4.7 APPENDIX: Chapter 4

Table 29: Explanatory Variables of all cross checked models.

| Model Codes | Variable 1 | Variable 2 | Variable 3 | Variable 4 | Variable 5 |
|---|---|---|---|---|---|
| QDS_M1 | GRS | RAR | Veg_C | PET | RWT |
| QDS_M2 | GRS | RAR | Alt_var | RAS | RCO |
| PSC_M1 | Fynbos_Area | Alt_Ave | Slope | PET | |
| PSC_MIN | Fynbos_Area | MIN | Slope | PET | |
| PSC_M2 | Veg_C | TD1 | | | |
| PSC_M3 | TMS-Witteberg | RCO | TD1 | PET | |

Table 30: Cross check results of all alternative route model AIC values.

| | | Model Codes from Table 29 | QDS_M1 | QDS_M2 | PSC_M1 | PSC_MIN | PSC_M2 | PSC_M3 |
|---|---|---|---|---|---|---|---|---|
| Analysis | QDS | Total_Div | **200.3** | 208.2 | 245.3 | 253.5 | 339.8 | 261.4 |
| | | Total_End | **184.2** | 188.3 | 227.7 | 231.5 | 311.5 | 241.2 |
| | | Fynbos_Div | **186.5** | 191.4 | 227.7 | 236.1 | 352.9 | 259.2 |
| | | Fynbos_End | 171.2 | **170.0** | 209.9 | 213.0 | 321.6 | 232.5 |
| | PSC | Total_Div | 77.6 | 96.5 | **63.7** | 68.0 | 109.4 | 69.8 |
| | | Total_End | 53.2 | 69.2 | 68.7 | 74.9 | **26.1** | 40.2 |
| | | Fynbos_Div | 100.1 | 104.1 | **65.7** | 68.8 | 128.0 | 87.3 |
| | | Fynbos_End | 75.3 | 64.4 | 47.9 | 47.1 | 35.9 | **33.8** |

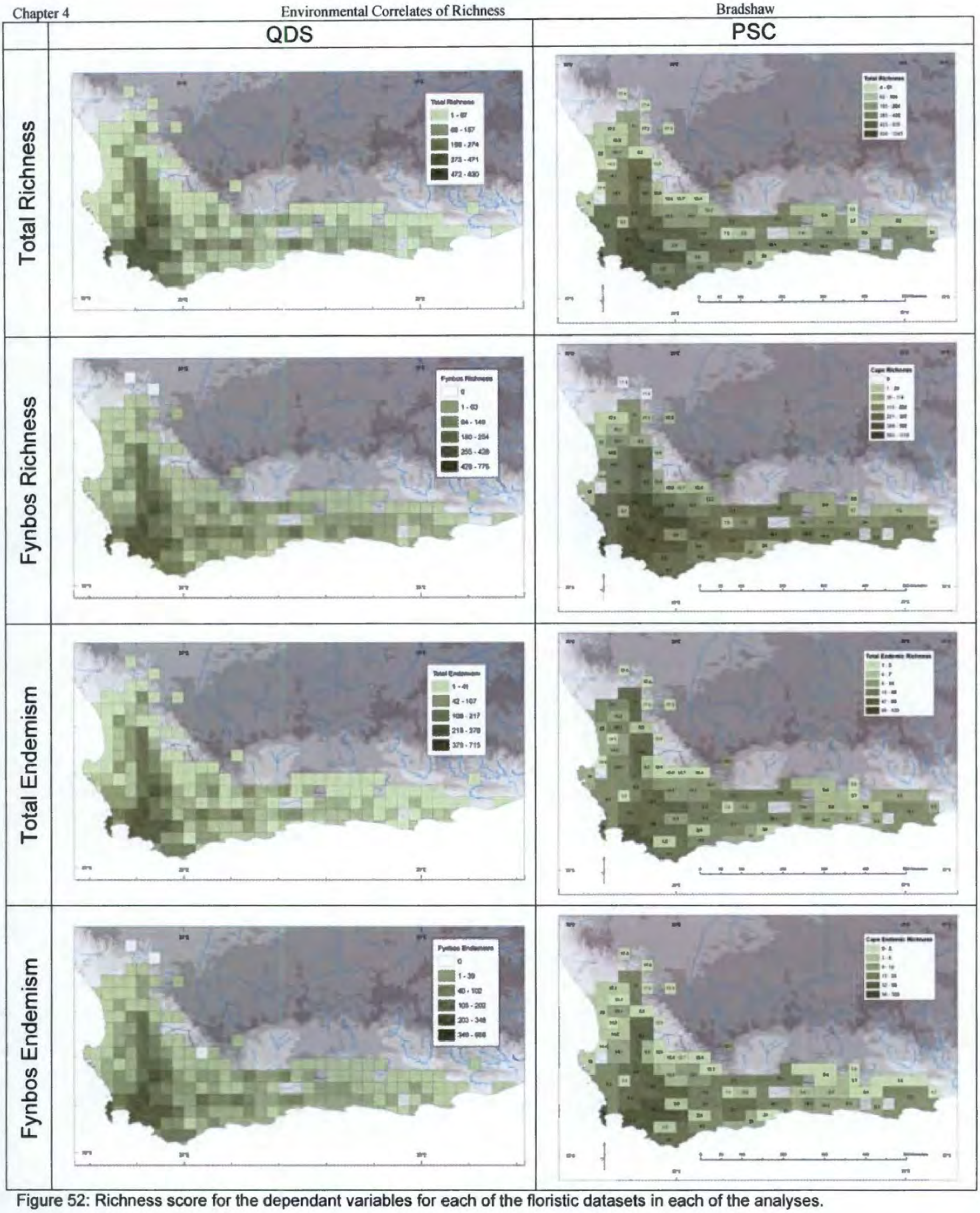


Figure 52: Richness score for the dependant variables for each of the floristic datasets in each of the analyses.

Table 31: Colinearity ($r^2$) of hypothesis variables evaluated in the QDS and PSC analyses. Explanations for the variables are in Table 23

| | | QDS | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Alt_Ave | Alt_Var | Terrestrial Area | FYNBOS_Area | GEOL_Cnt | GEOL_E | GRS | H2O_S | MAR | MAX | MIN | MST | MWT | PET | PEV | PRO | RAD | RAR | RAS | RCO | RCV | RWT | SLOPE | TDI | TMS_W_Area | VEG_Cnt | VEG_E |
| PSC | Alt_Ave | | 0.35 | 0.27 | 0.01 | 0.09 | 0.03 | 0.10 | 0.10 | 0.03 | 0.00 | 0.92 | 0.15 | 0.87 | 0.04 | 0.10 | 0.11 | 0.44 | 0.04 | 0.52 | 0.00 | 0.04 | 0.31 | 0.32 | 0.43 | 0.35 | 0.00 | 0.09 |
| | Alt_Var | 0.23 | | 0.12 | 0.19 | 0.14 | 0.05 | 0.04 | 0.02 | 0.14 | 0.08 | 0.33 | 0.00 | 0.20 | 0.05 | 0.02 | 0.01 | 0.05 | 0.44 | 0.05 | 0.00 | 0.12 | 0.59 | 0.87 | 0.00 | 1.00 | 0.24 | 0.11 |
| | Terrestrial Area | 0.00 | 0.10 | | 0.16 | 0.18 | 0.01 | 0.08 | 0.04 | 0.10 | 0.13 | 0.31 | 0.32 | 0.37 | 0.14 | 0.20 | 0.20 | 0.44 | 0.03 | 0.43 | 0.02 | 0.14 | 0.20 | 0.09 | 0.20 | 0.12 | 0.01 | 0.05 |
| | FYNBOS_Area | 0.02 | 0.15 | 0.60 | | 0.02 | 0.00 | 0.25 | 0.14 | 0.12 | 0.17 | 0.04 | 0.07 | 0.00 | 0.08 | 0.07 | 0.03 | 0.02 | 0.19 | 0.02 | 0.00 | 0.10 | 0.11 | 0.15 | 0.02 | 0.19 | 0.12 | 0.00 |
| | GEOL_Cnt | 0.02 | 0.26 | 0.41 | 0.18 | | 0.10 | 0.02 | 0.02 | 0.00 | 0.01 | 0.09 | 0.06 | 0.12 | 0.00 | 0.01 | 0.02 | 0.07 | 0.08 | 0.11 | 0.01 | 0.00 | 0.16 | 0.12 | 0.01 | 0.15 | 0.17 | 0.09 |
| | GEOL_E | 0.00 | 0.03 | 0.09 | 0.05 | 0.11 | | 0.00 | 0.01 | 0.01 | 0.01 | 0.01 | 0.00 | 0.01 | 0.01 | 0.01 | 0.00 | 0.00 | 0.04 | 0.00 | 0.02 | 0.01 | 0.03 | 0.03 | 0.00 | 0.05 | 0.06 | 0.14 |
| | GRS | 0.16 | 0.08 | 0.05 | 0.41 | 0.02 | 0.00 | | 0.28 | 0.70 | 0.38 | 0.09 | 0.46 | 0.23 | 0.49 | 0.56 | 0.58 | 0.42 | 0.19 | 0.43 | 0.02 | 0.71 | 0.02 | 0.04 | 0.20 | 0.04 | 0.11 | 0.02 |
| | H2O_S | 0.15 | 0.00 | 0.00 | 0.09 | 0.00 | 0.00 | 0.31 | | 0.16 | 0.18 | 0.05 | 0.14 | 0.16 | 0.18 | 0.03 | 0.00 | 0.15 | 0.13 | 0.18 | 0.40 | 0.14 | 0.03 | 0.01 | 0.25 | 0.01 | 0.00 | 0.04 |
| | MAR | 0.05 | 0.26 | 0.08 | 0.35 | 0.07 | 0.01 | 0.76 | 0.16 | | 0.39 | 0.05 | 0.48 | 0.15 | 0.54 | 0.70 | 0.66 | 0.40 | 0.39 | 0.37 | 0.11 | 0.98 | 0.07 | 0.15 | 0.16 | 0.14 | 0.15 | 0.00 |
| | MAX | 0.00 | 0.17 | 0.09 | 0.39 | 0.04 | 0.00 | 0.47 | 0.11 | 0.49 | | 0.00 | 0.76 | 0.05 | 0.63 | 0.53 | 0.20 | 0.49 | 0.19 | 0.40 | 0.02 | 0.39 | 0.00 | 0.06 | 0.10 | 0.08 | 0.06 | 0.00 |
| | MIN | 0.96 | 0.24 | 0.00 | 0.02 | 0.03 | 0.00 | 0.14 | 0.15 | 0.04 | 0.00 | | 0.16 | 0.90 | 0.03 | 0.12 | 0.16 | 0.46 | 0.06 | 0.54 | 0.00 | 0.07 | 0.26 | 0.29 | 0.36 | 0.33 | 0.00 | 0.07 |
| | MST | 0.14 | 0.05 | 0.11 | 0.40 | 0.02 | 0.00 | 0.60 | 0.12 | 0.56 | 0.79 | 0.12 | | 0.36 | 0.64 | 0.76 | 0.41 | 0.86 | 0.08 | 0.82 | 0.07 | 0.50 | 0.02 | 0.00 | 0.26 | 0.00 | 0.05 | 0.02 |
| | MWT | 0.89 | 0.09 | 0.00 | 0.10 | 0.01 | 0.00 | 0.33 | 0.25 | 0.15 | 0.04 | 0.89 | 0.32 | | 0.15 | 0.24 | 0.25 | 0.65 | 0.01 | 0.78 | 0.00 | 0.17 | 0.22 | 0.18 | 0.49 | 0.20 | 0.00 | 0.09 |
| | PET | 0.05 | 0.11 | 0.12 | 0.35 | 0.13 | 0.04 | 0.55 | 0.19 | 0.51 | 0.61 | 0.04 | 0.60 | 0.15 | | 0.71 | 0.38 | 0.52 | 0.22 | 0.45 | 0.08 | 0.54 | 0.00 | 0.04 | 0.15 | 0.05 | 0.13 | 0.01 |
| | PEV | 0.10 | 0.10 | 0.12 | 0.37 | 0.07 | 0.01 | 0.63 | 0.02 | 0.70 | 0.63 | 0.07 | 0.80 | 0.19 | 0.65 | | 0.72 | 0.68 | 0.16 | 0.60 | 0.31 | 0.73 | 0.00 | 0.05 | 0.16 | 0.02 | 0.14 | 0.01 |
| | PRO | 0.08 | 0.09 | 0.08 | 0.28 | 0.03 | 0.00 | 0.68 | 0.00 | 0.72 | 0.33 | 0.07 | 0.50 | 0.17 | 0.40 | 0.76 | | 0.43 | 0.06 | 0.41 | 0.38 | 0.74 | 0.03 | 0.05 | 0.10 | 0.01 | 0.09 | 0.01 |
| | RAD | 0.41 | 0.00 | 0.06 | 0.31 | 0.00 | 0.00 | 0.60 | 0.17 | 0.49 | 0.55 | 0.37 | 0.87 | 0.58 | 0.54 | 0.72 | 0.47 | | 0.02 | 0.95 | 0.06 | 0.44 | 0.11 | 0.04 | 0.42 | 0.05 | 0.03 | 0.04 |
| | RAR | 0.00 | 0.45 | 0.19 | 0.37 | 0.29 | 0.04 | 0.31 | 0.14 | 0.57 | 0.40 | 0.01 | 0.30 | 0.01 | 0.40 | 0.37 | 0.21 | 0.18 | | 0.01 | 0.00 | 0.31 | 0.23 | 0.31 | 0.03 | 0.44 | 0.23 | 0.03 |
| | RAS | 0.53 | 0.00 | 0.05 | 0.29 | 0.00 | 0.00 | 0.59 | 0.22 | 0.42 | 0.41 | 0.50 | 0.80 | 0.76 | 0.44 | 0.59 | 0.41 | 0.92 | 0.14 | | 0.03 | 0.40 | 0.11 | 0.04 | 0.45 | 0.05 | 0.03 | 0.06 |
| | RCO | 0.00 | 0.02 | 0.32 | 0.27 | 0.11 | 0.03 | 0.01 | 0.23 | 0.00 | 0.01 | 0.00 | 0.00 | 0.01 | 0.01 | 0.02 | 0.06 | 0.00 | 0.09 | 0.01 | | 0.13 | 0.09 | 0.08 | 0.01 | 0.00 | 0.10 | 0.01 |
| | RCV | 0.05 | 0.25 | 0.08 | 0.36 | 0.07 | 0.01 | 0.78 | 0.14 | 0.99 | 0.50 | 0.04 | 0.57 | 0.16 | 0.51 | 0.72 | 0.78 | 0.50 | 0.53 | 0.44 | 0.00 | | 0.06 | 0.13 | 0.17 | 0.11 | 0.13 | 0.00 |
| | RWT | 0.06 | 0.41 | 0.40 | 0.20 | 0.36 | 0.05 | 0.07 | 0.06 | 0.21 | 0.04 | 0.05 | 0.04 | 0.01 | 0.07 | 0.14 | 0.26 | 0.00 | 0.18 | 0.00 | 0.00 | 0.23 | | 0.63 | 0.02 | 0.59 | 0.21 | 0.09 |
| | SLOPE | 0.21 | 0.87 | 0.09 | 0.12 | 0.20 | 0.01 | 0.07 | 0.03 | 0.26 | 0.16 | 0.22 | 0.06 | 0.10 | 0.10 | 0.17 | 0.20 | 0.00 | 0.31 | 0.00 | 0.00 | 0.26 | 0.48 | | 0.01 | 0.87 | 0.21 | 0.08 |
| | TDI | 0.48 | 0.01 | 0.06 | 0.23 | 0.01 | 0.04 | 0.43 | 0.32 | 0.37 | 0.16 | 0.46 | 0.40 | 0.63 | 0.26 | 0.28 | 0.23 | 0.55 | 0.15 | 0.64 | 0.04 | 0.37 | 0.03 | 0.00 | | 0.00 | 0.09 | 0.00 |
| | TMS_W_Area | 0.00 | 0.10 | 1.00 | 0.59 | 0.42 | 0.10 | 0.05 | 0.00 | 0.08 | 0.09 | 0.00 | 0.10 | 0.00 | 0.12 | 0.12 | 0.08 | 0.05 | 0.19 | 0.05 | 0.32 | 0.08 | 0.40 | 0.09 | 0.06 | | 0.24 | 0.11 |
| | VEG_Cnt | 0.03 | 0.19 | 0.61 | 0.56 | 0.42 | 0.10 | 0.27 | 0.00 | 0.33 | 0.23 | 0.03 | 0.32 | 0.09 | 0.40 | 0.42 | 0.33 | 0.26 | 0.39 | 0.25 | 0.07 | 0.34 | 0.45 | 0.19 | 0.24 | 0.61 | | 0.09 |
| | VEG_E | 0.02 | 0.16 | 0.16 | 0.06 | 0.17 | 0.11 | 0.00 | 0.01 | 0.00 | 0.00 | 0.02 | 0.00 | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 | 0.09 | 0.00 | 0.09 | 0.00 | 0.20 | 0.14 | 0.01 | 0.16 | 0.17 | |

# General Summary

The Cape Floristic Region (CFR) - a global biodiversity hotspot - proved an excellent area to study patterns of endemism, taxon richness, floristic patterns, and how environmental conditions affect richness. The CFR is exceptionally rich in species and endemics (9087 species, 68.5% endemism). This richness is packed within a relatively small area (ca. 90 000 km$^2$) with a Mediterranean cool growing season, with relatively low moisture and low energy. Thus, the CFR provides an interesting contrast to hyper-diverse equatorial tropical forests, which are associated with warm-growing, high energy and high water conditions. High levels of beta and gamma diversity over relatively short geographic distances associated with a high level of hierarchical congruence in the distributional ranges of taxa, facilitated the retrieval of phytogeographical patterns.

## Chapter 2: Phytogeography

### Combined Dataset

In order to test congruence between the distributions of range restricted taxa, and to delimit chorological units, a large representative dataset was compiled and analysed, using comprehensive modern chorological weighted clustering techniques To avoid geographic circularity in establishing floristic boundaries, data were not confined to political or biotic geographic areas where possible. Multiple analyses were performed on each dataset, to more comprehensively analyse the data and to assess the statistical robustness of the patterns.

A hierarchical analysis was undertaken to determine how the individual Phytogeographical Centres (PCs) of the combined dataset are floristically related to each other, and to determine whether they combined into the higher level phytogeographical areas of proposed by previous studies (*cf.* Weimarck, 1941; Goldblatt and Manning, 2000).

The congruent phytogeographical patterns from the different clustering analyses undertaken on the combined dataset indicated substantial spatial structure and congruence in the distribution of range restricted taxa. Relatively good congruence between the phytogeographical patterns of this study and the two most significant and comprehensive previous studies (Weimarck, 1941; Goldblatt and Manning, 2000) indicated robust common broad-scale phytogeographical patterns within the CFR.

The large size of the dataset, and extensive analysis revealed additional finer phytogeographical sub-division, not previously recorded, including: six Phytogeographical Provinces (PP), 16 Centres (PC), and 36 Sub-Centres (PSC); compared to five equivalent Phytogeographical Provinces and nine equivalent Centres of Weimarck (1941), and six equivalent Phytogeographical Provinces of Goldblatt and Manning (2000). Additional floristic detail was retrieved in the Northwest PP, to the western showing the floristic distinctiveness of the Piketberg and Northwest Sandveld. Inland, the Hexriver, Groot Winterhoek and Greater Witteberg all displayed distinctive floristic development. In the Karoo Mountain PP, the importance of floristic development on the more mesic mountains in this xeric area was highlighted. The LBPP displayed east-west development, coinciding with major valleys, as well as montane and lowland differentiation. The Agulhas Plains PP was found to for three distinct areas.

Outliers of Cape Clades were endemic to areas outside the core CFR, and were usually situated in higher altitude, mesic sites, such as the Kamiesberg in the Succulent Karoo, and the

Drakensberg, Barberton, Pilgrim's Rest, Wolkeberg, and Soutpansberg in the high altitude temperate/montane sites in the summer rainfall areas. However, the phytogeographical patterns identified in this study for these areas outside the core CFR are coarse, and would undoubtedly be refined by the addition of clades centred in the Succulent Karoo or Drakensberg.

Hierarchical clustering of the Combined Dataset PCs revealed similar hierarchical patterns to previous phytogeographical studies on the CFR (Weimarck, 1941; Goldblatt and Manning, (2000). Phytogeographical Centres were found to cluster in the six traditional phytogeographical provinces (phytogeographical centres, *sensu* Goldblatt and Manning, 2000), the Southwest PP, Northwest PP, Langeberg PP, Agulhas Plains PP, Karoo Mountain PP and Southeast PP, forming the core CFR. The Gifberg, Nieuwoudtville and Vanrhynsdorp PCs were found to cluster outside the core CFR, and formed a southern Succulent Karoo area. There is conflict in the literature as to the inclusion or exclusion of these latter PCs in the CFR. Results here indicate weak high altitude archipelago-like affinities to the CFR, but stronger numeric affinities to the Succulent Karoo. Another notable deviation included the association of the Saldanha Peninsula and northwest coastal areas with this southern Succulent Karoo Centre, rather than to the Southwest PP and Northwest PP respectively. This may indicate a contraction of the CFR in response to aridification since the last glacial maximum when conditions are likely to have been cooler and wetter.

Relatively large numbers of Quarter Degree Squares (QDSs) were assigned to PCs, thus indicating that endemism was widespread in the CFR, but had its greatest concentration in the western winter rainfall areas, which also displayed the strongest phytogeographical development. While it was beyond the scope of this study and resolution of the data to determine precise boundaries between PCs, certain inferences can be made. The most numerous biotic element in the CFR comprises montane TMS fynbos taxa. Thus it is no surprise that phytogeographical development is more continuous in areas where this habitat is least interrupted, as dispersal would be least disrupted in these areas. For TMS fynbos taxa, large valleys and areas of lower altitude habitat can result in abrupt floristic turnover, forming boundaries between PCs. Less incised valleys pose less of a barrier, with lower turnover, and align with PSC boundaries within PCs. Phytogeographical development is more defined in the west (which has steep mountain slopes), with smaller, richer PCs, while in the east CFR, boundaries are less defined (topographically, slopes are less steep and more convex), and PCs have lower richness, and are larger. Different biotic elements may have different barriers to dispersal. Mountains may pose barriers to low altitude biotic elements. Lower altitude taxa are frequently endemic to particular substrates (littoral, limestone, granite and shale), and interfaces between these substrates could cause abrupt changes in floristic composition, resulting in phytogeographical boundaries. It may be possible to analytically quantify these boundaries on a more spatially resolved dataset of endemic taxa to determine the environmental barriers to dispersal.

## Clade/Group Datasets

The combined dataset was divided into numerous derivative datasets, including taxonomic (family), functional (geophyte) and threatened (RDL) datasets, to assess whether floristic patterns are repeated amongst these groups. Analysed as a single dataset, idiosyncratic patterns, particularly of less numerous clades, may be overwhelmed by numerically more dominant groups.

Certain datasets can be grouped together, based on their levels of phytogeographical congruence. Bruniaceae, Proteaceae (Proteeae) and Restionaceae have high levels of congruence. They display the greatest affinities to montane Mediterranean environments on TMS and are essentially restricted to the CFR. PC endemics of Ericaceae (*Erica*), Orchidaceae (Diseeae), Poaceae (Danthonieae) and possibly Rosaceae (*Cliffortia*), also show a higher preference for cooler mesic montane environments, but are less restricted to the CFR, being fairly well represented on the Eastern and Northeastern Escarpment as well. Fabaceae (*Aspalathus*), Geophytes and Rutaceae (Diosmeae) are unusual in that the NWPP contains the greatest numbers of endemic taxa. Additionally, these three datasets have well developed lower altitude PCs, which may be related to a lower moisture regime adaptation, or adaptation to non-TMS substrates. Low altitude PC formation is also significant in Asteraceae, Polygalaceae (*Muraltia*) and the RDL Taxa. Shared Phytogeographical patterns may possibly indicate shared evolutionary histories and/or selective pressures between the different clades. Congruence was never exact, and differences were explained based on different ratios of edaphic and topographic biotic elements in datasets. Where datasets displayed notable deviation from typical fynbos phytogeographical patterns, for example the Geophytes dataset, and to a lesser extent, Fabaceae and Rutaceae, additional research is recommended in order to better align these families phytogeographically.

By analysing taxonomic groups independently, additional insights into differences between earlier phytogeographical classifications of the CFR could be gained. Differences in the frequencies of biotic elements in the different datasets helped explain differences in the phytogeographical patterns of the two previous notable phytogeographical studies in the CFR (Weimarck, 1941; Goldblatt and Manning, 2000). For example, datasets with higher numbers of montane fynbos taxa tend to group the Agulhas Plains (or parts thereof) with the SWPP (e.g. Bruniaceae, Orchidaceae: Diseeae) as did Weimarck (1941), while taxa more strongly represented at lower altitude have more well developed independent Agulhas Plains (e.g. Rutaceae, Asteraceae and Fabaceae) similar to Goldblatt and Manning (2000), while other taxa show intermediate patterns.

The technique used herein to delimit PCs analysed individual clades, thus preventing more numerous clades, e.g. *Erica*, from obscuring individual floristic patterns of smaller clades. Idiosyncratic clade patterns hidden in the combined dataset include Rutaceae and Fabaceae, which had higher endemism and species richness in the NWPP rather than the SWPP. This reveals different development histories or selective pressures.

Habitat Analysis:

As QDSs and PCs can contain numerous habitats, habitat preferences of taxa endemic to PCs were recorded and analysed, to indicate the relative frequencies of biotic elements in the different PCs, which helped to identify habitats where endemic taxa occurred. Unequal treatment of taxon habitat data in the literature prevented a more rigorous statistical investigation of patterns. It was noted that the greater majority of PC endemic taxa were found to occur on TMS slope habitats. This is particularly noticeable in the more montane PCs. While TMS endemic elements are represented in lowland PCs, there is a proportionate increase of endemics on other habitats. Granite endemics are particularly abundant on the granite extrusions around Paarl and Stellenbosch, and on the Saldanha Peninsula, while limestone endemics are common on the Agulhas Plains. Additionally, in coastal areas, endemics can be found on quaternary littoral sand deposits. PC endemics also occur on rolling shale hills, but are not well represented. PC endemics on clay are more numerous than those on shale, especially on the Nieuwoudtville Escarpment, and lower altitudes in the Greater Langeberg PC. This means that PCs may contain multiple endemics biotic elements, or endemics in multiple habitats, the ratios of which vary depending on the location of the PC and the group being analysed. Different biotic elements would have different barriers to dispersal. Dispersal of TMS montane taxa could be inhibited by incised valleys, or substrate types. Similarly, dispersal of low altitude endemics could be inhibited by mountains, or substrate.

Regression Analysis:
The relationship between endemism, richness and area of PCs was investigated using simple log-log regression, to determine if the size of PCs alone could explain levels of richness and endemism. A strong positive, significant correlation was mostly found between PC endemism and non-endemic PC richness, and between endemism and PC area, and between non-endemic PC richness and PC area. Proteaceae is somewhat of an anomaly, with all three correlations being weak but significant. In many cases, the Peninsula had to be excluded to obtain statistically significant result, as it contained far greater endemism and richness than predicted by area. Conversely, the larger eastern, endemic depauperate summer rainfall centres had to be removed to obtain statistically significant results, as they contained much poorer endemism and diversity than predicted by area. While most PCs occurred in the 95% confidence interval, several occurred either above or below, indicating that PC area alone can't always adequately account for high or low levels of PC endemism or richness. This indicates that additional factors, such as environment and/or history are also influencing richness in these centres, and need to be investigated.

Chapter 3: Assessment of Methods

The performance of each of the weighting/clustering techniques implemented in the study (unweighted UPGMA, Bell weighted PAE, Bell weighted UPGMA, Int weighted UPGMA, MInt weighted UPGMA) was quantitatively assessed by a number of inter-related measures, namely: endemic PC taxa, PC richness, PC size, and the number of PCs generated, for each of the 15 datasets. These individual weighting techniques were then compared to the consensus of these results with further GIS refinement. It was found that although Bell weighting with UPGMA clustering produced slightly more optimal PCs for the criterion used in performance assessment, obtaining consensus from multiple analyses, and further GIS interrogation of candidate phytogeographical areas identified from cluster analysis can substantially enhanced the physical size and numbers of endemics of candidate phytogeographical areas. GIS interrogation, previously largely neglected, is a novel and efficacious approach to chorological delimitation. Further, it was found that conducting multiple clustering analyses could supplement weakly resolved trees, and was of benefit in highlighting areas of floristic congruence and conflict. These can be effectively interrogated and resolved in a GIS. This means that the gains of post clustering GIS interrogation may offset any differences in optimality of a single weighting technique by increasing the area and number of endemics in phytogeographical centres. However, this is potentially more beneficial for chorological studies which seek to classify areas into biotic units rather than for candidate centres of endemism used in cladistic biogeographic analysis.

Chapter 4: Environmental Correlates

In order to explain how well patterns of richness and endemism could be explained by environmental variables, a spatially sensitive regression technique (GWR) was used, that could account for spatial auto-correlation. Richness data were divided into derivative floristic datasets, including: total richness, total endemism, fynbos richness and fynbos endemism, to investigate whether different models were required to explain richness in these different datasets. Additionally, two types of input data were used, random uniform QDS, and floristically non-random irregular PSC identified in Chapter Two. It was found that GWR, incorporating environmental variables from both the energy-water hypothesis and habitat heterogeneity hypothesis explained much (78.3-91.2%) of the patterns in richness in the CFR, indicating the importance of both (multiple) hypotheses in understanding patterns of richness in the CFR, in agreement with other recent studies (Kreft and

Jetz, 2007). Potential evapo-transpiration and various measures of topographic heterogeneity provided high explanatory power. Length of growing/rain season was particularly important in the western winter rainfall CFR. Different models were required to optimally explain richness in the different types of input data (QDS versus PSC), and between richness and endemism in the CFR, indicating that comparisons between different studies should be made with caution. GWR displayed stronger explanatory power than global ordinary least squares regression in all analyses, and adequately accounted for spatial auto-correlation in the analysis. Thus, despite the high levels of beta and gamma diversity in the CFR, and the structured and congruent distributions of taxa forming floristic units, both the habitat heterogeneity and energy-water hypotheses still underpin gross regional levels of richness.

## Additional Research

While it was beyond the scope of this study and resolution of the data to determine precise boundaries between PCs, this could be undertaken on a more spatially resolved dataset of endemic taxa to determine the environmental barriers to dispersal.

An analysis of molecular dating of speciation events would shed additional understanding on the age and origin of endemic taxa in PCs. Previously, endemic taxa were either classified as palaeo-endemic or neo-endemic. Such qualitative classification could be refined. A quantitative classification of the speciation of endemics (perhaps into epochs) might be more informative, especially when compared to hypothesised historical environmental conditions, and shed more light on endemics in PCs, and PC formation.

# Appendix I: Phytogeography of Derivative Datasets

## Introduction

There are two reasons for undertaking separate analyses and interpretation of the individual sub-datasets, rather than relying exclusively on a single combined analysis. I refer to these reasons as geographical circularity and clade bias.

I define **geographic circularity** as the selection of certain taxa that are known to occur in an area of interest and then using these selected taxa to define the phytogeographical boundaries of the area of interest, to the exclusion of certain members of clades involved. Therefore, taxa are selected on geographic rather than on phylogenetic grounds. Goldblatt and Manning (2000) and Linder, Lovett, Mutke, Barthlott, Jurgens, Rebelo and Kuper (2005), used this approach in the analysis of African phytogeographical patterns. While this may yield satisfactory results in identifying different phytogeographical areas within the area of interest (internal floristic boundaries), phytogeographical boundaries between the CFR and other floristic areas may be less robust, and **external boundaries and floristic affinities may not be extended far enough**. This problem is further exacerbated by the use of political boundaries, which are usually even more biologically arbitrary. Some of the datasets that I utilised had been clipped to a pre-defined concept of the CFR. They excluded areas like the Kamiesberg and areas around Grahamstown, for example, the RDL Taxa Dataset and the Proteaceae Dataset, or the data sampling excluded these areas, for example, Asteraceae and Geophytes. In these datasets, the external floristic boundaries of the CFR cannot be determined with certainty. By using entire clades, rather than simply taxa that occur within a pre-defined geographic area, this circularity can be avoided. A further strength of this approach is the identification of outlier areas. These may be of historical interest, such as the floristic links between the CFR and the Kamiesberg, Grahamstown Mountains, Drakensberg Mountains, and East African Highlands. These areas would not be retrieved by a purely area-based approach that is geographically restricted to the CFR. Once outlying areas have been identified, they can be examined and compared to floristic patterns in other clades, in order to determine whether they are unique events associated with a particular taxon, or whether they are part of a repeated pattern. A decision can then be made on the floristic placement and interpretation of these areas. For example, the Kamiesberg peaks contain a number of phylogenetically diverse Cape Clade representatives and endemics, which suggests strong affinities to the core CFR, which is of considerable phytogeographical interest.

Thus, in order to reduce geographical circularity and subjectivity, I recommend the analysis of monophyletic clades.

However, the use of entire clades is not without its own problems and biases. Additional problems of determining phytogeographical boundaries can arise, for example, boundaries based on single clades or on dominant biotic elements can extend into areas where other clades or biotic elements are more dominant, but due to their absence from the analyses, their patterns are not taken into account. Similarly, if one is only considering a single clade, taxa with wider ranges may be used to determine boundaries, which extend over the boundaries of other more range-restricted taxa from other clades or floras. I refer to this as **clade bias**. The Zuurberg Sub-Centre of Weimarck (1941), which extends beyond the Sundays River, is a potential example of the effects of clade bias. Many authors consider the Sundays river to be the boundary of the CFR proper (Bolus, 1886, 1905; Marloth, 1908; Goldblatt and Manning, 2000), with only scattered occurrences of Cape clades beyond. Thus, inclusion of non CFR centred taxa would likely have resulted in its exclusion from the CFR. Clade bias jeopardises the accuracy of **external floristic boundaries and floristic relationships by extending them too far**. Examples of areas where this occurs in my study include the Southern Succulent Karoo PC and the Eastern Archipelago PC (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). By analysing purely Cape Clades, these areas are grouped with the CFR (for example, Polygalaceae, Proteaceae, Restionaceae and Diosmeae), due to clade bias. More taxonomically representative datasets, such as my Combined Dataset (Table 6) result in these areas clustering further away from the (core) CFR (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). However, clade specific results, stated and interpreted as such, are not necessarily incorrect, but discussions about entire floras are limited. As a whole, the QDSs peripheral to the core CFR are numerically dominated by non-Cape Clades, but include enclaves of Cape Taxa that are restricted to high altitude mesic sites. Higher resolution spatial data might be able to tease out endemic taxa at opposite ends of these topographic gradients and reduce this conflict. Similarly, the Eastern Escarpment is demarcated as a very large PC in *Erica*. While these patterns may be accurate and be of ecological and historical importance to the relevant clade, single clades may not reflect the most highly resolved floristic patterns across their ranges. The addition of clades centred on the Eastern Escarpment would reveal the finer floristic sub-divisions of the area.

Clade bias was also found to affect the **internal floristic boundaries** of the CFR (below the regional level). In Orchidaceae, the LBPP, KMPP and SEPP are grouped together into a single unit. Similarly, the KMPP and SEPP are grouped together in Bruniaceae.

The problems of clade circularity extend beyond taxa into ecological "guilds" of taxa.

Marloth (1908) identified a set of "Cape Clades" characterised by being centred in the CFR (which had then only been generally defined). Weimarck (1941) used this set of clades to delimit both the CFR and the centres in the CFR. These "Cape Clades" (Marloth, 1908; Weimarck, 1941) are heavily biased towards montane TMS elements (fynbos vegetation) and to a lesser extent, shale elements (Renosterveld vegetation). It is worth noting that fynbos comprises approximately 70% of the taxa in the area defined as the CFR (Cowling and Proches, 2005). Bias towards TMS Clades leads to the near exclusion of taxa like Aizoaceae and Crassulaceae, and may overwhelm their phytogeographical patterns even if they are included. Bayer (1984) was the first to note this bias towards Fynbos Clades. This study does not address this problem in detail, although it does include all RDL Taxa in the CFR. Analysing a set of clades separately should reduce the impact of clade bias and also help to identify clade-specific patterns. The completeness of datasets should always be borne in mind. Unfortunately, logistical problems, such as software limitations (matrix size), hardware limitations (computer speed) and data availability make it very difficult to analyse extensive and exhaustive datasets. Furthermore, due to historical biases in specimen collection and taxonomic description, Fynbos Clades are better known than Succulent Karoo Clades.

# Chapter 5: Asteraceae (Table 32, Figure 53)

## 5.1 Introduction

It is remarkable how few phytogeographical studies have been conducted on the Asteraceae in the CFR and in the Winter Rainfall area, considering that this family contributes more taxa and endemics, both at specific and generic level to the CFR Cape flora than any other family (Goldblatt and Manning, 2000). The poorly known taxonomic and phylogenetic relationships of the family undoubtedly have contributed to this current lack of knowledge. This situation is currently being addressed by various biologists (Nordenstam, 1994; Bayer, Puttock and Kelchner, 2000; Funk, Chan and Keeley, 2004; McKenzie, Muller, Skinner, Karis and Barker, 2006). Compounding this neglect is the "relatively" low rate of higher (tribal) taxonomic endemism in relation to the CFR, compared to other Cape Clades. Asteraceae have many more taxa that cross the traditional CFR-Succulent Karoo boundary than other Cape Clades (Nordenstam, 1969). For the Asteraceae (as well as Aizoaceae), the winter-summer rainfall boundary may be a more important floristic boundary than the 250mm winter rainfall isoline (Dahlgren, 1963c), which marks the boundary of the fynbos biome (Rutherford and Westfall, 1986). Three major "regional/climatic biotic" elements may be identified in the winter rainfall region: (1) elements restricted to the more mesic winter rainfall region (>250mm winter rainfall); (2) elements restricted to the more arid winter rainfall region (<250mm winter rainfall); and (3) elements that occur in both the mesic and arid winter rainfall regions. The latter lends support for call for a Greater Cape or Winter Rainfall region (Bayer, 1984; Jurgens, 1997; Born et al., 2006). Asteraceae are particularly common along the arid margins of the CFR and in arid fynbos areas (Campbell, 1985).

The most comprehensive floristic study, undertaken exclusively on Asteraceae in southern Africa was by Nordenstam (1969) on *Euryops*. Nordenstam (1969) used the phytogeographical centres of Weimarck (1941), as well as adding additional centres for *Euryops* outside the CFR, many of which are also significant for other taxa. In many ways *Euryops* does not show strong phytogeographical similarities to other Cape Clades. The highest levels of diversity and endemism occur mostly in the summer rainfall region in the Albany Centre, followed by the Stormsberg Centre to the north and the Drakensberg Centre to the northeast (Croizat, 1965; van Wyk and Smith, 2001). The Caledon Centre (PC in the SWPP) has high diversity, but relatively low endemism (Nordenstam, 1969),

Table 32: Taxonomic properties of the Centres identified for the Family Asteraceae (Figure 53).

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Southwestern Mtns | 14 | 162 | 119 | 69 | 156 | 0.16 | 0.15 |
| 1.1 | Bainskloof-Stellenbosch-SW Hottentots | 6 | 118 | 55 | 19 | 32 | 0.28 | 0.24 |
| 1.2 | Palmiet-Kleinriviersberge | 2 | 54 | 19 | 8 | 8 | 0.50 | 0.43 |
| 1.3 | RZE | 4 | 54 | 19 | 7 | 7 | 0.25 | 0.13 |
| 1.4 | S Central RZE | 1 | 40 | 10 | 7 | 7 | 1.00 | 1.00 |
| 2 | Northwestern Mtns | 28 | 137 | 94 | 66 | 158 | 0.09 | 0.07 |
| 2.1 | Nieuwoudtville Plateau | 3 | 19 | 14 | 9 | 12 | 0.44 | 0.38 |
| 2.2 | Gifberg-N West Coast | 4 | 15 | 11 | 7 | 10 | 0.36 | 0.25 |
| 2.3 | N Cedarberg | 5 | 44 | 14 | 6 | 12 | 0.40 | 0.28 |
| 2.4 | W Hexriver Mtns | 2 | 46 | 14 | 4 | 4 | 0.50 | 0.33 |
| 2.5 | Groot Winterhoek | 3 | 41 | 11 | 4 | 6 | 0.50 | 0.33 |
| 2.6 | S Cedarberg | 4 | 39 | 12 | 2 | 5 | 0.63 | 0.25 |
| 2.7 | NE Hexriver | 1 | 24 | 4 | 1 | 1 | 1.00 | - |
| 2.8 | E Cedarberg | 1 | 8 | 3 | 1 | 1 | 1.00 | - |
| 2.9 | W Hantamsberg | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 2.10 | Remainder | 2 | 6 | 0 | 0 | 0 | - | 1.00 |
| 3 | West and East Agulhas Plains-Potberg | 19 | 66 | 43 | 28 | 60 | 0.11 | 0.08 |
| 3.1 | East Agulhas Plain | 3 | 13 | 8 | 5 | 8 | 0.53 | 0.42 |
| 3.2 | E West Agulhas Plains | 4 | 24 | 9 | 4 | 9 | 0.56 | 0.42 |
| 3.3 | E East Langeberg Plains | 1 | 8 | 4 | 3 | 3 | 1.00 | 1.00 |
| 3.4 | Potberg-East Agulhas Plain | 4 | 20 | 9 | 2 | 5 | 0.63 | 0.25 |
| 3.5 | W West Agulhas Plain | 4 | 27 | 5 | 2 | 5 | 0.63 | 0.25 |
| 3.6 | W East Langeberg Plains | 1 | 4 | 2 | 2 | 2 | 1.00 | 1.00 |
| 3.7 | Remainder | 2 | 13 | 2 | 0 | 0 | - | 1.00 |
| 4 | W Karoo Mtns | 16 | 45 | 26 | 19 | 55 | 0.18 | 0.14 |
| 4.1 | Klein Swartberg | 2 | 12 | 8 | 6 | 9 | 0.75 | 0.70 |
| 4.2 | West Langeberg | 2 | 10 | 3 | 2 | 3 | 0.75 | 0.50 |
| 4.3 | SE Witteberg | 2 | 13 | 6 | 2 | 4 | 1.00 | 1.00 |
| 4.4 | Wabooms-Touwsberg | 2 | 6 | 4 | 2 | 2 | 0.50 | 0.00 |
| 4.5 | W West Langeberg | 1 | 7 | 2 | 1 | 1 | 1.00 | - |
| 4.6 | Remainder | 7 | 11 | 5 | 0 | 0 | - | 1.00 |
| 5 | Central and East Langeberg and Outliers | 8 | 38 | 19 | 17 | 37 | 0.27 | 0.23 |
| 5.1 | Central and East Langeberg | 6 | 36 | 18 | 15 | 35 | 0.39 | 0.35 |
| 5.2 | Remainder | 2 | 4 | 2 | 0 | 0 | - | 1.00 |
| 6 | Sandveld-Piketberg-Swartberg | 14 | 55 | 28 | 13 | 28 | 0.15 | 0.08 |
| 6.1 | Sandveld and Outliers | 10 | 46 | 21 | 9 | 19 | 0.21 | 0.11 |
| 6.2 | Piketberg | 3 | 15 | 6 | 3 | 7 | 0.78 | 0.67 |
| 6.3 | Remainder | 1 | 2 | 2 | 0 | 0 | - | 1.00 |
| 7 | W Southeastern Centre | 17 | 28 | 16 | 13 | 27 | 0.12 | 0.05 |
| 7.1 | Outeniqua-West Tsitsikamma | 7 | 17 | 7 | 5 | 11 | 0.31 | 0.14 |
| 7.2 | Tsitsikamma | 2 | 12 | 5 | 3 | 3 | 0.50 | 0.25 |
| 7.3 | Kouga | 2 | 4 | 1 | 1 | 2 | 1.00 | - |
| 7.4 | W Kouga-Suuranysberge | 2 | 2 | 1 | 1 | 2 | 1.00 | - |
| 7.5 | PE Plain | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 7.6 | Remainder | 3 | 6 | 1 | 0 | 0 | - | 1.00 |
| 8 | Peninsula | 3 | 54 | 23 | 10 | 17 | 0.57 | 0.52 |
| 9 | E Southeastern Centre | 7 | 21 | 11 | 6 | 12 | 0.29 | 0.14 |
| 10 | Groot Swartberg-E Rooiberg-Kammanassie | 4 | 15 | 7 | 6 | 11 | 0.46 | 0.35 |
| 10.1 | Groot Swartberg | 3 | 12 | 5 | 4 | 7 | 0.58 | 0.44 |
| 10.2 | E Kammanassie | 1 | 8 | 1 | 1 | 1 | 1.00 | - |
| 10.3 | Remainder | 1 | 2 | 0 | 0 | 0 | - | 1.00 |

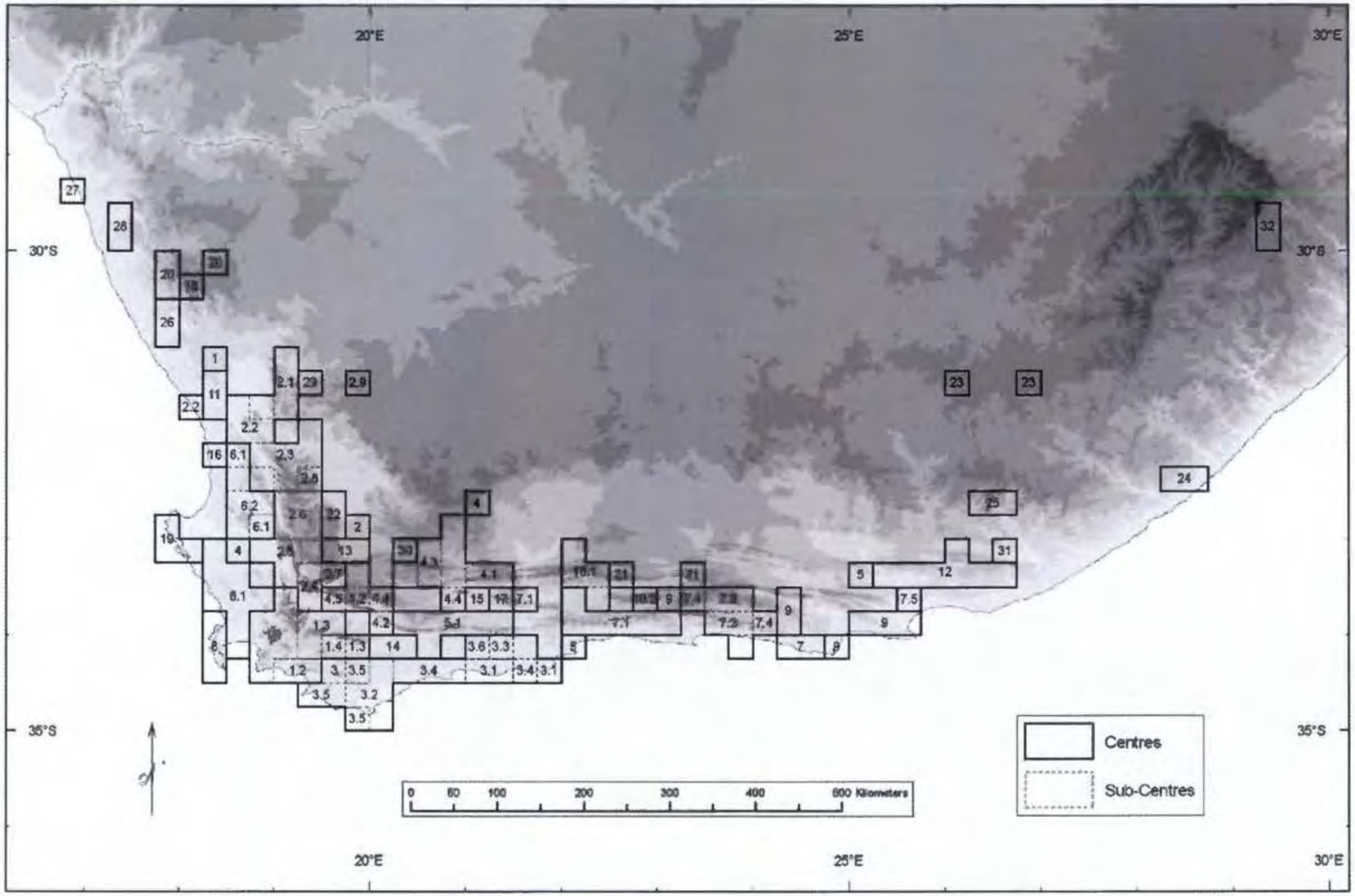


Figure 53: PC and PSC for the Asteraceae Dataset.

| Label | Centres Sub-Centres | Area | Diversity | Spp >0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 11 | W Vanrhynsdorp | 2 | 6 | 4 | 4 | 6 | 0.75 | 0.67 |
| 12 | Springbokvlakte-N of PE-Grahamstown_South | 7 | 6 | 4 | 4 | 11 | 0.39 | 0.19 |
| 13 | SE Kouebokkeveld-N Waboomsberg | 2 | 13 | 7 | 3 | 4 | 0.67 | 0.50 |
| 14 | E RZE-Central Langeberg Plains | 2 | 11 | 3 | 2 | 2 | 0.50 | 0.00 |
| 15 | W Little Karoo | 1 | 4 | 2 | 2 | 2 | 1.00 | 1.00 |
| 16 | West Coast | 1 | 3 | 2 | 1 | 1 | 1.00 | - |
| 17 | W Rooiberg | 1 | 2 | 2 | 1 | 1 | 1.00 | - |
| 18 | S Kamiesberg | 1 | 4 | 1 | 1 | 1 | 1.00 | - |
| 19 | Saldanha Peninsula | 3 | 4 | 1 | 1 | 3 | 1.00 | - |
| 20 | N Kamiesberg | 3 | 3 | 1 | 1 | 3 | 1.00 | - |
| 21 | E Groot Swartberg Mtns-Slypsteenberg-Antoniesberg | 2 | 3 | 1 | 1 | 2 | 1.00 | - |
| 22 | Swart Ruggens | 2 | 2 | 1 | 1 | 2 | 1.00 | - |
| 23 | Southern Drakensberg | 2 | 1 | 1 | 1 | 2 | 1.00 | - |
| 24 | Willowvale | 2 | 1 | 1 | 1 | 2 | 1.00 | - |
| 25 | Tarkastad-SADA | 2 | 1 | 1 | 1 | 2 | 1.00 | - |
| 26 | Garies-Kotzesrus | 2 | 1 | 1 | 1 | 2 | 1.00 | - |
| 27 | McDougall's Bay | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 28 | Buffelsbank-Komaggas | 2 | 1 | 1 | 1 | 2 | 1.00 | - |
| 29 | Soetlandsfonteinrivier | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 30 | North Witteberg | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 31 | Grahamstown_North | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 32 | Drakensberg | 2 | 1 | 1 | 1 | 2 | 1.00 | - |
| 33 | Outside | 38 | 32 | 4 | 0 | 0 | - | 1.00 |

which is in stark contrast to most Cape Clades (Levyns, 1964). Using the phytogeographical centres of Weimarck (1941), Nordenstam (1969) identified the following frequencies of endemic taxa in the CFR: SWPP 6, NWPP 4, LBPP 1, KMPP 3 and SEPP 9. So, although the Caledon (Sub-) Centre does not perform that well as a whole, the SWPP does. However, the SWPP does not perform as well as the SEPP and thus differs from most other TMS Cape Clades, which decrease in diversity and endemism to the north and east (Levyns, 1964).

Sections of *Euryops,* which may be natural groups, according to Nordenstam (1969), display strong localisation to particular floristic regions. Nordenstam's (1969) Section *Euryops* is largely restricted to the Cedarberg, while his Section Leptorrhiza's single species is distributed in the Succulent Karoo. Nordenstam's (1969) Section Psilosteum has an interesting distribution along the south and southeast coast, and may indicate a relictual relationship between the CFR and the Pondoland-Tongoland Centres, due to its presence there. This may corroborate the patterns and affinities in other taxa, like *Raspalia trigyna* (Bruniaceae) and *Leucodendron pondoense* (Proteaceae) (van Wyk, 1990), and other taxa in the Natal/Pondoland Sandstone Forest Endemics (van Wyk, 1989). Nordenstam's (1969) Sections Chrysops and Brachypus are largely Afromontane, although the former extends further south to the CFR, while the latter extends much further north to the Ethiopian Highlands.

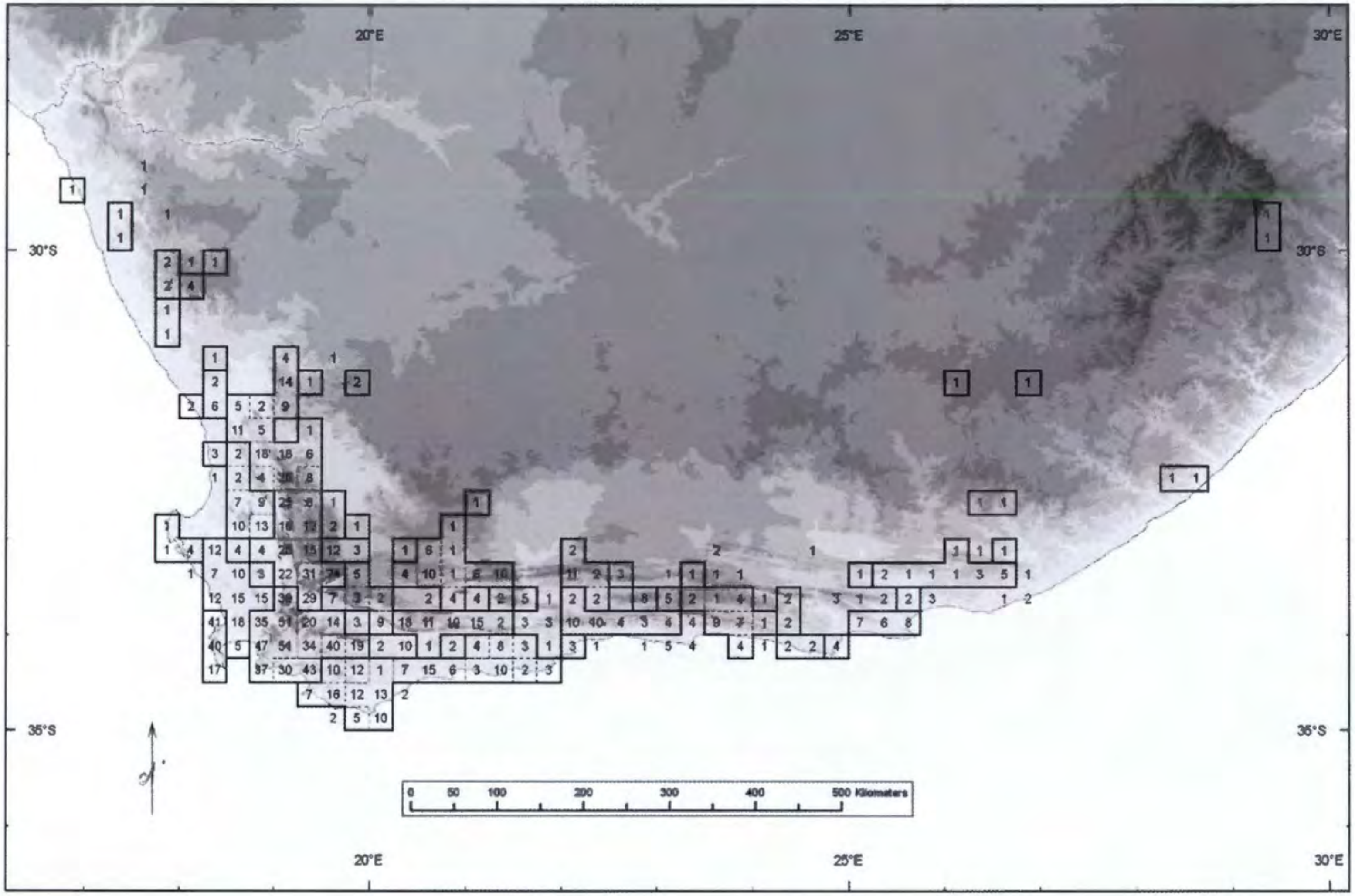


Figure 54: QDS Diversity for the Asteraceae Dataset.

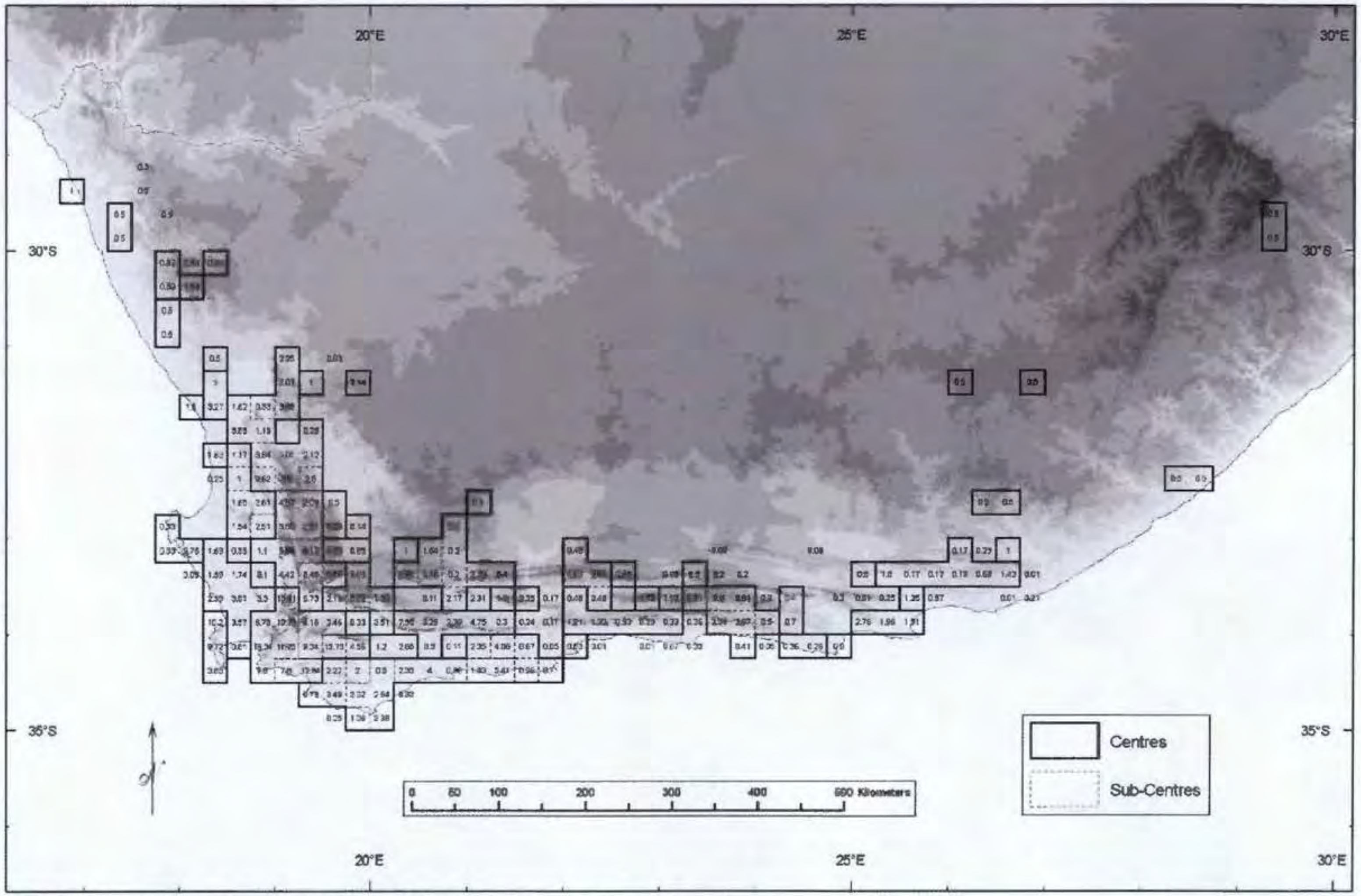


Figure 55: Sum of the Inverse Taxon Ranges for the Asteraceae Dataset.

Aside from *Euryops* that is relatively well-represented in the CFR (28 endemic taxa of the 43 occurring in the CFR, with 97 globally, according to Goldblatt and Manning (2000)), there may be other Asteraceae lineages with strong CFR affinities. Levyns' (1964) lists the genera *Metalasia* and *Stoebe*, as being of the Cape Flora, while Linder (2003) mentions the Relhaniinae, Arctoteae, Ursiniinae and the Amellus Group. However, lineages of Asteraceae may show greater floristic affinities to the Greater Cape Region of Born et al., (2006), than to my smaller core CFR, or the CFR areas as defined by Weimarck or Goldblatt and Manning (2000).

Asteraceae has 30 genera known to be endemic to the CFR. However, this number may decrease with further taxonomic and phylogenetic research, as additional polyphyletic and paraphyletic (due to autoapomorphies) relationships are discovered. Nevertheless, it is apparent that certain lineages of Asteraceae have strong affinities to the CFR. My analysis focuses on CFR endemic taxa (genera), which may bias the floristic patterns of my Asteraceae Dataset to those taxa of stronger CFR affinities, rather than the family as a whole.

I found that phytogeographical boundaries of my Asteraceae (Figure 53) correspond fairly closely to the PC boundaries of my Combined Dataset (Figure 18). However, there are a number of notable exceptions. There is a very well developed Agulhas Plains Centre (PC 3), and in general, the Asteraceae have well-developed PCs in both montane and low altitude areas, and in dry and more mesic habitats (Table 33). The diverse ecological preferences of this group have been noted in other studies, for example, "Phytogeography of the Genus *Euryops* (Compositae)" by Nordenstam (1969). *E. abrotanifolius* occurs from close to the sea to mountain summits, but avoids sandy areas of shale and littoral origin. Similarly, *E. pectinatus* is confined to montane TMS. *E. rehmannii* is widespread in the CFR, but is not a typical fynbos species, instead occurring in drier Renosterveld, or in the transition between arid fynbos and the Karoo. Similar patterns are found within *Elytropappus* (Levyns, 1935). *E. rhinoseroteris* is nearly geographically ubiquitous within the CFR, but occurs in the drier, lower altitude Renosterveld, while the remainder of the genus shows strong TMS preferences. Conflict within the dataset may be a result of taxa such as these, with diverse biotic preferences. However, it is anticipated that this will be kept to a minimum, by focussing on the more range-restricted species and CFR endemic genera.

There was some geographic conflict with the affinities of the West Hexrivier Mountains Sub-Centre (PSC 2.4) and the Groot Winterhoek Sub-Centre (PSC 2.5). Unweighted and Bell-shaped analyses suggest that sub-centres 2.4 and 2.5 should belong with the Southwest Centre (PC 1). PAE shows these OGUs to be independent at the PC level, indicating that delimitation of these OGUs are fairly well supported and that they should possibly be moved as whole units, rather than split. Merging them with the SWPP adds two more endemics, but *Osmitopsis nana* (4), although only recorded from 4 QDSs, occurs over a much wider area. This conflict may indicate a transitional area, containing overlapping taxa from the NWPP and the SWPP, or simply geographic coarseness of data.

### 5.1.1 The Relationship between endemism, diversity, and area in Asteraceae PCs

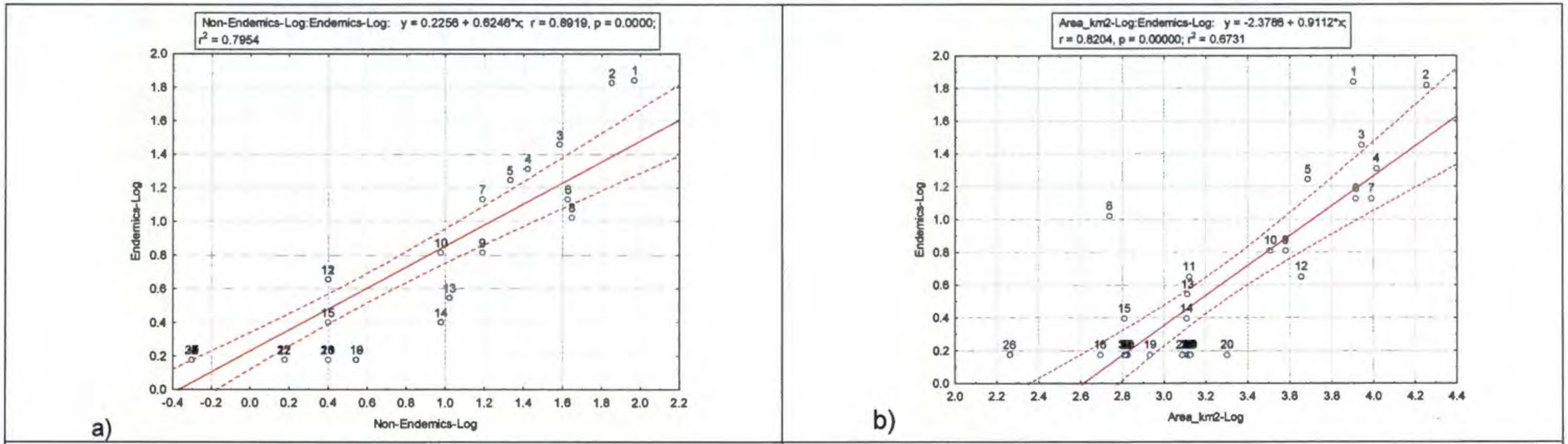
A highly significant and strong positive relationship ($r^2 = 0.80$, $p<0.001$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 56a), and between endemic taxa and PC area ($r^2 = 0.67$, $p<0.001$; Figure 56b), and non-endemic taxa and PC area ($r^2 = 0.49$, $p<0.001$; Figure 56c), but gets progressively weaker.

Endemism and diversity are disproportionally higher in the two westerly winter rainfall PCs (PC 1 and 2), especially in the Southwestern Mountains (PC 1). This is especially apparent considering the geographic size of the Southwest PC (Figure 56b and c). Similarly, the Peninsula Centre contains higher endemic (Figure 56b) and non-endemic taxa (Figure 56c) than predicted by area. Conversely, the relatively large size of the Zuurberg Centre (PC 12) results in an underrepresentation of endemic (Figure 56b) and non-endemic (Figure 56c) taxa by area. The SE Kouebokkeveld-N Waboomsberg (PC 13) and the E RZE-Central Langeberg Plains (PC 14) have relatively low levels of endemism (Figure 56a). Most of the PCs that only contain a single endemic are underrepresented (Figure 56a-c).

## 5.2 Phytogeographical Centres

### 5.2.1 Southwest Phytogeographical Province

The Southwest Mountains Centre of Asteraceae (PC 1) consolidates a number of SWPP PCs identified in the Combined Dataset, into a single PC, including Stellenbosch-Bainskloof (Combined Dataset, PSC 6.1), RZE (Combined Dataset, PC 8) and the Hottentots Holland-West Kleinrivierberge (Combined Dataset, PSC 1.1). In both the Combined Dataset and in the Asteraceae, the Peninsula (PC 8) is identified as an independent Centre, as is the Saldanha Peninsula (PC 18). In my Asteraceae Dataset, the Saldanha Peninsula shows strong affinities to the Sandveld-Piketberg-Swartberg Centre (PC 6), due to *Cotula duckettii* (4). However, more taxa would be required to determine if there are any links to the Succulent Karoo Biome, as suggested by the Combined Dataset results.



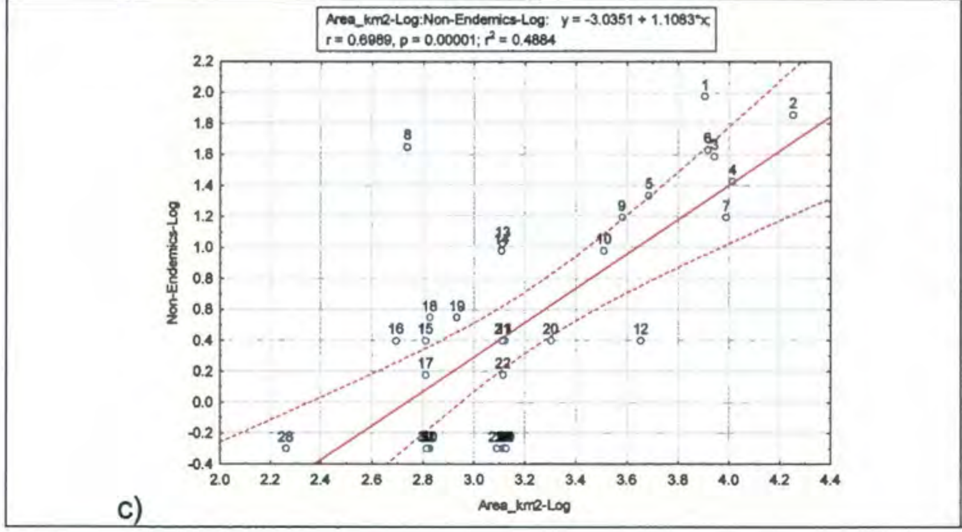


Figure 56a-c: The correlation between Endemism, diversity and Area in the Asteraceae Dataset.
The numbers on the graph correspond to the PC Asteraceae PC table above (Table 32) and the PC Maps (Figure 53).

Table 33: Habitat Data for Asteraceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliffs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats | Other | Unknown |
| 1 | Southwestern Mtns | | | | 6 | 9 | 7 | 3 | | 44 | | 3 | 1 | | | | | 3 | 58 | 1 | | 2 | 9 | 3 | | 12 | 2 | 4 | 1 | | | | | 2 | | 12 |
| 2 | Northwestern Mtns | | | | | | 6 | 3 | | 38 | 2 | 2 | 1 | 1 | | | | 4 | 40 | 1 | | 4 | 1 | 1 | 1 | 15 | 4 | 1 | | | | | | | | 14 |
| 3 | West & East Agulhas Plains-Potberg | | | | 1 | | | | | 5 | 2 | | | 14 | | | | 3 | 6 | | 8 | 4 | 2 | | | 3 | | | | | | | | 7 | 1 | 1 |
| 4 | W Karoo Mtns | | | | | | 3 | 2 | | 11 | | | | | | | | 1 | 12 | 1 | | | 1 | | 1 | 7 | | 1 | | | | | | | | 6 |
| 5 | Central & East Langeberg & Outliers | | | | | 1 | 3 | | | 10 | | 1 | | | | | | 1 | 9 | | | | | | 2 | 2 | | | | | | 2 | | | | 3 |
| 6 | Sandveld-Piketberg-Swartberg | | | | 6 | | | | | 6 | | | | | | | | | 6 | | 3 | 5 | | | | | | | | | | | | 2 | | |
| 7 | W Southeastern Centre | | | | | 1 | 1 | 2 | | 5 | 1 | | | | | | | 2 | 9 | 1 | | | 1 | 2 | | 7 | | | | | 1 | | | | 1 | 2 |
| 8 | Peninsula | | | | 1 | 1 | | | | 5 | | | | | | | | | 9 | | | | 2 | | | 3 | | | | | | | | 1 | | |
| 9 | E Southeastern Centre | | | | | | | | | 2 | | | | | | | | | 4 | | | 1 | | 1 | | 3 | | | | | | | | | | 1 |
| 10 | Groot Swartberg-E Rooiberg-Kammanassie | | | | | 1 | | 1 | | 4 | | | | | | | | 1 | 4 | 1 | | | 1 | | | 3 | | | | | | | | | | |
| 11 | W Vanrhynsdorp | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 4 |
| 12 | Zuurberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 4 |
| 13 | SE Kouebokkeveld-N Waboomsberg | | | | | | | 1 | 1 | 1 | | | | | | | | | 2 | | | | | | | 1 | | | | | | | | | | 1 |
| 14 | E RZE-Central Langeberg Plains | | | | | | | | | | | | | | | | | | 1 | | | | 1 | | | | | | | | | | | | | 1 |
| 15 | W Little Karoo | | | | | | | | | 1 | 1 | | | | | | | | 1 | | | 2 | | | | | 1 | | | | | | | | | |
| 16 | West Coast | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 17 | W Rooiberg | | | | | | 1 | | | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| 18 | S Kammiesberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 19 | Saldanha Peninsula | | | | 1 | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | |
| 20 | N Kammiesberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 21 | E Groot Swartberg Mtns-Slypsteenberg-Antoniesberg | | | | | | | | | | 1 | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| 22 | Swart Ruggens | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | | | | | | | | | |
| 23 | S Drakensberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 24 | Willowvale | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 25 | Tarkastad-SADA | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 26 | Garies-Kotzesrus | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 27 | McDougall's Bay | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 28 | Buffelsbank-Komaggas | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 30 | Soetlandsfonteinrivier | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 31 | N Witteberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 32 | Grahamstown_North | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | Totals | 0 | 0 | 0 | 15 | 13 | 21 | 12 | 1 | 133 | 7 | 6 | 2 | 15 | 0 | 0 | 0 | 15 | 162 | 5 | 11 | 19 | 18 | 7 | 4 | 57 | 9 | 6 | 1 | 0 | 1 | 2 | 0 | 13 | 2 | 61 |

In Asteraceae, as in Fabaceae, the Sandveld, ranging from Heerenlogement in the north to the Peninsula in the south is grouped together. The division into NWPP and SWPP Sandveld areas is apparent at the lower PSC level with northern (PSC 6.2) and southern (PSC 6.1) sub-centres, which, aside from a few outliers, correspond to the SWPP-NWPP boundary. This indicates that for the data I analysed, these lower altitude (Table 33) areas are more closely related to each other (share more PC endemic taxa), than to the neighbouring mountainous parts of the SWPP or the NWPP in which they occur. This may be to the arid tolerant nature of asterid taxa, enabling establishment on the lower lying areas.

### 5.2.2 Northwest Phytogeographical Province

The Northwest Mountains amalgamate a number of centres identified in the Combined Data analysis, such as the Cedarberg (Combined Dataset PC 8), Groot Winterhoek (PC 3), Gifberg (PC 15) and the Nieuwoudtville Plateau (PC 11). The large size accounts for the high diversity and endemism of this centre for this group, which is nearly as high as that of the Southwest Mountains, but it is double the area of the Southwest Mountains Centre (Table 32). Unlike most TMS Cape Clades, the centre of diversity for the Asterid NW Centre is the Nieuwoudtville Plateau (PSC 2.1), followed by the Gifberg (PSC 2.2). However, the differences in the numbers of endemics in the first five sub-centres of the Northwest Mountains Centre (PC 2) are not very great.

It is of methodological importance to observe that the two sub-centres with the most endemics are not what one would expect, especially when considering the QDS richness (Figure 54), or the inverse weighting (Figure 55), because the highest values are located in the northwest Hexrivier Mountains. Techniques to establish PCs that make use of QDS diversity, or inverse weighting, may therefore yield less optimal results. In terms of QDS richness, the Nieuwoudtville Plateau and the Gifberg have relatively low scores and aside from the central Nieuwoudtville QDS and southwest Gifberg QDS (Figure 54), and they have relatively low inverse weighting values (Figure 55). This possibly indicates a relatively low proportion of widespread taxa, which if present would have increased diversity. This may be on account of my sample bias, as the data collected focused on CFR endemic genera, whose diversity is concentrated in the southwest of the CFR. In addition, widespread taxa from neighbouring phytochoria do not contribute to the QDS richness score for those areas on the periphery.

The Hantamsberg (PSC 2.9) clusters with the NWPP, an affinity also observed by Weimarck, and Born et al., (2006), with the latter based on analyses from a more complete flora dataset.

It must be mentioned that the Swartruggens and Swartrugberg/Baviaansberg are independent of other PCs, notably the Cedarberg, and this is probably due to the paucity of more widespread taxa, linking the PCs together. The relationships of the Swartruggens and Swartrugberg/Baviaansberg (PC 22) to the surrounding centres in Asteraceae, should be studied, in order to determine if it forms part of the NWPP or KMPP, as there is conflict in its affinities of the Swartruggens and Swartrugberg/Baviaansberg to the NWPP/KMPP in the different groups analysed in my study.

### 5.2.3 Agulhas Plains Phytogeographical Province

The APPP of Asteraceae is very similar to that of my Combined Taxa Dataset, although, as with the previous two phytogeographical provinces, it consolidates a number of small, Combined Dataset PCs into a single larger unit. In Asteraceae, the APPP is strongly developed, with the eastern portions of the Kleinriviersberge (PC 1.2) and the East Langeberg Plains forming part of the APPP. The affinities of the Central Langeberg Plains are unknown, forming an independent centre (PC 14). This indicates once again in Asteraceae, as with the Sandveld-Piketberg-Swartberg PC (PC 6), that the plains and lowland areas have a strong and well-defined flora, which is generally independent of the neighbouring mountains. This differs from TMS Cape Clades, where there is usually a more direct relationship between the mountains and their neighbouring lowland areas, but this may also be on account of fewer widespread taxa in the dataset. Asteraceae also has a distinct and well-developed limestone endemic flora on the APPP (Table 33), which contributes to its independence, together with a high level of floristic development.

### 5.2.4 Karoo Mountains Phytogeographical Province

The KMPP is relatively well-developed in the Asteraceae Dataset, as one would expect for clades adapted to more arid conditions. It differs from the patterns observed in the SWPP, NWPP and APPP, as the centres are restricted almost entirely to mountainous areas, while the lowlands are relatively undeveloped. Most taxa occur on sandstone slopes and known distributions of endemics are spread from sea level to 1000 metres (Table 33). Selecting Asteraceae genera that are endemic to the CFR would have accentuated this pattern. Interestingly, the Klein Swartberg (PSC 4.1) is more closely related to the Witteberg (PSC 4.3) - although they are in different sub-centres - rather than to the Groot Swartberg (PSC 7.1), which is in a different PC. The Waboomsberg (PSC 4.4) and West Langeberg (PSC 4.2) also form part of the West Karoo Centre (PC 4) cluster, although they occur in separate sub-centres. Endemism and diversity are mostly concentrated in this West Karoo Centre (PC 4) of the KMPP. This area, the

Waboomsberg-West Langeberg-Witteberg appears to be an area of conflict and may possibly indicate an area of overlap between the NWPP and KMPP floras. The West Karoo Centre (PC 4) probably contains taxa with conflicting floristic affinities, particularly in the west, which may require a higher spatial resolution to resolve. Phylogenies would be required to determine taxon migration direction.

The Groot Swartberg (PSC 7.1) is fairly reduced in geographical size, and as in the Combined Dataset has affinities to the Kammanassieberge. It is interesting to observe the northward extension of the West Karoo Mountains (PC 4) through the Moordenaarskaroo to the southeast Roggeveldberge is due to *Euryops microphyllus* (2) and *Senecio haworthii* (5).

### 5.2.5 The Langeberg Phytogeographical Province

The Langeberg Centre (PC 5) is fairly restricted in extent to the Central and East Langeberg Mountains, with a minor extension onto the Central Langeberg Plains (PSC 5.1) and an outlier in the Far East Agulhas Plains. It is the smallest of the "traditional" phytogeographical provinces (centres of Weimarck and Goldblatt and Manning) identified for Asteraceae, and is encroached on all sides by surrounding PCs.

### 5.2.6 The Southeast Phytogeographical Province

The Southeast Centre consists of relatively low ranked PCs, which divide the traditional SEPP into a western Southeast PC (PC 7) and an eastern Southeast PC (PC 9). Unlike in the Combined Dataset, in Asteraceae the western area is larger and more dominant, which is probably due to clade bias of CFR representatives.

The Zuurberg Centre (PC 12) is equivalent to the montane region of Weimarck's (1941) Zuurberg Sub-Centre and contains fynbos and grassy fynbos endemics, but does not extend to the coastal areas.

### 5.2.7 Namaqualand Phytogeographical Centre

In Namaqualand, there are a number of PCs with endemic taxa. The best developed of these is the West Vanrhynsdorp Centre (PC 11), with four endemics. The remaining centres each have a single endemic. Two of these centres (PC 18 and 20) are centred on the Kamiesberg, while the remainder (PCs 26, 27 and 28) occur in less mountainous areas.

### 5.2.8 Summer Rainfall Region

Although the dataset analysed contains very few taxa outside the CFR, a number of small centres are delimited to the east of the CFR. Most of the centres (PCs 23, 25 and 32) are associated with high altitude floristic CFR Archipelagos extending along the escarpment *en route* to the Drakensberg. The remaining centre (PC 24) is situated close to the coast, near the Dwesa-Wild Coast Sub-Centre (PSC 6.1), of Orchidaceae.

## 5.3 Summary

The Asteraceae Dataset displays both well-developed montane and lowland PCs. There are well-developed PCs in all six Phytogeographical Provinces (*sensu* centres of Goldblatt and Manning, 2000), especially in the west and south. The Sandveld of the NWPP and SWPP consolidate together, rather than with the mountains of their respective Phytogeographical Provinces. The APPP is relatively well-developed. Levels of PP endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, NWPP, APPP, KMPP, LBPP and SEPP.

# Chapter 6: Bruniaceae (Table 34, Figure 57)

## 6.1 Introduction

Bruniaceae is one of the smaller Cape Clades that I analysed and it is mostly endemic to the CFR, with only two taxa represented outside its borders. One taxon, *Berzelia commutata*, extends beyond the borders of the CFR, in the CFR eastern archipelagos (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). The other taxon, *Raspalia trigyna*, occurs completely outside the CFR, in the Pondoland area. In this study, the PCs were strongly correlated with mountain ranges, aside from the relatively poorly developed West Agulhas Plain-Potberg Centre (PC 6) (Figure 57; Table 34). As is typical of montane fynbos CFR Clades, by far the greatest concentration of endemism is found in the Southwestern Mountains Centre (PC 1). The montane preferences of Bruniaceae PC can clearly be seen by the concentration of PCs in the mountainous regions (especially in the Southwest Centre) of the CFR, with notable "gaps" in the lowland areas of the CFR (Figure 57; Table 34).

A feature of the diversity patterns of endemics in Bruniaceae is the relatively sharp drop in levels of endemism from PCs to PSCs (Table 34). This indicates that, unlike in *Erica*, few of the Bruniaceae endemics are highly range-restricted. This is further reflected in the relatively high r-score (Table 34). For the Southwest Centre, the ratio between the r-score and number of endemics is 4.8 in Bruniaceae, while it is 3.3 in Ericaceae. Therefore, it appears that although taxa are restricted to certain PCs, they are relatively widespread within those PCs and not concentrated in PSCs. In the Combined Dataset, the Hottentots-W Kleinrivier Sub-Centre contains 83% of its PC endemics, while in Bruniaceae the Hottentots-W Kleinrivier Sub-Centre only contains 18.2% of its PC endemics. This pattern also occurs in the Northwestern Mountains Centre (PC 2) of Bruniaceae. A similar lack of very range-restricted taxa is also seen in my Rosaceae Dataset.

In the Southeast Centre (PC 5) collection records of *Berzelia commutata* (range of 10 QDSs) are widely distributed, with as many as six disjunctions. Its distributional pattern is similar to Orchidaceae in this eastern region of the CFR, merging the KMPP and SEPP. This may indicate that either the present distribution is a relic of a past climate, having retreated to favourable habitats within a once more widespread distribution, or that the species has specific ecological requirements, or that it has been under collected.

Table 34: Taxonomic properties of the Centres identified for the Family Bruniaceae (Figure 57).

| Label | Centre<br>Sub-Centre | Area | Diversity | Spp >0.5 | # Endems | r | Con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Southwestern Mtns | 20 | 60 | 40 | 22 | 103 | 0.23 | 0.20 |
| 1.1 | Hottentots-W Kleinrivier | 6 | 38 | 19 | 4 | 13 | 0.54 | 0.39 |
| 1.2 | Stellenbosch-Bainskloof Mtns | 2 | 30 | 3 | 2 | 3 | 0.75 | 0.50 |
| 1.3 | RZE | 4 | 32 | 6 | 2 | 6 | 0.75 | 0.50 |
| 1.4 | Remainder | 8 | 32 | 2 | 0 |  | - | 1.00 |
| 2 | Northwestern Mtns | 16 | 36 | 21 | 9 | 43 | 0.29 | 0.20 |
| 2.1 | Groot Winterhoek-Piketberg | 4 | 20 | 5 | 2 | 5 | 0.63 | 0.25 |
| 2.2 | Hexriver Mtns | 3 | 26 | 7 | 1 | 2 | 0.67 | - |
| 2.3 | Pakhuis-Swartberg Mtns | 4 | 15 | 2 | 1 | 4 | 1.00 | - |
| 2.5 | Remainder | 5 | 14 | 1 |  |  | - | 1.00 |
| 3 | Central and East Langeberg | 7 | 14 | 6 | 4 | 13 | 0.46 | 0.29 |
| 3.1 | East Langeberg | 3 | 8 | 3 | 2 | 6 | 1.00 | 1.00 |
| 3.2 | Central and Eastern Langeberg | 4 | 9 | 3 | 1 | 4 | 1.00 | - |
| 4 | S Peninsula | 2 | 12 | 2 | 1 | 2 | 1.00 | - |
| 5 | Southeastern Centre | 10 | 10 | 1 | 1 | 10 | 1.00 | - |
| 6 | E West Agulhas Plains-Potberg | 3 | 5 | 1 | 1 | 3 | 1.00 | - |
| 7 | Nieuwoudtville Plateau | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 8 | Outside | 55 | 19 | 3 | 0 | 0 | - | 1.00 |

## 6.1.1 The relationship between endemism, diversity, and area in Bruniaceae PCs

A highly significant relationship ($r^2 = 0.63$, p=0.033) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 60a). However, the relationship between endemic taxa and area ($r^2 = 0.75$, p=0.054; Figure 60b), and between non-endemic taxa and area was found to be marginally insignificant ($r^2 = 0.69$, p=0.088; Figure 60c). Although the significance values are not high, there is generally a strong positive relationship for all regression analyses in Bruniaceae.

Bruniaceae has high diversity and especially endemism in the Southwest PC (1). It has intermediate diversity and endemism in the Northwest PC (2), followed by low diversity and endemism in the Langeberg, while the remaining PCs trail behind (Figure 60a-c). This pattern is apparent in Restionaceae and to a lesser extent, Polygalaceae. In Bruniaceae, the Southwest PC (1) is the largest geographic PC, followed by the Northwest PC (2) and the Central and East Langeberg PC (3), which accounts for the levels of endemism in these three larger centres. The Southeast Centre (PC 5) contains fewer than expected endemic taxa relative to the geographic size of the PC (Figure 60b), which may be exacerbated by further collection.

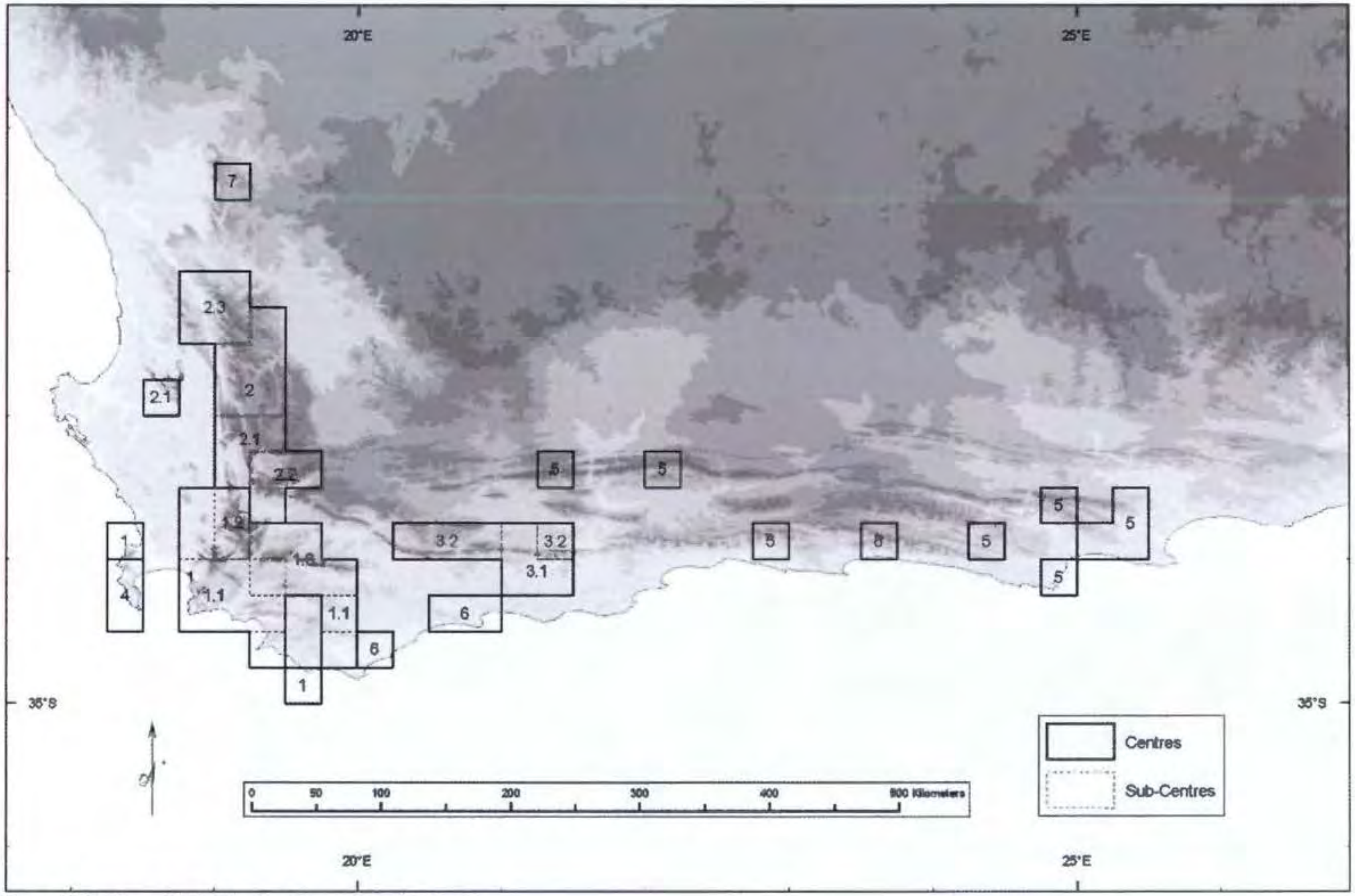


Figure 57: PC and PSC for the Bruniaceae Dataset.

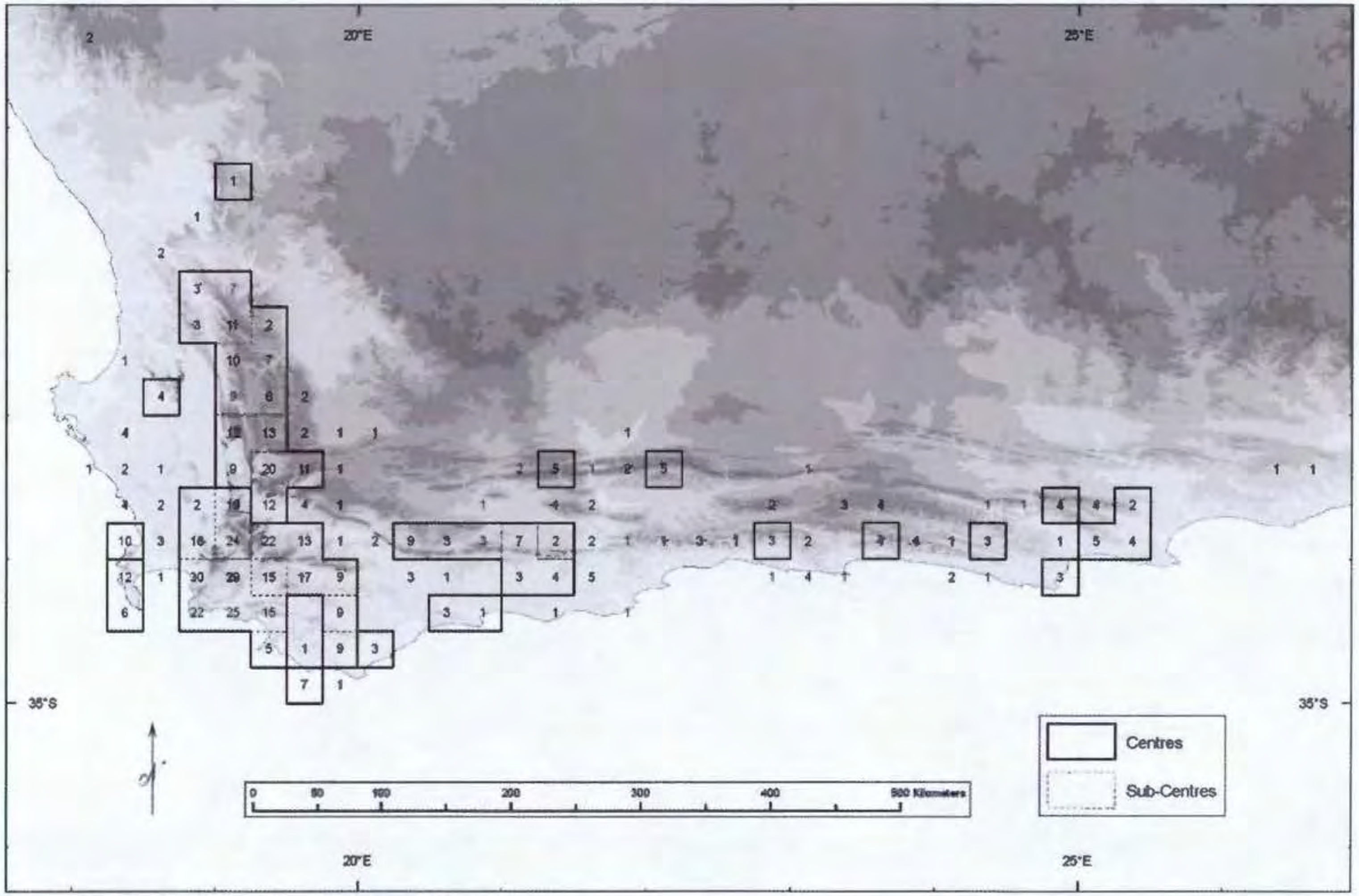


Figure 58: QDS Diversity for the Bruniaceae Dataset.

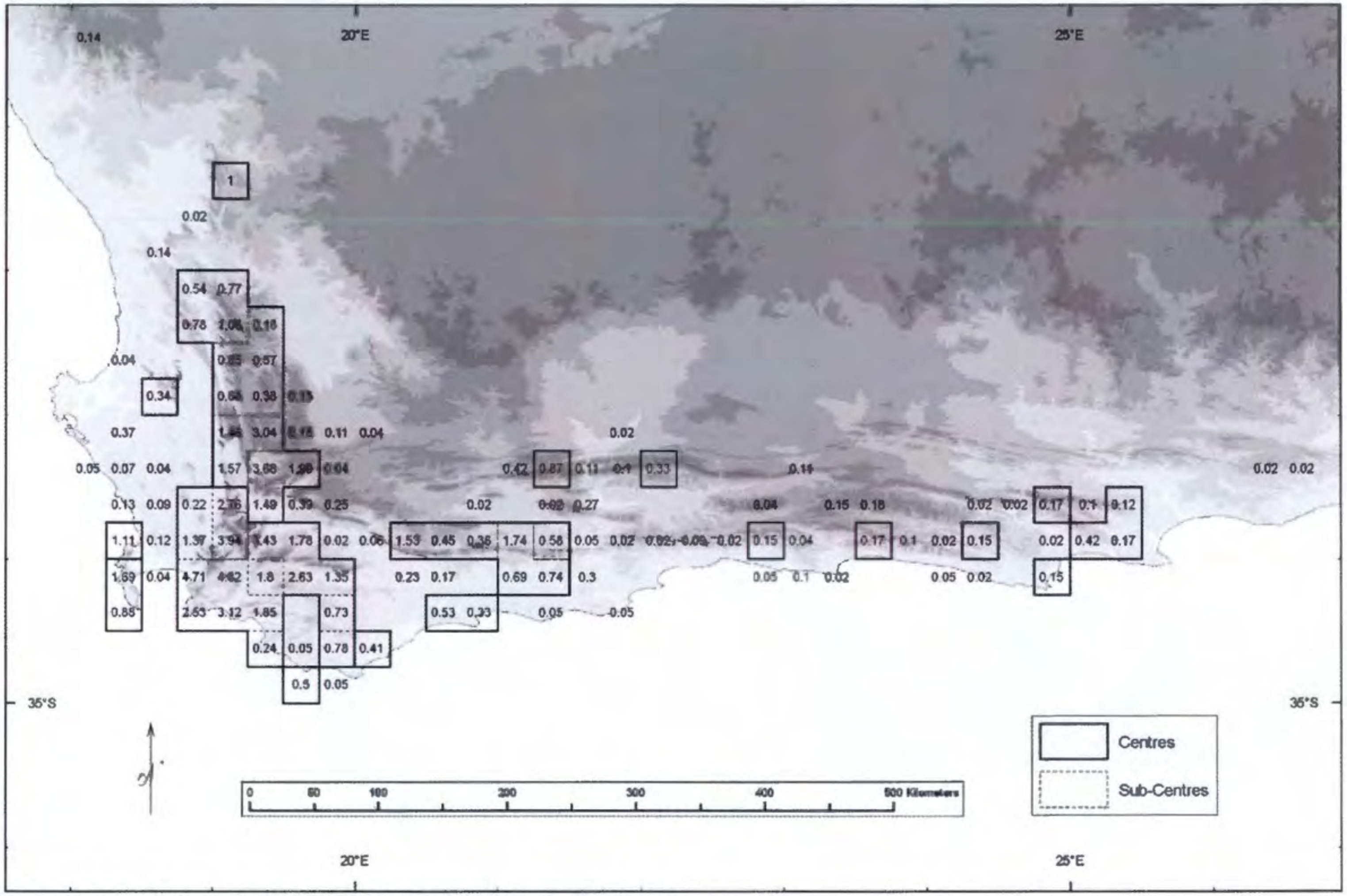


Figure 59: Sum of the Inverse Taxon Ranges for the Bruniaceae Dataset.

## 6.2 Phytogeographical Centres

### 6.2.1 The Southwest Phytogeographical Province

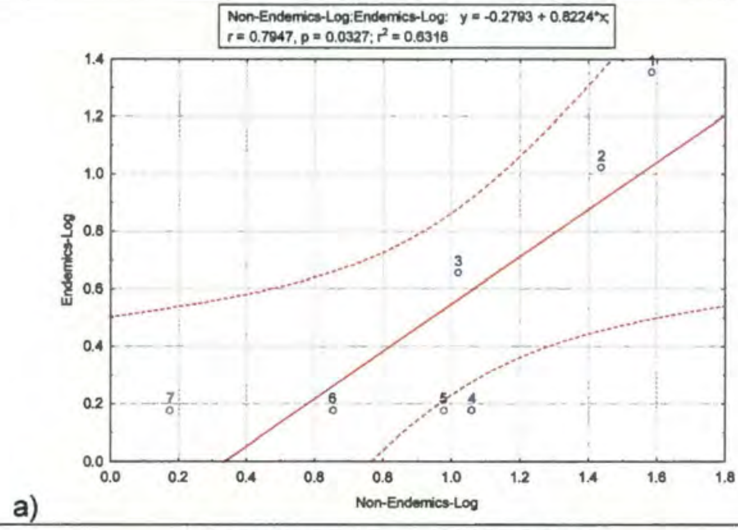
The greatest numbers of endemic taxa are found in the main SWPP PC, which is centred on the Southwest Mountains (Figure 57). The Southwest Mountains (PC 1) have twice as many endemics compared to the next richest centre and more endemics than all the other centres combined.

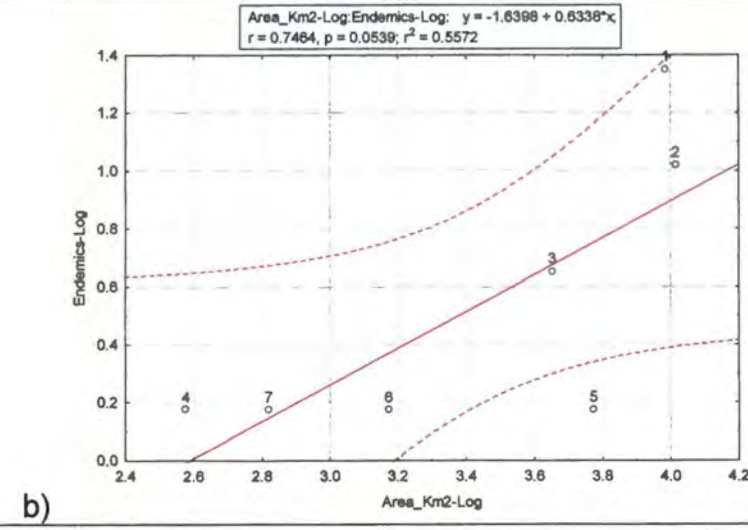
The South Peninsula emerges as a separate centre, based on two endemic species (Appendix II). *Brunia stokei* (5) and *Staavia verticillata* (5) join the Northern Peninsula (3318CD) to the remaining SWPP Mountains. However, *Audounnia captitata* (4) links the Southern Peninsula to the Hottentots-W Kleinrivier Sub-Centre (1.1), and *Staavia dregeana* (4) links the Peninsula as a whole to the northerly SWPP Mountains. This gives a strong indication of the floristic affinities of the Peninsula and may even motivate for the possible inclusion of my current Peninsula Centre (PC 4) as a sub-centre in the Southwest Mountains Centre (PC 1).

### 6.2.2 The Northwest Phytogeographical Province

The NWPP (PC 2) has the second highest number of endemics of the Bruniaceae PCs, followed by the Langeberg Centre (PC 3). The Piketberg (PSC 2.1) is a satellite of the Groot Winterhoek (PSC 2.1), rather than an independent centre, and is associated with the Cedarberg (PC 2 in part).

The Nieuwoudtville Escarpment (PC 7) has a single endemic taxon. There are two Bruniaceae Taxa on the Kamiesberg that show floristic links to the CFR, particularly the western CFR (NWPP and SWPP) and there are no taxa endemic to this northerly archipelago. Of the taxa that occur in the Kamiesberg, *Nebelia fragarioides* (10) is widespread in the two western phytogeographical provinces (the SWPP and the NWPP), while *Tittmannia laxa* (25) is centred in the two western phytogeographical provinces, but extends very slightly into western KMPP and LBPP.





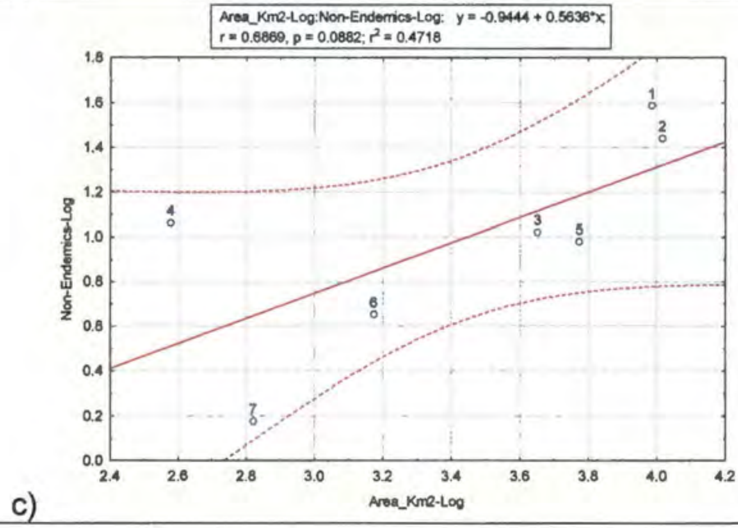


Figure 60a-c: The correlation between Endemism, diversity and area in the Bruniaceae Dataset.
The numbers on the graph correspond to the Bruniaceae PC table above (Table 34) and the PC Maps (Figure 57).

Table 35: Habitat Data for Bruniaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliffs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats/Dunes | Other | Unknown |
| 1 | Southwest Mountains | | | | | | | | | 18 | | | | 1 | | | | 1 | 15 | 8 | | | 2 | 1 | | 11 | | | | | | | | | 1 | 2 |
| 2 | Northwest Mountains | | | | | | | | | 7 | 1 | | | | | | | | 5 | 1 | | | 5 | | | 4 | | | | | | | | | | 1 |
| 3 | Central and East Langeberg | | | | | | | | | 3 | | | | | | | | | 3 | | | | 2 | 1 | | 1 | | | | | | | | | | |
| 4 | South Peninsula | | | | | | | | | 1 | | | | | | | | | | 1 | | 1 | | | | 1 | | | | | | | | | | |
| 5 | Southeast Centre | | | | | | | | | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| 6 | E West Agulhas Plains-Potberg | | | | | | | | | 1 | | | | 1 | | | | | 1 | | | | | | | | | | | | | | | | | |
| 7 | Nieuwoudville Plateau | | | | | | | | | 1 | | | | | | | | | | | | 1 | | | | 1 | | | | | | | | | | |
| | Totals | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 32 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 25 | 10 | 0 | 2 | 9 | 2 | 0 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 |

### 6.2.3 Remaining CFR Phytogeographical Provinces

The Langeberg Centre is reduced to the Central and Eastern Langeberg areas (PSC 3.2) and the East Langeberg Mountains (PSC 3.1), as well as the East Langeberg Plains (PSC 3.1).

There is a single endemic species on the limestone of the Agulhas Centre, *Berzelia cordifolia* and on this basis this centre can be recognized.

The KMPP and SEPP are combined in Bruniaceae by a single endemic species, *Berzelia commutata* (10).

### 6.2.4 Non-CFR Phytogeographical Centres

As *Raspalia trigyna* was not included in this analysis, no PCs outside the CFR were recovered. Inclusion of this taxon would have resulted in the formation of a single endemic taxon PC in the Pondoland region, as recorded by van Wyk and Smith (2001).

## 6.3 Summary

PC Endemism in Bruniaceae is distinctly montane, except perhaps in the eastern SEPP. The KMPP, SEPP and APPP are fairly poorly developed, with the KMPP and SEPP forming a single PC. Levels of PP endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, NWPP, LBPP and KMPP-SEPP.

# Chapter 7: Ericaceae (Table 36, Figure 61, Figure 62)

## 7.1 Introduction

*Erica* is the most speciose Cape genus and has strong montane preferences. *Erica* is most strongly centred in the winter rainfall area of southern Africa, although it has representatives in many of the high lying areas of east Africa, and some representatives

Table 36: Taxonomic properties of the Centres identified for the Family Ericaceae (Figure 61, Figure 62).

| Label | Centres Sub-Centres | Area | Diversity | Spp >0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Southern Mtns | 20 | 466 | 291 | 135 | 445 | 0.16 | 0.16 |
| 1.1 | Hottentots-Holland_Kleinriviersberge | 8 | 375 | 143 | 57 | 125 | 0.27 | 0.26 |
| 1.2 | Riviersonderend | 4 | 241 | 42 | 12 | 20 | 0.42 | 0.36 |
| 1.3 | Bainskloof-Stellenbosch | 3 | 236 | 24 | 5 | 10 | 0.67 | 0.58 |
| 1.4 | Remainder | 5 | 151 | 1 | 0 | 0 | - | 1.00 |
| 2 | Northern Mtns | 34 | 273 | 125 | 60 | 247 | 0.12 | 0.11 |
| 2.1 | Cedarberg Core | 8 | 149 | 38 | 10 | 18 | 0.23 | 0.14 |
| 2.2 | Hex-W Langeberg | 5 | 184 | 22 | 11 | 19 | 0.35 | 0.28 |
| 2.3 | Groot Winterhoek | 2 | 149 | 10 | 3 | 4 | 0.67 | 0.50 |
| 2.4 | Piketberg | 2 | 46 | 3 | 1 | 2 | 1.00 | - |
| 2.5 | Gifberg | 4 | 20 | 1 | 1 | 4 | 1.00 | - |
| 2.6 | Remainder | 13 | 110 | 2 | 0 | 0 | - | 1.00 |
| 3 | Peninsula | 3 | 141 | 39 | 24 | 47 | 0.65 | 0.64 |
| 4 | Langeberg | 11 | 209 | 49 | 21 | 46 | 0.20 | 0.16 |
| 4.1 | Eastern Langeberg | 6 | 171 | 23 | 10 | 16 | 0.27 | 0.19 |
| 4.2 | Western Langeberg | 2 | 99 | 9 | 5 | 7 | 0.70 | 0.63 |
| 4.3 | Remainder | 3 | 93 | 2 | 0 | 0 | - | 1.00 |
| 5 | Eastern Escarpment | 95 | 43 | 25 | 21 | 210 | 0.11 | 0.06 |
| 5.1 | N and E Drakensberg | 19 | 25 | 9 | 7 | 33 | 0.25 | 0.12 |
| 5.2 | Central and S Drakensberg | 15 | 22 | 2 | 2 | 16 | 0.53 | 0.07 |
| 5.3 | Amatola | 7 | 21 | 2 | 2 | 7 | 0.50 | 0.00 |
| 5.4 | Remainder | 54 | 19 | 7 | 0 | 0 | - | 1.00 |
| 6 | Greater Swartberg | 15 | 131 | 31 | 18 | 51 | 0.19 | 0.14 |
| 6.1 | Klein and Groot Swartberg Mtns | 7 | 100 | 24 | 14 | 33 | 0.34 | 0.29 |
| 6.2 | Remainder | 8 | 77 | 6 | 0 | 0 | - | 1.00 |
| 7 | W Southeastern Centre | 17 | 158 | 45 | 17 | 56 | 0.19 | 0.14 |
| 7.1 | E Outeniqua-Tsitsikamma | 6 | 108 | 9 | 5 | 9 | 0.30 | 0.13 |
| 7.2 | W Outeniqua | 3 | 111 | 8 | 3 | 5 | 0.56 | 0.33 |
| 7.3 | E Tsitsikamma | 2 | 56 | 3 | 2 | 2 | 0.50 | 0.00 |
| 7.4 | Remainder | 6 | 77 | 0 | 0 | 0 | - | 1.00 |
| 8 | West Agulhas Plain | 5 | 148 | 29 | 14 | 22 | 0.31 | 0.26 |
| 9 | N and E Southeastern Centre | 17 | 113 | 18 | 10 | 31 | 0.18 | 0.09 |
| 9.1 | Kammanassie-Kouga | 4 | 76 | 8 | 6 | 11 | 0.46 | 0.35 |
| 9.2 | Port Elizabeth | 1 | 20 | 1 | 1 | 1 | 1.00 | - |
| 9.3 | Remainder | 12 | 80 | 5 | 0 | 0 | - | 1.00 |
| 10 | Southern Sandveld | 7 | 81 | 10 | 6 | 11 | 0.26 | 0.11 |
| 10.1 | S Southern Sandveld | 1 | 52 | 4 | 2 | 2 | 1.00 | 1.00 |
| 10.2 | N Southern Sandveld | 2 | 32 | 3 | 2 | 3 | 0.75 | 0.50 |
| 10.3 | E Southern Sandveld | 1 | 34 | 2 | 1 | 1 | 1.00 | - |
| 10.4 | Remainder | 3 | 17 | 1 | 0 | 0 | - | 1.00 |

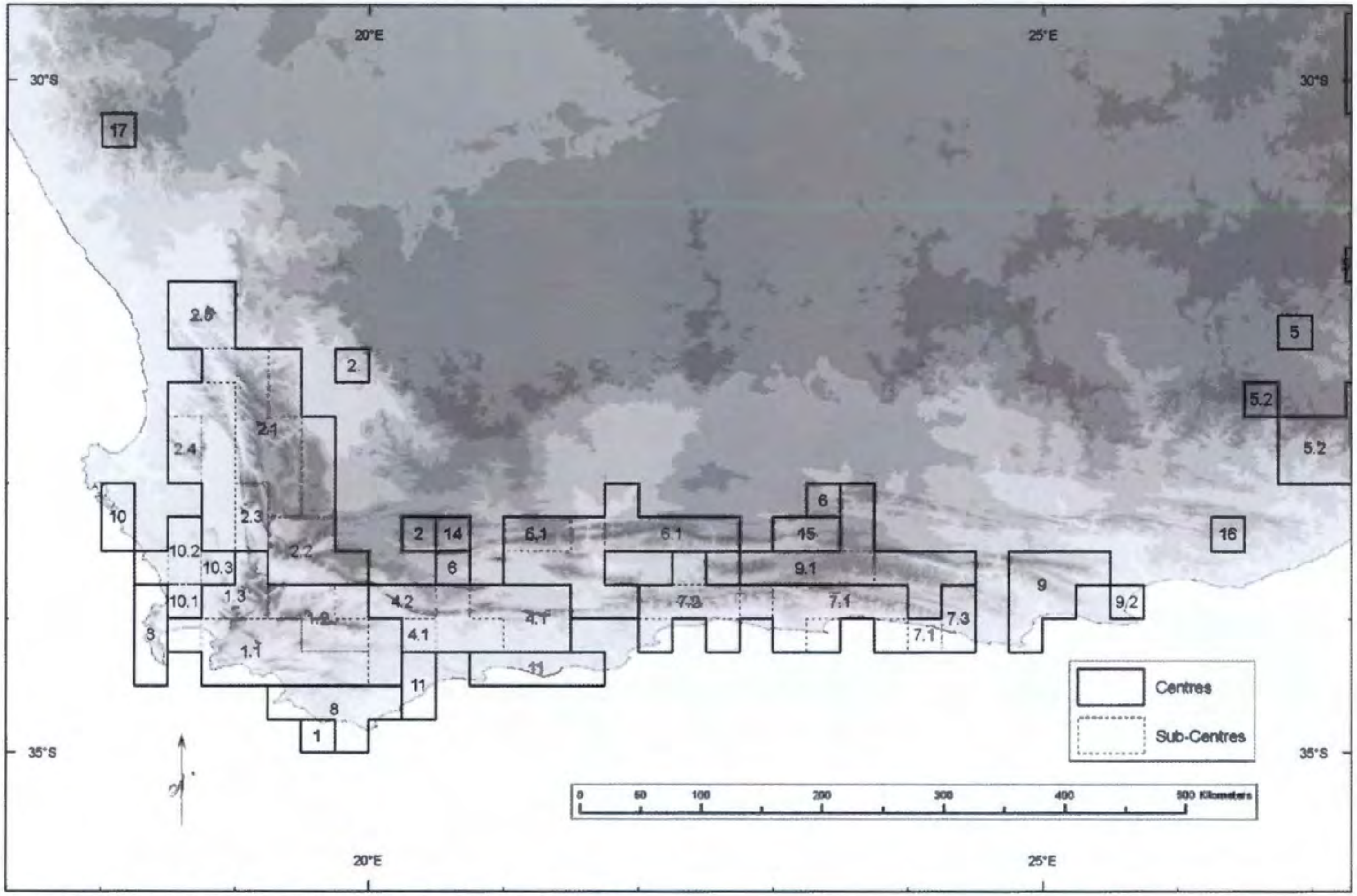


Figure 61: PC and PSC for the Ericaceae Dataset in the CFR.

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 11 | Potberg-East Agulhas Plain | 6 | 61 | 7 | 4 | 9 | 0.38 | 0.17 |
| 12 | NE Transvaal | 10 | 10 | 4 | 4 | 13 | 0.33 | 0.10 |
| 13 | Natal Coast | 16 | 11 | 2 | 2 | 16 | 0.50 | 0.00 |
| 14 | Witteberg | 1 | 31 | 1 | 1 | 1 | 1.00 | - |
| 15 | Slypsteenberg-Antoniesberg | 2 | 20 | 1 | 1 | 2 | 1.00 | - |
| 16 | Zuurberg | 1 | 10 | 1 | 1 | 1 | 1.00 | - |
| 17 | Kamiesberg | 1 | 8 | 1 | 1 | 1 | 1.00 | - |
| 18 | Western Transvaal | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 19 | Outside | 195 | 175 | 7 | 0 | 0 | - | 1.00 |

found as far afield as Scandinavia. Due to the widespread range of *Erica* analysed here, two maps were required. The first (Figure 61) concentrates on the CFR, while the second (Figure 62) covers the entire distribution of *Erica* PCs in South Africa. *Erica* has long been considered a classic CFR Clade (Levyns, 1964) and displays Levyns' (1938) pattern of having its greatest diversity and endemicity in the southwest, decreasing rapidly in diversity to the north and east, particularly outside the CFR. *Erica* is typical of mountainous mesic fynbos CFR flora, with the plains and lowlands displaying strong affinities to their neighbouring mountains (the Langeberg PC (PC 4) and the Northern Mountains PC (PC 2, see Figure 61). Although *Erica* shows similar phytogeographical boundaries to the Combined Dataset there are some differences, and a number of conflicts were noted between the PAE and UPGMA analyses.

PC formation in my analysis of *Erica* is distinctly montane. The Southern Strandveld (PC 10) and the Agulhas Plains Centres (PC 8 and 11) are the only PCs completely independent of mountains (Figure 61, Table 37), representing a mere 6.8% of QDSs that are assigned to PCs. This is also apparent in phytogeographical provinces, where lowland QDSs are generally not assigned to PCs, and when in PCs usually do not contribute to PSC formation. Thirteen of the 32 QDSs (41%) that form the Northern Mountains Centre (PC 2) are not assigned to sub-centres, as opposed to five of the 20 (25%) in the Southern Mountains Centre (PC 1), which indicates the absence of range-restricted endemics in the more arid and non-mountainous northern areas. In the Langeberg (PC 4), Southern Mountains (PC 1) and Northern Mountains (PC 2), about half the endemics occur at high altitude, and a quarter at middle and low altitude (Table 37). This emphasises the importance of montane and mesic habitats for the development of floristic units and endemism (and speciation) in *Erica*.

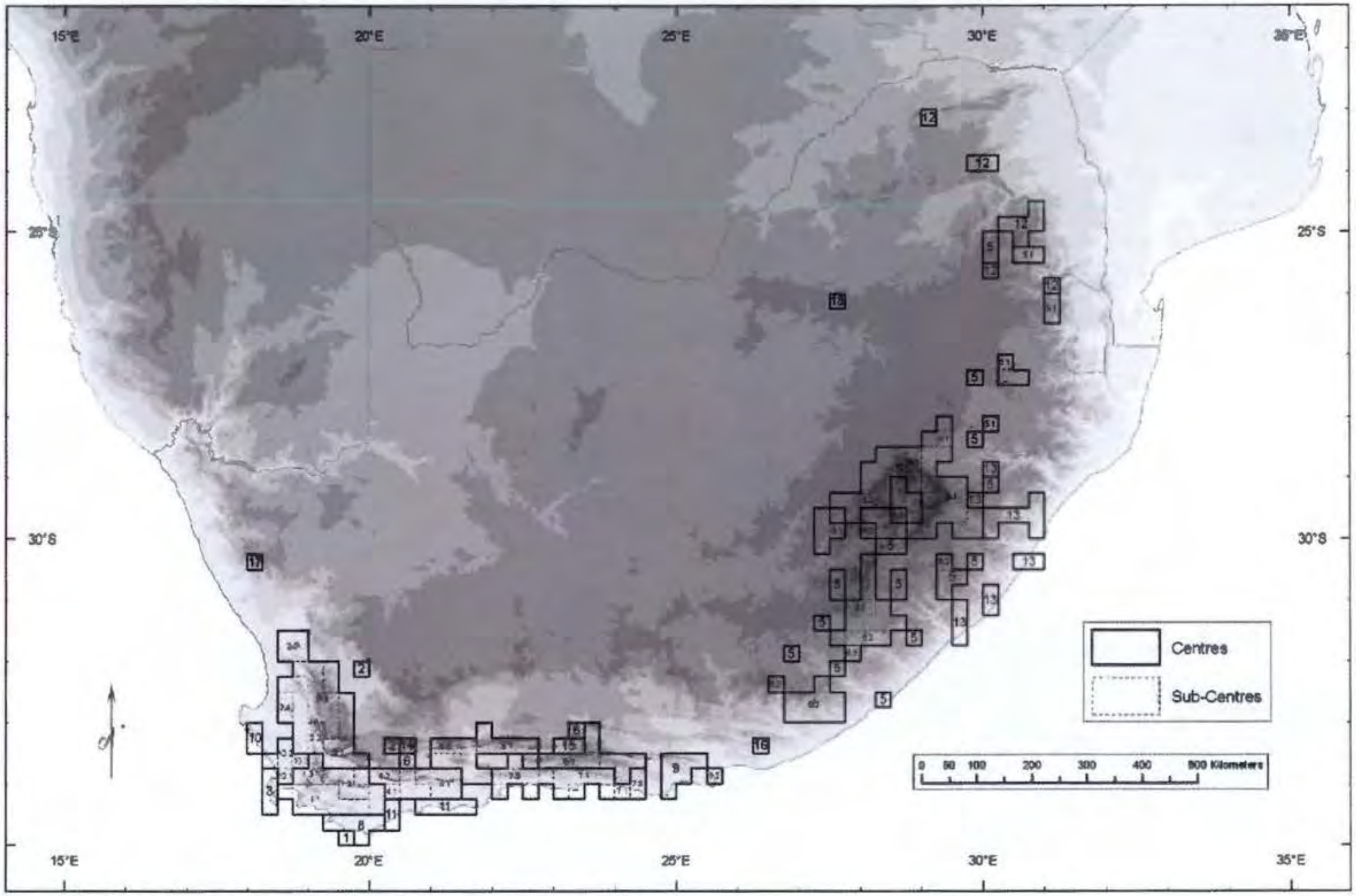
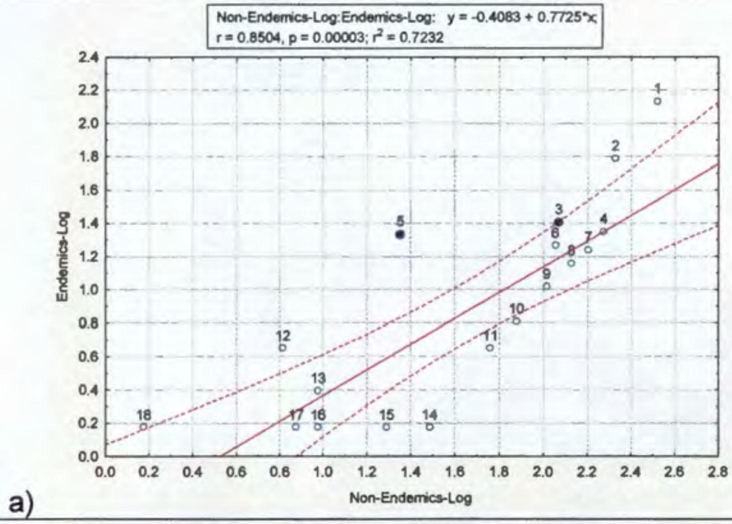
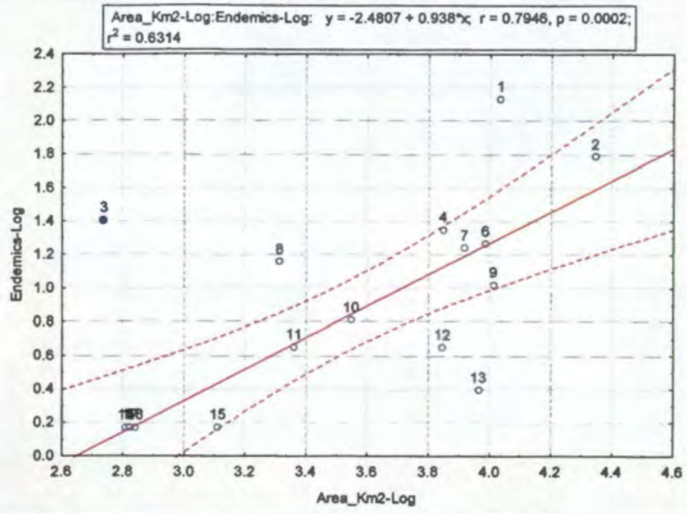


Figure 62: PC and PSC for the Ericaceae Dataset in Southern Africa.





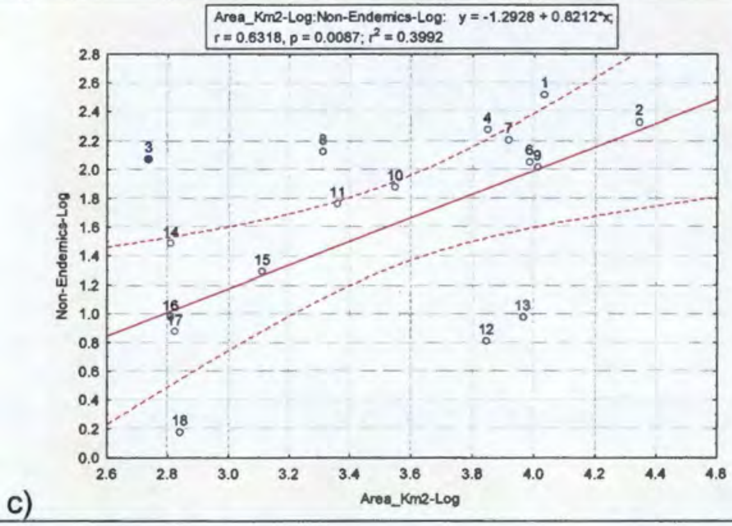


Figure 63a-c: The correlation between Endemism, diversity and area in the Ericaceae Dataset.
The numbers on the graph correspond to the *Erica* PC table above (Table 36) and the PC Maps (Figure 61 and Figure 62).

Table 37: Habitat Data for Ericaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliffs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats/Dunes | Other | Unknown |
| 1 | Southern Mtns | 34 | 29 | 45 | | | | | | | | 1 | | | | | | 16 | 94 | 9 | 14 | 4 | 28 | 2 | 1 | 28 | 12 | | | | | | | | | |
| 2 | Northern Mtns | 15 | 12 | 28 | | | | | | | | | | | | | | 29 | 43 | | | 14 | 3 | 2 | | 15 | 15 | | | | | | | 1 | | |
| 3 | Peninsula | 3 | 4 | 9 | | | | | | | | | | | | | | 9 | 10 | 6 | | 2 | 7 | | | 4 | 1 | | | | | | | | | |
| 4 | Langeberg | 5 | 6 | 11 | | | | | | | | | | | | | 1 | 6 | 18 | 1 | 1 | | 3 | | | 3 | | | | | | | | | | 2 |
| 5 | Eastern Escarpment | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | | | | | | | | | 20 |
| 6 | Greater Swartberg | 3 | 2 | 9 | | | | | | | | | | | | | | 3 | 9 | 1 | | | | | 2 | 4 | | | | | | | | | | |
| 7 | W Southeast Centre | 6 | 5 | 7 | | | | | | | | | | | | | | 1 | 5 | | | | 2 | | | | | 1 | | | | | | 1 | | 3 |
| 8 | West Agulhas Plains | 14 | | | | | | | | | | | | 2 | | | | | 1 | | 6 | 9 | | | | 3 | 6 | | | | | | | 4 | | |
| 9 | N & E Southeast Centre | 1 | 1 | 4 | | | | | | | | | | | | | | | 7 | | 1 | | | | 2 | 5 | | | | | | | | | | 2 |
| 10 | Southern Sandveld | 4 | | | | | | | | | | | 1 | | | | | | 1 | | | 3 | 2 | | | | 3 | | | | | | | | | |
| 11 | Potberg | 3 | | | | | | | | | | | | 3 | | | | | | 1 | 3 | | | | | | 2 | | | | | | | | | |
| 12 | NE Transvaal | 1 | | | | | | | | | | | | | | | | | 1 | | | 1 | | | | | 1 | | | | | | | | | 3 |
| 13 | Natal Coast | | | 1 | | | | | | | | | | | | | | 1 | | | | | 1 | | | | | | | | | | | | | 1 |
| 14 | Witteberg | | | 1 | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| 15 | Slypsteenberg-Antoniesberg | | | 1 | | | | | | | | | | | | | | 1 | | | | | | | | 1 | | | | | | | | | | |
| 16 | Grahamstown | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 17 | Kammiesberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 18 | Western Transvaal | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | Totals | 90 | 59 | 116 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 5 | 0 | 0 | 1 | 66 | 190 | 18 | 25 | 34 | 46 | 4 | 5 | 63 | 41 | 1 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 33 |

### 7.1.1 The relationship between endemism, diversity, and area in Ericaceae PCs

A highly significant and strong positive relationship ($r^2 = 0.72$, $p<0.001$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 63a), and between endemic taxa and PC area ($r^2 = 0.63$, $p<0.001$; Figure 63b), and non-endemic taxa and PC area ($r^2 = 0.40$, $p=0.009$; Figure 63c), which gets progressively weaker. However, it was necessary to exclude two outlying data points from the regression calculations (although they might still appear on the graphs), namely: the Peninsula (PC 3), which was significantly overrepresented with endemic and non-endemic taxa to PC area, and the Eastern Escarpment (PC 5), which was disproportionately large.

The high diversity and endemism in the Southwest (PC 1) and Northwest (PC 2) Mountains are again noticeable (Figure 63a). The Eastern Escarpment (PC 5) is overrepresented in endemics (Figure 63a), although this is likely as a result of its large geographical size. However, this large geographic size resulted in its exclusion from the remaining area-based regression (Figure 63b and c).

The Peninsula (PC 3, point excluded from regression) and West Agulhas Plains (PC 8) have higher endemic (Figure 63a) and non-endemic taxa (Figure 63b) than predicted by PC area. The Northeast Transvaal Centre (PC 12) and the Natal Coast Centre (PC 13) have low endemism relative to area (Figure 63b), and much lower than expected diversity (Figure 63c), as these PCs are quite distant from the CFR proper for a Cape Clade. However, the Northeast Transvaal Centre (PC 12) has higher endemic taxa than expected from its non-endemic component (Figure 63a).

## 7.2 CFR Phytogeographical Centres

### 7.2.1 The Southwest Phytogeographical Province

The Southwest Mountains PC (PC 1) occupies the bulk of the SWPP, with the Peninsula (PC 3) and the Southern Strandveld (PC 10) being represented as independent centres in my study of *Erica*. Although the Southwest Mountains PC of Ericaceae lump a large number of Combined Taxa Dataset PCs together, the divisions of the sub-centres in the SWPP correspond largely to the centres of the Combined Dataset.

In the PAE analysis, the Paarlberg (PSC 10.3) was merged with the Bainskloof-Stellenbosch Mountains (PSC 1.3), while in UPGMA it was assigned to the Sandveld (PC 10). However, this may have been a question of resolution. The higher areas of the Paarlberg (PSC 10.3) QDSs have floristic affinities to the Bainskloof-Stellenbosch Mountains (PSC 1.3) due to *E. chionophila* (5), while the lower lying areas share taxa with the Sandveld (PC 10) (*E. alexandri* (2)), and to other low altitude areas due to *E. setosa* (7), indicating dual affinities. There is no independent Saldanha Peninsula PC for *Erica,* further indicating its montane TMS preferences.

The Cape Peninsula (PC 3) has an astonishing 25 endemic species, ranking third richest in endemics, which is incredible when one considers its geographic size (only three QDSs with much ocean). The Peninsula has the highest number of endemics per QDS, 25/3 = 8.3/QDS (Table 36), followed by the Southern Mountains (137/20 = 6.85/QDS).

### 7.2.2 The Northwest Phytogeographical Province

The Northern Mountains (PC 2) cover the second largest area of *Erica* PCs, and is the largest PC in the core CFR. It clusters all the mountainous areas of the NWPP into a nearly continuous centre, except for the Kamiesberg and Nieuwoudtville Plateau. The Kamiesberg Mountains have low diversity and endemism, with a small isolated centre, containing a single endemic, which is probably due to an increase in aridity in this more northerly area. Surprisingly, the Nieuwoudtville Plateau does not have any endemics of its own and it is not even included in the NWPP PC. Although widespread taxa do occur here, it may be that moisture conditions are not able to support the endemic taxa in this area, or perhaps the area lacks sufficient altitude.

Erica PSCs of the Northern Mountains (PC 2) show less congruence to the PCs/PSCs of the Combined Taxa Dataset than *Erica* PSCs in the SWPP. Further evidence for the mesic montane affinity of the Ericaceae is apparent by the Olifant's River Valley and the flats between the Piketberg and Cedarberg not being assigned to a sub-centre. Most of these QDSs contain areas of much lower altitude than the QDSs assigned to the sub-centres. This further highlights the preference of *Erica* endemics for temperate, mesic, montane sites, particularly in the more arid NWPP. In addition, the Swartruggens, the Swartrugberge and the Baviaansberg are grouped with the Cedarberg, and the KMPP is poorly developed. This seems to be a pattern with the more mesic mountainous fynbos clades, which do not have a strong arid biotic element. Groups with a strong arid component seem to invade the Swartruggens the Swartrugberge and the Baviaansberg from the KMPP, and annex it to the KMPP.

### 7.2.3 The Langeberg Phytogeographical Province

As with many mesic montane TMS CFR elements, the Langeberg and associated plains form a well-developed centre. Here in the *Erica,* the Langeberg PC (PC 4) is the

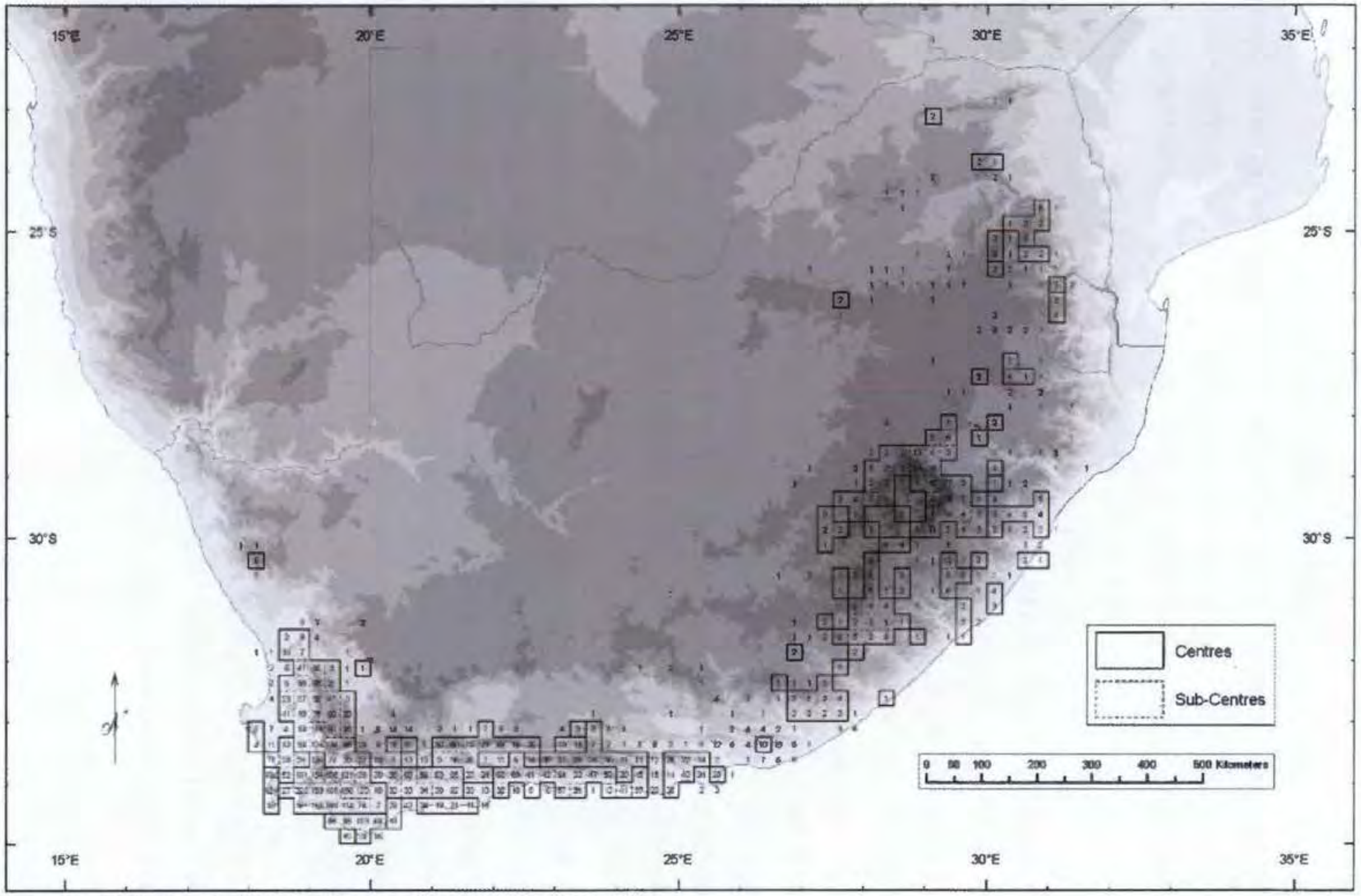


Figure 64: QDS Diversity for the Ericaceae Dataset in Southern Africa.

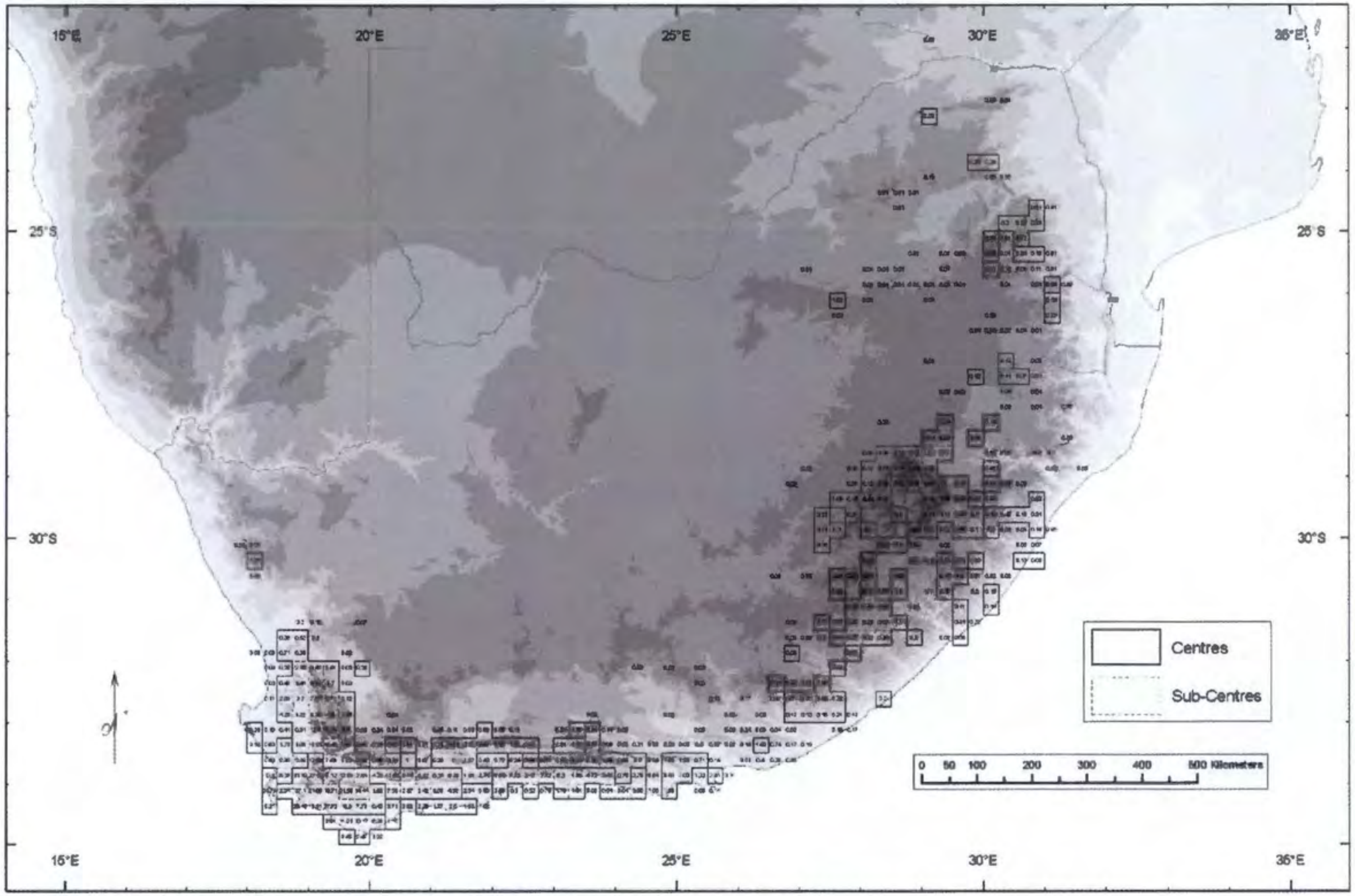


Figure 65: Sum of the Inverse Taxon Ranges for the Ericaceae Dataset in Southern Africa.

forth richest of the PCs I identified. Interestingly, the eastward extension of the Langeberg is curtailed by the southward migration of the Swartberg Centre (PC 6) along the Gamka-Gouritz River Valleys and not the westward migration of the SEPP, as in the Combined Dataset.

### 7.2.4 The Karoo Mountain Phytogeographical Province

Apart from the Greater Swartberg PC (PC 6), the KMPP is relatively poorly developed phytogeographically in *Erica*. The Klein and Groot Swartberg combine to form a single sub-centre (PSC 6.1) of the Greater Swartberg PC. The bigger ratio of high altitude to middle and low altitude endemics (Table 37) in the Swartberg (PC 6) (when compared to PCs in less arid environments (PC 1, 2 and 4)) once again indicates the importance of mesic montane sites for endemic *Erica* Taxa in more arid areas.

The Greater Swartberg PC also includes areas to the south, such as the Rooiberg, the eastern parts of the Langeberg and western parts of the Outeniqua Mountains; although these areas do not differentiate into separate sub-centres. This curious pattern is due to *Erica recta* (8) and *E. muirii* (5), which are possibly synonymous (Goldblatt and Manning, 2000), and occur on dry lower slopes (Goldblatt and Manning, 2000). Thus, these endemic taxa may occur along the lower slopes of the Gamka/Gouritz River Valley. This pattern is also observed in the Geophytes Dataset. Contrary to the Combined Dataset and the map of Goldblatt and Manning (2000), the Kammanassie Mountains form part of the N and E Southeastern Centre (PC 9) in *Erica*, rather than the *Erica* Greater Swartberg Centre (PC 6).

### 7.2.5 The Agulhas Plains Phytogeographical Province

The West Agulhas Plains (PC 8) and Potberg-East Agulhas Plains (PC 11) correspond to the APPP of Goldblatt and Manning (2000). It is unusual for the Potberg area to be grouped with the East Agulhas Plains, rather than the West Agulhas Plains, as seen in most of my other analyses. However, there is conflict in the area. Currently, *Erica vernicosa* (3) groups the disjunct portion of the Potberg-East Agulhas Plains (PC 11) with the western portion, but *E. albertyniae* (5) would cause the Potberg and the western disjunct portion of the Potberg-East Agulhas Plains (PC 11) to merge with the West Agulhas Plains (PC 8), into a larger West Agulhas Plains Centre. The area has affinities in both directions, which only finer spatial data may be able to resolve. Unusually for CFR Clades, the actual Potberg QDS is not assigned to a PC, which may be due to under collection. However, *E. albertyniae* (5) is known to occur here, which would place the Potberg's floristic affinities to the west.

### 7.2.6 The Southeast Phytogeographical Province

The SEPP is divided predominantly into two centres. The West Southeastern Centre (PC 7) is situated in the southwest, and includes the Outeniqua and Tsitsikamma Mountains, and also coastal elements. In the northeast, the Kammanassie-Kouga Centre (PC 9) includes those mountains after which it is named and extends eastwards to include the area around the Grootwinterhoekberg-Vanstadensberg (PC 9), in a near continuous east-west axis, but interrupted where the Groot River cuts through the mountains, separating the Baviaanskloofberg from the more easterly Grootwinterhoekberg-Vanstadensberg.

The diminutive Zuurberg Centre (PC 16) represents the only PC development in the Zuurberg Sub-Centre (Weimarck, 1941).

## 7.3 Non-CFR Phytogeographical Centres

The Eastern Escarpment Centre (PC 5), which is centred on the Drakensberg, is by far the largest PC geographically, occupying 95 QDSs and is three times larger than the next largest PC. The centre has very low diversity compared to its CFR counterparts, particularly relative to its size. However, nearly half the taxa (21 of 43) are endemic to the area (Table 36), which is a far higher ratio of endemism to diversity than other PCs that occur in the core CFR. This is due to its large geographical size. Similar patterns are also observed in my Poaceae and Orchidaceae analyses. It would be interesting to determine whether the *Erica* taxa occurring here are monophyletic or due to repeated invasions from the CFR Taxa, and to investigate possible directions of taxon and gene migration. Studies of *Moraea*, *Disa*, and *Pentaschistis* indicate that migration is mostly from the CFR to the Drakensberg (Galley et al., 2006).

*Erica* also has a few endemic taxa in other recognised phytogeographical regions. These include the Northeastern Escarpment Centre (PC 12), which is situated mostly in the Pilgrim's Rest-Sabie area, with outliers south to Barberton, north to the Wolkberg-Haenertsburg and the Blouberg areas. These have been identified as floristically important for Orchids and Grasses in this study, and also in other floristic studies (van Wyk and Smith, 2001; Goldblatt and Manning, 1998, for *Gladiolus*).

*Erica* is also represented by two endemics in the lower lying areas between the Drakensberg and the Natal Coast, with observable floristic congruence with Orchidaceae.

The small Western Transvaal Centre in *Erica* (PC 18) shows no geographic congruence with other groups analysed in my study.

## 7.4 Summary

PC formation and endemism in *Erica* is predominantly montane, but not exclusively so (Table 37). There is low altitude PC development in the SWPP and the APPP (Table 37). PC development is the epitome of mesic TMS Cape (fynbos) Clades, and phytogeographic patterns are highly congruent with the results of other floristic studies on the fynbos biotic element (Marloth, 1908; Weimarck, 1941). Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, NWPP, LBPP, Eastern Escarpment, KMPP and SEPP.

# Chapter 8: Fabaceae (Table 38, Figure 66)

## 8.1 Introduction

Globally, Fabaceae is one of the larger angiosperm families and is well-represented in the CFR. It contains clades that are considered typical Cape Clades (Linder, 2003), notably the genus *Aspalathus* (Dahlgren, 1960, 1961a, 1961b, 1961c, 1962, 1963a, 1963b, 1963c, 1965, 1966), and at the tribal level, Liparieae, Podalyrieae and Psoraleeae.

*Aspalathus* is one of the better-studied Cape Clades, with taxonomic and phytogeographical work undertaken by Dahlgren (Dahlgren, 1960, 1961a, 1961b, 1961c, 1962, 1963a, 1963b). Dahlgren (1963c) demonstrated that *Aspalathus* follows the traditional CFR pattern identified by Levyns (1962; 1964), having its highest diversity in the southwest, decreasing to the north and east. Dahlgren (1963c) found the highest diversity to occur in three-degree (1°) squares from the Hottentots Holland Mountains to the Groot Winterhoek. Dahlgren (1963c) adopted the phytogeographical classification of taxa proposed by Weimarck (1941). Dahlgren's (1963c) frequencies of endemic taxa are listed as: SWPP 63; NWPP 47; LBPP 16; SEPP 13; KMPP 11; and Knysna 3. Dahlgren (1963) did not identify an Agulhas Plains flora, or a Bredasdorp sub-centre in the SWPP. Dahlgren's (1963c) endemism frequencies largely follow those of other CFR Clades, with endemism being especially concentrated in the two westerly centres. As *Aspalathus* was revised relatively recently, it was also used in the Phytogeographical paper of Oliver et al., (1983), which largely corroborates the earlier findings and floristic patterns of Dahlgren (1963c).

In my study, Fabaceae shows certain phytogeographical similarities with other 'typical' CFR elements (see also Linder, 2003). However, it does show notable differences as well. My dataset is mostly comprised of *Aspalathus* (which was a little over 82% of the taxa that I analysed), thus the dataset is not entirely monophyletic, but mostly so.

Firstly, and most importantly, I found that the PC with the greatest number of endemics is the Northern Mountain Centre (PC 1). This geographically large PC consolidates three PCs from the Combined Dataset, including: the Groot Winterhoek (PSC 2.1), the Cedarberg (PSC 1.2) and the northern Hexrivier Mountains (PSC 1.1). Overall, I found endemism to be higher in the NWPP PC than in the SWPP PC (Table 38), although there is only a marginal difference in diversity. This differs from the findings of Goldblatt and

Table 38: Taxonomic properties of the Centres identified for the Family Fabaceae (Figure 66).

| Label | Centres<br>Sub-Centres | Area | | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Northwest Mtns | 18 | 111 | 57 | 39 | 92 | 0.13 | 0.11 |
| 1.1 | Groot Winterhoek-S Cedarberg | 9 | 94 | 33 | 21 | 38 | 0.20 | 0.16 |
| 1.2 | N Cedarberg | 7 | 57 | 18 | 11 | 19 | 0.25 | 0.17 |
| 1.3 | Remainder | 3 | 13 | 2 | 0 | 0 | - | 1.00 |
| 2 | Agulhas Plains | 19 | 90 | 32 | 18 | 53 | 0.15 | 0.11 |
| 2.1 | Potberg-East Agulhas Plain | 8 | 53 | 19 | 8 | 19 | 0.30 | 0.20 |
| 2.2 | Western Agulhas Plain | 4 | 47 | 7 | 2 | 5 | 0.63 | 0.25 |
| 2.3 | N West Agulhas Plain | 1 | 8 | 2 | 1 | 1 | 1.00 | - |
| 2.4 | Remainder | 6 | 46 | 2 | 0 | 0 | - | 1.00 |
| 3 | Swartberg-Witteberg | 14 | 41 | 20 | 14 | 27 | 0.14 | 0.07 |
| 3.1 | Groot Swartberg-Anysberg | 3 | 16 | 6 | 2 | 4 | 0.67 | 0.33 |
| 3.2 | Witteberg | 2 | 16 | 3 | 2 | 3 | 0.75 | 0.50 |
| 3.3 | Klein Swartberg | 3 | 12 | 3 | 2 | 5 | 0.83 | 0.67 |
| 3.4 | Rooiberg | 2 | 9 | 3 | 2 | 3 | 0.75 | 0.50 |
| 3.5 | N Witteberg | 1 | 5 | 1 | 1 | 1 | 1.00 | - |
| 3.6 | Remainder | 3 | 9 | 4 | 0 | 0 | - | 1.00 |
| 4 | Worcester-Bonnievale | 8 | 71 | 15 | 12 | 25 | 0.26 | 0.19 |
| 4.1 | Worcester-Bonnievale Core | 5 | 63 | 15 | 9 | 17 | 0.38 | 0.30 |
| 4.2 | Remainder | 3 | 22 | 2 | 0 | 0 | - | 1.00 |
| 5 | Southeastern Centre | 21 | 46 | 14 | 10 | 33 | 0.16 | 0.06 |
| 5.1 | W Southeastern Centre | 13 | 41 | 9 | 7 | 20 | 0.22 | 0.09 |
| 5.2 | Central Southeastern Centre | 6 | 18 | 2 | 2 | 6 | 0.50 | 0.00 |
| 5.3 | Remainder | 2 | 14 | 0 | 0 | 0 | - | 1.00 |
| 6 | Hottentots-W Kleinrivier-S RZE | 9 | 94 | 30 | 9 | 27 | 0.33 | 0.25 |
| 6.1 | Hottentots-W Kleinrivier-S RZE Core | 8 | 94 | 29 | 8 | 23 | 0.36 | 0.27 |
| 6.2 | Remainder | 1 | 12 | 0 | 0 | 0 | - | 1.00 |
| 7 | Sandveld/Piketberg | 9 | 56 | 18 | 9 | 17 | 0.21 | 0.11 |
| 7.1 | Piketberg | 3 | 34 | 9 | 3 | 5 | 0.56 | 0.33 |
| 7.2 | Sandveld | 3 | 24 | 5 | 2 | 4 | 0.67 | 0.33 |
| 7.3 | W Sandveld | 1 | 14 | 1 | 1 | 1 | 1.00 | - |
| 7.4 | Remainder | 2 | 32 | 4 | 0 | 0 | - | 1.00 |
| 8 | Greater Peninsula | 6 | 68 | 15 | 9 | 22 | 0.41 | 0.33 |
| 8.1 | N Peninsula | 2 | 60 | 6 | 3 | 4 | 0.67 | 0.50 |
| 8.2 | Outliers | 2 | 32 | 5 | 1 | 2 | 1.00 | - |
| 8.3 | Remainder | 2 | 37 | 2 | 0 | 0 | - | 1.00 |
| 9 | Central-Eastern Langeberg | 7 | 50 | 12 | 7 | 16 | 0.33 | 0.21 |
| 9.1 | E Central-Eastern Langeberg | 5 | 37 | 8 | 5 | 10 | 0.40 | 0.25 |
| 9.2 | Central Langeberg and Plains | 2 | 29 | 3 | 1 | 2 | 1.00 | - |
| 10 | Nieuwoudtville-South Gifberg | 5 | 21 | 7 | 7 | 11 | 0.31 | 0.20 |
| 10.1 | Nieuwoudtville | 2 | 14 | 5 | 5 | 6 | 0.60 | 0.50 |
| 10.2 | South Gifberg | 2 | 12 | 1 | 1 | 2 | 1.00 | - |
| 10.3 | Remainder | 1 | 1 | 0 | 0 | 0 | - | 1.00 |
| 11 | Far Southeastern | 13 | 17 | 7 | 5 | 20 | 0.31 | 0.13 |
| 11.1 | PE | 3 | 15 | 3 | 2 | 4 | 0.67 | 0.33 |
| 11.2 | Grahamstown_South | 2 | 9 | 1 | 1 | 2 | 1.00 | - |
| 11.3 | Remainder | 8 | 8 | 2 | 0 | 0 | - | 1.00 |
| 12 | North Gifberg-West Coast | 5 | 9 | 5 | 5 | 9 | 0.36 | 0.20 |
| 12.1 | North Gifberg-West Coast Core | 3 | 6 | 5 | 3 | 5 | 0.56 | 0.33 |
| 12.2 | Remainder | 2 | 6 | 2 | 0 | 0 | - | 1.00 |
| 13 | Hankey-Uitenhage | 5 | 18 | 4 | 4 | 9 | 0.45 | 0.27 |
| 14 | Stellenbosch-Bainskloof Mtns | 6 | 80 | 14 | 3 | 6 | 0.33 | 0.00 |
| 15 | Kamiesberg | 3 | 8 | 2 | 2 | 5 | 0.83 | 0.67 |
| 16 | W Kammanassie | 1 | 7 | 1 | 1 | 1 | 1.00 | - |
| 17 | Katberg Pass | 2 | 3 | 1 | 1 | 2 | 1.00 | - |
| 18 | Joubertsberge | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 19 | Klein Roggeveldberge | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 20 | Saldanha | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 21 | Outside | 53 | 80 | 1 | 0 | 0 | - | 1.00 |

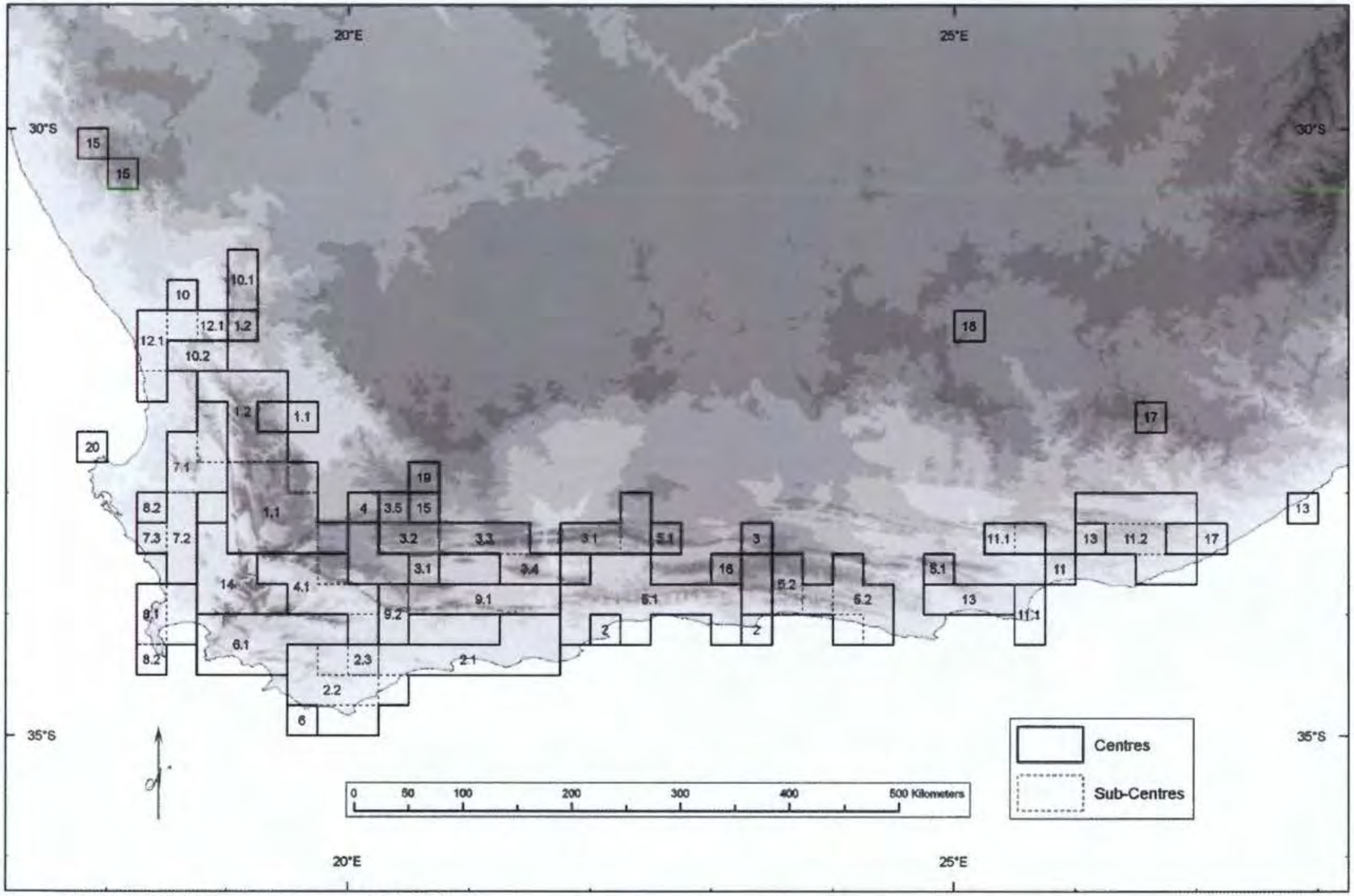


Figure 66: PC and PSC for the Fabaceae Dataset.

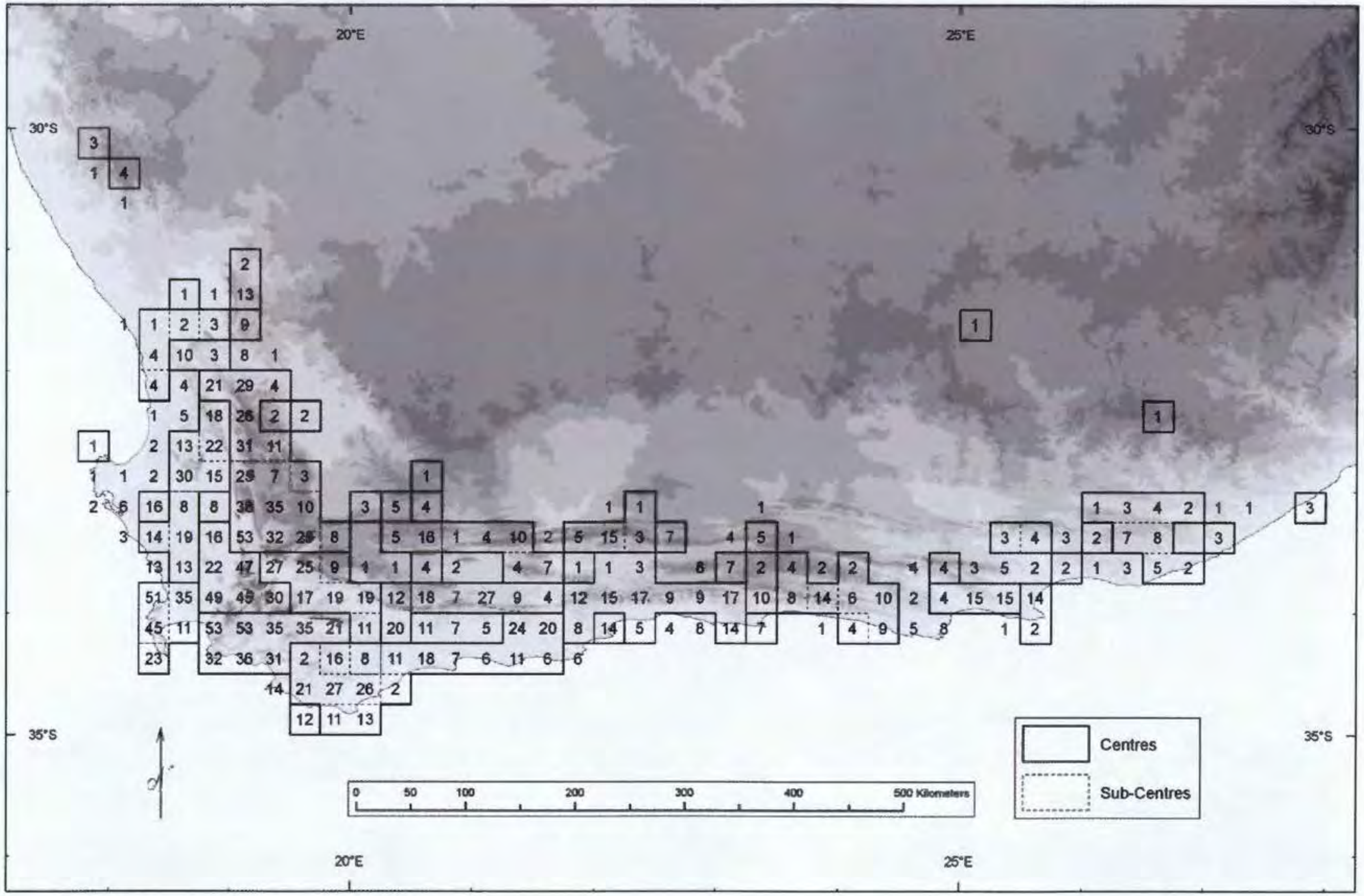


Figure 67: QDS Diversity for the Fabaceae Dataset.

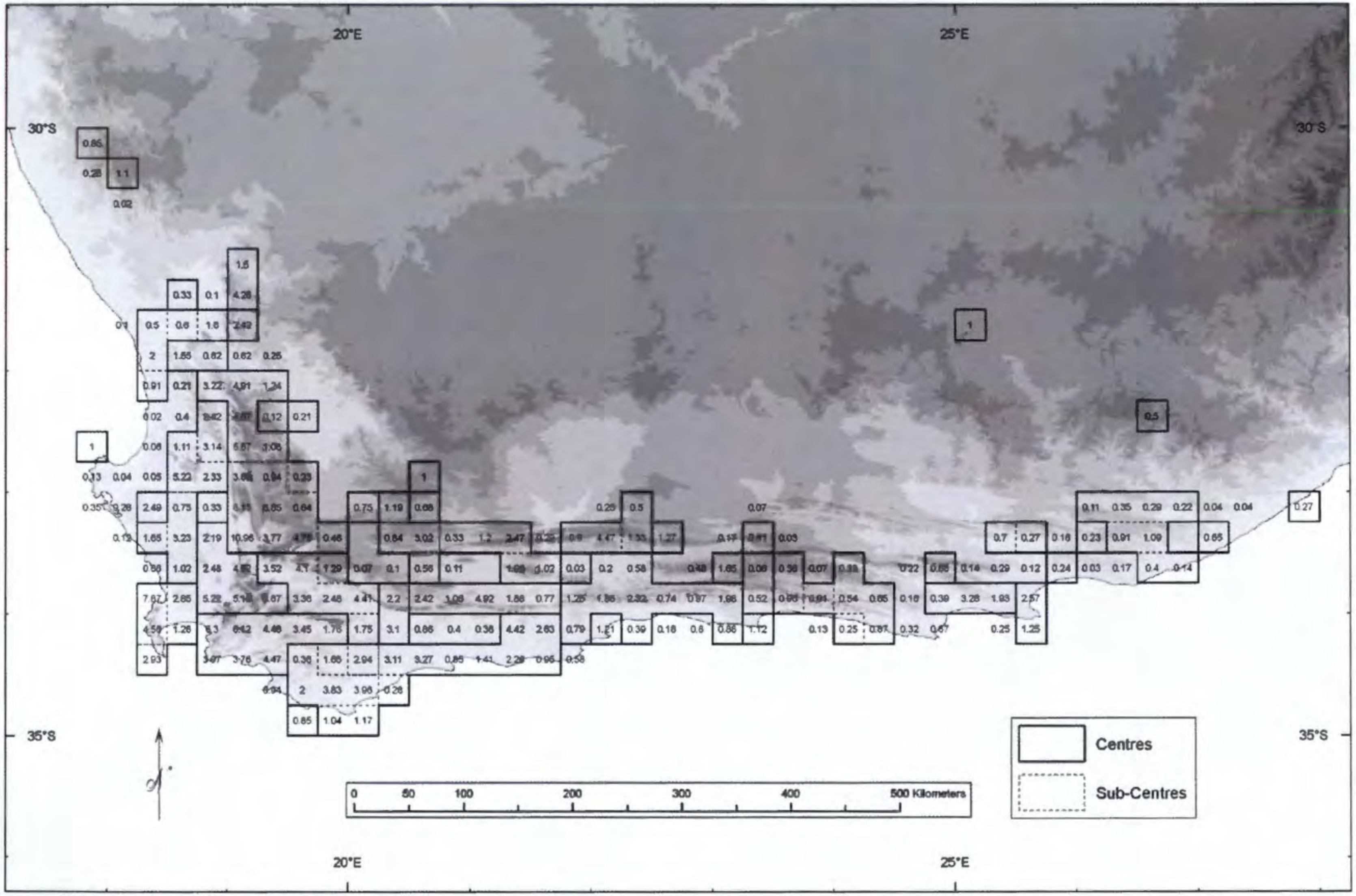


Figure 68: Sum of the Inverse Taxon Ranges for the Fabaceae Dataset.

Manning (2000), and Dahlgren's (1963) work on *Aspalathus*. The reasons for this difference are not entirely understood, but may have to do partly with the finer floristic subdivisions of the SWPP into four large PCs, while the NWPP is essentially one large PC. However, this does account for the large differences in endemism when the PCs are combined into larger units such as the SWPP and NWPP (Table 40).

The boundaries of the sub-centres are different from the phytogeographical boundaries of typical TMS montane clades. They do not seem to emphasise the importance of mountain ranges and peaks as being the central, or the most prominent features, of the PCs, especially in the SWPP, as I found in the 'typical' CFR Clade PCs that I identified in other datasets. The vast majority (77.8%) of the endemic taxa are located below 1000 metres (Table 39). There are almost equal counts of taxa between 0-500m and 500-1000m. The relatively high numbers of taxa at relatively low altitude (<500m) possibly account for the lower emphasis of mountain peaks and high altitude areas as central features to PC delimitation in the Fabaceae Dataset. Similarly, although 42.2% of endemics occur in mountain fynbos, 9.7% are represented in lowland fynbos, 15.1% are represented in a renosterbos-fynbos scrub and a further 5.4% in karroid type vegetation. So although more than 42.2% of endemics are found in true mountain fynbos, approximately 30.2% may be found at lower altitudes, or in non-mountain fynbos, which decreases the emphasis of high altitude areas on PC delineation. However, although a distinct lowland component of the endemic taxa can be identified in the Fabaceae Dataset, the exact edaphic affinities of these endemics need to be determined. This is largely due to the rather vague renosterbos-fynbos scrub vegetation type of Schutte (2000). It may well be that Fabaceae is better able to cope with arid, lower altitude conditions in the temperate phytogeographical provinces than other Cape Clades.

### 8.1.1 The relationship between endemism, diversity, and area in Fabaceae PCs

A highly significant and strong positive relationship ($r^2 = 0.68$, $p<0.001$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 69a), and between endemic taxa and area ($r^2 = 0.78$, $p<0.001$; Figure 69b), and non-endemic taxa and area ($r^2 = 0.61$, $p<0.001$; Figure 69c). The Saldanha Peninsula (PC 20) was excluded due to its small size and diversity, where there is a distinct lack of floristic development. No granitic or shale endemics are recorded in my Fabaceae Dataset, and there a relatively few endemics in sandy substrates (Table 39).

In Fabaceae, the Northwest PC (1) has significantly more endemic taxa than predicted by non-endemic taxa, or by geographic area (Figure 69a and b). It is atypical in Cape Clades for an NWPP PC (PC 1) to outperform the SWPP PC (PC 6, 7, 8, and 14), which is possibly due to the smaller geographic size and fragmentation of the SWPP. This is especially noticeable when considering that the Stellenbosch-Bainskloof Mountains (14) have significantly fewer endemics than expected from their numbers of non-endemics (Figure 69a), and the size of the PC area (Figure 69b). Interestingly, both the Hottentots-W Kleinrivier-S RZE (PC 6) and the Stellenbosch-Bainskloof Mountains (14) have high numbers of non-endemic taxa (Figure 69c), possibly indicating areas of floristic overlap, rather than PCs.

The Greater Peninsula (PC 8) again has higher than expected numbers of endemic and non-endemic taxa relative to PC area (Figure 69b and c). The Swartberg-Witteberg (PC 3) has higher than predicted endemism (Figure 69a). The two SEPP PCs, the Southeast Centre (PC 5) and the Zuurberg (PC 11) have lower than predicted endemism by geographic area (Figure 69b). Generally, the more winter xeric PCs, such as the Zuurberg (11), and the Gifberg (12) have lower than predicted numbers of non-endemic taxa (Figure 69c).

## 8.2 CFR Phytogeographical Centres

### 8.2.1 The Northwest Phytogeographical Province

The core PC of the NWPP, namely the Northern Mountains (PC 1), has external boundaries that are more or less similar to earlier phytogeographical centre delimitations by Weimarck and Goldblatt and Manning (2000), and also when compared to my Combined Dataset. The Groot Winterhoek (PSC 1.1) and the Cedarberg (PSC 1.2) combine to form the core areas and sub-centres of the Northern Mountains, but there the similarities to previous floristic studies end. The sub-centre boundaries are atypical, not separating the different mountain ranges into sub-centres. Instead, the southern Cedarberg, Groot Winterhoek, Hexrivier and Swartrugberge/Baviaansberg combine to form a single endemic rich and diverse sub-centre (PSC 1.1). It excludes the remaining areas of the central and northern Cedarberg and the Pakhuis Mountains, which cluster together into their own sub-centre (PSC 1.2). Furthermore, this extended Groot Winterhoek-S Cedarberg PSC (1.1) contains more endemic taxa and higher diversity than all my other Fabaceae PCs (Table 38). In most other groups (excluding the Geophytes and Diosmeae), the Hottentots Holland-Kogelberg-Kleinrivierberge has the highest taxon diversity and endemicity, following the pattern identified by Levyns (1938, 1962, 1964). The Northern Mountains Centre is larger in area than the centres of the SWPP.

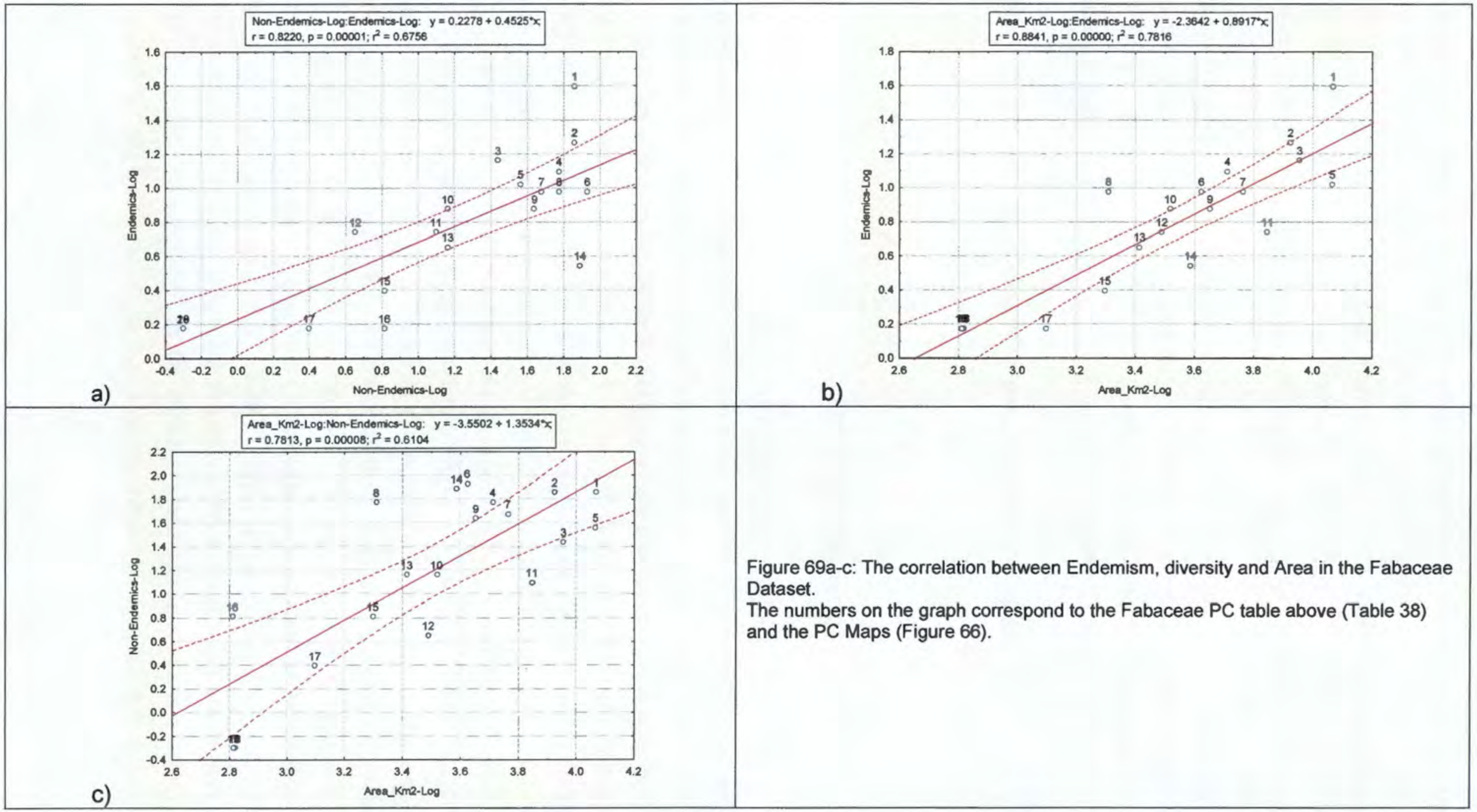


Figure 69a-c: The correlation between Endemism, diversity and Area in the Fabaceae Dataset.
The numbers on the graph correspond to the Fabaceae PC table above (Table 38) and the PC Maps (Figure 66).

Table 39: Habitat Data for Fabaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Clifs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | mtn fynbos | renosterbos-fynbos scrub | karroid type | lowland fynbos | coastal fynbos/Dunes | arid fynbos | subalpine fynbos | sandveld | Other |
| 1 | N Mtns | 3 | | 2 | 13 | 22 | 13 | 7 | | 1 | 1 | | | | | | | | 9 | | | 1 | | 1 | | 1 | | 22 | 6 | 4 | | | | | | 2 |
| 2 | Agulhas Plains | | | | 15 | 2 | 1 | 1 | | | | | | 5 | | | | 1 | | | | | | | | | | 3 | 4 | | 9 | 1 | | | | |
| 3 | Swartberg/Witteberg | | | | 1 | 5 | 7 | 2 | | 2 | 1 | | | | | | | | | | | | | | | | | 5 | 1 | 1 | | | | 1 | | |
| 4 | Worcester-Bonnievale | | | | 6 | 9 | 4 | | | | | | | | | | | | | | | | | | | | | 7 | 5 | 1 | 1 | 1 | 1 | | | |
| 5 | Southeastern Centre | 1 | | | 4 | 8 | 1 | 1 | | | | | | | | | | | 1 | | 1 | | | | | | | 7 | 2 | 1 | 1 | | 1 | | | |
| 6 | Hottentots-W Kleinrivier-S RZE | 3 | | | 7 | 3 | | | | | | | | | | | | | | | | | | 1 | | | | 8 | | | 1 | | | | | |
| 7 | Piketberg-Sandveld | 1 | | | 5 | 3 | 1 | | | | | | | | | | | | | | | | | | | | | 5 | 3 | | | | | | | |
| 8 | Greater Peninsula | | | | 5 | 4 | | | | | | | | | | | | | | | | | | | | | | 5 | 4 | | | | | | | |
| 9 | Central-Eastern Langeberg | 2 | | | 6 | 3 | | | | | | | | | | | | | 3 | | | | 1 | | | | | 6 | 1 | | 1 | | | | | |
| 10 | Nieuwouldtville-S Gifberg | | | | 1 | 5 | | | | | | | | | | | | | | 1 | | | 1 | | | | | 6 | | | | | | | | |
| 11 | Zuurberg Centre | 1 | | 1 | 2 | 3 | 1 | | | | | | | | | | | | | | | | | | | | | 2 | | | 1 | | | | | |
| 12 | North Gifberg-West Coast | | | | 3 | | | | | | | | | 1 | | | | 1 | | | | | | | | | | | | 2 | | | | | 1 | |
| 13 | Hankey-Uitenhage | 3 | | | 3 | 1 | | | | | | | | | | | | | 2 | | | 3 | | | | | 2 | 1 | | | 3 | | | | | |
| 14 | Stellembosch-Bainskloof Mtns | | | | 2 | 1 | 1 | | | 1 | | | | | | | | | 1 | | | | | | | | | 1 | | | 1 | | | | | |
| 15 | Kammiesberg | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| 16 | West Kammanassie | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| 17 | Katberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 18 | Joubertsberge | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 19 | Klein Roggeveldberge | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| 20 | Saldanha | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Totals | 14 | 0 | 3 | 74 | 70 | 30 | 11 | 0 | 4 | 2 | 0 | 0 | 6 | 0 | 0 | 0 | 2 | 16 | 1 | 1 | 4 | 2 | 2 | 0 | 1 | 2 | 78 | 28 | 10 | 18 | 2 | 2 | 1 | 1 | 2 |

In order to compensate for the fragmentation of the SWPP in PCs of small geographical size, all the PCs occurring in the SWPP area were merged and the floristic properties compared to a combined NWPP. The taxa in the Worcester-Bonnievale Centre (PC 4) were added to both the NWPP and SWPP due to the uncertainty of its affinities (Table 40). Even with the construction of these hierarchically high level phytogeographical provinces (Table 40), the NWPP still has far greater numbers of endemics (even when considering that the SWPP occupies a smaller area). This pattern is only apparent once these higher level phytogeographical provinces have been constructed. These results differ from Goldblatt and Manning (2000), suggesting that in my study, the NWPP has higher levels of diversity and endemism for the Fabaceae taxa analysed here, which comprises about 40% of CFR Fabaceae.

Table 40: Comparisons of the diversity and Endemism of the traditional SWPP and NWPP phytogeographical provinces for the Fabaceae Dataset.

| Province | Centre/Sub-Centre # | Area | # Taxa | Taxa >= 0.5 | # Endemics |
|---|---|---|---|---|---|
| SWPP | 6; 7.2; 7.3; 8; 14; 20 and 4 | 42 | 166 | 121 | 58 |
| NWPP | 1; 7.1; 10; 12 and 4 | 52 | 168 | 111 | 84 |

When examining QDS taxon diversity (Figure 67), very high numbers of diversity are recorded in the Hottentots-W Kleinrivier-S RZE QDSs, while there are far fewer QDSs with such high diversity scores in the NWPP. The inverse weighted species area map (Figure 68) shows better congruence with PC development, but does not entirely reveal the unusually rich levels of endemics of the NWPP PC formation. The two highest inverse weighting QDS values are in the Groot Winterhoek-S-Cedarberg sub-centre, while the third highest is found in the Peninsula, which as a centre, ranks relatively poorly. The QDS 3319AC is usually bisected by the boundary between the NWPP and SWPP, along the Kleinberg-Boontjies Rivers. In the Fabaceae Dataset, 3319AC is clustered with the NWPP. However, Goldblatt and Manning (2000) classify three of the five QDS endemics in the SWPP. Point locality data would increase the spatial resolution of floristic boundaries in conflicting QDSs like 3319AC and may lead to greater numbers of endemics; in this example, higher numbers of SWPP endemics. Fabaceae also has many low altitude biotic elements, indicating that higher montane areas might not be as important for endemic taxa, and that lower altitude areas, especially rivers (which have been used in the past as floristic boundaries (Weimarck, Goldblatt and Manning, 2000)) may not be as useful for phytogeographical boundaries in this clade. It may be that Fabaceae is slightly better able to cope with arid conditions in the Mediterranean centres of the CFR than other TMS Cape Clades, although not to the extent of having a specialised arid adapted taxa or clades. This diversity of biotic elements makes determining floristic boundaries more difficult. It may be more informative to undertake separate analysis on the different floristic elements. This is further supported by the

Swartruggens (PC 1) and Swartrugberge/Baviaansberg (PSC 1.1) forming part of the Northern Mountains (PC 1), rather than being incorporated into the KMPP PC.

Interestingly, as in Asteraceae, the Piketberg-Swartberg/Olifantsrivierberg and northern Sandveld flora (PSC 7.1) combine with the Sandveld (PSC 7.2 and 7.3) in the SWPP, although the principle sub-centres are separated in the region of the traditional NWPP-SWPP boundary (Weimarck; Goldblatt and Manning, 2000). As with Asteraceae, this may indicate a dedicated low altitude flora in Fabaceae, which has closer phytogeographical links to areas with similar environmental conditions, rather than to neighbouring montane areas.

There is one QDS in conflict with the NWPP, namely, 3218BD, which can be assigned to either the Sandveld/Piketberg Centre (PC 7), where it is located now, due to *Aspalathus pendula* (2), or to the Northwest Mountains Centre (PC 1), due to *A. decora* (2). The current delineation is maintained due to the relative increase in endemism afforded to the centre with fewer total endemics (PC 7).

Further north in the NWPP, the northern Gifberg and the flats to its west form a centre (PC 12) that separates the Nieuwoudtville Plateau (PSC 10.1) slightly from the South Gifberg (PSC 10.2), which may likely form a single centre (combining PC 10 and PC 12) with additional collecting. Further north, in Namaqualand, is a Kamiesberg outlier (PC 15).

### 8.2.2 The Southwest Phytogeographical Province

The difference between Fabaceae PCs and other montane TMS Cape Clades (fynbos) is also apparent in the SWPP, particularly in the Hottentots-W Kleinrivier-S RZE Centre (PC 6). Instead of this southwest corner PC being located on the Hottentots Holland and Kleinrivier Mountains as in other fynbos datasets, it appears that the lower areas between the northerly Franschhoek-RZE Mountains and the southerly Palmietberge-Kleinrivierberge comprise the central area of the centre, with the mountain watersheds, especially the RZE, as boundaries. Although eight out of the nine endemics occur in mountain fynbos, seven occur below 500 metres (Table 39), highlighting the importance of lower altitude habitats for endemism in Fabaceae. Another floristic deviation is that the traditional boundary (of Weimarck; Goldblatt and Manning; and my fynbos datasets) between the NWPP and the SWPP, south of the West Langeberg - the centre of the Bree River Valley, bisects the middle of another centre, the Worcester-Bonnievale Centre (PC 4). Many of these endemics are low altitude taxa and less than half of them occur in true mountain fynbos (Table 39). The affinities of this PC to either the NWPP or SWPP are as yet uncertain and require further analysis. In most Cape Clades, endemism and consequently PCs are centred on the TMS mountain ranges (Marloth, 1908; Weimarck), with rivers as the principal boundaries. Lower altitude non-TMS endemic elements do not appear to conform to this pattern.

An unusual feature of two of the core SWPP PCs, the Hottentots-W Kleinrivier-S RZE (PC 6) and Stellenbosch-Bainskloof Mountains (PC 14), is that there is a very low conversion rate of PC taxon diversity into PC taxon endemism, which is unusual for SWPP PCs in my study. In the Hottentots-W Kleinrivier-S RZE (PC 6), only about 30% of the represented taxa have half their ranges in the PC, while about 30% of those are strictly endemic to the PC. The conversion rate is even lower in the Stellenbosch-Bainskloof Mountains (PC 14), where about 20% of the represented taxa have half their ranges in the PC and about 20% of those are strictly endemic to the PC. This is in stark contrast to the Northern Mountains (PC 1), where about 51% of the represented taxa have half their ranges in the PC and about 68% of those are strictly endemic to the PC. Even when the SWPP fragments are combined (Table 39), resulting in more similar area and taxon diversity, the SWPP still does not contain as many endemics, suggesting that taxa in the SWPP have a relatively wider distribution. The average range size of endemic taxa in the SWPP is 3.43 QDSs, while in the NWPP it is 2.12 QDSs. Alternatively, this may also be due to disproportionate collector efforts between the NWPP and SWPP, with under collection in the NWPP exaggerating the frequency of narrowly distributed taxa.

Both the NWPP and the SWPP Sandveld (PSCs 7.1 and 7.2 respectively) merge with the Piketberg, Swartberg and Olifantsrivierberg into a single centre (PC 7). Importantly, the NWPP and SWPP components are in different sub-centres, separated along the traditional SWPP-NWPP boundary. However, in the very south, the Cape Flats region of the Sandveld occurs in a different PC and is more closely affiliated with the Peninsula and the Table Mountain Complex (PC 8). This also represents a deviation from Cape Clades with stronger TMS affinities, where the Peninsula usually displays stronger floristic affinities to the more distant sandstone mountains across the Cape Flats, rather than to the Cape Flats itself. The Peninsula has two relatively high diversity QDSs (Figure 67), the northern of the two QDSs (3318CD) has the third highest QDS inverse weighting score for my Fabaceae dataset. This shows the distinctiveness and importance of this area, even in clades which are not as strongly associated with mountain ranges. The Saldanha Peninsula (PC 20) is poorly developed, and contains a single, very range-restricted endemic taxon, *Aspalathus gerrardii* (1).

There is one QDS in conflict in the SWPP, namely, 3318DD, which can be assigned to either the Stellenbosch-Bainskloof Mountains Centre (PC 14), where it is located now, due to *Rafnia ericifolia* (2), or to the Greater Peninsula Centre (PC 8), due to *Aspalathus humilis* (2). The current delineation is maintained due to the relative increase in endemism afforded to the centre with fewer total endemics.

### 8.2.3 The Agulhas Plains Phytogeographical Province

The APPP (PC 2) is larger and better developed in Fabaceae than compared with most of the other clade/group datasets that I analysed, in terms of area, taxon diversity, endemism and delineation. This is quite surprising, considering the relatively low QDS richness and QDS inverse weighting scores in the area.

The eastern parts of the Kleinrivierberge (PSC 2.2) combine with the APPP rather than the Hottentots-W Kleinrivier-S RZE Centre (PC 6). This again indicates that the lower altitude areas surrounding the mountains are often more dominant in determining QDS affinities in forming PCs in Fabaceae, rather than the higher mountain areas, as in other montane TMS Cape Clades. Endemic taxa in lowland habitats are by far the most dominant taxa (78.9% occurring below 500 metres) in the Agulhas Plains Centre (PC 2).

The APPP also migrates slightly northwards in the east, occupying a QDS of the East Langeberg Plain (PSC 2.1). The sub-centres show some, although not complete similarity to the usual patterns of floristic sub-division, with the Potberg-East Agulhas Plains Sub-Centre (PSC 2.1) being the richest sub-centre, rather than the West Agulhas Plains (PSC 2.2), as occurs more frequently in fynbos groups.

### 8.2.4 The Langeberg Phytogeographical Province

The Langeberg Centre (PC 9) performs relatively poorly in Fabaceae, and only comprises two sub-centres. The larger sub-centre consolidates the full length of the Central and Eastern Langeberg (PSC 9.1 of the Combined Taxa Dataset), in the mountainous portion and ends eastwards, at the Gouritsrivier Valley. The absence of any high altitude endemics (above 1000 metres) in the Langeberg may contribute to its relatively poor floristic performance. Remarkably, only one QDS from the Langeberg Plains is included in the centre in the western Central Langeberg Plain (PSC 9.2). This results in a noticeable gap in the assigning of QDSs to centres in the area between the LBPP and APPP. Although at least one QDS has a relatively high diversity (11 taxa in 3420BA, Figure 67), closer examination of this area reveals no taxa that are exceptionally range-restricted (Figure 68). The highest inverse weighting score is 0.86 in the most diverse QDSs, while the other values are much lower (0.40 and 0.36, see Figure 68). There are three taxa occurring in the general area collected from five QDSs. However, all widespread and are represented in numerous PCs. Thus, the absence of range-restricted taxa, compounded by conflict with other centres, seems to have resulted in this gap. The reasons for this are peculiar, as the group as a whole is well-represented by endemic taxa in lowland areas. Although the majority of the endemic Langeberg taxa in this study occur in mountain fynbos, they occur mostly at low altitude, below 500m (Table 39). These endemics are usually associated with mountains. The reason for this gap on the LBPP Plains may be due to a combination of topography and climate. This depauperate area represents a low altitude area, outside the winter rainfall area that was delimited by Schulze (1997), resulting in it receiving very little rain in winter, and able to support lower diversity (and endemism).

### 8.2.5 The Karoo Mountain Phytogeographical Province

The KMPP is very similar in pattern to the LBPP above. Essentially, it consists of one major centre (PC 3), with the sub-centres being strongly associated with major mountain ranges, namely, the Groot Swartberg (PSC 3.1), the Witteberg (PSC 3.2), the Klein Swartberg (PSC 3.3) and the Rooiberg (PSC 3.4). In the KMPP, it is very noticeable that the majority of taxa occur in mountain fynbos, at high altitude, predominantly 500-1500m (Table 39). The KMPP of Fabaceae has the highest proportion of endemic taxa found between altitudes of 1000-1500m of all Fabaceae PCs. It seems that as PCs become progressively more **'winter arid'** (climatic demarcation based on Schulze, 1997), that endemic taxa will have a greater preference for the more mesic montane areas.

### 8.2.6 The Southeast Phytogeographical Province

In Fabaceae, the SEPP is composed predominantly of the Southeast Centre (PC 5), which is centred in the western parts of the SEPP, on the Outeniqua-Tsitsikamma Mountains. This may be due to the fact that the winter rainfall pattern is stronger here. There are extensions of this centre, northwards into the Karoo (PSC 5.1) and south to the coast (PSC 5.1 and 5.2). The remainder of the SEPP comprises smaller PCs.

The far eastern SEPP contains a PC close to Port Elizabeth, the Hankey-Uitenhage Centre (PC 13), which contains four endemic taxa and includes an outlier in the Zuurberg area, and further east in East London, due to *Aspalathus intermedia* (5). This taxon and the fragmented nature of PCs in this area indicate that additional collection may result in the consolidation of PCs here in the east SEPP.

Further east is the Zuurberg Centre (11), which roughly corresponds to the Zuurberg Centre of Weimarck (1941). Although it is fairly common for Cape Clades in this area to have PC development on the Zuurberg Mountains, it is more unusual to have PC development in the lower lying areas, as *Aspalathus* does here. However, in many other Fabaceae PCs, this lower altitude PC development is more apparent, except in the central LBPP and KMPP. This low altitude PC development is largely due to very few taxa, such as *Aspalathus frankenioides* (9), and *Lessertia carnosa* (2). Due to this lower altitude development, it would be interesting to determine how the Zuurberg Centre (11) corresponds to the Albany Centre (van Wyk and Smith, 2001; Croizat, 1965).

## 8.3 Non-CFR Phytogeographical Centres

Although the Fabaceae Taxa sampled here were geographically biased towards the CFR, there is some PC development outside the core CFR. My Katberg Pass Centre (PC 17) and Joubertsberge Centre (PC 18) occur close to the Sneeubergen Centre that Nordenstam (1969) identified for *Euryops*. The Sneeubergen Centre (Nordenstam, 1969) overlaps with the northern area of the Albany Centre of van Wyk and Smith (2001). Both PCs (17 and 18) have endemic *Aspalathus* Taxa, which may once again indicate the historical importance of the East African Highlands corridor as a conduit for gene dispersal of Cape Clades.

## 8.4 Summary

In Fabaceae (*Aspalathus*), the phytogeographical delimitations of the western temperate traditional phytogeographical centres (NWPP, SWPP and APPP) differ noticeably from the traditional CFR phytogeographical patterns (Weimarck), with a bias towards lower altitude biotic element endemism and PC development. Here, mountain ranges/ridges occur largely on the periphery of PCs, rather than being central. The Sandveld of the NWPP and SWPP consolidate together, rather than with the mountains of their respective Phytogeographical Provinces. Taxon endemism in the SWPP PCs is uncharacteristically poor for a CFR Clade (Levyns, 1964; Linder, 2003).

However, in the less Mediterranean centres in the east of the CFR (LBPP, KMPP and even the SEPP), endemism is more strongly associated with montane TMS areas. Lower altitude endemic taxa, and consequently PC development may be facilitated by the greater abundance of winter rainfall availability in the west, even at lower altitudes (0-500 m (-1000m)). Conversely, in the more arid areas of the CFR, the lower winter moisture availability in the east may force taxa to occur at higher altitudes, for example, in the KMPP and LBPP.

Patterns and levels of PC endemism are unusual in the different phytogeographical provinces and are approximately as follows (highest to lowest): NWPP, (combined) SWPP, APPP, KMPP, SEPP and LBPP.

# Chapter 9: Geophytes (Table 41, Figure 70)

## 9.1 Introduction

The Geophyte Dataset is not a monophyletic dataset, mostly comprising families from Asparagales and in a few other taxonomic orders. Although my Geophyte Dataset contains a few monophyletic clades, such as *Haemanthus* and *Ferraria*, it largely consists of range-restricted RDL Geophyte Taxa, which may obscure historical patterns and may rather highlight current ecological conditions, or threats.

Earlier phytogeographical studies on endemism in the CFR (Marloth, 1908; Weimarck) neglected the floristic distributions of geophytes. Until recently, the general model of a CFR endemic plant was one that was described as a dwarf, or low, non-sprouting shrub, with soil-stored seeds, which are ant-dispersed (Cowling and Holmes, 1992; Trinder-Smith, Cowling and Linder, 1996; McDonald, Juritz, Cowling and Knottenbelt, 1995). Plants that form a symbiotic relationship with soil microbes were also considered to have a predisposition to endemism in the CFR (Cowling et al., 1992). Examples include Fabaceae, while it has been postulated that root symbiosis occurs in Ericaceae as well (Cowling and Holmes, 1992). High levels of pollinator specialisation can also predispose taxa to speciation and endemism (van der Niet, Johnson and Linder, 2006). The greater the number of such characteristics a plant possesses, the higher its probability of being an endemic. More recent studies have highlighted the floristic importance of geophytes in the CFR (Goldblatt and Manning, 2000, 2002; Proches, Cowling and du Preez, 2005; Proches and Cowling, Goldblatt, Manning and Snijman, 2006).

The boundaries of geophyte floristic units are very different from other taxa in the CFR. In addition, patterns of diversity and endemism are also very different. The Geophytes Dataset has considerably more endemic taxa in the South Namaqualand Centre (PC 1) than in any other centre. It has nearly two and a half times the number of endemics than the S NWPP-N SWPP Centre (PC 2), which is ranked second. Furthermore, diversity and endemism are mostly concentrated on the Nieuwoudtville Escarpment (PC 1.1). The Geophyte Dataset is my only dataset in this study where the Nieuwoudtville Escarpment performs so well. This is observed at both the PC geographical level (Figure 70) and lower QDS geographical level (Figure 71). Diversity at the QDS level indicates the middle of the Nieuwoudtville Plateau as a centre of diversity and endemism for my Geophyte Dataset. Thus my data suggests that the centre of diversity and endemism for geophytes is not in the Hottentots-Kogelberg fulcrum, as was observed in montane TMS Cape (fynbos) elements by Levyns (1938, 1962 and 1964), but around the Nieuwoudtville Plateau.

The diversity and endemism in the remaining PCs are fairly comparable with other datasets and the Combined Dataset, although the boundaries of the floristic units deviate from the conventional fynbos patterns. The positions of the PCs, particularly the Southern NWPP-Northern SWPP Centre (PC 2) and the South Southwest Mountains (PC 3) have similarities to the patterns of my Fabaceae Dataset. This indicates that as with Fabaceae, that Geophytes have a higher number of endemic taxa in lower altitude environments (<1000 metres), rather than on high slopes and ridges. When analysing the properties of Geophyte endemic taxa (Table 42), this indeed appears to be the case. There are also increased numbers of endemics on the richer, shale derived (clay) soils (Table 42), and on granite and limestone substrate types, rather than on the more nutrient poor TMS soils that many Cape (fynbos) Clades prefer, such as Restionaceae, *Erica* and Proteaceae. The South Namaqualand Centre (PC 1) and the East KMPP-West SEPP Centre (PC 4) show the highest levels of endemism for the speciose PCs, 68.6% and 64.4% of their taxa being endemic respectively. These constitute the two largest Geophyte PCs by area, in my Geophyte Dataset, which contributes to their high endemism. Interestingly, both these two centres occur in the more arid areas of the winter rainfall region. In TMS centred clades, these levels of endemism are usually associated with the more mesic, southwest areas of the CFR. Although it should be borne in mind that my Geophyte Dataset is biased towards range restricted taxa, nevertheless comparisons can be made between the PCs of my dataset.

A number of the Geophyte phytogeographical units directly associated with "CFR" PCs extend outside the core CFR, as defined by Goldblatt and Manning (2000), and Weimarck (1941), notably the Vanrhynsdorp Sub-Centre (PSC 1.3). As the Geophyte Dataset was assembled mostly from taxa restricted to the geographical confines of the CFR, it cannot be verified whether the Vanrhynsdorp Sub-Centre (PSC 1.3) is a northern extension of the NWPP, or part of the Succulent Karoo. It may even contain taxa with affinities to both these areas. Similarly, due to the geographical cropping of the dataset, it is not possible to determine if, or where the floristic boundary between the Succulent Karoo and the CFR might lie for Geophytes. It is also not possible here to determine whether the Geophyte Flora constitutes a Greater Cape Flora (as proposed by Born et al., 2006), or if it comprises distinct CFR and Succulent Karoo Floras.

Table 41: Taxonomic properties of the Centres identified for the artificial group Geophytes (Figure 70).

| Label | Centres Sub-Centres | Area | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Southern Namaqualand | 20 | 118 | 96 | 81 | 136 | 0.08 | 0.07 |
| 1.1 | Nieuwoudtville Escarpment | 3 | 57 | 41 | 30 | 37 | 0.41 | 0.39 |
| 1.2 | Gifberg-Soutpansberg | 5 | 49 | 32 | 21 | 29 | 0.28 | 0.24 |
| 1.3 | Knersvlakte-Hardeveld | 3 | 20 | 14 | 11 | 14 | 0.42 | 0.37 |
| 1.4 | Nieuwoudtville Surrounds | 3 | 18 | 6 | 2 | 4 | 0.67 | 0.33 |
| 1.5 | N West Coast | 3 | 13 | 4 | 2 | 4 | 0.67 | 0.33 |
| 1.6 | Remainder | 3 | 6 | 0 | 0 | 0 | - | 1.00 |
| 2 | S NWPP-N SWPP | 17 | 98 | 59 | 34 | 56 | 0.10 | 0.07 |
| 2.1 | Berg-Bree Catchment | 6 | 59 | 22 | 15 | 20 | 0.22 | 0.17 |
| 2.2 | Piketberg | 3 | 26 | 8 | 6 | 8 | 0.44 | 0.33 |
| 2.3 | Southeast Sandveld | 4 | 46 | 10 | 5 | 10 | 0.50 | 0.38 |
| 2.4 | NE Hex-W Langeberg | 2 | 13 | 3 | 2 | 3 | 0.75 | 0.50 |
| 2.5 | Porterville-Skurweberg | 2 | 15 | 2 | 2 | 3 | 0.75 | 0.50 |
| 3 | S Southwest Mtns | 15 | 81 | 50 | 30 | 69 | 0.15 | 0.12 |
| 3.1 | Hottentots-RZE-Overberg | 10 | 60 | 31 | 16 | 34 | 0.21 | 0.16 |
| 3.2 | Peninsula | 3 | 33 | 11 | 8 | 12 | 0.50 | 0.43 |
| 3.3 | W Kleinrivier-Gansbaai | 2 | 18 | 3 | 2 | 3 | 0.75 | 0.50 |
| 4 | E KMC-West SEC | 28 | 45 | 31 | 29 | 65 | 0.08 | 0.05 |
| 4.1 | Outeniqua-Kammanassie | 7 | 20 | 8 | 8 | 16 | 0.29 | 0.18 |
| 4.2 | Klein Swartberg-Rooiberg-Gamkaberg | 3 | 14 | 6 | 6 | 8 | 0.44 | 0.33 |
| 4.3 | Kouga-Meiringspoort | 3 | 10 | 4 | 4 | 6 | 0.50 | 0.33 |
| 4.4 | Groot Swartberg | 3 | 10 | 3 | 3 | 5 | 0.56 | 0.33 |
| 4.5 | West Klein Swartberg | 1 | 6 | 1 | 1 | 1 | 1.00 | - |
| 4.6 | Tsitsikamma-Outeniqua | 3 | 6 | 1 | 1 | 3 | 1.00 | - |
| 4.7 | SE Baviaanskloofberg | 1 | 3 | 1 | 1 | 1 | 1.00 | - |
| 4.8 | Far West Klein Swartberg | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 4.9 | Remainder | 6 | 9 | 0 | 0 | 0 | - | 1.00 |
| 5 | Cedarberg-Kouebokkeveld | 11 | 64 | 40 | 27 | 54 | 0.18 | 0.15 |
| 5.1 | NW Cedarberg | 3 | 41 | 21 | 13 | 22 | 0.56 | 0.53 |
| 5.2 | Kouebokkeveld-Swartberg | 6 | 37 | 15 | 10 | 19 | 0.32 | 0.24 |
| 5.3 | Remainder | 2 | 9 | 0 | 0 | 0 | - | 1.00 |
| 6 | West LBPP-KMPP | 18 | 41 | 23 | 18 | 45 | 0.14 | 0.09 |
| 6.1 | Central Langeberg | 8 | 25 | 12 | 8 | 19 | 0.30 | 0.20 |
| 6.2 | W Langeberg-Waboomsberg | 4 | 20 | 8 | 5 | 8 | 0.40 | 0.25 |
| 7 | Saldanha Peninsula | 6 | 27 | 15 | 12 | 23 | 0.32 | 0.26 |
| 7.1 | Northwest | 2 | 16 | 8 | 5 | 6 | 0.60 | 0.50 |
| 7.2 | Southeast | 4 | 21 | 7 | 4 | 9 | 0.56 | 0.42 |
| 8 | South Sandveld | 5 | 41 | 16 | 11 | 22 | 0.40 | 0.34 |
| 9 | Klein Roggeveld-Witteberg | 5 | 13 | 8 | 7 | 11 | 0.31 | 0.20 |
| 10 | St Francis-Port Elizabeth-Grahamstown | 4 | 10 | 5 | 5 | 8 | 0.40 | 0.25 |
| 11 | Kamiesberg-Steinkopf Escarpment | 12 | 11 | 5 | 4 | 20 | 0.42 | 0.22 |
| 11.1 | NW Namaqualand Escarpment | 6 | 8 | 1 | 1 | 6 | 1.00 | - |
| 11.2 | Kamiesberg | 2 | 7 | 1 | 1 | 2 | 1.00 | - |
| 11.3 | Remainder | 4 | 9 | 1 | 0 | 0 | - | 1.00 |
| 12 | W West Agulhas Plains | 3 | 13 | 6 | 3 | 5 | 0.56 | 0.33 |
| 13 | Kwadouwsberg | 2 | 7 | 3 | 3 | 4 | 0.67 | 0.50 |
| 14 | Potberg | 3 | 14 | 2 | 2 | 5 | 0.83 | 0.67 |
| 15 | Vanstadens-NW Baviaanskloofberg | 3 | 5 | 2 | 2 | 4 | 0.67 | 0.33 |
| 16 | N Namaqualand Lowlands | 17 | 5 | 2 | 2 | 18 | 0.53 | 0.06 |
| 17 | Doring River Valley | 1 | 4 | 2 | 2 | 2 | 1.00 | 1.00 |
| 18 | Karoopoort-East | 1 | 4 | 2 | 2 | 2 | 1.00 | 1.00 |
| 19 | Slypsteenberg-Steytlerville-Kleinpoort | 3 | 3 | 2 | 2 | 4 | 0.67 | 0.33 |
| 20 | E West Agulhas Plains | 1 | 6 | 2 | 1 | 1 | 1.00 | - |

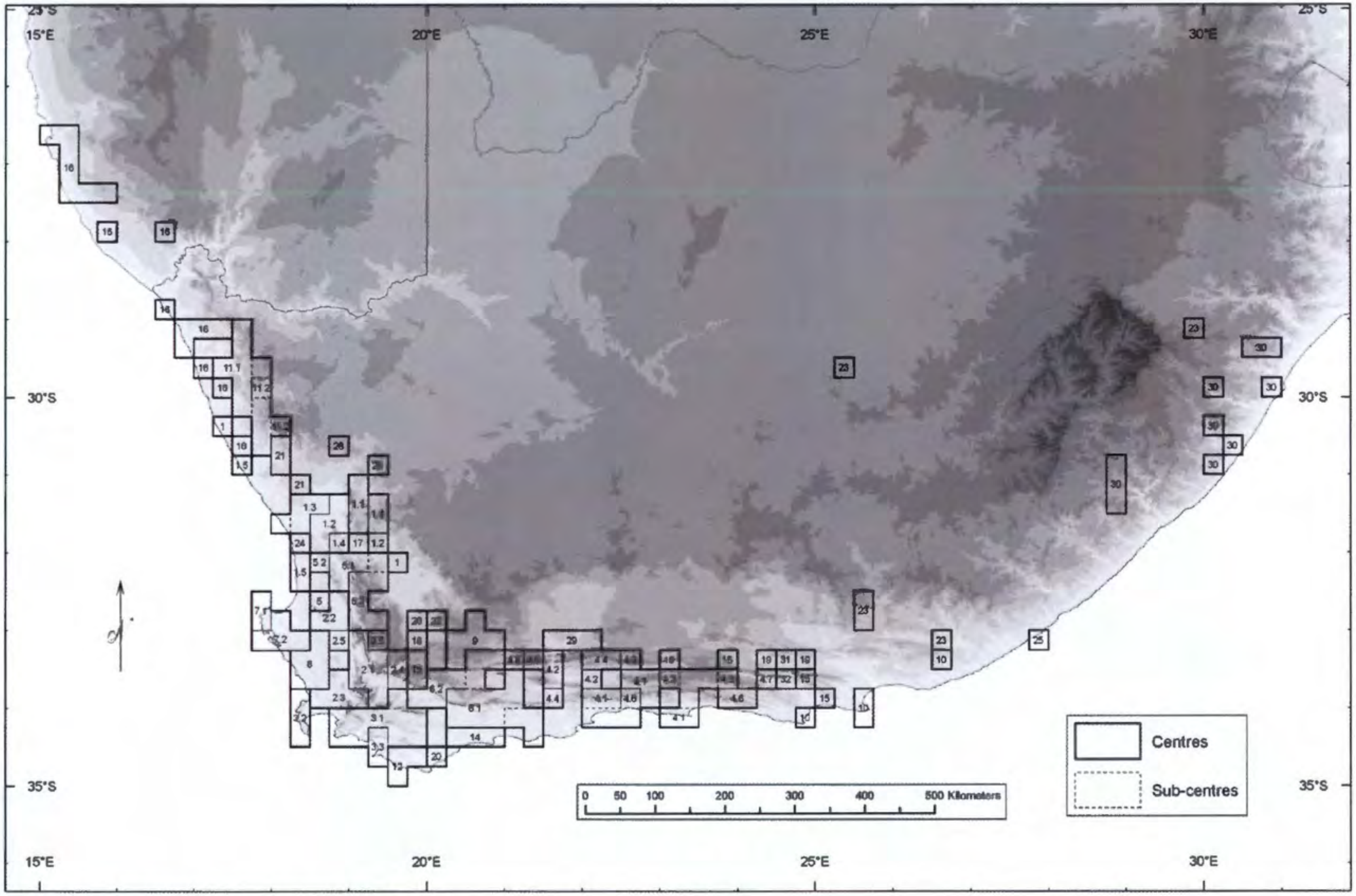


Figure 70: PC and PSC for the Geophyte Dataset.

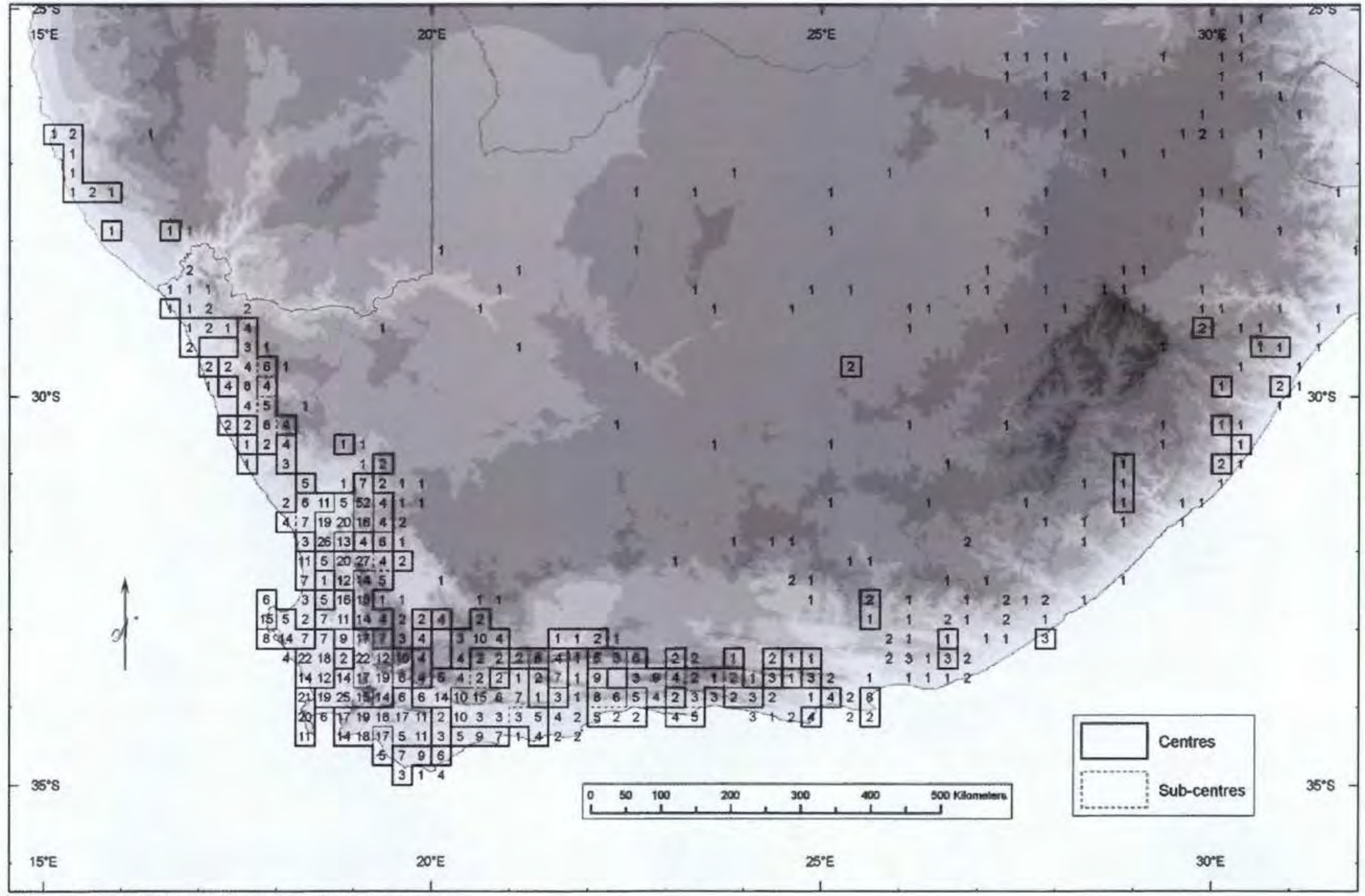


Figure 71: QDS Diversity for the Geophytes Dataset.

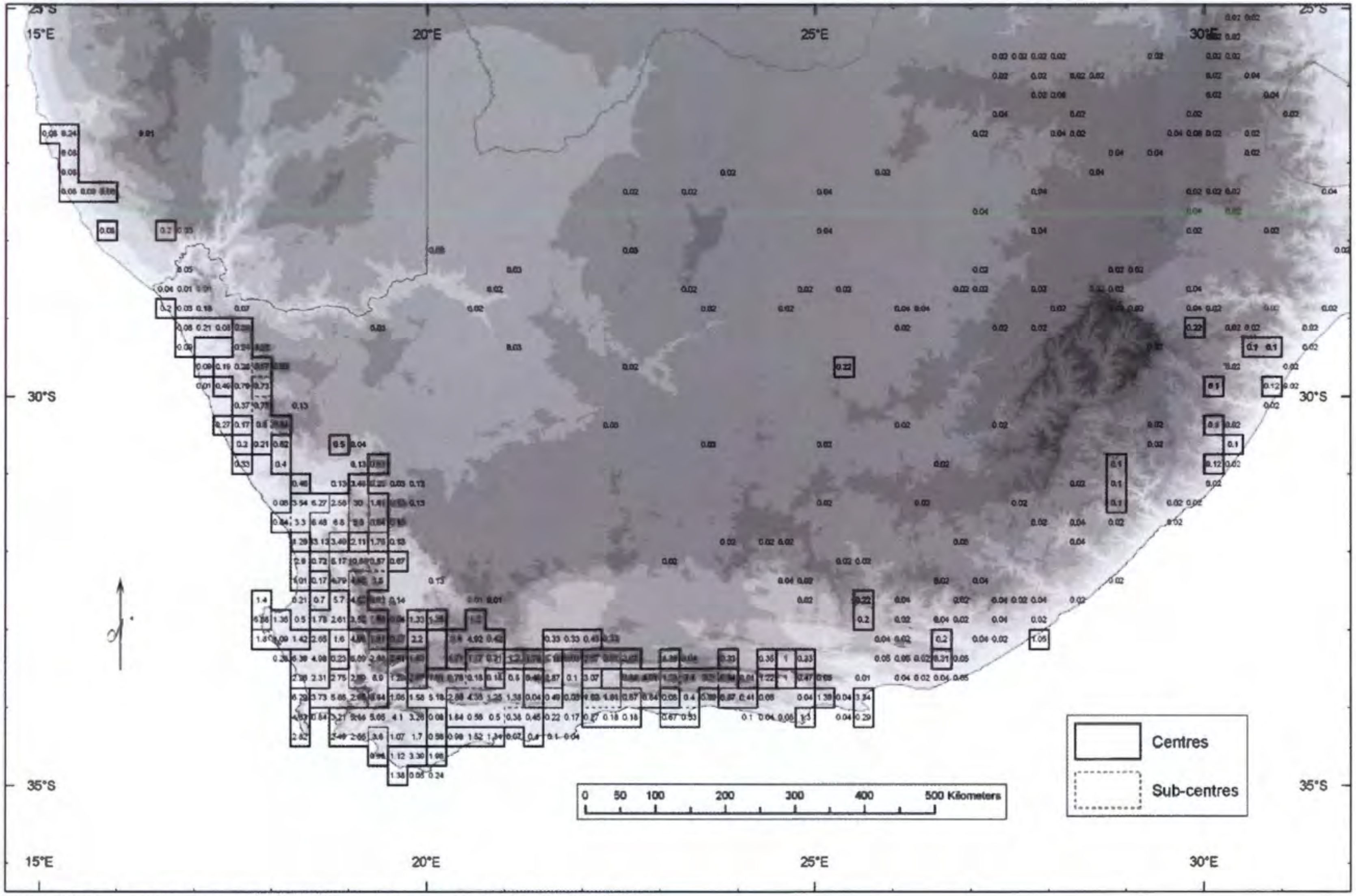


Figure 72: Sum of the Inverse Taxon Ranges for the Geophyte Dataset.

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 21 | N7-Nuwerus-Garies | 3 | 6 | 1 | 1 | 3 | 1.00 | - |
| 22 | Touwsrivier | 1 | 4 | 1 | 1 | 1 | 1.00 | - |
| 23 | Summer Rainfall Area | 5 | 4 | 1 | 1 | 5 | 1.00 | - |
| 24 | Doringbaai | 1 | 3 | 1 | 1 | 1 | 1.00 | - |
| 25 | East London | 1 | 3 | 1 | 1 | 1 | 1.00 | - |
| 26 | South Tankwa | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 27 | Windhoek | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 28 | Springbok-Loeriesfontein | 2 | 2 | 1 | 1 | 2 | 1.00 | - |
| 29 | Southern Groot Karoo | 3 | 2 | 1 | 1 | 3 | 1.00 | - |
| 30 | Natal Midlands | 10 | 2 | 1 | 1 | 10 | 1.00 | - |
| 31 | Groot-Losberg | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 32 | East Baviaanskloofberg | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 33 | Outside | 282 | 43 | 7 | 2 | 80 | 0.14 | -0.72 |

The Saldanha Peninsula Centre (PC 7) is very well developed in the Geophyte Dataset, relative to my other datasets (with the exception of the Combined and RDL Datasets to which it contributes). The hierarchical relationships between Geophyte PCs need to be investigated to determine whether the Saldanha Peninsula Centre has affinities to the SWPP, NWPP, or sSK. The Combined Dataset Analysis seems to suggest Succulent Karoo affinities (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26), which is probably due to the dominance of the Geophyte contribution.

Taxa ignored for the purposes of GIS PC identification included *Ferraria glutinous* (53) and *Haemanthus montane* (27), as they are very widespread and occur mostly in summer rainfall regions.

### 9.1.1 The relationship between endemism, diversity, and area in the Geophyte PCs

In my Geophyte Dataset, a highly significant and strong positive relationship ($r^2 = 0.74$, $p<0.001$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 73a), between the number of endemics and the geographic size of the PC ($r^2 = 0.71$, $p<0.001$) (Figure 73b), and between the number of non-endemics and the geographic size of PCs ($r^2 = 0.77$, $p<0.001$) (Figure 73c). The N Namaqualand Lowlands (PC 16), East London (PC 25) and the Natal Midlands (PC 30) were excluded due to under under-representation in my dataset, resulting in them being outliers.

Endemism is significantly overrepresented in the Nieuwoudtville Escarpment PC (1), both when compared to non-endemic taxa and geographic area of the PC (Figure 73a and b). Endemism is also high in the E KMPP-West SEPP (4) when compared to non-endemic taxa. A number of PCs (3, 5, 7 and 8) contain higher than expected numbers of endemic

(Figure 73b) and non-endemic (Figure 73c) taxa, relative to PC area, while a few PCs (2 and 10) are nearly overrepresented in both endemic and non-endemic taxa. Conversely, a number of PCs (11, 16 and 30) have lower than predicted endemic and non-endemic taxa relative to PC area. These PCs are geographically peripheral to the CFR and under sampled in my dataset, with only two genera represented in them. The Agulhas Plains PCs (12, 14 and 20) have more non-endemic taxa than predicted by PC area (Figure 73c), but expected levels of endemism relative to PC area (Figure 73b), resulting in a decrease in endemism relative to the non-endemic taxa (Figure 73a).

## 9.2 CFR Phytogeographical Centres

### 9.2.1 The South Namaqualand Centre (including the NWPP)

As in my Fabaceae and Rutaceae (Diosmeae) Datasets, the Geophyte NWPP contains the PC with the greatest diversity and number of endemics (Table 41), which represents a deviation from the patterns in most fynbos clades (Levyns, 1938, 1964). Furthermore, the boundaries of the NWPP are substantially different to those of the Combined Dataset and the Fynbos Clades that I analysed. In the Geophyte Dataset, the NWPP is divided into three PCs, one of which crosses the northern boundary of the CFR (PC 1), extending west of Vanrhynsdorp. Another (PC 2) crosses the southern boundary of the traditional NWPP through the Tulbagh-Bree River Valleys (Goldblatt and Manning, 2000; Weimarck, 1941). In both cases where PCs show conflict with traditional floristic boundary demarcations, it would be interesting to analyse these taxa further, both in terms of their phylogenies and ecological preferences, and to determine the hierarchical affinities and relationships of the floristic units.

The North Northwest Mountains Centre (PC 1) is centred on the Nieuwoudtville Escarpment and extends southeast along the Matsikammiesberg-Gifberg Escarpment. It extends further southwest onto the flats around and west of Vanrhynsdorp, extending to the coast, at the mouths of the Olifantsrivier and Verlorevlei. North Northwest Mountains PC extends over the traditional CFR boundary (Goldblatt and Manning, 2000; Weimarck, 1941) and contains elements of fynbos, renosterveld and succulent Karoo floras (Table 42). Similarly, as it contains taxa in both the higher lying escarpment and surrounding flats, it may artificially combine disparate biotic elements into a single floristic unit. Thus, this PC may require further spatial refinement, and/or sub-division. Ultimately, it remains to be determined whether this PC, as a single unit, or together with some of its PSCs are part of the core CFR, or not.

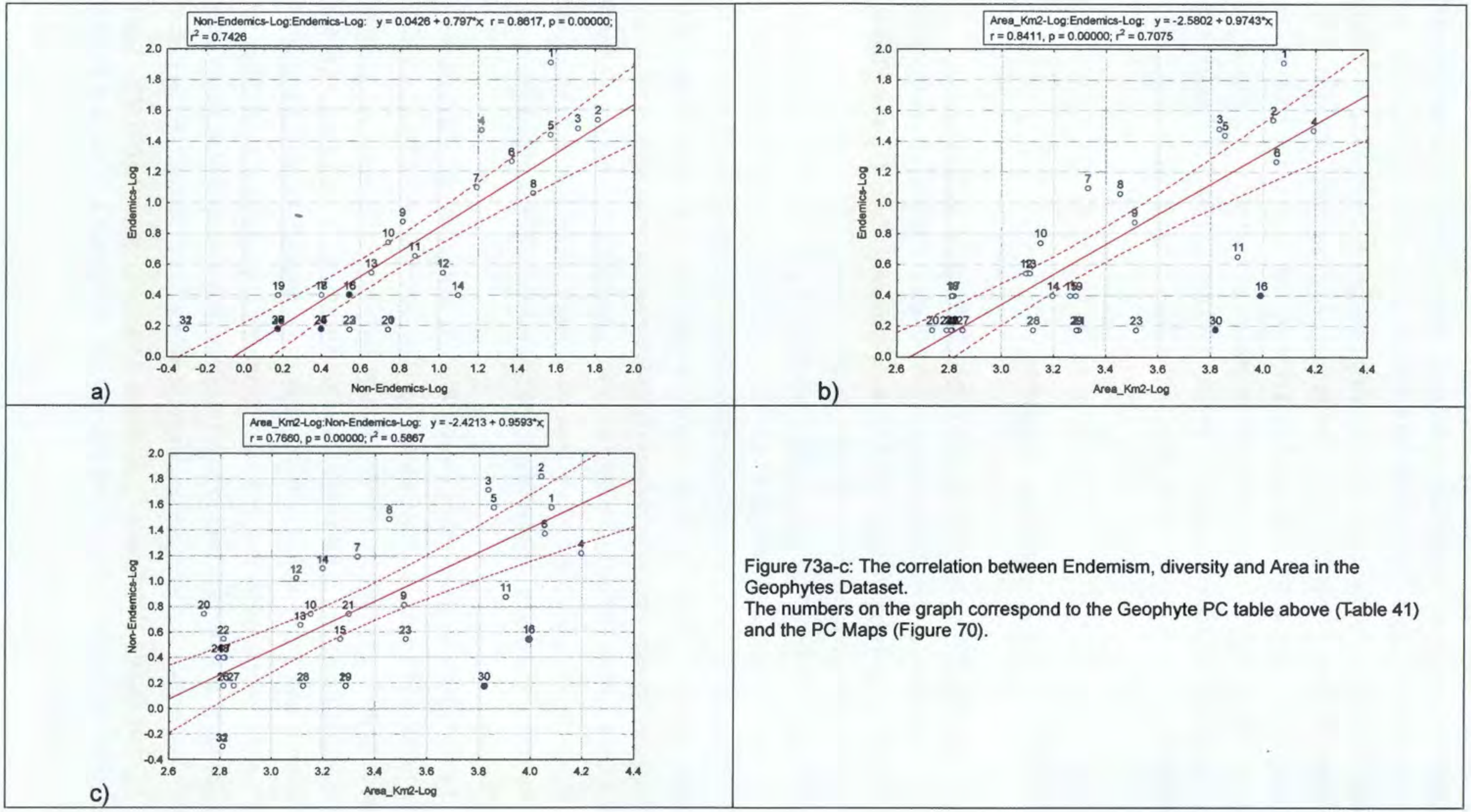


Figure 73a-c: The correlation between Endemism, diversity and Area in the Geophytes Dataset.
The numbers on the graph correspond to the Geophyte PC table above (Table 41) and the PC Maps (Figure 70).

Table 42: Habitat Data for the Geophyte Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliffs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats/Dunes | Other | Unknown |
| 1 | Southern Namaqualand | | | | | 5 | 1 | 1 | | 16 | 1 | 11 | | | | | 1 | | 12 | 2 | | 12 | 5 | 1 | 3 | 13 | | 2 | 5 | | 2 | | | 2 | | |
| 2 | S NWC-N SWC | | | | 2 | 1 | 3 | | | 7 | 1 | 10 | 2 | | | | | | 13 | 1 | 1 | 6 | 6 | | 1 | 8 | 2 | 3 | 7 | | | | | | | |
| 3 | S Southwest Mtns | | | | 3 | 1 | | | | 12 | | 11 | 2 | | | | | | 12 | 1 | 1 | 3 | 3 | | | 9 | 3 | 4 | 6 | | | | | 2 | | |
| 4 | E KMC-West SEC | | 1 | 3 | 2 | 4 | 1 | | | 5 | | 3 | | | 1 | | | | 10 | 1 | 3 | | 5 | 2 | 3 | 5 | | 1 | 4 | | 1 | | | 1 | | |
| 5 | Cedarberg-Kouebokkeveld | | | | | 1 | 1 | 1 | | 15 | | | | | | | | | 11 | 2 | | 2 | | 2 | 2 | 15 | 4 | | | | | | | | | |
| 6 | West LBC-KMC | | | | 5 | | | | | 4 | | 5 | 1 | | | 2 | | | 6 | | | 2 | 1 | | | | | 4 | 2 | 1 | 1 | 1 | | | | |
| 7 | Saldanha Peninsula | | | | 1 | | | | | | | 1 | 6 | 4 | | | | | 2 | 5 | 2 | 1 | | | | 2 | 4 | | | | | | | 1 | | |
| 8 | South Sandveld | | | | 3 | | | | | 2 | | 1 | 3 | | | | | | 1 | | | 5 | | | | 2 | 3 | | | | | | | 1 | | |
| 9 | Klein Roggeveld-Witteberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 10 | St Francious-Port Elizabeth-Grahamstown | | | | | | | | | | | | | | | | | | 3 | | | 2 | | | 1 | | 2 | | | | | 1 | | 1 | | |
| 11 | Kamiesberg-Steinkopf Escarpment | | | | | | | | | | | | | | | | | | | 1 | | | 1 | | | | | | | | | | | | | |
| 12 | W West Agulhas Plains | 1 | | | | | | | | | | | | 2 | | | | | 1 | | | | 1 | | | | | | 1 | | | | | 2 | | |
| 13 | Kwadouwsberg | | | | | | 1 | | | 3 | | | | | | | | | 1 | 2 | | | | | | | | | | | | | | | | |
| 14 | Potberg | 2 | | | | | | | | | | | | | | | | | 1 | | | 2 | | | | | 2 | | | | | | | | | |
| 15 | Vanstadens-NW Baviaansberg | | | | | | | | | 2 | | | | | | | | | 1 | | | | 2 | | | | | 2 | | | | | | | | |
| 16 | N Namaqualand Lowlands | 2 | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | | | | | | | | | |
| 17 | Doring River Valley | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | | | | 1 | | | | | |
| 18 | Karoopoort-East | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 19 | Slypsteenberg-Steylerville-Kleinpoort | 1 | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | |
| 20 | E West Agulhas Plains | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | | | | | | | | | |
| 21 | N7-Nuwerus-Garies | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 22 | Touwsrivier | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 23 | Summer Rainfall Area | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 24 | Doringbaai | | | | | | | | | | | | | | | | | | 1 | | | | | | | | 1 | | | | | | | | | |
| 25 | East London | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 26 | South Tankwa | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 27 | Windhoek | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 28 | Springbok-Loriesfontein | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 29 | Southern Groot Karoo | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 30 | Natal Midlands | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 31 | Groot-Losberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 32 | East Baviaansberg | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| | Totals | 6 | 1 | 3 | 16 | 12 | 7 | 2 | 0 | 66 | 2 | 42 | 14 | 6 | 1 | 2 | 1 | 0 | 76 | 16 | 7 | 38 | 24 | 5 | 10 | 55 | 24 | 16 | 25 | 1 | 5 | 2 | 0 | 10 | 0 | 0 |

Contrary to other datasets analysed here, the richest sub-centre of the NWPP is now situated in the northern most corner, on the Nieuwoudtville Escarpment (PSC 1.1). The Nieuwoudtville Escarpment Sub-Centre (PSC 1.1) is astonishing for its sheer number of endemic Geophyte Taxa, crammed into a small area. It has nearly as many endemics as the second richest full centre (PC 2), 30 endemics versus 34 endemics (Table 41). Furthermore, it is in an area nearly six times smaller, occupying 3 QDSs, versus 17 QDSs of the South NWPP-North SWPP PC (Table 41). The reasons for this remarkable level of Geophytic endemism on the Nieuwoudtville Escarpment are unknown. It is similar in size to the Cape Peninsula, occupying three QDSs, although the Peninsula is a much smaller landmass, not occupying the entire area of the QDSs. Both occupy peripheral geographical positions relative to the CFR. Unlike the Peninsula, the Nieuwoudtville Escarpment is not topographically isolated on all sides - the eastern side adjoins the rest of the Bokkeveld Escarpment. However, the eastern boundary may be precipitation dependant, thus effectively forming an island area. The much wetter Nieuwoudtville Plateau could provide a refuge for mesic relictual taxa. Furthermore, Goldblatt (1992) documented diverse edaphic conditions there. This may also account for speciation in a number of taxa. Goldblatt (1992) observes that three sister species of *Sparaxis* are locally endemic to the Nieuwoudtville Escarpment. *Sparaxis tricolor* and *S. elegans* occur in light clay soils in the Renosterveld, the former to the north, and the latter on the central plateau (Goldblatt, 1992); while *S. pillansii* is found on heavier clay soils which get seasonally water-logged. The three taxa mentioned, form the earliest diverging clade in *Sparaxis*. This suggests two things: (1) sister taxa in *Sparaxis* and possibly in other CFR Clades may evolve due to, or on different edaphic substrates, in relatively close geographical proximity (sympatric speciation), and (2) *Sparaxis,* as de Vos (1979) suggested for *Ferraria,* may have had the origin of their contemporary taxa in the more arid north, and may have invaded the core CFR more recently. This may extend to other members of Iridaceae and even other CFR Clades that have arid adapted elements. It would also be interesting to try and quantify the timing of these events, in both *Sparaxis* and *Ferraria*, to see if they coincide, to determine if this is a general synchronised pattern, or not. Sympatric processes like this may also serve to boost diversity greatly. If there is already allopatric speciation occurring on different mountain ranges, while locally sympatric speciation is occurring due to edaphic heterogeneity, it may result in the evolution of many more taxa. Further, the role of pollinator specificity should also not be ignored in promoting speciation and endemism (van der Niet et al., 2006), as many pollinators have narrow distributions (Colville, 2006).

The Gifberg area also contains high diversity and endemism of geophytes, which is observed to a lesser degree in my other datasets. The north and west Gifberg area (PSC 1.2) contains a QDS disjunct across the Nieuwoudtville Escarpment (PSC 1.1), the

Soutpansberg/Boegoeberge (PSC 1.2), due to two taxa *Haemanthus lanceifolius* (3), and *Pelargonium punctatum* (4). In the Geophyte Dataset, the Gifberg extends north along the escarpment due to *Babiana salterii* (2). However, 3118BD could equally be placed in the Vanrhynsdorp Sub-Centre (PSC 1.3), due to *Eriospermum calcareum* (2). The present classification is preferred, as many of the near endemics display a similar pattern. The Nieuwoudtville Surrounds Sub-Centre (PSC 1.4) is also disjunct across the Nieuwoudtville Escarpment (PSC 1.1), due to *Oxalis rubropunctata* (3). Bordering the Nieuwoudtville Escarpment to the south is the Doring River Valley Centre (PC 17). It is possible that with more collecting, these areas (PSCs 1.2, 1.4, and PC 17) may combine to form a single floristic unit.

The Vanrhynsdorp Sub-Centre (PSC 1.3) is quite well-developed in xerophytic taxa, such as Aizoaceae (Hartmann, 1991; Jurgens, 1991; Jurgens, 1997) and in the Combined Taxa Dataset (PSC 18.1), due to the contributions of the succulent RDL Taxa. Unlike the previous sub-centres discussed, it is situated on low altitude undulating terrain, rather than being associated with the escarpment. It has been noted that (at least *Ferraria*) the Vanrhynsdorp area is a centre of diversity and origin (de Vos, 1979). The Vanrhynsdorp floristic unit it is usually clustered outside the core CFR, as in this study (see my Combined Dataset), and in the literature (Marloth, 1908; Weimarck; Goldblatt and Manning, 2000). However, it still needs to be established whether this is the case for Geophytes.

There are additional, smaller, disjunct floristic units of the South Namaqualand Centre, located along the coast between Elandsbaai and Doringbaai (PSC 1.5 and PC 24 respectively), with an outlier near Groenrivier (PSC 1.5). Although the N West Coast PSC (1.5) is grouped with the South Namaqualand Centre (PC 1), it shows slight affinities to the Saldanha Peninsula (PC 7) due to *Ferraria densepunctulata* (4) and possibly other taxa.

The second major floristic unit in the NWPP straddles the traditional CFR boundary between the NWPP and the SWPP (our Combined Dataset; Goldblatt and Manning, 2000; Weimarck, 1941), and as such is referred to as the South NWPP-North SWPP Centre (PC 2). Aside from the central, most taxon diverse sub-centre, the Berg-Bree Catchment Sub-Centre (PSC 2.1), the remaining sub-centres are all largely in either the NWPP, or the SWPP.

The Berg-Bree Catchment Sub-Centre (PSC 2.1) in its entirety is unique to the Geophyte Dataset. However, the southeast of this sub-centre bears a resemblance to the Worcester-Bonnievale Centre (PC 4) of my Fabaceae Dataset. It is possible that there may be as many as three distinct floras here, with potentially overlapping distributions. These floras include a montane/fynbos flora, restricted to the NWPP, a montane/fynbos flora restricted to the SWPP (Table 42) and a strongly represented lower altitude valley/renosterveld flora (Table 42), possibly occurring in both the lower lying regions of both the SWPP and the NWPP, but hemmed in by the higher altitude montane areas of those centres. Thus, it may be of benefit to analyse the endemic taxa within this sub-centre (PSC 2.1) at a finer geographical and ecological scale, to determine their affinities, and the floristic boundaries in the area.

The Piketberg Sub-Centre (PSC 2.2) consists of QDSs that include the Piketberg Mountains (TMS) and the surrounding Swartland (shale) low altitude areas. In the Geophytes, the Piketberg shows stronger affinities to the Groot Winterhoek Mountains to the southeast, rather than to the Cedarberg. This is in contrast to the results of the Hierarchical Analysis for the Combined Dataset, but this may be due to fewer lower-lying areas being included with the Piketberg floristic unit in the Geophyte Dataset. These undoubtedly have strong affinities to the Olifantsrivier Mountains and Valley, which in turn, may have strong affinities to the Cedarberg.

Interestingly, the Northeast Hexrivier-West Langeberg (PSC 2.4) only contains dicotyledonous endemics (Appendix II). The remaining sub-centres of the South NWPP-North SWPP Centre (PC 2) in the NWPP are fairly small and would most likely be combined with the larger neighbours, with additional data. This is particularly so in the Porterville-Skurweberg Sub-Centre, which straddles the Groot Winterhoek (PSC 2.5). To the east, the Kwadouwsberg Centre (PC 13) combines QDSs that are usually assigned to different phytogeographical provinces in the Combined Datasets, namely the LBPP and KMPP).

The Cedarberg-Kouebokkeveld Centre (PC 5) is the last major floristic unit in the NWPP. It extends from the Pakhuis Mountains in the north, to the Kouebokkeveld Skurweberg in the south. To the west, the PC extends onto the Swartberg and the northern Olifantsrivierberg. The two sub-centres seem to divide PC 5 into northern and southern areas. The Northwest Cedarberg Sub-Centre (PSC 5.1) is situated on the Pakhuis Mountains and Olifantsrivierberg and includes part of the intervening Olifantsrivier Valley. The Kouebokkeveld-Swartberg Sub-Centre is centred on the Kouebokkeveld and extends southeast to the Swartberg (PSC 5.2). The majority of the endemic taxa in the Kouebokkeveld-Swartberg Sub-Centre prefer stony/rocky sloping ground on sandstone (Table 42). Lower altitude elements appear under-represented in this area in my dataset and therefore contribute little to PC/PSC development here. Interestingly, further east, the drier Swartruggens and Swartrugberg/Baviaansberg, which are in the rain shadow of the higher westerly mountains, are not assigned to any centre.

Previous phytogeographical studies of Iridaceae (Goldblatt, 1991) have described the family as following a classic Levyns' (1938) pattern of species distribution. In their Appendix: Statistics for Families of the Cape Flora, Goldblatt and Manning (2000), reported that there are more species and endemics in the SWPP than the NWPP for Iridaceae (Table 43). Despite containing slightly more species, this does not represent a classic "fynbos" CFR pattern at the family level, in which the values for taxon richness and endemism can decrease by as much as 50% from the SWPP to the NWPP in montane TMS CFR Clades, such as in my datasets of Bruniaceae, *Erica,* Proteaceae and Restionaceae. There may be clades within Iridaceae at lower taxonomic levels that show greater similarity to more typical CFR floristic patterns, but my current dataset is not complete enough to analyse this, and it is beyond the scope of the current study.

Table 43: Taxon Diversity and Endemism recorded in Goldblatt and Manning (2000) for the Families of Geophytes analysed in this study in the Northwestern (NWPP) and Southwest (SWPP) Phytogeographical Provinces.

| Family | NWPP | SWPP |
|---|---|---|
| Amaryllidaceae | 48 (14) | 39 (10) |
| Convallariaceae (Eriospemaceae) | 30 (7) | 18 (1) |
| Geraniaceae | 98 (17) | 88 (13) |
| Hyacinthaceae | 126 (22) | 93 (17) |
| Iridaceae | 356 (123) | 379 (132) |
| Oxalidaceae | 78 (35) | 56 (37) |
| Totals | 805 (225) | 733 (217) |

The remaining families of Geophytes in this study nearly all have greater numbers of taxa and endemics in the NWPP, rather than the SWPP (Table 43). This was recorded by Goldblatt and Manning (2000), and they seem to display even less of a "Cape Clade" floristic pattern than Iridaceae. The only minor exception is Oxalidaceae (Table 43), which has two more endemics in the SWPP than the NWPP.

It is difficult to make direct comparisons to the taxonomic frequencies presented by Goldblatt and Manning (2000), due to the differences in the positions of their floristic boundaries. The positions of the boundaries of the PCs presented here, as well as the relationships between the different floristic units have been influenced by the strong contributions made by the Geophytic RDL Taxa, and to a lesser degree, by the relative absence of taxa of larger distributional ranges. However, from the floristic patterns I have identified for my Geophyte Dataset, it appears that the traditional floristic boundaries of the CFR, based largely on montane fynbos TMS Taxa, may not be appropriate for Geophytes, nor potentially for other plant groups that are not found exclusively in montane, TMS derived, nutrient poor habitats. This should receive further attention.

### 9.2.2 The Southwest Phytogeographical Province

The PCs of the Geophytes Dataset in the SWPP differ from the Combined Dataset and montane TMS Clades in a number of ways. The most noticeable is the association of the Hottentots Holland and Kogelberg Mountains with the northern QDSs of the West Agulhas Plains Dataset (Figure 70). These are in the different PCs of my Combined Dataset (Figure 18), and occasionally even in different phytogeographical provinces (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26) of my hierarchical analysis of my Combined Dataset. Furthermore, instead of the PCs being centred on higher altitude areas, taxa are endemic to lower-lying areas and associated vegetation types (Table 42). This is evident in the South Southwest Mountains Centre (PC 3), where the PCs are not centred on either the RZE, or Kleinrivier Mountains, but on the lowlands between them (Figure 70, Table 42). The mountain watersheds effectively define the northern and southern boundaries of this PC. This is in marked contrast to the more montane TMS Cape Clades, but is similar to the floristic patterns of Fabaceae in this area.

The RZE and Kleinrivier Mountains share certain taxa, although none of these taxa were found to contribute to the endemism of the Hottentots Holland and Kogelberg Mountains Sub-Centre (PSC 3.1). Analysis of the habitat preferences of endemic taxa indicate that about two fifths of the taxa are shale/clay endemics (Table 42), probably located at low altitude. The recorded altitude of the endemic taxa is fairly low, mostly below 500 metres (Table 42). It is these low altitude endemics that may link the endemic TMS Taxa in the RZE and Hottentots-Kleinrivier regions together. Thus, although the Hottentots Holland-Kogelberg Mountains and the RZE each have their own endemics, they are probably grouped together, because of the overlap of TMS and non-TMS endemic taxa in QDS, that occur between these two montane TMS regions, rather than the higher altitude taxa on the TMS Substrates. This floristic pattern in the Geophyte Dataset represents a departure from traditional CFR elements, which prefer TMS Substrates more exclusively. They may also reflect the abundance and diversification of Geophytes on the heavier clay soils of the Malmesbury Shale series, or on the geologically recent quaternary littoral deposits (Table 42). Similar patterns were also observed in the Fabaceae Dataset (Figure 66, Table 39).

The Peninsula (PSC 3.2) is reasonably prominent in my Geophyte Dataset, as it is in many of my datasets, once again highlighting its unique biogeographical history. The close relationship between the Peninsula Mountains and those of the remaining SWPP are clearly illustrated in many of my datasets (Orchidaceae, Poaceae, Polygalaceae, Restionaceae and Rutaceae). The hierarchical analysis of the Combined Dataset further confirms the close affinity between the Peninsula Mountains to the remaining SWPP Mountains. The Peninsula (PSC 3.2) also has affinities to the Stellenbosch Mountains (PSC 3.1). However, the level of affinity depends on the geographic scale and hierarchical relationships used in the analyses. Apart from montane TMS elements, the Peninsula also has numerous lower altitude taxa. It is likely that these taxa have significant affinity to the surrounding low altitude PCs, containing shale and littoral endemic elements (PC 8, and part of PSC 2.3). Both on the Peninsula and near Stellenbosch, there is substantial integration of higher altitude montane and lower altitude flats, hills or valleys, which undoubtedly result in antagonistic and conflicting classifications of their respective QDSs.

For most groups analysed in my study the Berg-Bree River Axis provides a clear boundary between the NWPP and SWPP. However, this is not the case in the Geophyte

Dataset, where the Berg-Bree Catchment Centre (PSC 2.1) is bisected by the Berg-Bree River Axis. The Fabaceae Dataset displays similar patterns. However, the vast majority of endemic Geophyte Taxa in this sub-centre (11 of 15) have a distributional range of a single QDS. Of the remaining endemics, *Lachenalia polyphylla* (2) and *Moraea nubigena* (2) occupy the extreme northern and southern areas of the sub-centre respectively. *Ixia mostertii* (2) is central in the sub-centre. However, it is only recorded from the northern side of the Berg-Bree River Axis (Goldblatt and Manning, 2000). The only PC endemic that crosses the Berg-Bree River Axis is *Gladiolus exilis* (3) (Goldblatt and Manning, 2000; Goldblatt and Manning, 1998). Thus, at a finer geographical scale, the traditional NWPP-SWPP boundary is almost exclusively preserved, although whether this is floristically meaningful or not requires further research, as this low altitude area appears to constitute a distinct floristic unit.

The Southeast Sandveld Sub-Centre (PSC 2.3) and the South Sandveld Centre (PC 8) occupy most of the Sandveld (Mucina and Rutherford, 2006; Acocks, 1988). The Southeast Sandveld Sub-Centre (PSC 2.3) is the only sub-centre of the South NWPP-North SWPP Centre (PC 2) that occurs exclusively in the SWPP.The South Sandveld Centre (PC 8) is very well developed, with a high number of endemics (Table 41), relative to its size. The Geophyte Dataset has some of the highest numbers of endemic taxa recorded in a PC in this lowland region.

The remaining centre of the SWPP, the Saldanha-West Coast-Sandveld Centre (PC 7), is also well developed in the Geophyte Dataset, having relatively high numbers of endemics (Table 41). The hierarchical analysis of the Combined Dataset seemed to indicate stronger ties to the Southern Succulent Karoo, rather than affinities to the SWPP. It may be interesting to investigate the hierarchical relationships further on a more complete Geophyte Dataset.

### 9.2.3 The Agulhas Plains Phytogeographical Province

For Geophytes, my results indicate a much-reduced Agulhas Plains Flora, consisting of a few geographically reduced PCs. These include the Western West Agulhas Plains (PC 12), the Eastern West Agulhas Plains (PC 20) and the Potberg (PC 14). It appears that the three larger PCs to the north: the South Southwest Mountains (PC 3), the Western LBPP-KMPP (PC 6) and the Eastern KMPP-Western SEPP (PC 4), have extended their ranges south, and incorporated part of the Agulhas Plains, particularly in the west. This southward extension of inland PCs is not as significant on the eastern Agulhas Plains. In most of my datasets where the East Agulhas Plains forms a PC, it rarely extends beyond a single QDS inland from the coast. Although it is well known for containing many limestone endemics, which have been noted in my other datasets, only two geophyte limestone endemics (Table

42) were noted in the APPP. However, more limestone endemics were identified in the Saldanha-West Coast-Sandveld Centre (PC 7). In the Geophyte Dataset, the Potberg Centre (PC 14) contains two sandstone endemic taxa. I found that generally, datasets with poorly defined APPP floras are poorly developed in the Potberg, the Geophyte Dataset appears to be an exception.

### 9.2.4 The Langeberg Phytogeographical Province

The Geophyte Dataset boundaries of the LBPP are atypical when compared to the Combined Datasets and those of montane TMS CFR Clades. Within the Geophyte Dataset, PC development is concentrated in the Western portion of the LBPP. The PC extends northwards into the western KMPP, over the Waboomsberg, incorporating the QDS with the Anysberg and eastern Witteberg, traditionally placed in the KMPP. It also stretches westward onto the flats to the northeast of the RZE, similar to the Combined Dataset. The LBPP is more restricted in the east, not extending beyond Garcia's Pass in the Mountains, and not quite reaching the Gouritz River in the flats. The West LBPP-KMPP PC (PC 6) also extends south of the Langeberg Mountains, to include almost the entire adjacent LBPP Plains, and extend to the coast near Stilbaai in 3421AD and possibly along the Goukou River, which may illustrate the importance of rivers as floristic corridors, (as with the Gouritz River, in the Swartberg-Rooiberg Sub-Centre (PSC 4.1), in the KMPP).

The Central Langeberg Sub-Centre (PSC 6.1) is conventional and is centred on the Central Langeberg and the plains immediately to the south. The West Langeberg-Waboomsberg Sub-Centre (PSC 6.2) is more unusual and combines floristic areas from four different Phytogeographical areas (Goldblatt and Manning, 2000; Weimarck, 1941). It may also possibly include the valley in the Langeberg between Ashton and Montagu, as many endemic taxa are restricted to lower altitudes. This is potentially a very interesting low altitude corridor of gene flow and could be investigated further for confirmation.

### 9.2.5 The Karoo Mountain-Southeast Phytogeographical Province

PC formation in the KMPP is fairly good, although as with the Western LBPP-KMPP (PC 6), it is not exclusive to the KMPP, and the East KMPP-West SEPP Centre (PC 4) extends into the SEPP. The eastern KMPP and western SEPP merge into a nearly continuous PC, although for the most part, the boundaries of the sub-centres largely coincide with the traditional floristic boundaries of the KMPP-SEPP. It is probable that the floristic units demarcated here may contain both KMPP and SEPP biotic elements and that the QDS scale of resolution is too coarse to differentiate between the two. Mountains seem to be a fairly dominant feature of the PCs in this region, although to a lesser extent than was observed in the Fabaceae Dataset.

Cluster analysis produced a much more disjunct and fragmented pattern in the eastern KMPP and western SEPP than depicted here (Figure 70), but subsequent GIS analyses consolidated many of these smaller units. The original units have been retained as sub-centres. Taxa that group these usually separate areas of the KMPP and SEPP together are *Freesia verrucosa* (5) and *Lachenalia haarlemensis* (5), mostly in the northern parts; while *Borbartia aphylla* (9) groups together most of the QDSs in the traditional western SEPP. *Freesia speciosa* (7) is a western Little Karoo endemic, though it was not recovered as a PC endemic here, as it occurs in the Central Langeberg, Klein Swartberg and Rooiberg. A more comprehensive dataset may help resolve some of the phytogeographical conflict in this area.

Part of the East KMPP-West SEPP Centre (PC 4) extends into the LBPP, due to *Geissorhiza uliginosa* (3) and possibly along the Gamkarivier-Gouritsrivier Valley, as its preferred habitat includes waterfalls and wet cliffs (Goldblatt and Manning, 2000). To the north of the western KMPP is the Klein Roggeveld-Witteberg Centre (PC 9), which contains a fairly high number of endemics. On the northern boundary of the KMPP there are also a number of smaller PCs (PC 15, 19 and 29), usually with only a single endemic.

A hierarchical analysis of the affinities of all these floristic units, as well as the sub-centres in the KMPP and western SEPP would be informative. It would help determine where their affinities lie. This would be most profitable on a more comprehensive dataset.

The orientations of many of the sub-centres in the KMPP-SEPP generally follow the east-west lying mountain ranges in this region. The dominant floristic unit in the central region of the KMPP is the Outeniqua-Kammanassie Sub-Centre (PSC 4.1). In the east, there is considerable overlap of PCs in the KMPP and the SEPP. This is primarily due to *Ornithogalum rogersii* (3), which occupies the most peripheral QDSs in nearly all the Outeniqua-Kammanassie Sub-Centre (PSC 4.1) fragments; and *Gladiolus fourcadei* (2), which joins the Kammanassie to Knysna. In the Combined Dataset and in most other contemporary phytogeographical studies (see Goldblatt and Manning, 2000), the Kammanassie is placed in the KMPP, although Weimarck (1941) included it in his "Knysna Interval", which is similar to the results found in my Geophytes Dataset. Further investigation is required to determine whether the Kammanassie Mountains belong in the KMPP, or the SEPP, in the Geophyte Dataset.

Unlike in many other datasets, the Swartberg is poorly developed as a consolidated floristic unit. Both the Klein and Groot Swartberg contain relatively small fragmented floristic units, defined by relatively few endemics, aside from the Klein Swartberg-Rooiberg-Gamkaberg Sub-Centre (PSC 4.2).

The Kouga-Meiringspoort Sub-Centre (PSC 4.3) is another unusual and disjunct sub-centre. The western and Central QDSs are combined due to *Eriospermum aequilibrae* (2), and the central and eastern QDSs are affiliated due to *Oxalis fourcadei* (2). The remaining endemics all occur in the Meiringspoort QDS (3322BC) in the northwest.

The Tsitsikamma-Outeniqua Sub-Centre (PSC 4.4) is another fragmented sub-centre, although this likely reflects incomplete locality data for *Gladiolus sempervirens* (3).

The eastern remainder of the SEPP is very fragmented and disjunct, a common feature in this area for many of the clade/guild datasets of my study. It most likely reflects under collection, or possibly the transition into a different floristic region. The best-developed floristic unit is the St Francis-Port Elizabeth-Grahamstown Centre (PC 10). Most of the endemic taxa of this PC occupy a single QDS, except for *Bobartia macrocarpa* (4), the taxon that links them all together into a consolidated PC. The Vanstadens-NW-Baviaanskloofberg Centre (PC 15) is formed due to *Eriospermum ciliatum* (3), while *Cyrtanthus staadensis* (1) is endemic to the south-eastern tip.

## 9.3 Non-CFR Phytogeographical Centres

### 9.3.1 Namaqualand/Succulent Karoo Region

The Kamiesberg-Steinkopf Escarpment (PC 11) forms the largest floristic unit situated entirely in Namaqualand. However, it is a very much more impoverished relative to the other PCs, due to the geographical bias of the dataset (see Methods 2.1.1.2). The sub-centre division of the Kamiesberg-Steinkopf Escarpment (PC 11) (based on the distribution of *Haemanthus unifoliatus* (6)) along the escarpment could have been made on the distribution of *Haemanthus amarylloides polyanthus* (6), which occupies most of the more southerly QDSs of the PC. However, the area defined by the species level taxon was retained over the sub-species level taxon. These may co-occur, in which case the sub-centre could be extended southwards along the escarpment.

There is a minor PC along the N7, between Garies and Vanrhynsdorp (PC 21). This area is very accessible to collectors being situated along the main arterial road through Namaqualand. There is also evidence of a lower altitude PC on the northwest coastal plains of Namaqualand (PC 16). The disjunction over the Orange River is most likely due to strict access restrictions in the Diamond Mining Areas and thus a reflection of poor collecting, and may not be a true biological pattern.

### 9.3.2 Summer Rainfall Phytogeographical Centres

A few centres in the summer rainfall region are displayed (PCs 23, 25 and 30). My dataset was very limited in this area. The PCs that I retrieved in this region all contain only a single endemic and will not be discussed in detail here. They have been recorded for consistency and possibly as a starting point for further PC investigation in this region. However, there appear to be many Geophyte PCs and hotspots outside the CFR, and readers are encouraged to consult the works of Goldblatt and Manning (1998) on the genus *Gladiolus*.

## 9.4 Summary of the Geophyte Dataset

The Geophytes comprise a phylogenetically heterogeneous dataset and are grouped together on account of their life forms. Although, initially somewhat neglected as a significant contributor to floristic patterns in the CFR, the importance of this life form is becoming increasingly recognised (Manning, Goldblatt, and Snijman, 2002; Proches et al., 2005; Proches et al., 2006). The geographic distributions of diversity and endemism, and the phytogeographical boundaries of PCs are very atypical in Geophytes, compared to other CFR Taxa. This is possibly because of the greater abundance of low altitude elements on non-TMS Substrates and the coarse spatial resolution of my dataset. This makes naming of the Geophyte PCs problematic, as they do not coincide with recognised floristic units. Names provided here are provisional, and require refinement to lowland features defining centres, rather than the montane features used in the naming of montane fynbos floristic units. In addition, this floristic spatial incongruence also resulted in complex and cumbersome descriptions of floristic unit geographic distributions.

Even though there was substantial low altitude floristic development in many PCs, low altitude PC development in the APPP is poor. Goldblatt and Manning (2000) only record six endemics for *Oxalis* in the APPP. Many taxa appear under-collected in the eastern CFR, having disjunct distributions, resulting in disjunct floristic units. Patterns and levels of PC endemism are unusual in the different phytogeographical provinces, and are approximately as follows (highest to lowest): combined south Namaqualand-NWPP, NWPP combined with the SWPP, east KMPP-west SEPP and the LBPP. Levels of endemism within PCs on the Saldanha Peninsula are extremely high compared to the other datasets analysed in this study.

# Chapter 10: Orchidaceae (Table 44, Figure 74 and Figure 75)

## 10.1 Introduction

The Orchidaceae Dataset analysed here represents both the complete BOL orchid flora of Southern Africa (incorporated in the publication of Linder and Kurzweil (1999)) and the RDL Dataset for orchids. To emphasise the phytogeographical affinities of the different sub-familial Orchid clades, endemics are numbered (Table 44) and listed (Appendix II) according to their tribes. Unlike some taxa that have diversified extensively in the CFR and have few representatives elsewhere in Africa (for example, Restionaceae, *Erica,* Diosmeae and Proteaceae), Orchidaceae is relatively well-represented both within and outside the CFR. It may be for this reason that Orchidaceae were until fairly recently (Linder, 1983) mostly neglected from discussions on CFR phytogeography (Levyns, 1938, 1962, 1964; Oliver et al., 1983). Linder (1983) demonstrated that there were strong affinities between the sub-tribe Disinae in the CFR and the temperate regions of southern Africa, but that Disinae exhibited typical Cape Clade patterns (Levyns, 1964), with decreasing diversity and endemism north of the CFR (Linder, 1983). It is largely at these sub-familial taxonomic levels that high levels of endemism and interesting phytogeographical patterns start emerging (Linder, 1983; Linder et al., 2005). In my study, Orchidaceae divides the CFR into three prominent floristic centres (PC 2, 4 and 6) (Figure 74 and Figure 75).

Sub-Family Orchioideae contributes the greatest number of endemic Orchidaceae Taxa, with 103 of the 113 PC endemic taxa for the entire dataset. The strong temperate nature of endemic Orchid Taxa is strongly emphasised in this study, particularly taxa from the Tribe Diseae. The Natal Coast Centre (PC 6) is the only well-supported centre (i.e. a centre with more than one endemic taxon) where the number of endemic taxa from other sub-families exceeds those from Orchioideae, but only by one (Table 44). Within Sub-Family Orchioideae, Tribe Diseae contributes the largest number of endemics, with 83, while Tribe Orchideae only contributes 28. Taxa from Diseae contribute the largest number of endemics to the centres in the central and southern areas (which are largely cooler and less tropical), while Orchideae contribute more endemics in the northern centres, which include the Barberton-Wolkberg-Soutpansberg (PC 3), the Natal Coast (PC 6), the Western Transvaal (PC 7), Ngome (PC 9) and the Mbazwana Area (PC 16) Centres.

Temperate and taxonomic patterns of endemic orchids are particularly apparent in my study, with the Eastern Escarpment (PC 1) and Southwest (PC 2) Centres containing the greatest numbers of endemics, followed by three other centres with montane characteristics, although less mesic cool/temperate habitats. The Natal Coast Centre (PC 6) contains the highest numbers of endemics of the more tropical PCs, and is ranked sixth richest in endemism. While endemism in most fynbos Cape Clades is largely restricted to mesic, montane environments in the winter rainfall area, Orchidaceae is also well represented in summer rainfall montane environment, that are cool and temperate, as well as in sub-tropical and tropical environments. Orchid PC development on mountains is even more pronounced in the more arid areas of the CFR (Figure 75, Centre 5, 12, and 13), where QDS with large areas of lower altitude xeric habitats are excluded from PCs.

A large portion of the endemic taxa found in the temperate phytogeographical provinces belong to the large genus *Disa*. This genus contains about 162 species and is largely restricted to Africa, south of the Sahara (Linder and Kurzweil, 1999). *Disa* taxa also occur on Madagascar and Reunion islands, while one species reaches the Arabian Peninsula (Linder and Kurzweil, 1999). Southern Africa contains 131 species, while 92 are represented in the CFR, of which 78 are endemic to the CFR (Goldblatt and Manning, 2000). At the sub-generic level within *Disa*, particularly the section level, most taxa show more localised geographical patterns, although there are a few sections, which are more widespread. Sections largely restricted to the CFR and/or winter rainfall region include: *Disella*, *Monadenia*, *Amphigena*, *Coryphaea* and *Phlebidia*. Section *Disa* is well-represented in the CFR, while *Herschilianthe* prefers temperate environments in both the winter and summer rainfall regions. Section *Stenocarpa* is also found in both rainfall regions, while *Repandra* and *Hircicornes* are mostly summer rainfall taxa. Taxa that are more tropical include *Micranthae* and *Aconitoideae*.

Readily apparent within this study is the relatively disjunct and widespread nature of Orchidaceae PCs, when compared to the other datasets I analysed. This may be due to the specific moist microhabitat requirements of Orchids, which may be isolated, but scattered over a large area. Evidence for this is reflected in the adaptive reproductive strategy of Orchids, whereby large quantities (in excess of 8000 seeds per plant) of easily dispersed seeds are produced (Linder, 1983). This contrasts markedly with many other CFR Taxa, which make use of serotiny, or myrmechochory, with dispersal distances of mere metres (Linder, 1985b; Slingsby and Bond, 1985). Despite this, patterns of endemism within the Orchids still emerge. Thus, unlike many Cape Taxa, seed dispersal, or the lack there of, may not be a primary driver of speciation, or endemism within Orchids. However, orchids are pollinator specific, with highly complex pollinator symbiotic relationships (Johnson and Steiner, 2003; Johnson, Linder and Steiner, 1998).

Table 44: Taxonomic properties of the Centres identified for the group Orchidaceae (Figure 74 and Figure 75).

| Labels | Centre | Area | Diversity | Taxa | Endemics | | | | r | con | CON |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sub-Centre | | | >=0.5 | Tot | Diseae | Orchideae | Other | | | |
| 1 | Eastern Escarpment | 63 | 166 | 66 | 30 | 23 | 7 | - | 180 | 0.10 | 0.06 |
| 1.1 | Drakensberg Core | 12 | 88 | 23 | 7 | 7 | - | - | 19 | 0.23 | 0.10 |
| 1.2 | Kokstad | 3 | 59 | 3 | 1 | 1 | - | - | 3 | 1.00 | - |
| 1.3 | Amatola | 3 | 72 | 2 | 1 | 1 | - | - | 3 | 1.00 | - |
| 1.4 | Remainder | 45 | 139 | 12 | 0 | - | - | - | 0 | - | 1.00 |
| 2 | Southwestern Centre | 19 | 151 | 58 | 22 | 21 | - | 1 | 75 | 0.18 | 0.14 |
| 2.1 | SW Mountains | 10 | 150 | 45 | 13 | 13 | - | - | 34 | 0.26 | 0.20 |
| 2.2 | Remainder | 9 | 73 | 6 | 0 | - | - | - | 0 | - | 1.00 |
| 3 | Barberton-Wolkberg-Soutpansberg | 22 | 106 | 21 | 15 | 6 | 7 | 2 | 39 | 0.12 | 0.06 |
| 3.1 | Barberton-Mbabane | 5 | 69 | 7 | 5 | 1 | 3 | 1 | 9 | 0.36 | 0.20 |
| 3.2 | Pilgrim's Rest-Sabie | 5 | 44 | 5 | 5 | 2 | 3 | - | 10 | 0.40 | 0.25 |
| 3.3 | Haenertsburg | 5 | 46 | 3 | 2 | 1 | 1 | - | 6 | 0.60 | 0.20 |
| 3.4 | East Soutpansberg | 1 | 8 | 1 | 1 | - | - | 1 | 1 | 1.00 | - |
| 3.5 | Remainder | 6 | 23 | 1 | 0 | - | - | - | 0 | - | 1.00 |
| 4 | Langeberg-Southeastern Centre | 33 | 153 | 37 | 13 | 13 | - | - | 58 | 0.14 | 0.06 |
| 4.1 | Central and Eastern Langeberg | 13 | 93 | 9 | 6 | 6 | - | - | 18 | 0.23 | 0.08 |
| 4.2 | Eastern SEPP | 5 | 79 | 2 | 2 | 2 | - | - | 7 | 0.70 | 0.40 |
| 4.3 | Eastern Outeniqua-Western Tsitsikamma | 3 | 67 | 1 | 1 | 1 | - | - | 3 | 1.00 | - |
| 4.4 | Western Outeniqua | 1 | 21 | 1 | 1 | 1 | - | - | 1 | 1.00 | - |
| 4.5 | Remainder | 11 | 98 | 2 | 0 | - | - | - | 0 | - | 1.00 |
| 5 | Northwestern Centre | 29 | 125 | 26 | 12 | 12 | - | - | 52 | 0.15 | 0.07 |
| 5.1 | Pakhuis-Olifants | 7 | 53 | 4 | 3 | 3 | - | - | 11 | 0.52 | 0.29 |
| 5.2 | Groot Winterhoek-Hexrivier | 7 | 102 | 3 | 2 | 2 | - | - | 8 | 0.57 | 0.14 |
| 5.3 | Nieuwoudtville | 2 | 19 | 1 | 1 | 1 | - | - | 2 | 1.00 | - |
| 5.4 | Remainder | 11 | 87 | 2 | 0 | - | - | - | 0 | - | 1.00 |
| 6 | Natal Coast | 21 | 89 | 12 | 10 | 1 | 5 | 4 | 24 | 0.11 | 0.02 |
| 6.1 | East Coast Core | 7 | 49 | 5 | 4 | - | 1 | 3 | 10 | 0.36 | 0.14 |
| 6.2 | Mtunzini-Ngoya | 3 | 8 | 2 | 2 | - | 1 | 1 | 4 | 0.67 | 0.33 |
| 6.3 | Valley of a Thousand Hills | 3 | 29 | 2 | 1 | - | 1 | - | 3 | 1.00 | - |
| 6.4 | Libode-Ngqueleni | 1 | 8 | 1 | 1 | - | 1 | - | 1 | 1.00 | - |
| 6.5 | Tongaat | 1 | 4 | 1 | 1 | - | 1 | - | 1 | 1.00 | - |
| 6.6 | Remainder | 3 | 21 | 1 | 0 | - | - | - | 0 | - | 1.00 |
| 7 | Western Transvaal | 7 | 30 | 3 | 2 | - | 2 | - | 8 | 0.57 | 0.14 |
| 8 | Kouga | 2 | 36 | 1 | 1 | 1 | - | - | 2 | 1.00 | - |
| 9 | Ngome | 2 | 25 | 1 | 1 | 1 | - | - | 2 | 1.00 | - |
| 10 | Piketberg | 1 | 11 | 1 | 1 | - | 1 | - | 1 | 1.00 | - |
| 11 | NE Wolkberg | 1 | 9 | 1 | 1 | 1 | - | - | 1 | 1.00 | - |
| 12 | Kamiesberg | 1 | 6 | 1 | 1 | - | - | 1 | 1 | 1.00 | - |
| 13 | Northern Namaqualand | 10 | 6 | 1 | 1 | 1 | - | - | 10 | 1.00 | - |
| 14 | NE Barberton | 1 | 4 | 1 | 1 | - | 1 | - | 1 | 1.00 | - |
| 15 | SE Barberton | 1 | 1 | 1 | 1 | - | 1 | - | 1 | 1.00 | - |
| 16 | Mbazwana Area | 1 | 1 | 1 | 1 | - | - | 1 | 1 | 1.00 | - |
| 17 | Outside | 337 | 290 | 34 | 0 | - | 0 | - | 0 | - | 1.00 |

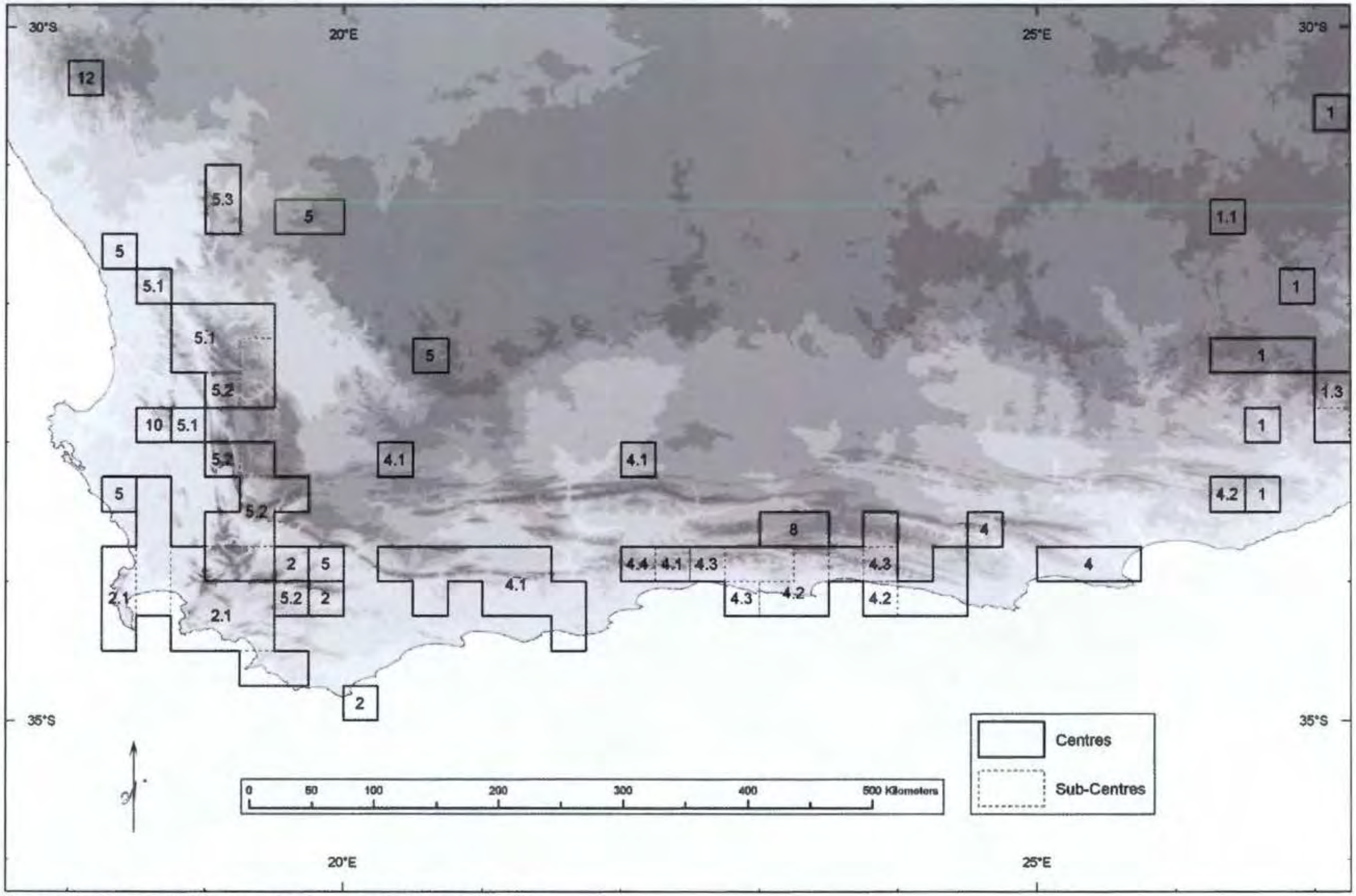


Figure 74: PC and PSC for the Orchidaceae Dataset in the CFR.

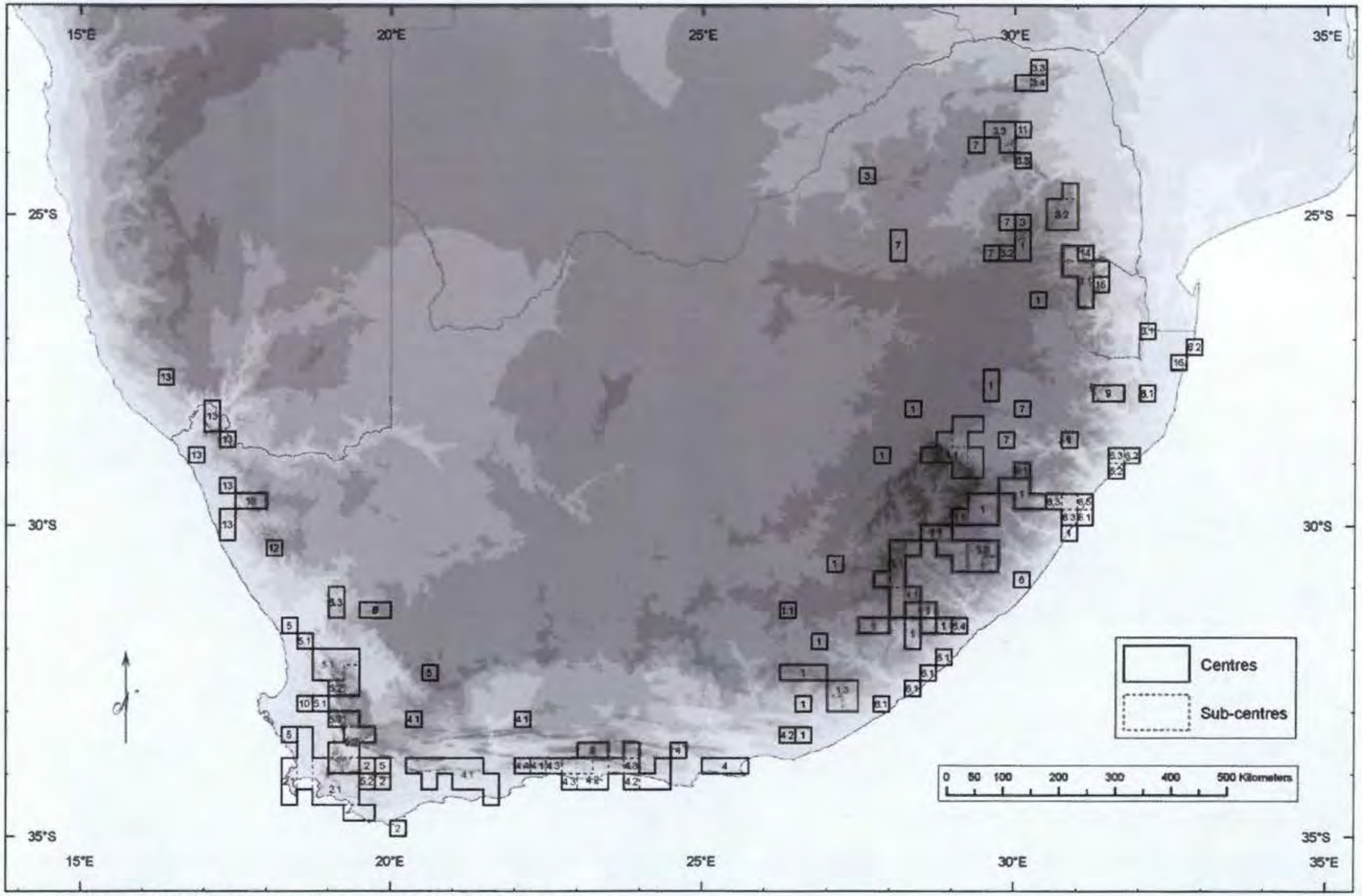


Figure 75: PC and PSC for the Orchidaceae Dataset in Southern Africa.

As with many other datasets, there appears to be a fair amount of collector bias, with areas near roads and major cities, or academic/botanical institutions being very well sampled. The Cape Peninsula and Durban have been particularly well collected (Figure 76). Furthermore, preference for localised, unusual microhabitats makes collecting very difficult and may account for many of the gaps between my PCs (Figure 74, Figure 75 and Figure 76).

A number of fairly widespread tropical African species of Orchidaceae have managed to cross the arid Limpopo Interval (Weimarck) and have established with varying success in South Africa. Some appear to be fairly restricted, to scattered, disjunct, high altitude sites in the northeast of South Africa. Others are more widespread and extend further south, into the Drakensberg, while others extend even further south along the humid east coast of South Africa. This pattern has also been noted for tropical invertebrates (Poynton, 1961). A more extreme example is *Holothrix macowaniana*. Although restricted to forests in the Eastern Cape, it is also found in the Zimbabwean highlands.

### 10.1.1 The relationship between endemism, diversity, and area in the Orchidaceae PCs

In my Orchidaceae Dataset, a highly significant and strong positive relationship ($r^2 = 0.63$, $p<0.001$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 78a). A highly significant and strong positive relationship also occurs between the number of endemics and the geographic size of the PC ($r^2 = 0.79$, $p<0.001$) (Figure 78b), and between the number of non-endemics and the geographic size of the PC ($r^2 = 0.64$, $p<0.001$) (Figure 78c).

In the Orchidaceae Dataset, the Eastern Escarpment (PC 1) contains the highest number of endemic taxa, due to its very large geographic area of 63 QDSs (Figure 78b). It has higher than expected endemism relative to its non-endemic taxa (Figure 78a), but not when compared to its geographic area (Figure 78b).

By contrast, the Southwestern Centre (PC 2) has high levels of endemism and especially diversity. Numbers of endemic taxa exceed those predicted by non-endemic taxa. Furthermore, levels of endemic (Figure 78b) and non-endemic taxa (Figure 78c) are higher than predicted by PC area. Endemism is low in the Western Transvaal (PC 7; Figure 78a and b). The Kouga PC (8) and the Ngome PC (9) have relatively high numbers of non-endemic taxa, relative to PC area (Figure 78b), and endemism (Figure 78a).

The Northern Namaqualand Centre (13) contains fewer than expected endemic (Figure 78b) and non-endemic taxa (Figure 78c), considering its area, due to its less hospitable xeric climate.

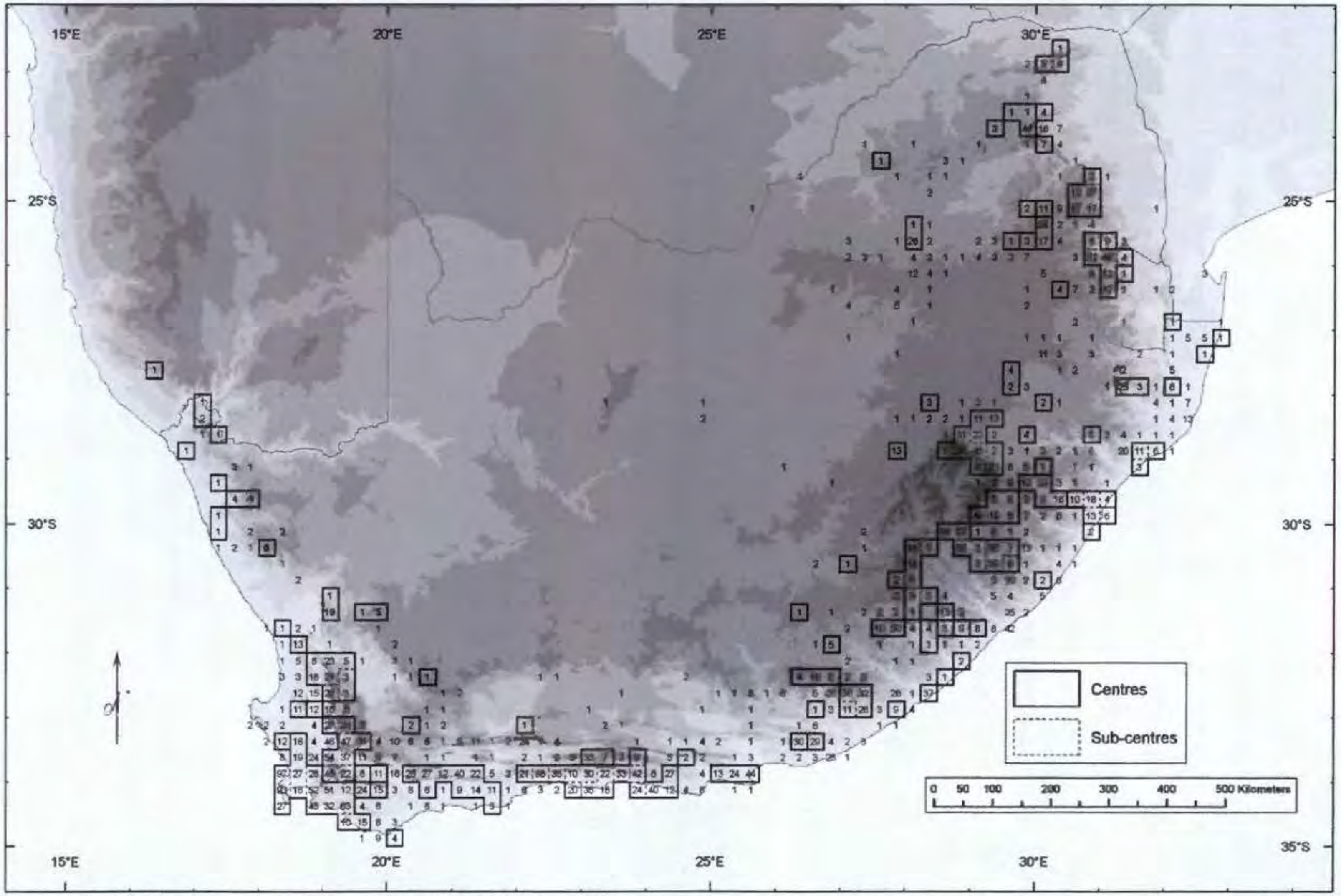


Figure 76: QDS Diversity for the Orchidaceae Dataset in Southern Africa.

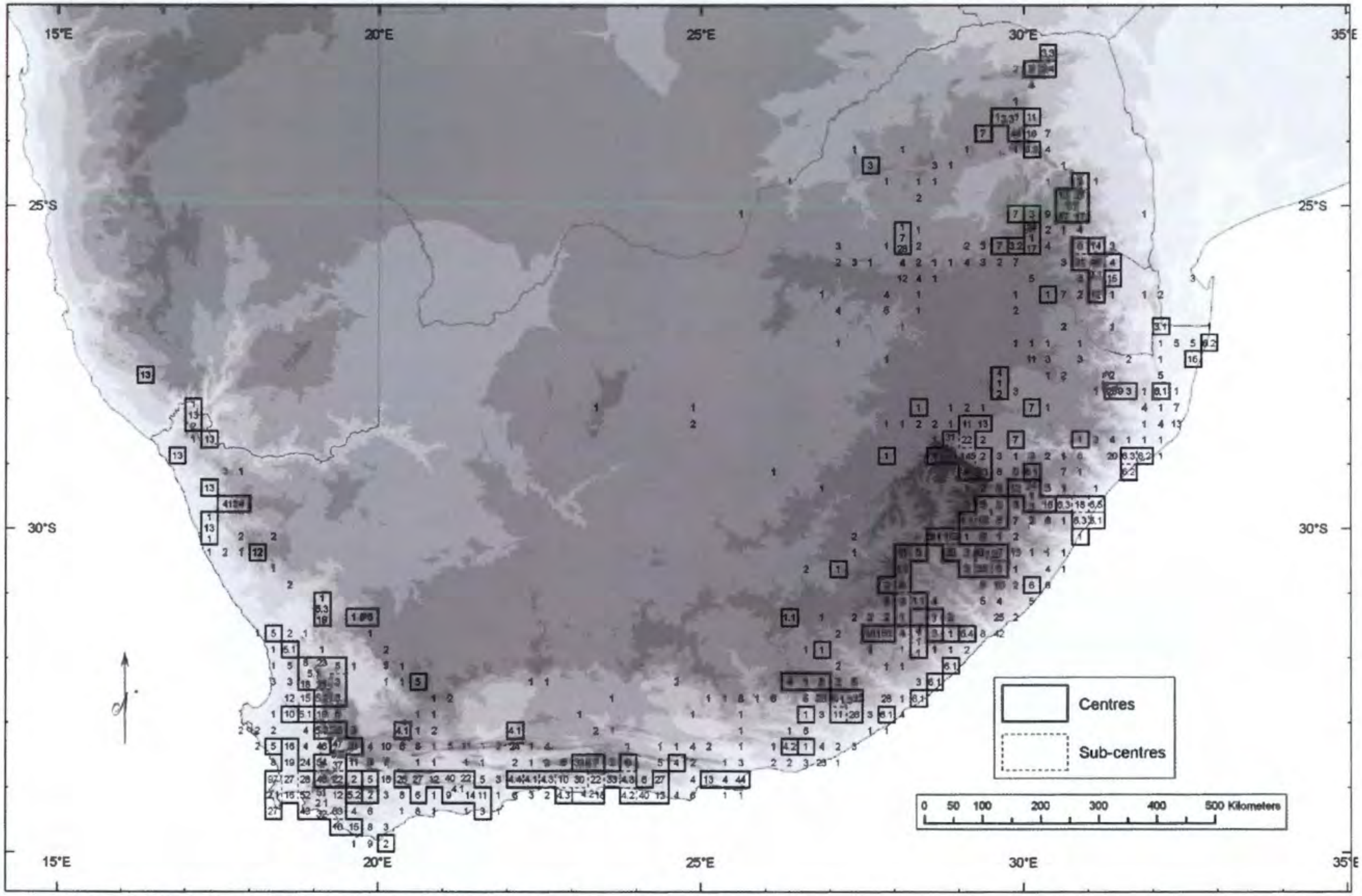


Figure 77: Sum of the Inverse Taxon Ranges for the Orchidaceae Dataset in Southern Africa.

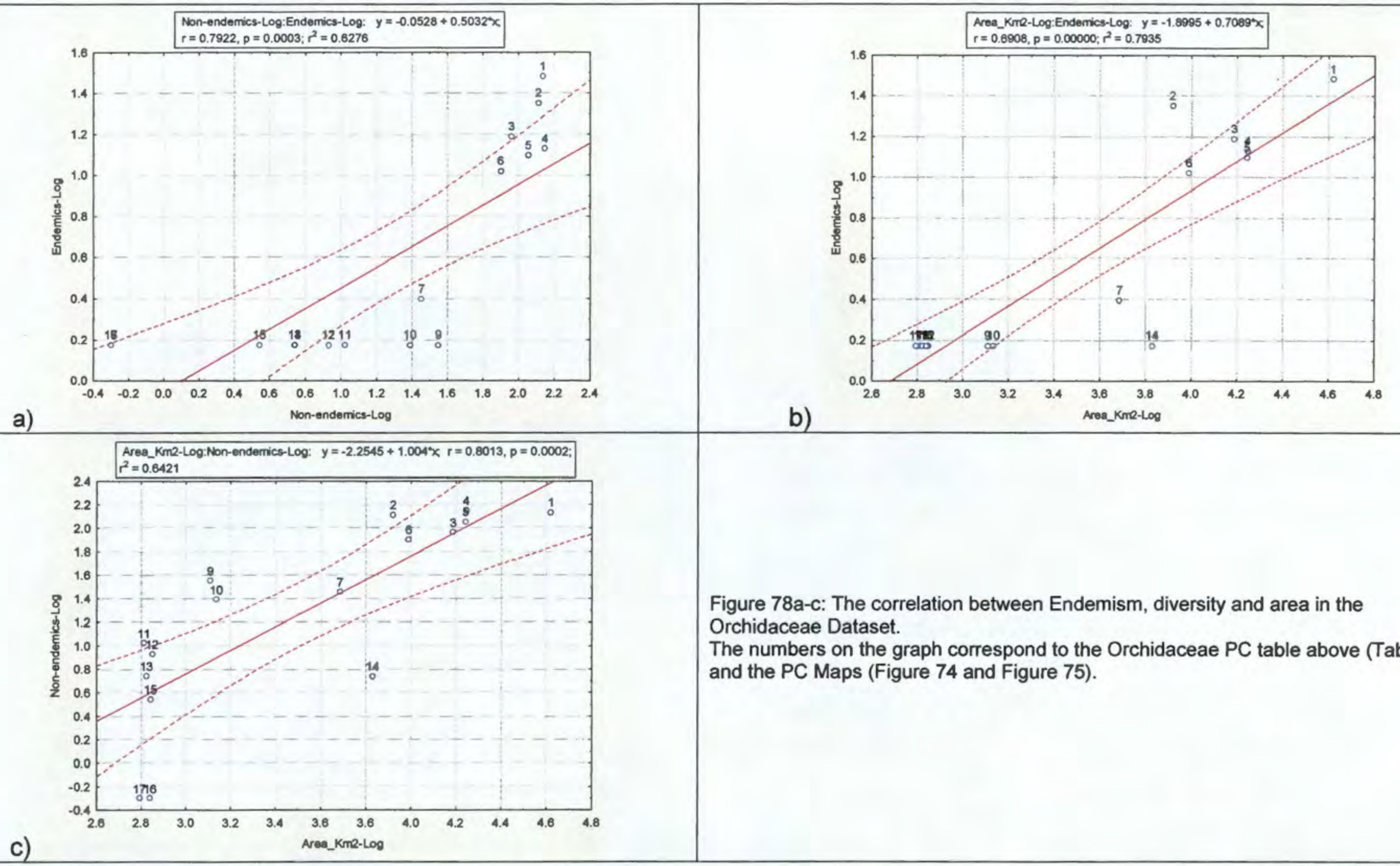


Figure 78a-c: The correlation between Endemism, diversity and area in the Orchidaceae Dataset.
The numbers on the graph correspond to the Orchidaceae PC table above (Table 44) and the PC Maps (Figure 74 and Figure 75).

Table 45: Habitat Data for the Orchidaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Conglomerate | Loam | Limestone/Calcareous | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliffs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats/Dunes | Other | Unknown |
| 1 | Eastern Escarpment | | | | | | 9 | 14 | 21 | | | | | | | | | 2 | 6 | 9 | | | 11 | | 2 | 6 | | | | 2 | | 23 | | | | |
| 2 | Southwestern Centre | | | 1 | 7 | 2 | 1 | | | 8 | | | | | | | | 3 | 6 | | | 3 | 6 | 1 | 2 | 3 | 4 | 1 | | 1 | | | | 3 | | |
| 3 | Northeastern Escarpment | | | | | | 4 | 3 | | | | | | | | | | 6 | 2 | 2 | 1 | | 5 | 1 | 2 | 3 | | | | 1 | | 7 | 1 | | | |
| 4 | Langeberg-Southeastern Centre | | | | 5 | 5 | 1 | | | 4 | | | | | | | | | 9 | | | 1 | 3 | 1 | 3 | 3 | | 2 | | | | | | | | |
| 5 | Northwestern Centre | | | 1 | | | | | | 4 | | 4 | 1 | | | | | | 4 | 1 | | 4 | 2 | 1 | 1 | | 2 | | 2 | | | | | | | |
| 6 | Natal Coast | | | | 1 | 3 | 2 | 1 | | | | | | | | | | | | | | | 3 | | | | | | | 4 | | 2 | | 4 | | |
| 7 | Western Transvaal | | | | | | 1 | | | | | | | | | | | | | | 1 | | | | | 1 | | | | | | 2 | | | | |
| 8 | Kouga | | | | | 1 | 1 | | | | 1 | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| 9 | Ngome | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 10 | Piketberg | | | | | | | | | 1 | | | | | | | | | | | | | | | | 1 | | 1 | | | | | | | | |
| 11 | Krokodilpoortberg | | | | | 1 | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | |
| 12 | Kamiesberg | | | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | |
| 13 | Northern Namaqualand | | | | | | | | | | | | | | | | | | 1 | 1 | | | | | 1 | 1 | | | | | | | | | | |
| 14 | Vaalkrans | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | | | | | | |
| 15 | Malandela Hills | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | |
| 16 | Mbazwana Area | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| 17 | Outside | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | 1 | 0 | 3 | 13 | 12 | 21 | 19 | 21 | 17 | 1 | 4 | 2 | 0 | 0 | 0 | 0 | 11 | 29 | 13 | 2 | 8 | 30 | 5 | 11 | 19 | 6 | 4 | 3 | 9 | 0 | 35 | 1 | 8 | 2 | 0 |

## 10.2 CFR Phytogeographical Centres

### 10.2.1 Southwest Phytogeographical Province

In Orchidaceae, the SWPP is remarkable for its extremely high diversity and its high numbers of endemics. It is ranked marginally behind the geographically larger Eastern Escarpment Centre, for diversity, which is nearly three times its size (Table 44). The Southwest Centre has the best area to endemism and area to diversity ratios of all the well-supported centres. The fact that the Southwest Centre (PC 2) has similar diversity to the much larger Eastern Escarpment Centre (PC 1) indicates that the relationship between area, diversity and endemism is not as simplistic as a positive linear correlation. Once again, this highlights the unique diversity of the CFR, particularly the Southwest Centre (Levyns, 1964; Goldblatt and Manning, 2000). The SWPP diversity and endemism is even more notable in Orchidaceae, as the Northwest Centre (PC 5) crosses the Berg River Valley into the Bainskloof/Wemmershoek Mountains, decreasing the geographic area of the SWPP, relative to the other datasets that I analysed.

As is common in Cape Clades (Linder, 2003), the majority of Orchid endemics (21 of 22) that were identified in this study are from a single clade, the Tribe Diseae (Table 44 and Appendix II). Furthermore, all but five endemics are from the genus *Disa*. At the sub-generic level, four endemics are from Section *Herschelianthe* (excluding an endemic hybrid), four from *Disa*, three from *Monadenia*, three from *Disella* and one from *Phlebidia*. Although similar to other Cape Clades in regards to the dominance of limited clades (Linder, 2003).

The only other orchid tribe with an endemic in the SWPP is Cymbidieae, with one taxon. The lack of high-level taxonomic diversity of endemic Orchids in the SWPP and the absence of epiphytes, may be due to the relatively uniform physiognomy of the fynbos biome, which offers very little opportunity for epiphytic establishment, both spatially and temporally. Suitable epiphytic habitats may take several years to develop and periodic burning may regularly remove these arboreal habitats in mature fynbos, and favour resprouting from subterranean organs. Possibly even more significant, is summer aridity and low humidity. All (or nearly all) endemic CFR Orchids are tuberous geophytes, which is one of the adaptive strategies used by taxa in the CFR against seasonal aridity.

In Orchidaceae, the Southwestern Centre (PC 2) is concentrated in the southwest parts of the CFR. Low-lying regions of the CFR are very poor for independent PC formation, although in the more montane SWPP, NWPP and LBPP-SEPP, there are a few lowland endemics (at least 8 of 46 endemics) (Table 45). There is no PC development on the Saldanha Peninsula in Orchidaceae.

Internally, the Southwestern Centre (PC 2) does not have many sub-divisions, consisting of a core, mountainous area (PSC 2.1) in the extreme southwest corner of the traditional SWPP, which consists solely of taxa from Tribe Diseae. All but three of these endemics belong to the genus *Disa* (Appendix II). Despite the SWPP having the highest area to endemism ratio, endemism is even further concentrated within the Southwest Mountains Sub-Centre (PSC 2.1) (SWPP). The Southwest Mountains Sub-Centre (PSC 2.1) has the greatest number of endemics of all the sub-centres and has almost as many endemics as all the PCs ranked below it (PCs 3 to 16). It also has the highest area to endemism ratio of all the Orchidaceae phytogeographical areas (Table 44). From the QDS taxon diversity values and the QDS inverse weighting (Figure 76 and Figure 77 respectively), it is clear that the Southwest Mountains Sub-Centre (PSC 2.1) is a very speciose area for Orchid Taxa. The highest QDS diversity for Orchids is also found in the CFR - the Peninsula has QDS values of 97 and 93, nearly double the richest values outside the CFR.

### 10.2.2 Northwest Phytogeographical Province

In Orchidaceae, the Northwest Centre (PC 5) crosses the Berg-Bree River Axis and clusters the Bainskloof/Wemmershoek Mountains with the NWPP. In the Combined Dataset and in other studies (Weimarck; Goldblatt and Manning, 2000), these mountains are placed in the SWPP. However, in my study, the Int_Exp analysis was the only Orchidaceae clustering analysis that grouped the Bainskloof/Franschhoek Mountains in the SWPP. My remaining Orchidaceae analyses: PAE, Bell4, Int1 and MInt) grouped these mountains with the Northwestern Centre to varying degrees. In Orchidaceae, it appears that the boundary for the NWPP should be extended to include an additional mountain range to the south, ending in the Jonkershoek and Riviersondereinde River Valleys, although this should be verified. There are a number of gaps in the NWPP, where QDSs are not assigned to any PC. This is most likely due to under collection.

The Northwest Centre (PC 5) has a number of outlying QDSs, situated in the Hantam and Klein-Roggeveld Mountains, due to the endemic *Corycium deflexum* (5). These taxa, together with *Cliffortia* (Weimarck, 1934), which at that time, Weimarck had recently revised, lend support to Weimarck's proposition of the Doorn River Interval, with the Hantam and Klein-Roggeveld Mountains showing affinities to the NWPP. The Doorn and Tankwa River Lowlands, situated in the rain shadow of the NWPP Mountains, are extremely arid, and pose a formidable barrier to the mesic fynbos taxa of the CFR. However, with a more comprehensive dataset, the Hantam and Klein-Roggeveld Mountains would most likely form a distinct independent centre, or sub-centres, as proposed by van Wyk and Smith (2001) and Manning et al., (2002). Thus these disjunct records are of historical interest for the CFR.

As with the other PCs in the CFR (the Southwestern Centre (PC 2) and Langeberg-Southeastern Centre (PC 4)) nearly all PC endemic taxa (aside one from the Southwestern Centre (PC 2)) belonging to the Sub-Family Orchideae are members of the Tribe Diseae. At the sub-centre level, all CFR PSC endemic taxa belong to the Diseae (Table 44 and Appendix II).

My current sub-centre delimitation reflects a northern (PSC 5.1) and southern (PSC 5.2) component. However, an initial UPGMA analysis indicated a sub-centre pattern more similar to that of Poaceae, with a west and east component, with a very long north-south axis, linking the Bainskloof/Wemmershoek, Groot Winterhoek and the Cedarberg. This was due to the strong congruence between the ranges of *Disa esterhuysiana* (4) and *Disa telipogonis* (4). Subsequent GIS analyses revealed higher sub-centre endemism along more traditional geographical sub-centre delimitation (Figure 74). This may indicate that the Northwest PC contains disparate biotic elements that may be in conflict, producing two alternative floristic patterns (north-south versus west-east components). The linear north-south distributions of *Disa esterhuysiana* (4) and *Disa telipogonis* (4) seem to indicate that they prefer the relatively high, moist (Linder and Kurzweil, 1999; Table 45) westward facing mountains, which would create a rain shadow on the more easterly mountains, resulting in increasing aridity. The position and orientation of the Groot Winterhoek-Hexrivier Sub-Centre (PSC 5.2) QDS may indicate that this is still important for the endemic taxa in this sub-centre. The QDS of the Pakhuis-Olifants Sub-Centre (PSC 5.1) are less linear and are centred in a less topographically complex area. The remaining sub-centre, on the Nieuwoudtville Plateau (PSC 5.3) usually contains some Cape Clade endemics, but I found it to be particularly important for Geophytes, although in Orchidaceae, it is only defined by a single endemic.

### 10.2.3 The Langeberg-Southeast Phytogeographical Province

The LBPP and SEPP areas are combined in Orchidaceae to form a single centre (PC 4), as in Bruniaceae. Other studies have also merged these two centres together (Oliver et al., 1983). It is noteworthy that although this PC does contain portions of the 'all year rainfall area' (Schulze, 1997), all the endemic taxa are from Tribe Diseae (13 taxa). Thus, even in PCs that receive predominantly year round rainfall, there are no epiphytic endemics. The closest epiphytic PC endemics appear in the south-westerly extensions of the Natal Coast (PC 6) and Eastern Escarpment (PC 1) Centres. *Tridactyle bicaudata* var (*rupestris*) (5) is recorded as far west as the Kouga Mountains (3323DB). However, it is not endemic to any of my PCs.

Most PSCs are restricted to either the LBPP or SEPP of the Combined Dataset, within the traditional phytogeographical provinces. The Langeberg-KMPP Sub-Centre (PSC 4.1) is centred on the Langeberg, but includes two QDS outliers in the KMPP, due to *Disa gladiflora ssp capricornis* (4) in the northwest, and *Disa schlechteriana* (3) in the northeast. There is a disjunction across the Gouritz River Valley, to the remaining three PSCs in the east. The remaining sub-centres are all fairly weakly supported. The Eastern SEPP Sub-Centre (4.2) is centred in the Plettenberg Bay area, but has a disjunct record of *Pterygodium newdigitatae* (5) from near Grahamstown. *Satyrium muticum* (5) links the Langeberg-KMPP Sub-Centre (PSC 4.1) and Eastern SEPP Sub-Centre (4.2) disjunctly, possibly across the Knysna Interval of Weimarck. The Eastern SEPP Sub-Centre (4.2) and the remaining LBPP Sub-Centres show some geographic overlap, and although there might be some habitat differentiation, more extensive collection may result in these sub-centres merging together.

### 10.2.4 Unrecovered CFR Phytogeographical Centres

#### 10.2.4.1 The Karoo Mountain Area

There is no independent centre in the KMPP for Orchidaceae, although there are outliers from the LBPP (PC 4.1 in part). Aside from the arid conditions here, sampling has been quite biased, as is indicated by the number of taxa collected near Seweweekspoort Pass in the Klein Swartberg and the Swartberg Pass in the Groot Swartberg, which are easily accessible by road.

#### 10.2.4.2 The Agulhas Plains Area

There are no independent centres associated with the Agulhas Plains region, and unusually, no Potberg Centre development. The SWPP has invaded from the west and the LBPP-SEPP from the north and east, but interestingly do not include any Orchid limestone endemics, or TMS endemics on the Potberg Mountains.

## 10.3 Non-CFR Phytogeographical Centres

### 10.3.1 The Eastern Escarpment Phytogeographical Centre

The Eastern Escarpment Centre (PC 1) contains the largest number of Orchid endemics of all the Orchid centres I identified. This is expected, as it covers the largest geographic area of all the PCs (with more than twice the number of QDSs than the centre ranked second). As with other taxonomic groups I analysed, the Eastern Escarpment Centre (PC 1) covers a very large phytogeographical area. As such, the high levels of diversity and endemism are not unexpected, as diversity and endemism are positively correlated with geographic size (Figure 78a-c). The Eastern Escarpment Centre (PC 1) and the Southwest Centre (PC 2) contain similar levels of diversity. However, endemism in the Drakensberg is calculated at 18%, while in the Southwest Centre it is approximately 14.5%, which is fairly low by Cape Clade standards in the SWPP. The Eastern Escarpment Centre (PC 1) represents a portion of the Grassland Biome (Low and Rebelo, 1996) and is more or less centred on the higher lying, topographically complex areas, containing the Drakensberg and southern Drakensberg. There is also further PC development north of the Drakensberg.

What is very notable in the Eastern Escarpment Centre (PC 1) is that only two tribes are represented by endemic taxa, both from the Sub-Family Orchioideae. These tribes are much better represented in more cool/temperate areas in southern Africa (Linder, 1983; Linder, Kurzweil and Johnson, 2005). In the Eastern Escarpment Centre (PC 1), Diseae contains 23 endemics and Orchideae seven endemics. This supports the findings of Linder (1983), that the phytogeographical patterns of the Sub-Tribe Disinae, largely correspond to the general patterns in the Cape and Afro-Montane Floras, and that the further north that these Orchid PCs are located, the higher the proportion of Orchideae endemics are within them (Linder, 1983).

Nearly half the endemic taxa found in the Eastern Escarpment Centre (PC 1) belong to the genus *Disa*. Seven of these 11 *Disa* endemics belong to the section *Stenocarpa*. This seems to indicate that this clade is centred in the Drakensberg Centre and is undergoing active speciation here, resulting in neo-endemics. Furthermore, two pairs of sub-species are endemic to this Eastern Escarpment Centre (PC 1), which lends further support to this hypothesis. Galley et al., (2006) notes in situ speciation of two *Disa* clades in the Drakensberg, resulting in radiations of 12 and 26 taxa. The remaining Orchid endemic taxa are from different sections, including *Disella* (the rest of the section appears to be largely a winter rainfall group), *Repandra* (summer rainfall), *Austroalpinae* (grasslands of southern, central and eastern Africa) and *Intermediae* (which is not well known (Linder and Kurzweil, 1999)).

At the sub-centre level, all Orchid endemic taxa belong to the Tribe Diseae. The genus *Disa* is by far the most dominant, due to the more range-restricted nature of the taxa and represents all but two of the sub-centre endemics, which are from *Corycium*. The Drakensberg Core Sub-Centre (PSC 1.1) is the most strongly supported, being the only sub-centre with more than one Orchid endemic.

## 10.3.2 The Northeastern Escarpment Phytogeographical Centre

The Northeastern Escarpment Centre (PC 3) is very rich in Orchid endemics, considering its size. It is also second only to the Southwest Mountains Centre (PC 2) in its ratios of Orchid diversity to area and endemism to area.

The Northeastern Escarpment Centre (PC 3) is largely congruent with Northeast Mountain Grassland Vegetation of Low and Rebelo (1996), and the Wolkberg Centre of van Wyk and Smith (2001). Nordenstam (1969) recovered a Barberton Centre for *Euryops*, which stretched from Barberton in the south to Lydenburg in the north, but excluded the more northerly Soutpansberg. Similarly, in their revision of *Gladiolus*, Goldblatt and Manning (1998) also grouped the southerly areas together, and referred to them as the Mpumalanga Highlands. This is congruent with the results of van Wyk and Smith (2001), who identified the Soutpansberg as the most distantly related of these Northeastern Escarpment floristic areas.

Geographically, the Northeastern Escarpment Centre (PC 3) stretches from Barberton in the South, tapering off to the QDS just north of the Eastern Soutpansberg, principally along the north-eastern escarpment of the Transvaal Drakensberg. There appear to be very well-developed phytogeographical areas within the larger area PC (3) and the sub-centres identified in my study (PSC 3.1, 3.2, 3.3 and 3.4) are treated as centres in their own right by van Wyk and Smith (2001). The Northeastern Escarpment Centre (PC 3) is characterised by a lack of geographical continuity, with the sub-centres being separated by relatively large incised valleys. This may provide some clues as to speciation in this region. Interestingly, two Orchid sister taxa, *Schizochilus cecili ssp culveri* (4) and *Schizochilus cecili ssp transvaalensis* (3), both occur in this PC (3), but in different sub-centres (3.1 and 3.2 respectively), and in different habitats (on rock ledges and the escarpment respectively (Linder and Kurzweil, 1999)). This may indicate that the endemic taxa may prefer the higher altitude mesic sites and that the incised valleys may provide some barrier to gene flow. Further investigation is required into life histories and environmental parameters, to determine exactly what barriers may have contributed to divergence. There is noticeable latitudinal tribal replacement of endemic taxa within the two, cool (temperate) tribes. Diseae and Orchideae are more abundant in the southerly PCs, but are replaced by a Vandeae endemic in the PCs to the north.

The most endemic rich sub-centre of the Northeastern Escarpment Centre (PC 3) for Orchids, the Barberton-Mbabane Sub-Centre (PSC 3.1), is a noted centre of diversity, for Geophytes, namely *Gladiolus* (Goldblatt and Manning, 1998) and *Watsonia* (Goldblatt, 1989); and was also recovered in the asterid genus *Euryops* (Nordenstam, 1969). van Wyk and Smith (2001) also highlighted this area as a phytogeographical centre. The

Orchid Taxa here are mostly from the Tribes Orchideae and Diseae, although there is a single Cymbidieae endemic present.

Similarly, the Pilgrim's Rest-Sabie Sub-sentre (PSC 3.2) is also a noted centre of diversity for *Gladiolus* (Goldblatt and Manning, 1998), *Watsonia* (Goldblatt, 1989) and *Euryops* (Nordenstam, 1969). My Pilgrim's Rest-Sabie Sub-centre (PSC 3.2) forms part of van Wyk and Smith's (2001) considerable enlarged Wolkeberg Centre, which extends in a crescent from west of Barberton in the South, through Pilgrim's Rest-Sabie, north to the Wolkeberg, then westwards nearly reaching Naboomspruit. I found distinct phytogeographical development around the Wolkeberg (PSC 3.3).

There is a disjunction to the final Orchid sub-centre to the north, the Eastern Soutpansberg Sub-Centre (PSC 3.4). Once again, investigating phylogenetic relationships of the endemic taxa may prove interesting. van Wyk and Smith (2001) also identified this area as a phytogeographical centre for succulents, and referred to it as the Soutpansberg Centre.

### 10.3.3 Natal Coast Phytogeographical Centre

The Natal Coast (PC 6) covers parts of the areas of two principle biomes, the new Indian Ocean Coastal Belt Forest and the Savannah Biome, with occasional outliers in the Grassland and Albany Thicket Biomes (Mucina and Rutherford, 2006). Floristically, this covers the Pondoland-Tongaland Centre, more recently referred to as the Maputaland-Pondoland Centre (van Wyk and Smith, 2001). The presence of higher humidity habitats in a forest environment, allows for the establishment of epiphytic Orchid Taxa, which are largely absent from the CFR and other cool/temperate phytogeographic regions in South Africa. This is the only centre that features a high number of endemic Orchid Taxa from a sub-family other than Orchioideae, namely Epidendroideae, which are predominantly epiphytic. By contrast, the CFR has no epiphytic Orchids endemic to PCs. Although, the PC (6) is situated along the coast, it does penetrate inland due to *Stenoglottis longifolia* (2) (2930AA) (Orchideae), *Disperis woodii* (5) (3128DA) (Diseae) and *Tridactyle bicaudata var rupestris* (5) (Vanadeae) in 3323DB. The PC includes taxa from diverse habitats (Table 45), from coastal forests to montane grasslands, indicating that the centre needs to be differentiated further, at a finer habitat scale. Linder (1983) did not differentiate between the Natal Coastal Centre (PC 6), the Eastern Escarpment Centre (PC 1) and the Northeastern Escarpment Centre (PC 3) PC, as identified here. However, Linder et al., (2005) did differentiate between the Grassland and Savannah biomes, although at a coarse geographic level.

The higher numbers of endemic taxa from different taxonomic groups may be due to the greater diversity of habitats and biomes represented in the Natal Coast Centre (PC 6)

(Linder et al., 2005; and Appendix II). Tribal endemic frequency is as follows: the Orchideae contributes five endemics the Vandeae three endemics, while Diseae and Gastroideae are each represented by one endemic taxon. Tribal endemism frequency is notably different between the western predominantly winter rainfall PCs (PC 2, 4 and 5) and the summer rainfall temperate PCs (PC 1 and 3), and the more tropical summer rainfall PCs (PC 6). The Natal Coast PC (6) is dominated by Orchideae endemics and endemics from other tribes, and only contains one Diseae endemic.

*Diaphananthe millarii* (3) (Tribe Vandeae) is the only species of this genus that is endemic south of the arid Limpopo River Basin. This may provide clues as to modes of speciation of tropical taxa in South Africa. The Limpopo Basin is a noted barrier to plant dispersal (Weimarck, 1941). During more mesic geological periods, tropical taxa may have crossed this barrier and subsequently became isolated when conditions became more arid once again. Alternatively, dispersal may occur due to unique or unusual dispersal events across this barrier, resulting in isolation. This population fragmentation may result in speciation due to founder effects. Phylogeography may identify a similar pattern in *Diaphananthe xanthopollinia* (5), at a lower taxonomic, or population level, which is widespread in central and eastern Africa. A few of the more tropical taxa do cross the Limpopo Basin and phylogeography may shed light on the amount of gene flow between these southern populations and those to the north.

Due to the coarse geographical level at which my analysis was undertaken, it is difficult to make specific comment on finer phytogeographical patterns and floristic sub-divisions. It seems that species turnover in this region may be more closely linked to local habitat turnover rather than geography, which is reflected in the diversity of life history adaptations of the endemic taxa (epiphytes, lithophytes, geophytes (Linder and Kurzweil, 1999)). However, sub-centres were identified tenuously for my Orchid Dataset. The Dwesa-Wild Coast Sub-Centre (PSC 6.1) is centred in the southern and central areas of the Natal Coast Centre, although this centre does include outliers further north. As mentioned earlier, this phytogeographical area may contain disparate phytogeographical units, with both temperate and sub-tropical/tropical affinities, and may require further sub-division into more appropriate sub-centres. The Mtunzini-Ngoya Sub-Centre (PSC 6.2) is centred in the extreme north. The Valley of a Thousand Hills (PSC 6.3) is also dominant towards the north, but includes QDSs to the south that overlaps with the geographical area of the Dwesa-Wild Coast Sub-Centre (PSC 6.1). The remaining Orchid sub-centres each contain a single endemic Orchid species. Interestingly, all the sub-centres, aside from the Valley of a Thousand Hills Sub-Centre (PSC 6.3) contain an endemic taxon from the Orchideae Tribe.

### 10.3.4 Western Transvaal Phytogeographical Centre

Although occupying relatively few QDSs, the Western Transvaal Centre (PC 7) is fairly widespread geographically, due to *Habenaria kraenzliniana* (4) from Sub-Family Orchideae, which is disjunct and which extends far to the south. Whether this is a genuine disjunction, or whether it is due to under collection needs to be confirmed. The precise phytogeographical affinities of the centre are vague and difficult to ascertain, as it covers a large area.

## 10.4 Additional minor Phytogeographical Centres of Orchidaceae

Most of the remaining Orchid centres are geographically small and only have a single endemic taxon. In many of these small centres, further collecting may indicate that they should be merged with better defined neighbouring centres, in the same manner as the Southern Sandveld Centre (PC 8).

The Kamiesberg (PC 12) and Northern Namaqualand (PC 13) Centres are quite remote, geographically, and may possibly have interesting evolutionary histories. *Disperis purpurata ssp pallescens* is endemic to the Richtersveld/Northern Namaqualand Centre (PC 13) (Bruyns, 1989; Linder and Kurzweil, 1999), but was not included in my dataset.

Minor (single endemic, single QDS) PCs that cluster around the sub-centres of the Northeastern Escarpment Centre (PC 3), such as the NE Wolkberg Centre (PC 11), the NE Barberton Centre (PC 14) and the SE Barberton Centre (PC 15), should in all likelihood be merged into their larger neighbours. However, there is no empirical evidence from my dataset to support this. The dataset analysed is limited to collections from the Bolus Herbarium.

### 10.5 Summary

The dominant contributor of Orchid endemic taxa in the CFR and temperate Southern Africa, is Diseae and is the dominant, or near dominant contributor of endemics in nearly all Orchid PCs identified here. In the CFR, Orchid PC development is nearly restricted to the more mesic SWPP, NWPP and mountainous areas of a combined LBPP-SEPP, and is noticeably absent from the KMPP and APPP. Orchidaceae has important PCs both inside and outside the CFR.

Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: Eastern Escarpment, SWPP, Northeastern Escarpment, NWPP and combined LBPP-SEPP, and NWPP.

# Chapter 11: Poaceae (Table 46, Figure 79 and Figure 80)

## 11.1 Introduction

The two photosynthetic pathways utilised by grass clades (Gibbs Russell, Watson, Koekemoer, Smook, Barker, Anderson, and Dallwitz, 1990), generally equivalent to Poaceae sub-families, have important ecological and biogeographic implications. C4 grasses are usually dominant in warmer areas, while C3 grasses are more prevalent in temperate areas (Hartley, 1958a, 1958b, 1973; Hartley and Slater, 1960). Apart from the study of Gibbs-Russell (1987), who found these photosynthetic pathways have important phytogeographical implications in southern Africa, biogeographical studies of Poaceae in southern Africa have been largely neglected.

Similarly, until fairly recently, Poaceae (Linder, 1989) had been largely ignored in phytogeographical discussions of CFR Taxa. However, within Poaceae, the tribe Danthonieae (Barker, Linder, Harley, and Morton, 2000) is largely centred in the CFR (Linder, 1989), and displays similar patterns to montane TMS Cape Clades. My dataset is almost exclusively restricted to the phytogeographical patterns of Tribe Danthonieae in Southern Africa, a $C_3$ photosynthesiser, with a few additional RDL Taxa grasses. Where these RDL Taxa have contributed to PC formation, their higher taxonomic relationships have been included (Appendix II). However, *Ehrharta eburnean* (2) is the only PC endemic from a tribe other than Danthonieae in my limited grass dataset.

Floristic patterns for Danthonieae show similarities to other Cape Clades, particularly Cape Clades that are represented in the Drakensberg. This is perhaps a little surprising, as grasses are relatively inconspicuous in the CFR. Furthermore, Acocks (1953) observed that Restionaceae may replace grasses in the CFR at higher altitudes; and Bond and Goldblatt (1984) suggested that Restionaceae and Cyperaceae have replaced grasses as ecological dominants in the CFR.

Diversity and endemism of Danthoineae Taxa are highest in mesic montane areas of the CFR, with good PC and PSC differentiation in these habitats in the western CFR phytogeographical provinces. This includes the Northwestern Mountains Centre (PC 4), the Southwestern Mountains Centre (PC 1) and the Agulhas Plains Centre (PC 5). The remaining CFR floristic areas, the LBPP, the KMPP and the SEPP are very fragmented, due to low QDS diversity, and they appear to be under collected. However, further east, there is a well-developed Southeastern Escarpment Centre (PC 2), which is concentrated in the temperate montane areas of that region, in the Grassland Biome of Mucina and

Rutherford (2006). There appears to be some sample bias, with the Peninsula (PSC 1.3 and PC 1 in part) and the Stellenbosch (PSC 1.2) areas being overrepresented.

Table 46: Taxonomic properties of the Centres identified for the group Poaceae (Figure 79 and Figure 80).

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Southwestern Mtns | 21 | 76 | 27 | 14 | 70 | 0.24 | 0.18 |
| 1.1 | Elandskloofberge-NW Hexrivier | 2 | 47 | 2 | 2 | 3 | 0.75 | 0.50 |
| 1.2 | Hottentotsholland | 2 | 47 | 2 | 1 | 2 | 1.00 | - |
| 1.3 | N Peninsula | 1 | 38 | 1 | 1 | 1 | 1.00 | - |
| 1.4 | Kogelberg | 1 | 28 | 1 | 1 | 1 | 1.00 | - |
| 1.5 | Remainder | 15 | 63 | 10 | 0 | 0 | - | 1.00 |
| 2 | Southeastern Escarpment | 84 | 30 | 17 | 12 | 158 | 0.16 | 0.08 |
| 2.1 | NE Drakensberg | 25 | 22 | 10 | 7 | 54 | 0.31 | 0.19 |
| 2.2 | SW Drakensberg | 6 | 12 | 6 | 1 | 6 | 1.00 | - |
| 2.3 | Remainder | 53 | 20 | 3 | 0 | 0 | - | 1.00 |
| 3 | Northwestern Mtns | 13 | 66 | 11 | 10 | 25 | 0.19 | 0.10 |
| 3.1 | W Cedarberg-Swartberg-Groot Winterhoek | 10 | 61 | 9 | 7 | 17 | 0.24 | 0.12 |
| 3.2 | Piketberg-E South Gifberg | 3 | 25 | 2 | 2 | 4 | 0.67 | 0.33 |
| 4 | Namaqualand | 29 | 40 | 5 | 5 | 38 | 0.26 | 0.08 |
| 4.1 | Kamiesberg | 2 | 17 | 2 | 2 | 3 | 0.75 | 0.50 |
| 4.2 | Nieuwoudtville Plateau | 1 | 18 | 1 | 1 | 1 | 1.00 | - |
| 4.3 | Remainder | 26 | 34 | 2 | 1 | 23 | 0.88 | - |
| 5 | Agulhas Plains | 10 | 32 | 4 | 4 | 17 | 0.43 | 0.23 |
| 5.1 | Agulhas-Potberg-East Agulhas Plain | 6 | 26 | 4 | 3 | 9 | 0.50 | 0.25 |
| 5.2 | Remainder | 4 | 22 | 1 | 0 | 0 | - | 1.00 |
| 6 | Witteberg-NE Hex-W Langeberg-Skurweberg | 8 | 40 | 2 | 2 | 9 | 0.56 | 0.13 |
| 7 | Port Elizabeth-E Cape | 9 | 22 | 2 | 2 | 11 | 0.61 | 0.22 |
| 8 | Central Langeberg-W Outeniqua | 2 | 20 | 2 | 2 | 2 | 0.50 | 0.00 |
| 9 | East Langeberg Plains | 3 | 27 | 1 | 1 | 3 | 1.00 | - |
| 10 | Klein Swartberg | 1 | 12 | 1 | 1 | 1 | 1.00 | - |
| 11 | West Langeberg and Plains | 1 | 12 | 1 | 1 | 1 | 1.00 | - |
| 12 | Zuurberg | 1 | 5 | 1 | 1 | 1 | 1.00 | - |
| 13 | S Namibia | 5 | 5 | 1 | 1 | 5 | 1.00 | - |
| 14 | Swartkop | 1 | 4 | 1 | 1 | 1 | 1.00 | - |
| 15 | Oesterbaai | 1 | 3 | 1 | 1 | 1 | 1.00 | - |
| 16 | Northeastern Escarpment | 5 | 3 | 1 | 1 | 5 | 1.00 | - |
| 17 | Goukamma | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 18 | Amsterdam Island | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 19 | Outside | 324 | 70 | 21 | 0 | 0 | - | 1.00 |

## 11.1.1 The relationship between endemism, diversity, and area in the Poaceae PCs

In my Poaceae Dataset, a significant and positive relationship ($r^2 = 0.49$, $p<0.005$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 83a). Further, there is a significant and strong positive relationship between the number of endemics and the geographic size of the PC ($r^2 = 0.68$, $p<0.005$) (Figure 83b), and between the number of non-endemics and the geographic size of the PC ($r^2 = 0.56$, $p<0.005$) (Figure 83c), and it is weaker. The western Northern Transvaal PC (16) was found to unduly influence the regression analysis and was therefore excluded.

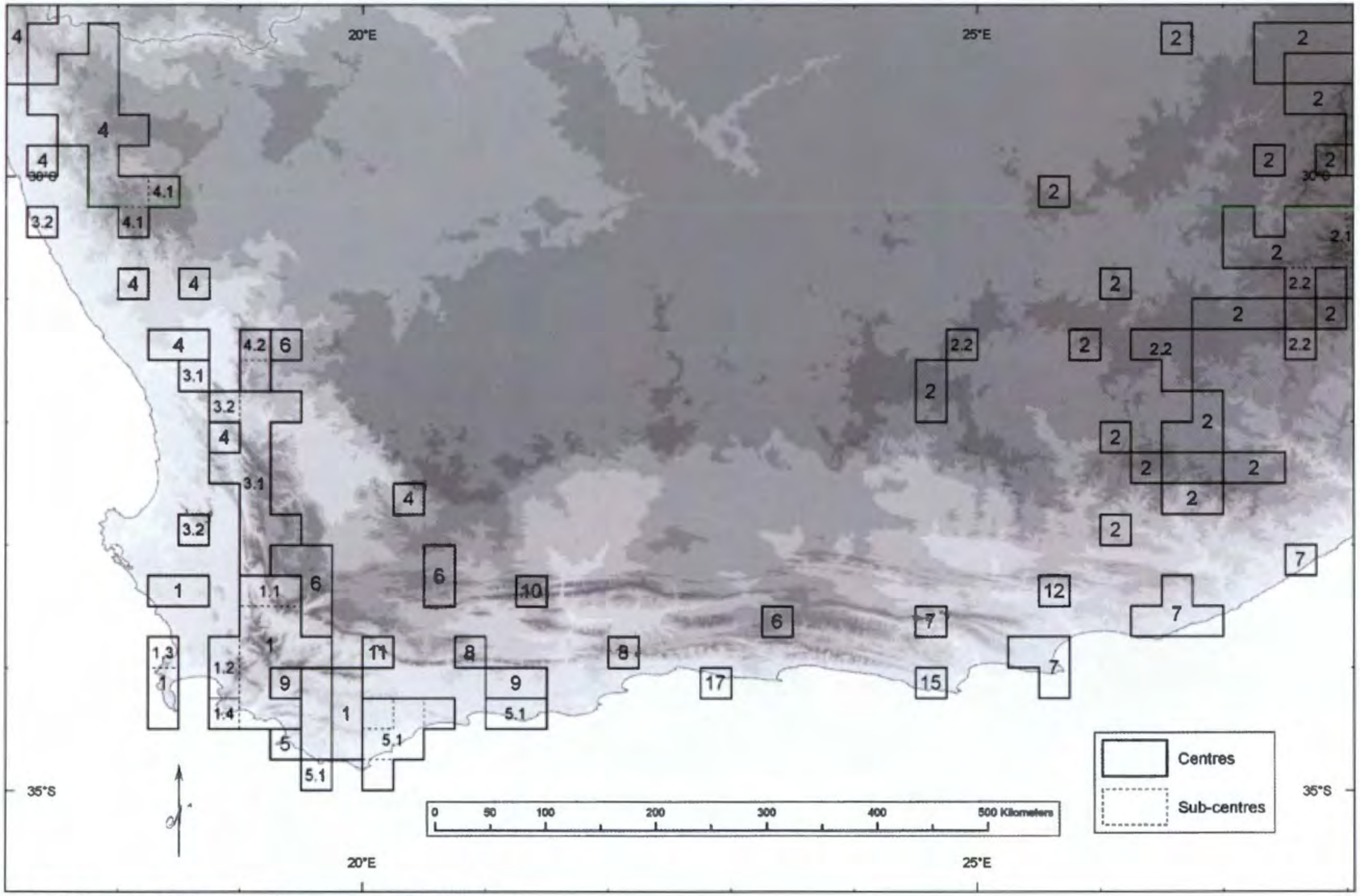


Figure 79: PC and PSC for the Poaceae Dataset in the CFR.

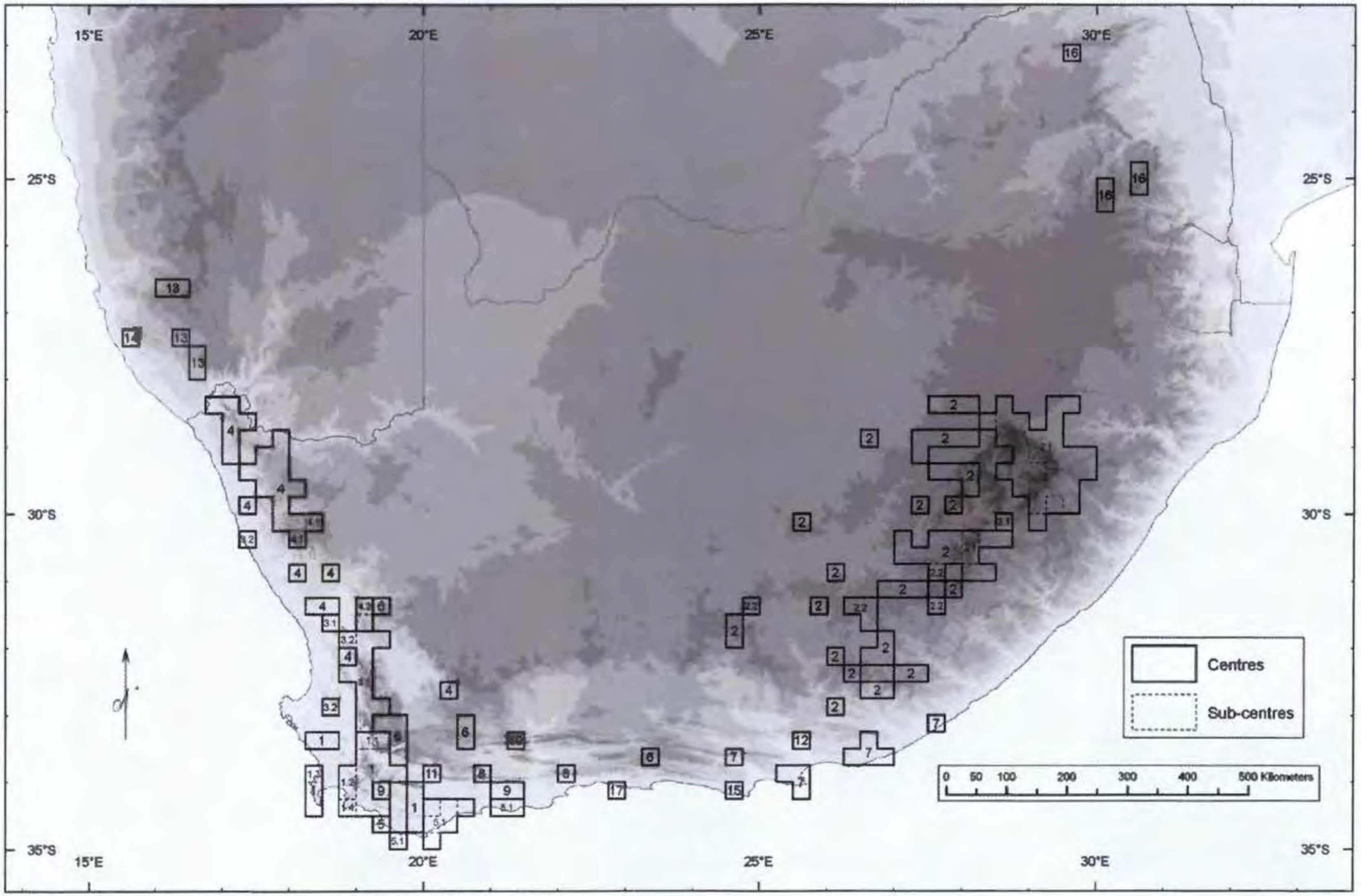


Figure 80: PC and PSC for the Poaceae Dataset in Southern Africa.

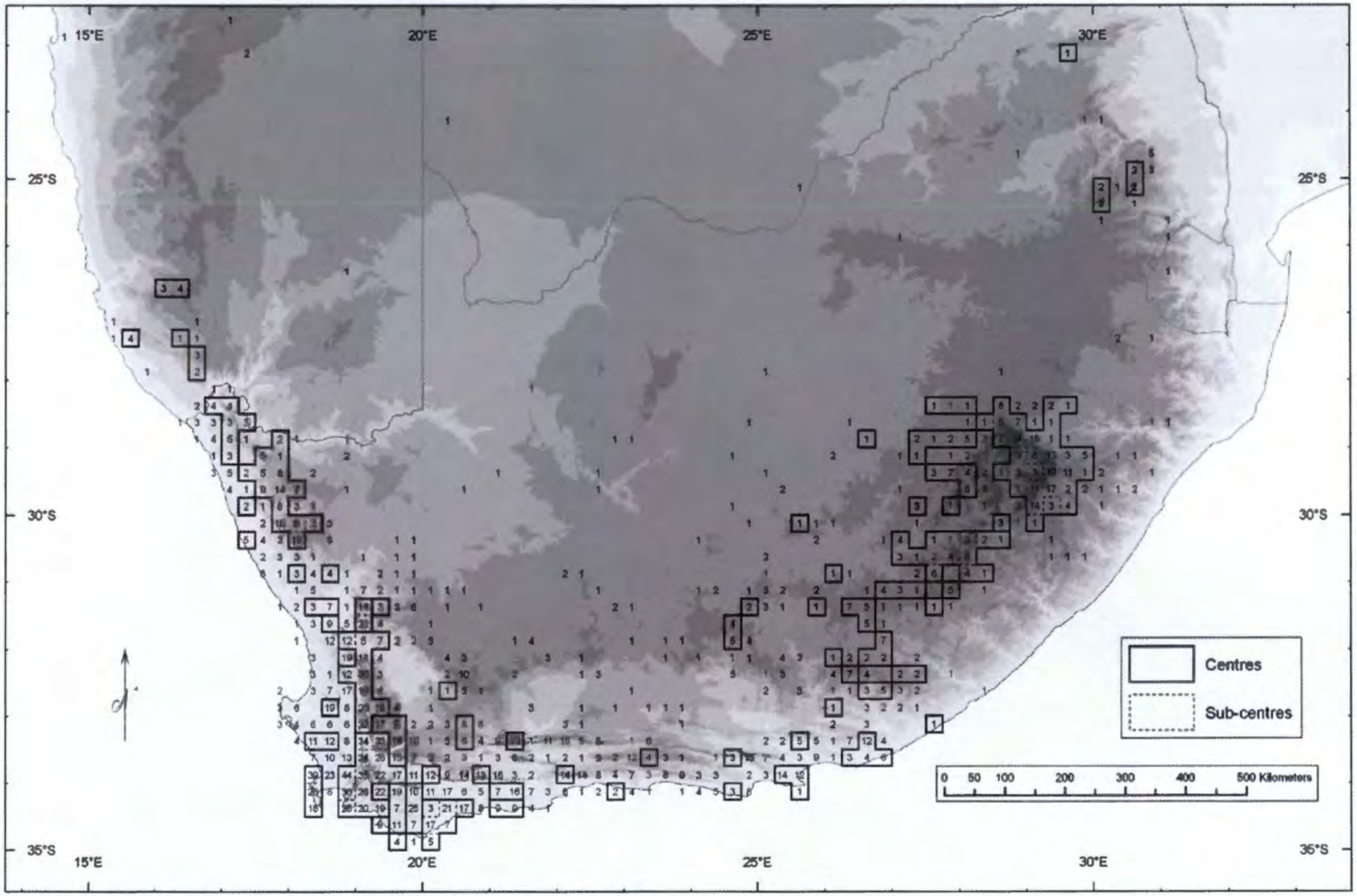


Figure 81: QDS Diversity for the Poaceae Dataset in Southern Africa.

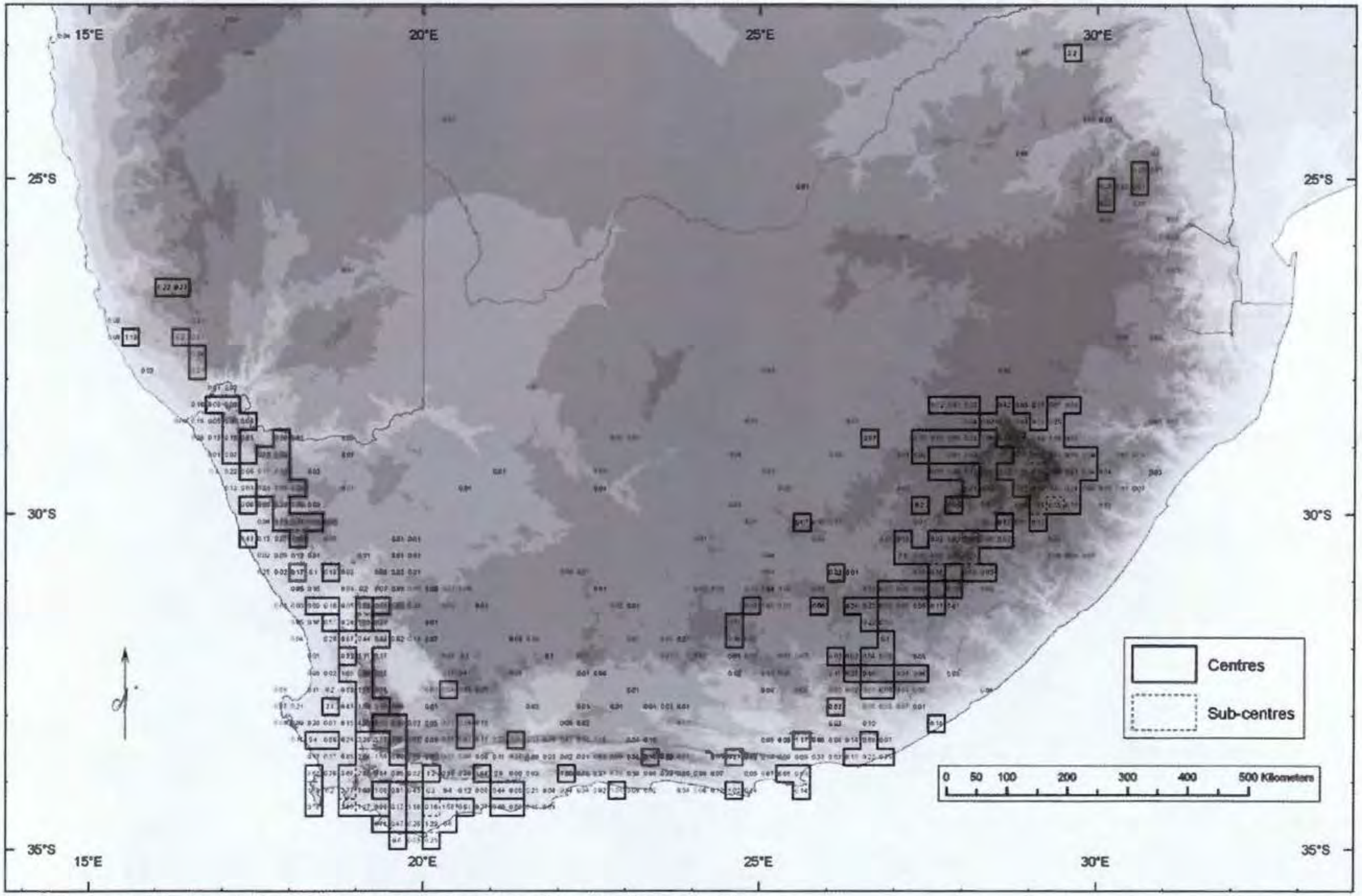


Figure 82: Sum of the Inverse Taxon Ranges for the Poaceae Dataset in Southern Africa.

Table 47: Habitat Data for the Poaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliifs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats | Other | Unknown |
| 1 | Southwestern Mtns | 3 | | 3 | | | | | | 7 | 2 | | | | | | 1 | 2 | 9 | | | | 3 | | | 3 | 1 | | | | | | | | | |
| 2 | Drakensberg | 1 | | 3 | | | | | | 3 | | | | | | | 1 | 1 | 3 | 2 | | | | 3 | 1 | 1 | | | | | | 4 | | | | |
| 3 | Northwestern Mtns | | | 4 | | | | | | 4 | | | | | | | | | 8 | | | | 1 | | 4 | 3 | | 1 | | | | | | | | |
| 4 | Namaqualand | | | | | | | | | | | 1 | 1 | | | | 1 | | 1 | | | 1 | | | 1 | 1 | | | | | | | | | | |
| 5 | Agulhas Plains | | | | | | | | | | | | | 3 | | | | | 1 | 2 | | 2 | | | | | 1 | | | | | | | | | |
| 6 | Witteberg-NE Hex-W Langeberg-Skurweberg | | | | | | | | | | | | | | | | | | 1 | | | | | | 2 | 2 | | | | | | | | | | |
| 7 | Port Elizabeth-E Cape | 1 | | | | | | | | 1 | | | | | | | | | 1 | | | | | | | | 1 | | | | | | | 1 | | |
| 8 | Central Langeberg-W Outeniqua | | | | | | | | | | | | | | | | | | | 1 | | | 1 | | | | | | | | | | | | | |
| 9 | East Langeberg Plains | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | |
| 10 | Klein Swartberg | | | 1 | | | | | | | | | | | | | | 1 | | | | | | | | 1 | | | | | | | | | | |
| 11 | West Langeberg & Plains | | | | | | | | | | | | | | | | | | 1 | 1 | | | | | 1 | | | | | | | | | | | |
| 12 | Zuurberg | | | | | | | | | | | | | | | | | | 1 | | | 1 | | | | | | | | | | | | | | |
| 13 | S Namibia | | | | | | | | | | | | | | | | | | | | | 1 | | | 1 | | 1 | | | | | | | | | |
| 14 | Swartkop | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| 15 | Oesterbaai | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | |
| 16 | W N Transvaal1 | | | 1 | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | |
| 17 | Goukamma | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | |
| 18 | Amsterdam Island | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 19 | Outside | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Totals | 7 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 15 | 2 | 1 | 1 | 3 | 0 | 0 | 4 | 4 | 26 | 6 | 0 | 5 | 6 | 3 | 10 | 11 | 6 | 1 | 0 | 0 | 0 | 4 | 0 | 4 | 0 | 0 |

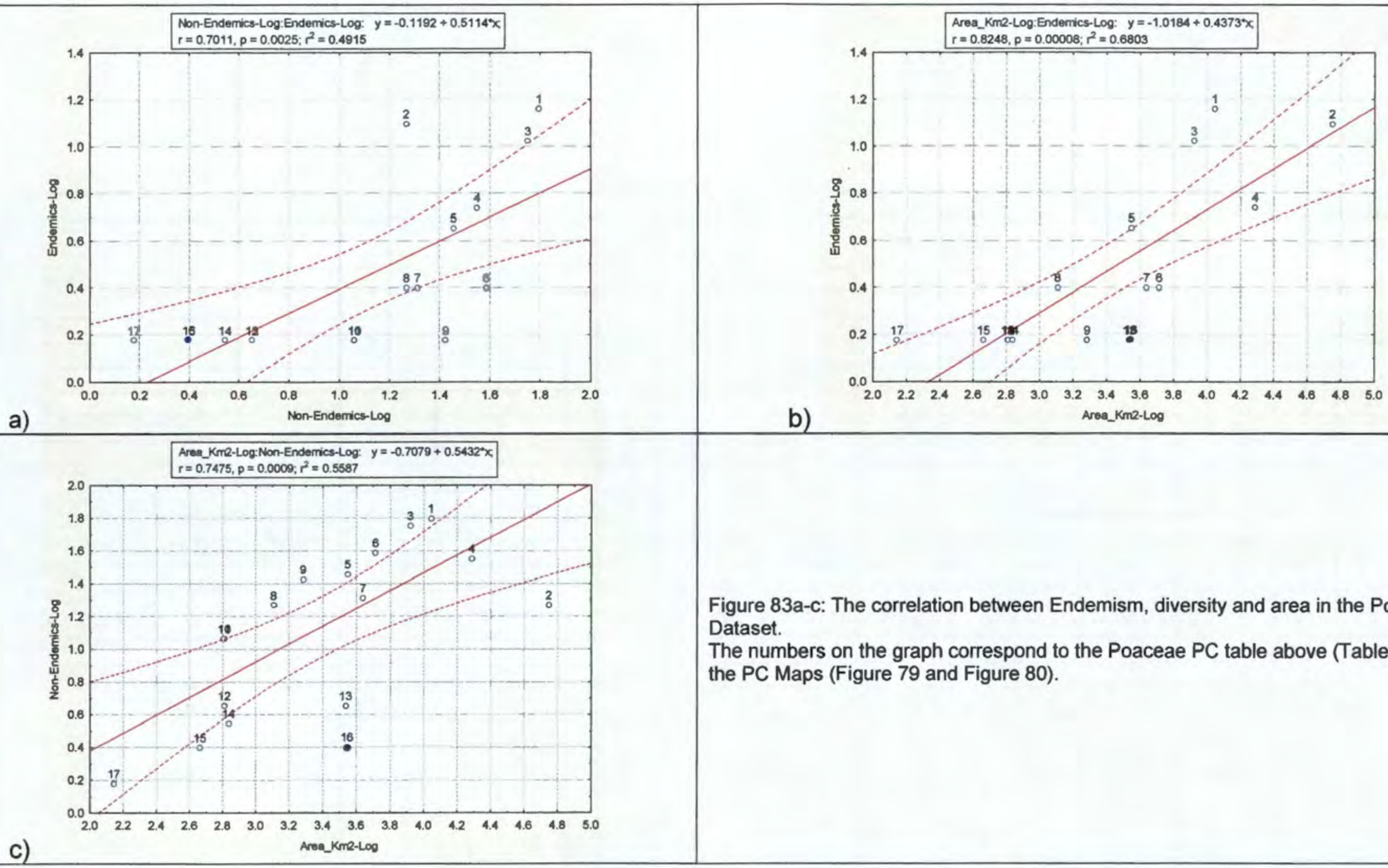


Figure 83a-c: The correlation between Endemism, diversity and area in the Poaceae Dataset.
The numbers on the graph correspond to the Poaceae PC table above (Table 46) and the PC Maps (Figure 79 and Figure 80).

The Southwestern Mountains (PC 1) and the Northwestern Mountains (PC 3) have higher than expected endemism in relation to non-endemic taxa (Figure 83a), and also have higher than expected levels of endemic (Figure 83b) and non-endemic taxa (Figure 83c) in relation to PC size.

The Southeastern Escarpment Centre (PC 2) has higher than expected endemism in relation to non-endemic PC taxa (Figure 83a) due to its large geographic size (84 QDSs) However, endemism is not significantly more different than its PC area would predict (Figure 83b), while non-endemic taxa are underrepresented relative to PC area (Figure 83c). Importantly my analysis focuses on the Danthonioideae and ignores other grasses present in the Drakensberg. Inclusion of all Drakensberg grasses may result in geographically smaller PCs.

The Witteberg-NE Hex-W Langeberg-Skurweberg (6) and East Langeberg Plains (9) have lower than expected taxon endemism in Poaceae (Figure 83a), and concomitantly, they have high levels of non-endemic taxa in relation to PC geographic size. The numbers of endemic taxa do not deviate significantly from what the PC area would predict. In the Southern Namibian PC (13), diversity is low, relative to the PC area (Figure 83c), due to aridity. As my Poaceae Dataset focuses almost exclusively on Cape Danthonioideae, which are largely restricted to the CFR, PCs (4, 13, 14 and 16) that are geographically distant from the core CFR and have relatively few Danthonioideae Taxa. The inclusion of other grass taxa would increase the diversity of these distant PCs and retrieve more appropriate floristic patterns.

## 11.2 CFR Poaceae Phytogeographical Centres

### 11.2.1 The Southwest Phytogeographical Province

In Poaceae, the Southwestern Mountains Centre (PC 1) extends further north than the Bree River, which is the traditionally recognised boundary of the SWPP (Weimarck; Goldblatt and Manning, 2000). It incorporates the western Hex River Mountains into the Southwestern Mountains Centre (PC 1). Bell-weighting (PAE and Bell analyses) indicates that the Elandsberg and Hex River Mountains are an independent PC, while Integration Weighting (Int and MInt analyses) indicates a relationship between the north-western Hex River Mountains and the Bainskloof-Stellenbosch Mountains. There is no independent Sandveld PC for Poaceae, or a Saldanha Peninsula PC, although part of the Sandveld area is included in the Southwestern Mountains Centre (PC 1).

Although the Southwestern Mountains Centre (PC 1) has a similar number of Poaceae endemics, compared to the Southeastern Escarpment Centre (PC 2), which is ranked second, it is only a quarter of the geographic size, and has more than 2.5 times the diversity (Table 46). Thus the CFR, and in particular, the SWPP, are extremely important for Danthonioideae in southern Africa. The majority of Danthonioideae diversity is centred in the SWPP, although this group of grasses does not form a physiognomically conspicuous part of the SWPP Flora. This highlights one of the principal differences between vegetation and floristic studies. Vegetation map studies focus on the physiognomically obvious or dominant taxa, to characterise an area, such as *Themeda triandra* in the grassland biome (Acocks, 1953, 1988). Floristic studies, on the other hand focus on taxon frequencies of either diversity and/or endemism. This has important conservation implications. If the conservation objective is to protect biodiversity, taxa and/or Phytogeographical Centres need to be protected. Alternatively, if one where trying to protect an assemblage, or habitat (landscape), one would have to consider dominant taxa, or keystone taxa.

Endemism of Danthonioideae in the Southwestern Mountains Centre (PC 1) is mostly centred on TMS slopes of the mountains of the south-western Cape (Table 47). Danthonioideae sub-centres are weakly developed, with very few endemics and should be accepted with caution. In addition, Danthonioideae Sub-Centre QDS clustering in the SWPP shows incongruence with my Combined Dataset. The Danthonioideae Peninsula PSC (1.3) is restricted to the northern parts (single QDS) of the Peninsula. The Kogelberg PSC (1.4) is independent of the Hottentots Holland and Kleinrivierberge, and restricted to a single QDS in the southwest. The Hottentots Holland is grouped with the Stellenbosch Mountains (PC 1.2) and restricted to two western QDSs. Interestingly, the converse of what was observed in Orchidaceae occurs here. The SWPP Danthonioideae PC crosses the Berg River Valley extending into the western parts of the Hex River Mountains and Ceres Valley (PC 1.1). This forms the richest sub-centre for Danthonioideae, and is atypical for fynbos clades. There is no sub-centre development in the Sandveld and there is no centre development on the Saldanha Peninsula.

### 11.2.2 The Northwest Phytogeographical Province

The Northwest Mountains (PC 3) occupy one of the smallest areas of the major PCs in Danthonioideae, and has the greatest diversity and endemism relative to its geographic size for Danthonioideae in the CFR. PC formation is concentrated in the western parts of the NWPP Mountains, on a similar north-south mountain axis as the Orchidaceae. It runs from the southern Koebeeberge-Boegoeberge, through the Cedarberg and southwards to the Groot Winterhoek (PSC 3.1). In Poaceae, even with arid adapted taxa (Appendix II), endemic taxa are concentrated in high altitude regions (Table 47). These mountainous areas may provide a refuge for taxa during drier geological periods.

Unlike in many of my other datasets, there is no direct relationship between the Piketberg (PSC 3.2) and the Groot Winterhoek. The Northwest Mountains (PC 3) have an outlier northwest of the Cedarberg, along the Namaqualand West Coast, due to the distribution of *Pentaschistis pillansii* (3). The disjunctions may indicate poor collection across its range.

### 11.2.3 The Karoo Mountain Phytogeographical Province

The Karoo Mountain Centre is fairly poorly developed in Poaceae, consisting primarily of a small fragmented PC (6), which occurs in both the KMPP and the NWPP. The exact affinities of this centre are unknown, though geographically it has a larger area in the KMPP. A hierarchical PC analysis should reveal where its affinities lie.

The Witteberg (PC 6) combines with the north-eastern Hex River (Matroosberg) Mountains, extending south to include parts of the West Langeberg. It also extends further north to include the Swartrugberg and the Baviaansberg, and west to the Skurweberg. Further disjunct outliers are found near the Nieuwoudtville Plateau and on the west Kouga Mountains. This possibly indicates that its distribution extends along the narrow, but very long, arid band forming the interior boundary of the CFR (Hartmann, 1991, 1993).

The only other area of significance for Poaceae in the KMPP is a small (single QDS) centre, located on the Klein Swartberg (PC 10), containing a single endemic.

### 11.2.4 The Agulhas Plains Phytogeographical Province

There is a relatively strongly developed Agulhas Plains Poaceae Flora (PC 5), although it still displays a few disjunctions. This is a little surprising, considering how poorly the eastern CFR is developed in my Poaceae (Danthonioideae) dataset. There is very little geographically localised sub-centre development, with no distinct, or independent West APPP, or Potberg areas as retrieved in other datasets. Rather, only a core sub-centre within the centre is identified, which merely excludes peripheral QDSs. As the coastal shelf in this area may have experienced cyclic periods of submersion, it would be interesting to calibrate the age of the taxa here, to shed light on any historical or evolutionary processes.

### 11.2.5 The Langeberg-Southeast Phytogeographical Province

The LBPP and SEPP are fairly weakly developed in Poaceae, consisting of a few fragmented areas containing small numbers of endemics, with rarely more than two endemic taxa per PC. In the LBPP area, two disjunct centres, the Central Langeberg-West Outeniqua Centre (PC 8) and the East Langeberg Plains Centre (PC 9) are recorded.

The best developed PC for Poaceae in the SEPP is the Port Elizabeth-E Cape Centre (PC 7), which contains two endemics. This PC extends eastwards outside the traditional CFR boundary; although most of it is included in Weimarck's (1941) Zuurberg Centre. *Merxmuelleria papposa* (4) occurs within the core CFR, while the more easterly endemic, *Pentaschistis heptamera* (7), is a coastal species and reminiscent of *Thamnochortus glaber* (14 QDS range) in the Restionaceae Dataset, and the eastern Zuurberg Centre (PC 11) in the Fabaceae Dataset. There is a genuine Zuurberg endemic, *Pentaschistis angustifolia* (1), in my Poaceae Zuurberg Centre (PC 12). In the western SEPP, there are two single QDS centres, each with a single endemic along the coast, in the western and central SEPP (PCs 15 and 17).

## 11.3 Non-CFR Poaceae Phytogeographical Centres

### 11.3.1 The Eastern Highlands Phytogeographical Centres

There are two independent Poaceae PCs situated in the high altitude areas of the eastern escarpment. The Northeastern Escarpment PC (16) contains only a single endemic, while the Southeastern Escarpment Centre (PC 2), centred on the Drakensberg, contains a high number of endemic taxa and is ranked second (in numbers of endemic taxa) of all the Danthonioideae PCs. The geographical patterns and taxonomic frequencies of these non-CFR centres are similar to other Cape Clades that reach the Drakensberg. They exhibit low diversity, comprising relatively widespread taxa, forming geographically large PCs, with relatively high endemism (*cf. Erica*, Orchidaceae).

It is perhaps a little surprising that Danthonioideae also contains a large number of endemics in the Drakensberg. Although grasses are physiognomically dominant in this area, the ecologically dominant grasses from the higher lying areas of the Drakensberg are mostly from the Pooideae Sub-Family (Gibbs-Russell, 1986, Linder, 1989). Pooideae, like the Arundinoideae Sub-Family of Danthonioideae, is also a $C_3$ photosynthesiser (Gibbs-Russell, 1986). Linder (1989) provides a brief list of the common high altitude Pooideae grasses in the Drakensberg area, while Acocks (1953, 1988) provides a more comprehensive list for high altitude and surrounding lower lying areas of the Drakensberg, which almost always includes *Themeda triandra*, a Panicoid grass that is physionomically dominant in the Drakensberg.

### 11.3.2 The Namaqualand Phytogeographical Centre

There is a well-developed Namaqualand Centre (PC 4), which clusters the Kamiesberg, Vanrhynsdorp and Nieuwoudtville Escarpment areas together into a single PC. This may contribute to these three regions clustering together in the hierarchical relationships between PCs in my Combined Dataset (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). The Centre stretches from the northern Cedarberg to the Richtersveld and corresponds fairly well to the escarpment areas of the Succulent Karoo Region of Jurgens (1991). In the Namaqualand Centre, two PSCs are identified: the Kamiesberg Mountains (PSC 4.1) and the Nieuwoudtville Plateau (PSC 4.2).

Although *Tribolium utriculosum* is not very range restricted (occupies 23 QDSs in Namaqualand PC Remainder PSC 4.3, Table 46), it is included as defining the Namaqualand PC, as it is restricted to the winter rainfall area. *Merxmuelleria dura* (13) could also be added without conflict, but extends into the summer rainfall region, and is more widespread than the 13 QDS from which it has been collected, and is thus excluded. Interestingly, *Merxmuelleria dura* shows affinities to the Hantam-Roggeveld sub-centres of Weimarck, and may be of historical interest.

### 11.3.3 Other Potential Phytogeographical Centres for Poaceae

A few nominal PCs, scattered in Southern Africa, each containing a single endemic, could be considered as Poaceae PCs. These include a Southern Namibia Centre (PC 13) on the Huib-Hoch Plateau and a Swartkop PC (14) nearer the coast. *Pentaschistis insulare* (1) is found on Amsterdam Island (PC 18) in the Indian Ocean, which may be as a result of a chance long distance dispersal event, with subsequent genetic drift.

## 11.4 Summary

The greatest contribution to Poaceae endemism in the CFR comes from the Danthonieae, especially the *Pentaschistis* Clade. In the CFR, PC development is most significant in the west, in the SWPP, NWPP and APPP, while the eastern PCs are comparatively small, scattered and disjunct. There are fairly well developed PCs outside the CFR, found on the Eastern Escarpment (temperate summer rainfall) and in Namaqualand (arid winter rainfall). Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, Southeastern Escarpment, NWPP, Namaqualand and APPP.

# Chapter 12: Polygalaceae (Table 48, Figure 84)

## 12.1 Introduction

Within Polygalaceae, the genus *Muraltia* is the most prominent Cape Clade (Levyns, 1964; Linder, 2003). My Polygalaceae Dataset comprises 113 *Muraltia* taxa and six *Polygala* taxa, and will essentially reflect the floristic patterns of *Muraltia*. Unlike most other Cape Clades whose highest QDS diversities are in the Caledon division (Levyns,

Table 48: Taxonomic properties of the Centres identified for the group Polygalaceae (Figure 84).

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Central Southwest Centre | 10 | 53 | 26 | 16 | 39 | 0.24 | 0.19 |
| 1.1 | Peninsula | 3 | 31 | 11 | 7 | 11 | 0.52 | 0.44 |
| 1.2 | Stellenbosch Mtns | 3 | 31 | 8 | 4 | 8 | 0.67 | 0.56 |
| 1.3 | Wemmershoek-N RZE | 3 | 21 | 2 | 1 | 3 | 1.00 | - |
| 1.4 | Remainder | 1 | 15 | 0 | 0 | 0 | - | 1.00 |
| 2 | Northwest Centre | 29 | 38 | 17 | 11 | 55 | 0.17 | 0.09 |
| 2.1 | NWC-Sandveld/Piketberg | 11 | 22 | 2 | 2 | 12 | 0.55 | 0.09 |
| 2.2 | Hexriver Mtns | 2 | 14 | 1 | 1 | 2 | 1.00 | - |
| 2.3 | Skurweberg | 1 | 11 | 1 | 1 | 1 | 1.00 | - |
| 2.4 | N Northwest Centre | 6 | 10 | 1 | 1 | 6 | 1.00 | - |
| 2.5 | SW Gifberg | 1 | 5 | 1 | 1 | 1 | 1.00 | - |
| 2.6 | Remainder | 5 | 19 | 0 | 0 | 0 | - | 1.00 |
| 3 | Hottentots-Holland-Overberg | 7 | 38 | 18 | 9 | 19 | 0.30 | 0.21 |
| 3.1 | Overberg | 5 | 31 | 10 | 5 | 11 | 0.44 | 0.30 |
| 3.2 | Hottentots-Holland | 2 | 18 | 6 | 2 | 3 | 0.75 | 0.50 |
| 4 | Karoo Mtn Centre | 19 | 26 | 9 | 8 | 33 | 0.22 | 0.11 |
| 4.1 | Witte-Klein-Boesmanspoortberg | 6 | 13 | 3 | 2 | 7 | 0.58 | 0.17 |
| 4.2 | Touwsberg-Rooiberg | 4 | 13 | 2 | 2 | 5 | 0.63 | 0.25 |
| 4.3 | Meiringspoort | 1 | 6 | 1 | 1 | 1 | 1.00 | - |
| 4.4 | Anysberg | 1 | 3 | 1 | 1 | 1 | 1.00 | - |
| 4.5 | Remainder | 7 | 14 | 2 | 0 | 0 | - | 1.00 |
| 5 | W Langeberg-Potberg | 6 | 30 | 5 | 5 | 11 | 0.37 | 0.21 |
| 5.1 | W Langeberg | 3 | 15 | 3 | 2 | 3 | 0.50 | 0.00 |
| 5.2 | Potberg | 2 | 14 | 2 | 2 | 3 | 0.75 | 0.50 |
| 5.3 | Remainder | 1 | 10 | 0 | 0 | 0 | - | 1.00 |
| 6 | West Agulhas Plains | 9 | 24 | 7 | 4 | 12 | 0.33 | 0.11 |
| 6.1 | Core West Agulhas Plains | 6 | 18 | 6 | 3 | 8 | 0.44 | 0.17 |
| 6.2 | Remainder | 3 | 15 | 1 | 0 | 0 | - | 1.00 |
| 7 | Zuurberg | 8 | 6 | 2 | 2 | 11 | 0.69 | 0.38 |
| 8 | W East Agulhas Plains | 3 | 12 | 1 | 1 | 3 | 1.00 | - |
| 9 | Central Southeast Centre | 6 | 9 | 1 | 1 | 6 | 1.00 | - |
| 10 | West Southeast Centre | 3 | 9 | 1 | 1 | 3 | 1.00 | - |
| 11 | West Coast | 2 | 7 | 1 | 1 | 2 | 1.00 | - |
| 12 | Port Elizabeth | 1 | 5 | 1 | 1 | 1 | 1.00 | - |
| 13 | East Suurberg | 2 | 1 | 1 | 1 | 2 | 1.00 | - |
| 14 | Outside | 76 | 38 | 11 | 0 | 0 | - | 1.00 |

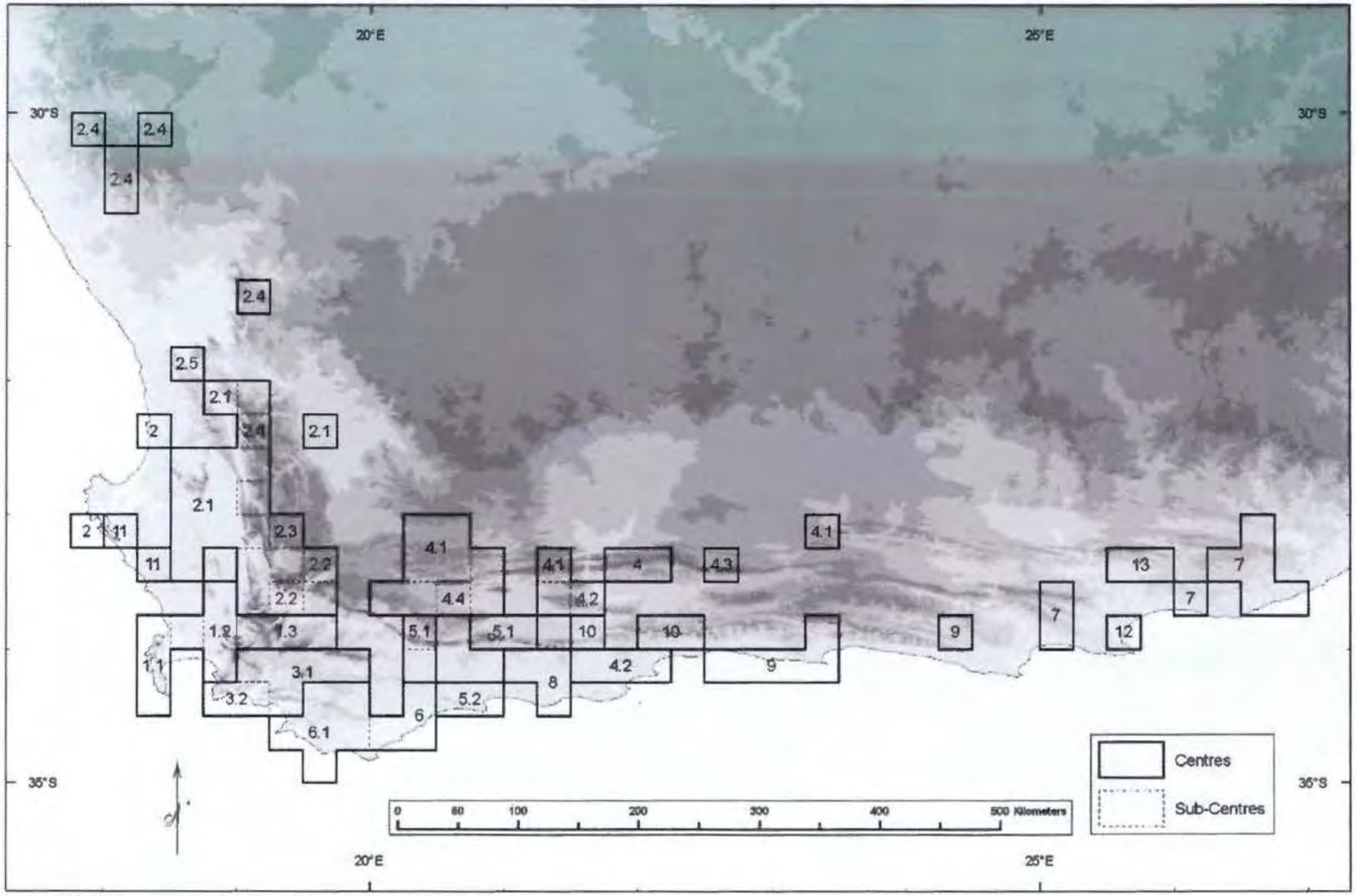


Figure 84: PC and PSC for the Polygalaceae Dataset.

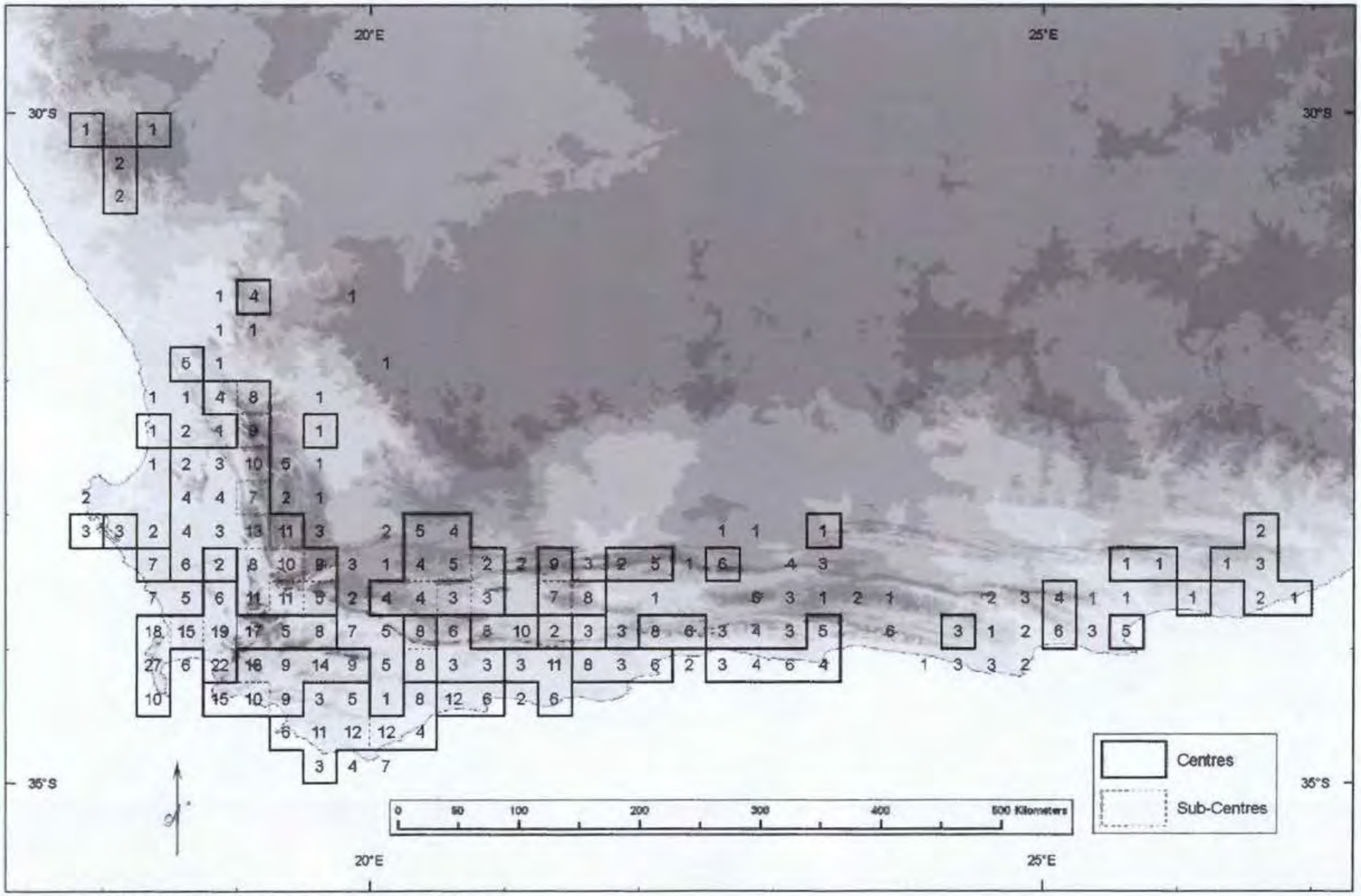


Figure 85: QDS Diversity for the Polygalaceae Dataset.

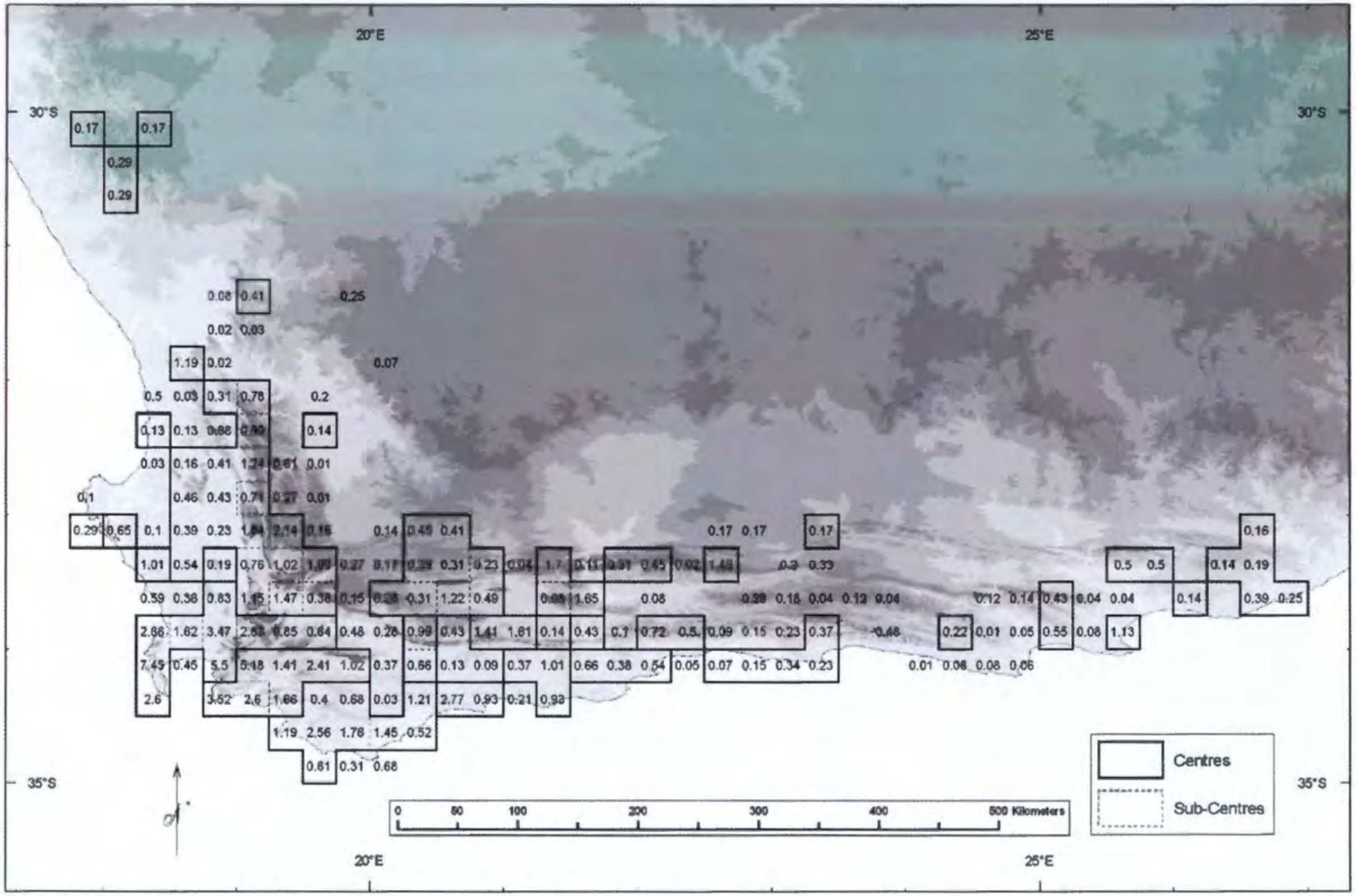
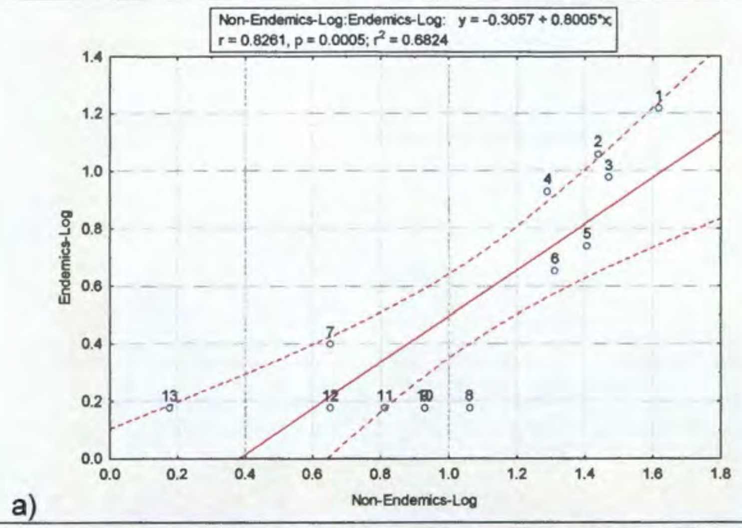
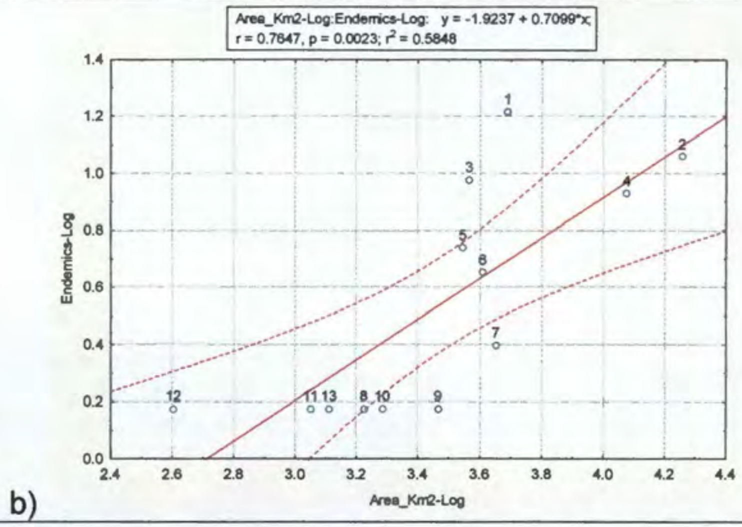


Figure 86: Sum of the Inverse Taxon Ranges for the Polygalaceae Dataset.





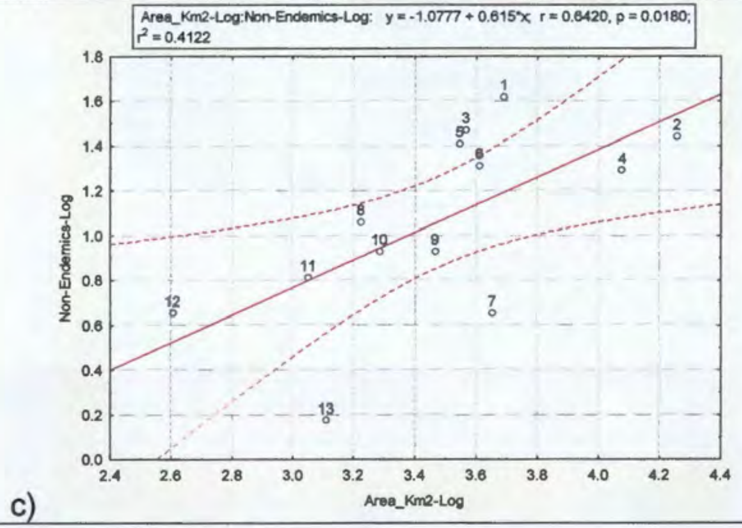


Figure 87a-c: The correlation between Endemism, diversity and area in the Polygalaceae Dataset.
The numbers on the graph correspond to the Polygalaceae PC (Table 48) and the PC Maps (Figure 84).

Table 49: Habitat Data for the Polygalaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliifs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats | Other | Unknown |
| 1 | Central Southwest Centre | 1 | | 1 | | | | | | 10 | | | | | | | | | 15 | | 2 | 4 | 1 | | 2 | 10 | | | | | | | | | | |
| 2 | Northwest Centre | 1 | | | | | | | | 6 | | 1 | | | | | | | 10 | | | 1 | | | 2 | 6 | 1 | | | | | | | | | |
| 3 | Karoo Mtn Centre | | | | | | | | | 1 | | | | | | | | | 5 | | | | | | 1 | 5 | | | | | | | | | | |
| 4 | Hottentots-Holland-Overberg | | | | | | | | | 5 | | | 1 | | | | | | 8 | | 1 | 1 | | | | 6 | | | | | | | | 1 | | |
| 5 | W Langeberg-Potberg | | | | | | | | | 5 | | | | | | | | | 5 | | | | | | | 4 | | | | | | | | | | |
| 6 | West Agulhas Plains | | | | | | | | | 2 | | | | 2 | | | | | 2 | | 2 | | | | | | | | | | | | | | | |
| 7 | Zuurberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 8 | W East Agulhas Plains | 1 | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | |
| 9 | Central Southeast Centre | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 10 | West Southeast Centre | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | |
| 11 | West Coast | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | |
| 12 | Port Elizabeth | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 13 | East Suurberg Mountains | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Totals | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 29 | 0 | 1 | 1 | 4 | 0 | 0 | 0 | 0 | 46 | 0 | 7 | 6 | 1 | 0 | 5 | 32 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |

1938, 1964), I found that *Muraltia* has its highest QDS diversity on the Cape Peninsula (Figure 85). However, the second and third highest QDS diversity scores for *Muraltia* occur in the QDSs with the Hottentots-Holland and Stellenbosch Mountains, which is more typical of Cape Clades. Whether this represents over collection on the Peninsula, or is a real pattern, still needs to be determined. *Muraltia* follows the typical Cape Clade pattern (Levyns, 1938, 1964) of decreasing in diversity to the north and east, from this south-western area of the CFR.

The geographical positioning of Polygalaceae phytogeographical centres and its sub-centre boundaries are slightly atypical. They indicate low altitude biotic elements, especially on littoral flats, as observed in Asteraceae, Fabaceae, Geophyte and the RDL Taxa Datasets of my study.

The two main SWPP PCs for Polygalaceae, the Central Southwest Centre (PC 1) and the Hottentots-Holland-Overberg Centre (PC 3), are relatively small, geographically, but have the highest and second highest diversity, and the highest and third highest endemism values of all the PCs respectively (Table 48). As is common in other Cape Clades, the Northwest Centre (PC 2) is ranked second, but occupies more than double the area of the richer Central Southwest Centre (PC 1). The Karoo Mountain Centre (PC 4) for Polygalaceae performs surprisingly well, both in terms of diversity and endemism; especially considering it occupies fewer QDSs than the Northwest Centre (PC 2), and only has one less endemic taxa (Table 48).

There were a number of erroneous, disjunct localities in the dataset I analysed, which I verified in the Cape Plants Conspectus (Goldblatt and Manning, 2000), and if the questionable localities were found to be erroneous here, they were deleted.

### 12.1.1 The relationship between endemism, diversity, and area in the Polygalaceae PCs

In my Polygalaceae Dataset, a significant and strong positive relationship ($r^2 = 0.68$, $p=0.0005$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 87a). This significant relationship also occurs between the number of endemics and the geographic size of the PC ($r^2 = 0.58$, $p=0.002$) (Figure 87b), and between the number of non-endemics and the geographic size of the PC ($r^2 = 0.41$, $p=0.02$) (Figure 87c), but gets progressively weaker.

None of the regressed endemic/non-endemic PC data points are very far from the 95% confidence lines in the Polygalaceae Dataset (Figure 87a). The Northwest Centre (2) and the Karoo Mountain Centre (4) have slightly more endemics than predicted from their numbers of non-endemic taxa, while the western East Agulhas Plains (8) is slightly underrepresented (Figure 87a). Polygalaceae is poorly represented in the eastern CFR, with the Central Southeast Centre (9) having fewer endemics than predicted by PC area. The East Suurberg Mountains (13) has lower non-endemic taxa than predicted from the PC area.

The two main SWPP PCs, the Central Southwest Centre (1) and the Hottentots-Holland-Overberg Centre (3) both have significantly higher than expected numbers of endemic (Figure 87b) and non-endemic (Figure 87c) taxa than expected from their PC area. This again highlights the importance and significance of this area within the core CFR. Conversely, the Zuurberg (PC 7) has less than expected numbers of endemic (Figure 87b) and non-endemic (Figure 87c) taxa than expected from its PC area, and is a peripheral floristic unit of the CFR.

## 12.2 CFR Phytogeographical Centres

### 12.1.1 The Southwest Phytogeographical Province

In my Polygalaceae Dataset, the SWPP has by far the greatest number of endemics of all the traditional CFR phytogeographical areas (Goldblatt and Manning, 2000; Weimarck, 1941). The Central Southwest Centre (PC 1) alone has approximately 1.45 times more Polygalaceae endemics than the next richest centre, in a PC that is 34.5% smaller geographically. In addition, the other major SWPP PC, the Hottentots-Holland-Overberg Centre (PC 3), has the third highest number of Polygalaceae endemic taxa, in an even smaller area (Table 48). Combining these two PCs into a single phytogeographical unit, results in a combined total of 33 endemic Polygalaceae Taxa. This represents more than 2.27 times more Polygalaceae endemic taxa than the next richest Polygalaceae centre, the Northwest Centre (PC 2). This combined SWPP PC is 58.6% the geographic size of the Northwest Centre (PC 2). In both these SWPP PCs (1 and 3), there are more endemic taxa than QDSs, resulting in a very high endemism to area ratio. Furthermore, the diversity of these combined PCs (1 and 3) is 71 taxa, which is nearly double the diversity of any other PC that was identified in the Polygalaceae. These figures for the SWPP, both individual PCs and combined, illustrate how remarkable the SWPP is in terms of diversity and endemism for Polygalaceae (and for many other plant families) in the already remarkable CFR.

The boundary between the two SWPP PCs is slightly anomalous. Usually the Hottentots-Holland QDS (3418BB) is combined with the Kogelberg QDS (3418BD) to the south, but here it is grouped with the Stellenbosch Mountains to the north. The West Agulhas Plains Centre (PC 6) extends northwards, including the East Kleinriviersberge in the APPP. There is no independent RZE phytogeographical unit, as in the Combined Dataset and in other more montane clades. Instead, the Overberg Sub-Centre (PSC 3.1) to the south and the Wemmershoek-North RZE Sub-Centre (PSC 1.3) to the north, are divided along the ridge of the RZE. A similar pattern was observed in the Fabaceae, Geophyte and RDL Taxa Datasets.

Although the boundaries of the Peninsula Sub-Centre (PSC 1.1) are congruent with most other datasets, the boundaries of the remaining two PSCs are not. *Muraltia alba* (3) is nearly endemic to the Stellenbosch Mountains Sub-Centre (1.2), but shares part of its QDS distribution (3319CC) with *Muraltia ferox* (3) in the Wemmershoek-N RZE Sub-Centre (PSC 1.3). The latter sub-centre delimitation is unusual, as its QDSs are usually separated into different floristic areas in most of my other datasets (compare with the Combined Dataset). It is deeply incised by low altitude river valleys and in most of my datasets, the western QDSs are typically included in the Stellenbosch-Bainskloof Mountains, and its eastern QDSs are frequently incorporated into the RZE.

In the Hottentots-Holland-Overberg Centre (3), the Overberg Sub-Centre (3.1) is atypical and seems to emphasise the lower lying areas south of the RZE and north of the Kleinrivierberge as a PCs, rather than the RZE itself. This is due to *M. caledoniensis* (4) and *M. concave* (2), of which the former occupies lower altitude hills and slopes (Table 49). However, in Polygalaceae, the Overberg Sub-Centre (PSC 3.1) contains no shale or clay endemics (Table 49). The Kogelberg and its eastern adjoining QDS are joined together, which is fairly common in other datasets. However, there does not appear to be any significant PC development on the Kleinrivierberge further east of this QDS, which is unusual for a Cape Clade.

*Muraltia aspalathoides* (4) is nearly endemic to the Overberg Sub-Centre, but has an outlying locality in the Quoin Point QDS (a fairly common pattern), which places it in conflict with *Muraltia gilletiae* (3), of the Core West Agulhas Plains Sub-Centre. *M. gilletiae* is favoured in the PC delimitation, due to its smaller range. Interestingly, both occur on sandstone slopes, so there is no edaphic separation of ranges in the QDS that they share.

There is a small limestone (Table 49) PC, due to *Muraltia harveyana* (2), between Langebaan and Yzerfontein, along the West Coast (PC 11).

### 12.1.2 The Northwest Phytogeographical Province

PC development in the NWPP is well defined, by a single, nearly continuous centre, the Northwest Centre (PC 2), except for two disjunctions. These occur over the lower lying Doring River Valley, between the Cedarberg-Gifberg and the Nieuwoudtville Escarpment and the larger disjunction between Nieuwoudtville and the Kamiesberg. It is common in Cape Clades for the NWPP to have a high number of endemics, although not as high as the SWPP. Polygalaceae is no exception, with the Northwest Centre (PC 2) being ranked joint second for diversity and second for endemism. The Northwest Centre (PC 2) is the largest PC I identified for Polygalaceae (at 29 QDSs, see Table 48) and this contributes to its high number of endemic taxa and ranking.

Polygalaceae endemic taxa are noticeably absent from the eastern Cedarberg, Skurweberg, Swartruggens and Swartrugberge, and even the central Witteberg. This gap in assigning QDSs to Polygalaceae PCs extends all the way to the APPP in the south, and provides a clear separation between the westerly PCs (in the NWPP and SWPP), and the central PCs (the KMPP and LBPP). QDS taxon diversity in this area is also relatively low (Figure 85) and has low inverse weighting scores (Figure 86), in comparison to the surrounding QDSs that have been assigned to the PCs surrounding it. This may explain why these QDSs are not assigned to a PC. Whether *Muraltia* is genuinely absent from these areas, or if it has merely been under collected here, still needs to be determined. *Muraltia macrocarpa* (6) is a fairly range-restricted taxon that occupies the "gap" between the KMPP and the NWPP, but is also found in both these phytogeographical provinces. It is therefore not used in extending or enlarging either of these PCs due to conflict.

As in a few of my other datasets (Geophytes, Rutaceae, Orchidaceae, Poaceae, Rosaceae and Rutaceae) the boundary between the SWPP PC and the NWPP PC for Polygalaceae does not coincide with the Berg River as in my Combined Dataset, or the literature (Goldblatt and Manning, 2000; Weimarck, 1941). In Polygalaceae, the NWPP seems to extend as far south as Du Toits Kloof. The reason and significance of this incongruence is unknown, but it seems to indicate that the Berg River may not be an effective barrier to gene flow in all clades, especially those with low altitude elements, and therefore it does not always correspond to a floristic boundary.

Sub-Centre development in the Northwest Centre (PC 2) is poor. This is mostly due to a marginal overlap between different biotic elements on the periphery of their distribution ranges thus causing conflict. This may be resolved with higher resolution spatial data. In terms of area size, there is a well-developed low altitude sub-centre, the NWPP-Sandveld/Piketberg Sub-Centre (PSC 2.1), due to *Muraltia arachnoidea* (5), which occurs on lower sandstone slopes (Table 49), and *Muraltia origanoides* (7), which occurs mostly west of the NWPP Mountains. Interestingly, these two endemic taxa only share a single QDS, 3218DD. *Muraltia arachnoideae* (5) is situated in the north, while *M. origanoides* (7), occurs further south. The establishment of this sub-centre is largely at the cost of a more developed mountain montane phytogeographical area. The southern montane sub-centres (PSCs 2.2 and 2.3) are nearly all each restricted to single a QDS. However, there are numerous montane elements that could group these individual montane QDSs into a single, larger, consolidated floristic area. These higher altitude taxa are in conflict with the low altitude endemics in the NWPP-Sandveld/Piketberg Sub-Centre (PSC 2.1) in 3219CA and 3319AA, and the low altitude floristic unit is upheld at the expense of the high altitude floristic area due to higher total endemism. These montane biotic elements have been tabulated (Table 50).

Table 50: A list of potential montane Polygalaceae NWPP endemics.

| *Taxon* | Distribution |
|---|---|
| *Muraltia pillansii* (5) | Between the Groot Winterhoek and Pakhuis mountains |
| *Muraltia crassifolia* (2) | Distributed from the southern Hexriver-West Langeberg Mountains in the south to the Pakhuis Mountains in the north |
| *Muraltia polyphylla* (6) | Occurs from the Limietberg-SW Hexriver Mountains in the south to the Cedarberg in the north. |
| *Muraltia acicularis* (8) | May tentatively also be included in this group, but is slightly more widespread, and not endemic to the NWPP, with one locality in 3319CC, which is in Wemmershoek-N RZE Sub-Centre (PSC 1.3). |

In the northern parts of the NWPP are two sub-centres: the Southwest Gifberg (PSC 2.5), which is the typical area for PC development for most Cape Clades; and the North Northwest Mountains Sub-Centre (2.4), a widespread and disjunct PSC which extends from the northern Cedarberg, over the Nieuwoudtville Escarpment, to the Kamiesberg, where it is centred. This association of the Kamiesberg to the NWPP agrees with the phytogeographical classification of Weimarck (1941).

### 12.2.3 The Karoo Mountains Phytogeographical Province

It is uncharacteristic for the KMPP PC to contain such a high proportion of endemics in a Cape Clade, relative to the SWPP and NWPP. It occupies a smaller geographical area than the NWPP PC, making its levels of diversity and endemism more remarkable. However, the PC is fairly disjunct, consisting of mountainous QDSs and may even include LBPP elements. It has only two less Polygalaceae endemics than the NWPP, but it is possible that the number of endemic taxa may be reduced, due to taxonomic errors.

Another unusual feature is the extension of the Karoo Mountain Centre (PC 4) and the Rooiberg-Albertinia Sub-Centre (PSC 4.2) into the eastern Langeberg Plains, due to *Muraltia cliffortiafolia* (4). This is reminiscent of the patterns observed in *Erica* and the Geophyte Datasets, where there appears to be a phytogeographical north-south link, in the region of the Gouritz River. The Witte-Klein-Boesmanspoortberg Sub-Centre (PSC 4.1) is centred on the Witteberg, but includes disjunct localities in the Klein Swartberg (3321AD) and Boesmanspoortberg (3323AB), both due to *Muraltia vulnerans* (6). The remaining two sub-centres each have a single endemic occupying a single QDS. In general, the sub-centre boundaries are not very resolved geographically in the Karoo Mountain Centre and there are numerous disjunctions, and a few instances of interdigitization.

### 12.2.4 The Langeberg Phytogeographical Province

PC development for Polygalaceae in the LBPP is poor, with many disjunctions. The West Langeberg-Potberg Centre (PC 5) is the only PC that shows significant development in the Langeberg, with only the West Langeberg Sub-Centre (PSC 5.1) occurring in the LBPP. The remaining sub-centre, the Potberg Sub-Centre (PSC 5.2), is found much further to the south and is centred on the Potberg Mountains. The pattern here appears to be similar to that of the Rooiberg-Albertinia Sub-Centre (PSC 4.2); and is joined together due to *Muraltia acerosa* (5). The peripheral parts of the Langeberg have been included in the surrounding PCs, such as the Western East Agulhas Plains, the West Southeast Centre (PC 9) and especially the Rooiberg-Albertinia Sub-Centre (PSC 4.2).

*Muraltia plumosa* (5) is nearly endemic to the West Langeberg-Potberg Centre (PC 5), but is in conflict with *Muraltia gilletiae* (3) in 3419DC, of the Central Southwest Centre (PC 1).

### 12.2.5 The Agulhas Plains Phytogeographical Province

There is extremely good PC development in the West Agulhas Plains (PC 6), especially in the core sub-centre (PSC 6.1). Two of the endemics occur on sandstone and two on limestone (Table 49). The West Eastern Agulhas Plains (PC 8) form an independent PC, which is disjunct across the Potberg and contains the limestone endemic *Muraltia barkerae* (3), suggesting ecological affinities to the western APPP.

*Muraltia pungens* (7) is nearly endemic to APPP, but has conflict with *M. schlechteri* (3) in 3419BB, which is endemic to the Central Southwest Centre (PC 1). The latter configuration is favoured due to its smaller taxon range.

### 12.2.6 The Southeast Phytogeographical Province

As with many other traditional CFR Clades analysed here (Bruniaceae, Poaceae and to a lesser extent, Restionaceae, Rosaceae and Proteaceae), the SEPP shows very poor PC development, except surprisingly in the Zuurberg (as defined by Weimarck). There are five impoverished PCs in the SEPP: two in the west and two in the east, each with a single endemic taxon. The remaining PC, the Zuurberg PC (7), is centred in the Zuurberg floristic region, east of the Sundays River, but it also has a disjunct area on the Groot Wintershoekberg-Vanstadensberg. Further collecting may result in some coalescence of these three eastern PCs.

The PCs in the west of the SEPP generally cover a larger area than those in the east. The Central Southeast Centre (PC 9) is situated mostly in Weimarck's Knysna Interval.

The remaining Polygalaceae PCs are more typical, although the West Southeast Centre (PC 10) extends the potential Western SEPP even further west than in the Combined Dataset, although this is only by a single QDS.

*Polygala bowkerae* (1) occurs around Port Elizabeth, just inside Weimarck's Cockscomb Sub-Centre (PC 12), while *Muraltia lancifolia* (2) occurs to the north, in the East Zuurberg (PC 13). The Polygalaceae endemics of the Zuurberg PC (7) occur mostly in Weimarck's Zuurberg Sub-Centre, but both have outliers in his Cockscomb Sub-Centre,

## 12.3 Non-CFR Phytogeographical Centres

Although *Muraltia*, and *Polygala* occur outside the CFR, these extraneous taxa were not included in this analysis.

## 12.4 Summary

*Muraltia* is by far the largest contributor of endemics from Polygalaceae in the CFR and has long been considered a Cape Clade (Levyns, 1964; Linder, 2003). There is evidence from the positions of PC boundaries that there are numerous lower altitude endemic taxa, as well as more numerous montane endemics, which may be phytogeographically antagonistic in establishing PCs at the QDS scale of resolution. Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, NWPP, KMPP, LBPP and APPP.

# Chapter 13: Proteaceae: Proteeae (Table 51, Figure 89)

## 13.1 Introduction

The activities of the Protea Atlas Project (http://protea.worldonline.co.za/default.htm) make Proteaceae the most comprehensively recorded geographical dataset in my study. This large collecting effort has most probably resulted in relatively low numbers of taxa being restricted to one and two QDSs, and the increase in the numbers of taxa occurring in three and four QDS taxa (in comparison to other datasets analysed in my study). Collections from peripheral populations, or taxa that "just overlap" into neighbouring QDSs may have been neglected in less extensively collected plant groups, but recorded in Proteaceae, due to the massive collecting effort. Thus, the numbers of taxa that are very range-restricted (i.e. recorded from a single QDS) are decreased and the frequency of intermediate range-restricted taxa may have been increased relative to other datasets.

Possible biological reasons for the relatively large number of endemics and range-restricted taxa in Proteaceae may be due to low dispersal capabilities and adaptation to regular burning. This has resulted in limited gene flow concomitant with high generation turnover (Goldblatt and Manning, 2002).

At a relatively early stage in modern Cape biogeography, Levyns (1964) recognised that the distribution of Proteaceae in the CFR followed the traditional Cape distribution pattern very closely. The boundaries of the PCs in Proteaceae, as identified here, follow a nearly traditional montane, fynbos phytogeographical pattern of the CFR (Weimarck; Goldblatt and Manning, 2000). This is particularly so in the west, although there are a few anomalies. Both the traditional Southwest and Northwest Centres are divided into numerous smaller PCs. Proteaceae displays typical mesic montane phytogeographical patterns. However, there are well-developed lowland areas associated with the mountainous regions, for example, the East Langeberg-West Outeniqua (PC 7).

### 13.1.1 Taxonomy and monophyly of Cape Proteaceae

Of the 14 indigenous Proteaceae genera in Southern Africa, all but *Brabejum* belong to the tribe Proteeae (Johnson and Briggs, 1975). Most are centred in the CFR, especially in the southwest centre in the Caledon Division (Levyns, 1964), aside from *Faurea*, which is found in the summer rainfall region. *Protea* is the only other genus that is well-represented outside the CFR, although more than half of *Protea* taxa are still endemic to the CFR. Although it has never been disputed that Proteeae is a significant Cape Clade, its origins remain controversial. Some biogeographers advocate an African origin (Levyns, 1964), while others suggest a Gondwanan origin. Interpretation depends largely on the taxonomic, or clade level being discussed. While Tribe Proteeae is African, Family Proteaceae is ultimately Gondwanan. My dataset consists of all Proteeae represented in the CFR, the single *Brabejum* taxon in the CFR and the single *Faurea* taxon represented in the CFR.

### 13.1.2 Comparisons of previously floristic studies on Cape Proteaceae

Rebelo and Siegfried (1990) generated a map on Proteaceae Phytogeographical Centres (Figure 88). In general, there is fairly good floristic congruence between the Proteaceae Chorion map of Rebelo and Siegfried (1990) and the Cape Flora map of Goldblatt and Manning (2000). The most significant spatial differences occur at the higher floristic hierarchical levels (zones, districts and provinces) of Rebelo and Siegfried (1990). Rebelo and Sigfried (1990) group their Bredasdorp and Mossel Bay Districts within their South-western Province, and do not recognise an independent Agulhas Plains Centre, while Goldblatt and Manning (2000) do. Rebelo and Sigfried's (1990) grouping of Bredasdorp District with the South-western Province is strikingly similar to the classification of Weimarck. The rest of Rebelo and Siegfried's South-western Province (1990) corresponds largely with the Southwest Centre of Goldblatt and Manning (2000). Similarly, there is fairly good congruence between the North-western Province (Rebelo and Sigfried, 1990) and the Northwest Centre (Goldblatt and Manning, 2000), and between the Inland Mountain Province (Rebelo and Sigfried, 1990) and the Karoo Mountain Province (Goldblatt and Manning, 2000).

There is less congruence in the Langeberg region, which Goldblatt and Manning (2000) identify as a phytogeographical centre in its own right. However, Rebelo and Siegfried (1990) classify it as part of their larger Coastal Mountain Complex, but exclude the lower lying regions to the south of the Central Langeberg, which remain unclassified. The Coastal Mountain Complex (Rebelo and Sigfried, 1990) corresponds more closely to a combined Langeberg-Southeast Centre of Goldblatt and Manning (2000). However, there are other notable differences. The Southeast Centre of Goldblatt and Manning (2000) extends from approximately Mossel Bay to Port Elizabeth, while in Rebelo and Siegfried (1990), the Coastal Mountain Complex extends from the LBPP to past the Krom River, and includes three distinct areas. Subdivision of the Coastal Mountain Complex occurs between the LBPP and SEPP, then at the Storms River Mouth. From the Krom River east including all of Weimarck's Zuurberg Sub-Centre is the South-eastern Province of Rebelo and Sigfried (1990), which terminates near the Great Fish River.

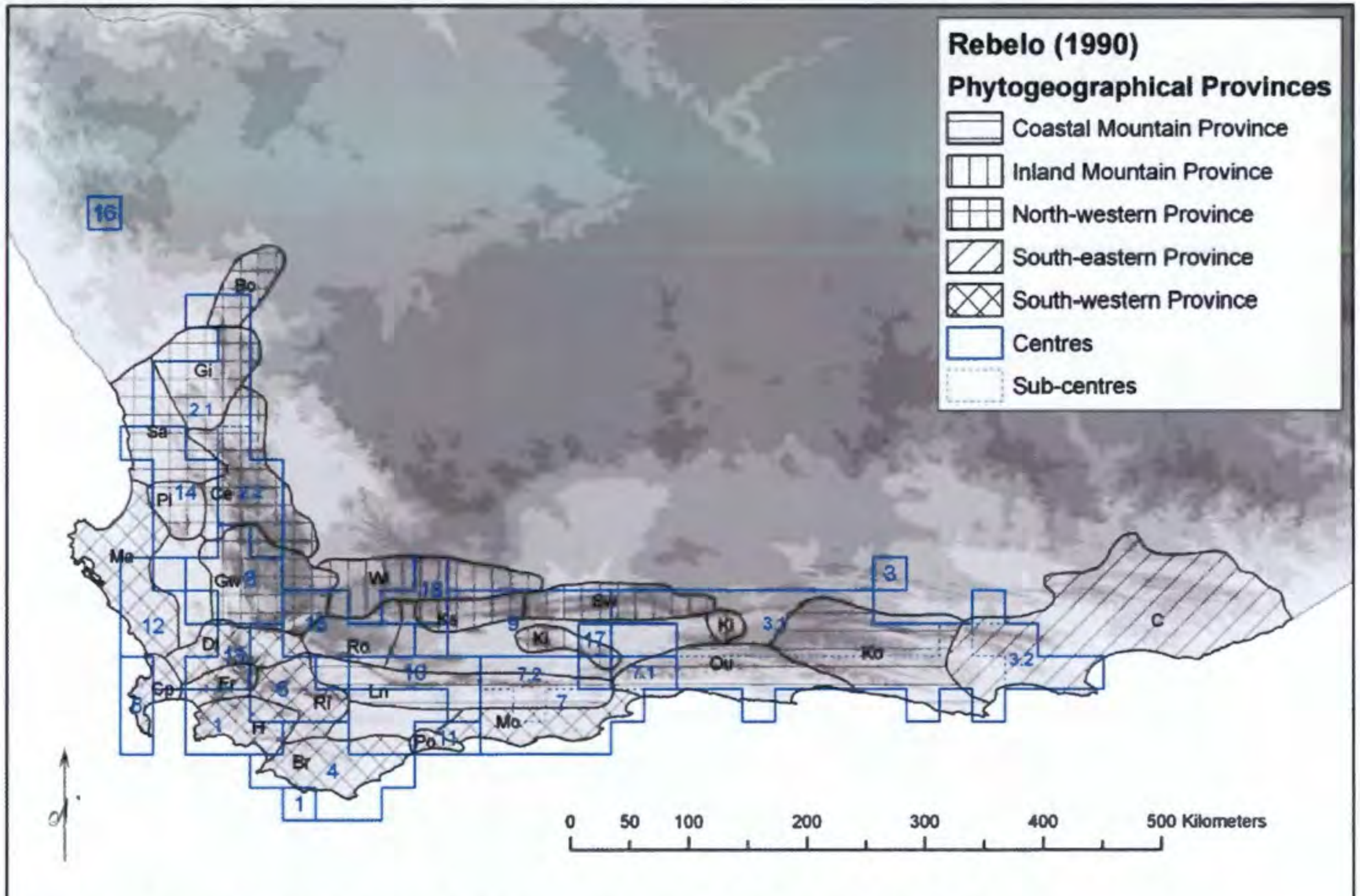


Figure 72: Centres of Endemism in Proteaceae (Rebelo, 1990), compared to our floristic units (in blue).

Cp) Peninsula District, Fr) Franshoek District, H) Houwhoek District, Ri) Riviersonderend District, Dt) Du Toits Kloof District, Gw) Groot Winterhoek District, Ln) Langeberg District, Br) Bredasdorp District, Po) Potberg District, Pi) Piketberg District, Ma) Malmesbury District, Wi) Witteberg District, Ks) Klein Swartberg Zone, Ce) Cedarberg District, Sa) Sandveld Zone, Gi) Gifberg Zone, Bo) Bokkeveld Zone, Mo) Mosselbay District, Sw) Swartberg Zone, Ou) Outeniqua District, Ki) Karoo Island Zone, Ko) Kouga District, C) Cockscomb District

Figure 88: Phytogeographical Centres in Proteaceae (Rebelo, 1990).

Table 51: Taxonomic properties of the Centres identified for the group Proteaceae (Figure 89).

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Hottentots-Kleinrivier | 6 | 159 | 42 | 17 | 49 | 0.48 | 0.45 |
| 2 | Northern Mtns | 16 | 85 | 19 | 13 | 46 | 0.22 | 0.16 |
| 2.1 | Pakhuis-Gifberg-Nieuwoudtville | 10 | 42 | 8 | 6 | 19 | 0.32 | 0.18 |
| 2.2 | Cedarberg | 6 | 77 | 9 | 4 | 15 | 0.63 | 0.50 |
| 3 | Southeast Centre-E Karoo Mtns | 37 | 70 | 27 | 11 | 114 | 0.28 | 0.21 |
| 3.1 | E Karoo-N Central Southeastern Mtns | 23 | 59 | 15 | 3 | 33 | 0.48 | 0.22 |
| 3.2 | Groot-Winterhoekberge-Elandsberge | 5 | 28 | 1 | 1 | 5 | 1.00 | - |
| 3.3 | Remainder | 16 | 53 | 9 | 0 | 0 | - | 1.00 |
| 4 | Bredasdorp | 9 | 94 | 21 | 8 | 28 | 0.39 | 0.30 |
| 5 | Peninsula | 3 | 70 | 13 | 8 | 17 | 0.71 | 0.67 |
| 6 | Riviersonderend | 6 | 152 | 20 | 6 | 13 | 0.36 | 0.23 |
| 7 | E Langeberg-Outeniqua | 14 | 88 | 15 | 6 | 21 | 0.25 | 0.10 |
| 7.1 | Outeniqua | 2 | 53 | 5 | 3 | 5 | 0.83 | 0.75 |
| 7.2 | E Langeberg | 4 | 66 | 5 | 2 | 6 | 0.75 | 0.50 |
| 7.3 | Remainder | 8 | 41 | 3 | 0 | 0 | - | 1.00 |
| 8 | Groot Winterhoek | 6 | 108 | 15 | 5 | 14 | 0.47 | 0.33 |
| 9 | Klein and W Groot Swartberg-Rooiberg | 9 | 53 | 7 | 4 | 18 | 0.50 | 0.33 |
| 10 | West and Central Langeberg | 5 | 70 | 6 | 4 | 7 | 0.35 | 0.13 |
| 11 | Potberg | 3 | 53 | 4 | 4 | 8 | 0.67 | 0.56 |
| 12 | Malmesbury Centre | 7 | 79 | 13 | 2 | 12 | 0.86 | 0.71 |
| 13 | Stellenbosch-Bainskloof | 3 | 135 | 9 | 2 | 3 | 0.50 | 0.00 |
| 14 | Piketberg-Olifantsrivierberg | 8 | 60 | 6 | 2 | 10 | 0.63 | 0.25 |
| 15 | E Hex-W Langeberg | 6 | 89 | 4 | 2 | 7 | 0.58 | 0.17 |
| 16 | Kamiesberg | 1 | 3 | 2 | 2 | 2 | 1.00 | 1.00 |
| 17 | Gamka | 1 | 17 | 2 | 1 | 1 | 1.00 | - |
| 18 | Witteberg | 3 | 32 | 1 | 1 | 3 | 1.00 | - |
| 19 | Outside | 69 | 153 | 1 | 0 | 0 | - | 1.00 |

## Comparisons between my Study and Previously Floristic Studies on Cape Proteaceae

My study shows good congruence with both the above floristic maps, once again, particularly the boundaries of the lower floristic units (PSCs, PCs). At These floristic levels, my boundaries are similar to the map of Rebelo and Siegfried (1990), particularly in the two western-most centres. In my study, the Langeberg is considerably enlarged and in the east, it includes substantial lowland areas to the southeast. I retrieved west-east divisions in both the Langeberg Centre (PCs 10 and 7) and Groot Swartberg Centre (PCs 9 and 3). However, in the previous studies (Goldblatt and Manning, 2000; Rebelo and Siegfried, 1990; Weimarck) they both form continuous areas respectively.

In my study, the SEPP-East Karoo Mountains Centre (PC 3) is enlarged, and is equivalent to the combined Outeniqua and Kouga Districts of Rebelo and Siegfried (1990). My Groot-Winterhoekberge-Elandsberge Sub-Centre (3.2) boundary corresponds to the western boundary of their South-eastern Province (Cockscomb District). My East Langeberg-Outeniqua Centre (7) overlaps the central portions of the Coastal Mountain Province (Langeberg District) and extends south into their Southwest Province (Mossel Bay District).

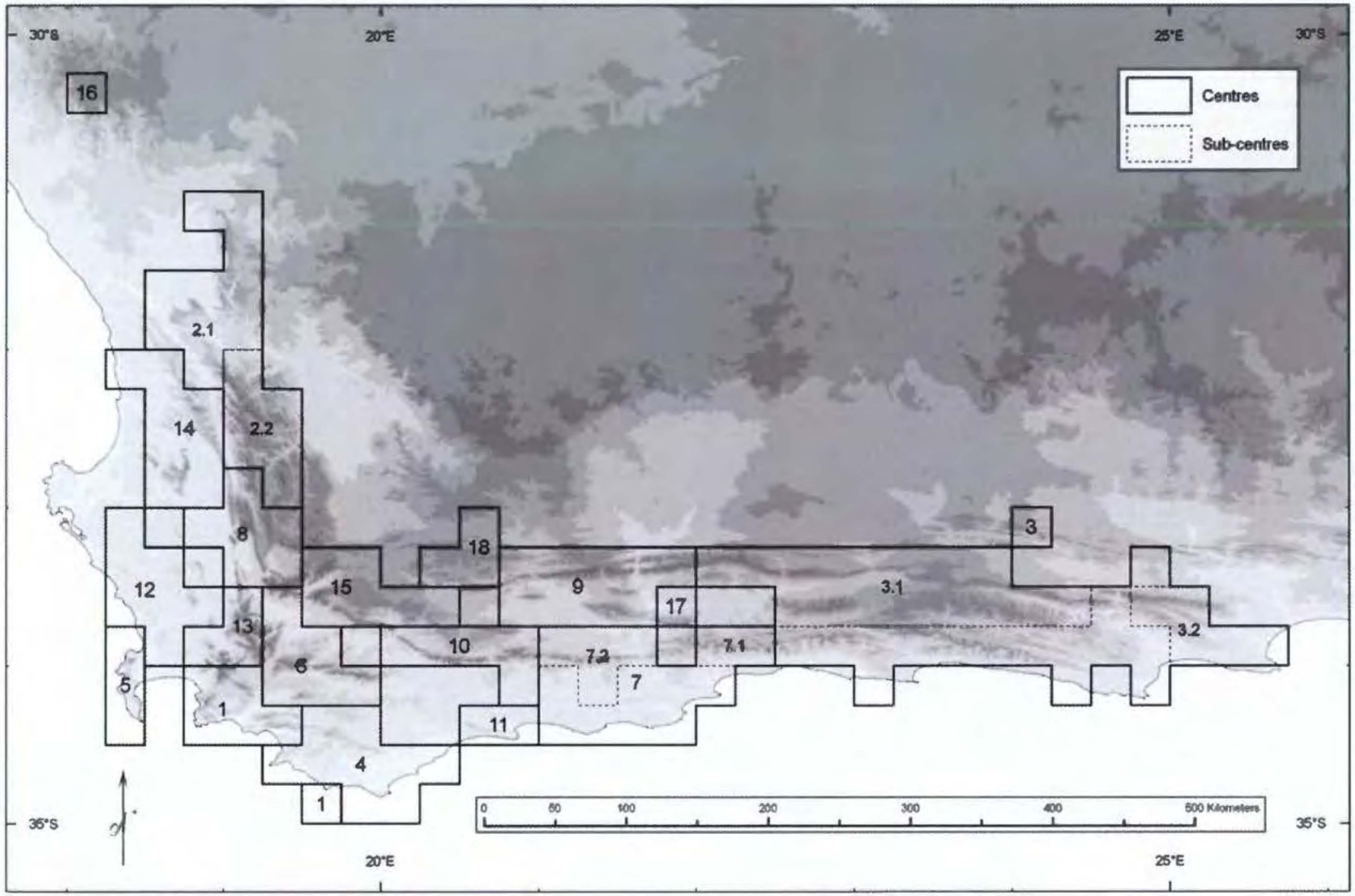


Figure 89: PC and PSC for the Proteaceae Dataset.

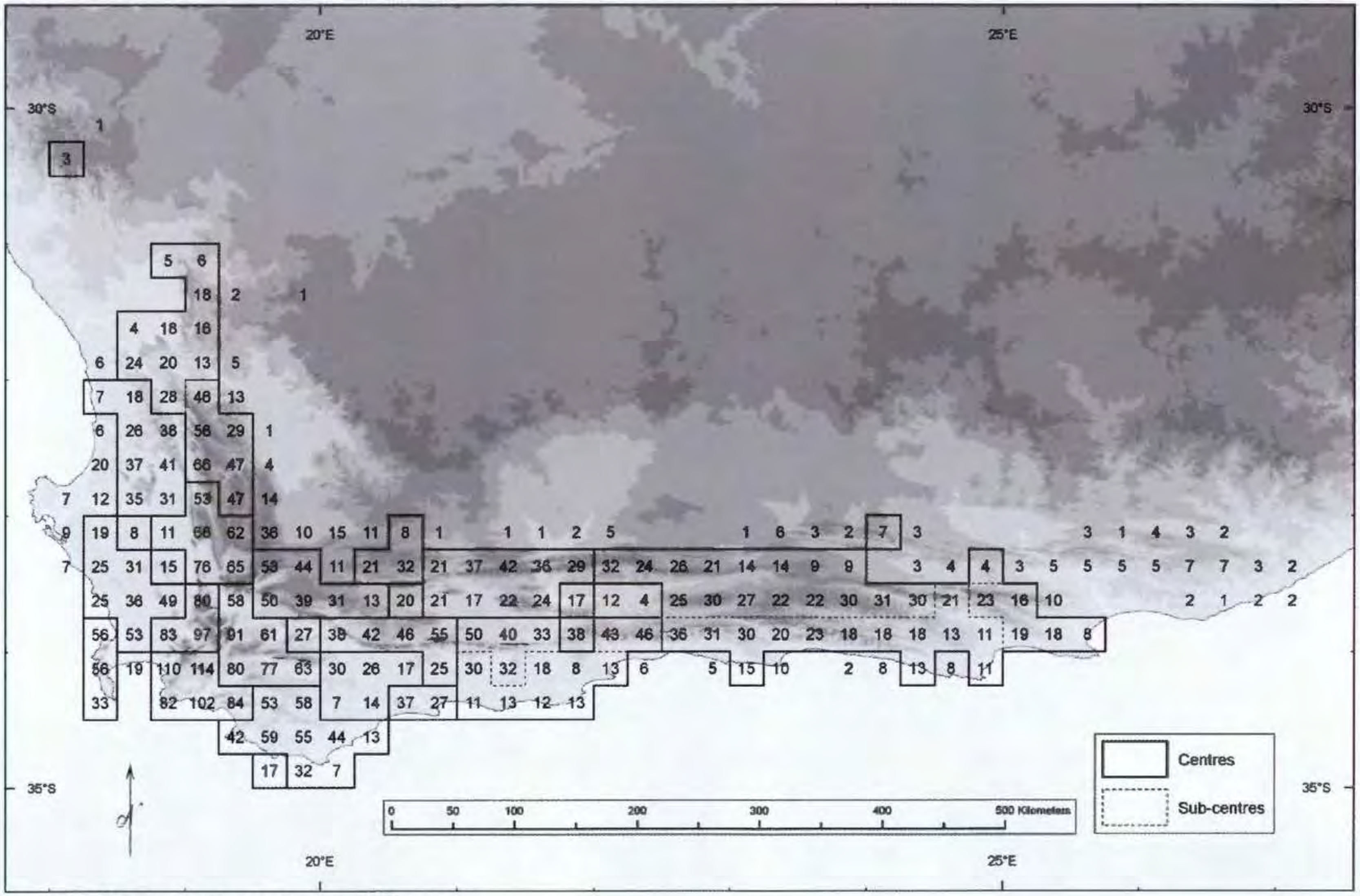


Figure 90: QDS Diversity for the Proteaceae Dataset.

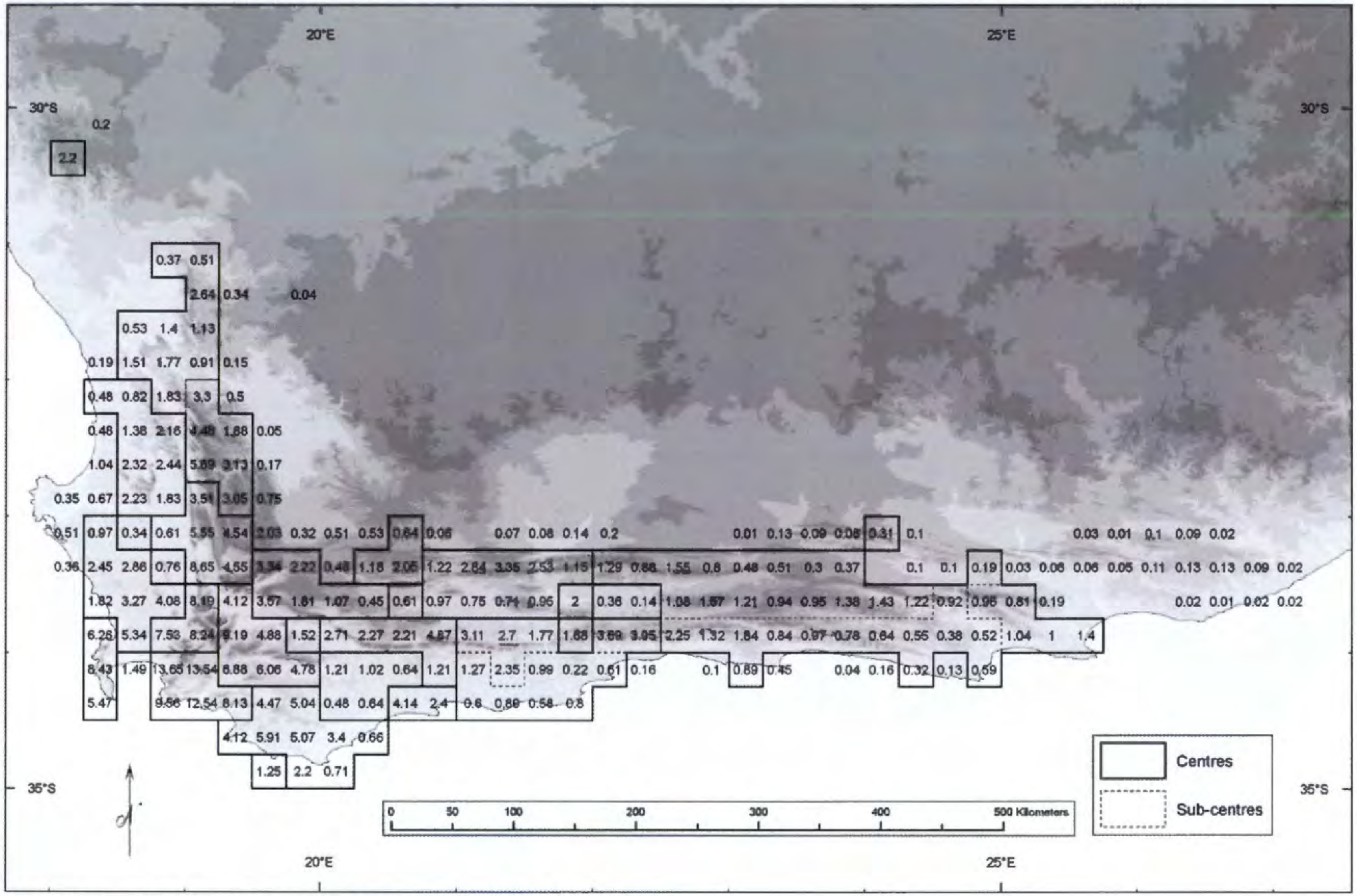


Figure 91: Sum of the Inverse Taxon Ranges for the Proteaceae Dataset.

Table 52: Habitat Data for the Proteaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliffs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats | Other | Unknown |
| 1 | Hottentotts-Kleinrivier | 1 | | 1 | 10 | 5 | 4 | | | 7 | 2 | | | | | 1 | 1 | | 7 | | 1 | 2 | 6 | 1 | | 1 | 2 | | | | | | | | | |
| 2 | Northern Mtns | | | 2 | 1 | 6 | 5 | 4 | | 9 | | | | | | | | 8 | 4 | | | 1 | | | 1 | 2 | 4 | | | | | | | | | |
| 3 | Southeast Centre-E Karoo Mtns | | | 3 | 3 | 4 | 6 | 3 | 2 | 9 | 1 | | | | | | | 1 | 10 | | | | | | 2 | 2 | | | | 1 | | | | | | |
| 4 | Peninsula | | | | 7 | 2 | | | | 4 | | | | | | | | | 6 | | | 3 | 1 | 1 | 1 | 3 | 1 | | | | | | | | | |
| 5 | Bredasdorp | | | | 6 | | | | | 1 | | 2 | | 1 | | 1 | | | 3 | 1 | | 4 | | | | 1 | 1 | | | | | | | 1 | | |
| 6 | Riviersonderend | | | 1 | | 4 | 3 | | | 5 | | | | | | | | 1 | 5 | | | | | | | | 1 | | | | | | | | | |
| 7 | Groot Winterhoek | | | 1 | 1 | 2 | 2 | 1 | | | | | | | | | | 1 | 3 | | | 1 | 2 | | | 1 | 1 | | | | | | | | | |
| 8 | E Langeberg-Outeniqua | | | | 1 | 3 | 1 | | | 2 | | | | | | | | 1 | 2 | 1 | | 1 | | | 2 | 1 | 1 | | | 1 | | | | | | |
| 9 | Klein & W Groot Swartberg-Rooiberg | | | | | 2 | 4 | 2 | | 2 | | | | | | | | | 4 | | | | | | 1 | 1 | | | | | | | | | | |
| 10 | West & Central Langeberg | | | 1 | 1 | 2 | | 1 | | 3 | 1 | | | | | | | | 3 | | | | | | | | | | | | | | | | | |
| 11 | Potberg | | | | 3 | | | | | 1 | | | | | | | | | 2 | | | | | | | | 1 | | | | | | | 1 | | |
| 12 | Stellenbosch-Bainskloof | | | | 1 | 1 | | | | 1 | | | | | | | | | 1 | | | 1 | | | | | 1 | | | | | | | | | |
| 13 | Malmesbury Centre | 1 | | | 2 | | | | | | 1 | | 1 | | | | | | 2 | | | 2 | | | | | 1 | | | | | | | | | |
| 14 | Piketberg-Olifantsberg | | | | 1 | 1 | | | | 1 | | | | | | | | | 1 | | | 1 | | | | | 1 | | | | | | | | | |
| 15 | NE Hexrivier-Waboorns-West Langeberg | | | 1 | 1 | 1 | 2 | 1 | | 1 | | | | | | | | 1 | 1 | | | | | | | 1 | | | | | | | | | | |
| 16 | Kammiesberg | | | | | | 2 | 1 | | | | | 2 | | | | | | 2 | | | | | | | | | | | | | | | | | |
| 17 | Gamka | | | | | 1 | | | | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| 18 | Witteberg | | | | | | | 1 | | 1 | | | | | | | | | 1 | | | | | | 1 | | | | | | | | | | | |
| | Totals | 2 | 0 | 10 | 38 | 34 | 29 | 14 | 2 | 48 | 5 | 2 | 3 | 1 | 0 | 2 | 1 | 13 | 58 | 2 | 1 | 16 | 9 | 2 | 8 | 13 | 15 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 |

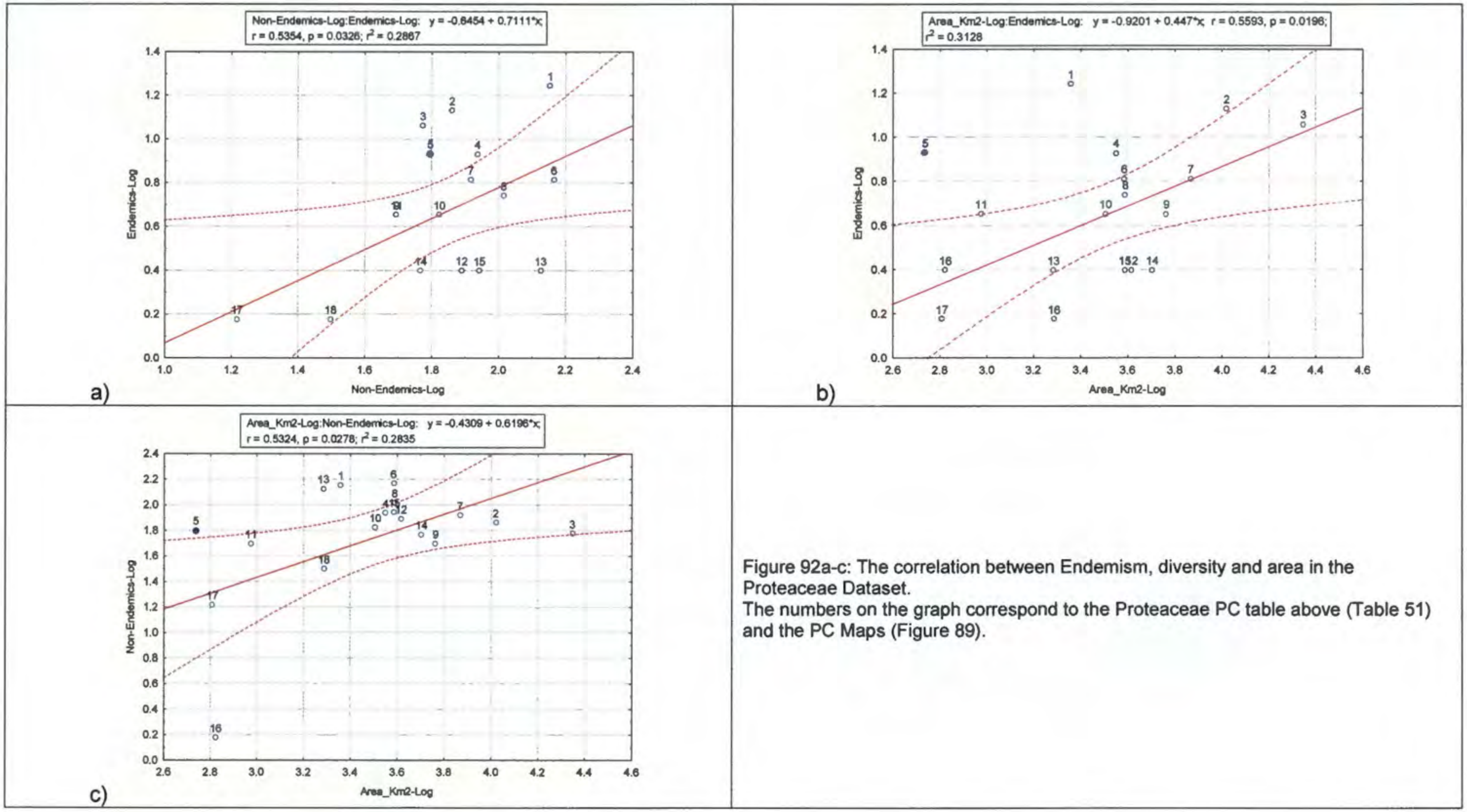


Figure 92a-c: The correlation between Endemism, diversity and area in the Proteaceae Dataset.
The numbers on the graph correspond to the Proteaceae PC table above (Table 51) and the PC Maps (Figure 89).

### 13.1.1 The relationship between endemism, diversity and area in the Proteaceae PCs

In general, regression of endemism, diversity and area indicates a weak relationship (Figure 92a-c). The reasons for this are not entirely clear, but it may be due to the high concentration of diversity and endemism in the south-western PC and the rapid tapering-off of these values to the north and east. Thus levels of endemism may be more dependent on how far west and south the PCs are (Levyns, 1964), rather than how large. In all my regression analyses for Proteaceae, excluding the Peninsula (PC 5) data point helped in obtaining significant correlations. In my regression of endemic and non-endemic taxa (Figure 92a), I excluded the Kamiesberg PC (16), in order to obtain a significant relationship ($r^2 = 0.29$, p=0.033), but the relationship is very weak. The Kamiesberg appears to be an outlier in the regression of non-endemic taxa and PC area (Figure 92c). However, its removal results in a statistically insignificant relationship, and a poorer $r^2$ value, and so was retained in the PC area regressions. Significant relationships were also obtained between PC endemism and PC area ($r^2 = 0.31$, p=0.020), and the number of non-endemic PC taxa and PC area ($r^2 = 0.28$, p=0.028), but as stated previously, the relationship is weak.

PC endemism is significantly higher than expected in three of the western montane Proteaceae PCs, namely the Hottentots-Kleinrivier (1), the Northwest mountains (2) and the Peninsula (5), when regressed both against non-endemic PC taxa (Figure 92a) and PC area (Figure 92b). PC endemism is fairly high in the Bredasdorp PC (4) and is higher than predicted by PC area (Figure 92b), and falls just outside the 95% confidence interval w.r.t. non-endemic taxa (Figure 92a). The Hottentots-Kleinrivier PC (1) is significantly higher than predicted in all three regressions (Figure 92a-c), highlighting just how remarkable and important the area is for biodiversity. It is very surprising that the Stellenbosch-Bainskloof Mountains (PC 13) have so few endemic taxa (Figure 92a), considering how many non-endemic taxa it has (Figure 92a and c). This is a recurring pattern in my study and may indicate an area of floristic overlap, rather than a phytogeographical centre. The RZE (PC 6) also has significantly higher than expected numbers of non-endemic taxa (Figure 92c), but this does not translate into high numbers of endemics (Figure 92a and b). The low numbers of endemics may be due to inappropriate PC boundaries, or it may indicate that it is better to merge the PC with a neighbouring PC. Alternatively, the high diversity and low endemism may indicate that the RZE PC is actually an area of overlap between different floristic areas.

PCs that contained fewer than expected endemics were in lower altitude areas, such as the Malmesbury PC (12) and the Piketberg/Olifantsrivierberg PC (14) (Figure 92a and b). The reason for the poor performance of the East Hex River-West Langeberg (PC 15) is unknown (Figure 92a and b), although this PC is situated in a more arid area of the CFR. The Kamiesberg (16) contained fewer than expected non-endemic taxa (Figure 92c), probably due to its disjunct and arid characteristics. The arid Witteberg (18) had fewer than predicted endemic taxa (Figure 92b), but is not as distant from the CFR as the Kamiesberg, which may account for its higher number of non-endemic taxa (Figure 92b). The large size of the Southeast Centre-E Karoo Mountains PC (3) accounts for its high ratio of endemism (Figure 92a) and for its unremarkable performance in the area based regression analyses (Figure 92b and c).

## 13.2. CFR Phytogeographical Centres

### 13.2.1 Southwest Phytogeographical Province

The SWPP contains three of the six most endemic rich Proteaceae PCs (1, 5, 6) and a few minor PCs (12 and 13). This is quite remarkable, considering the relatively small geographic size of each of these PCs (Table 51, Figure 89). The Hottentots Holland-W Kleinrivier Mountains (Kogelberg) (PC 1) contains the greatest taxonomic richness and endemism for Proteaceae. It is congruent with the Houwhoek District of Rebelo and Siegfried (1990), which also had the highest endemism of the floristic units that they identified, but not the highest diversity. Despite its relatively small size (six QDSs), the Hottentots Holland-W Kleinrivier Mountains (Kogelberg) (PC 1) has more than double the number of endemics than the second richest Proteaceae PC. The Peninsula Centre (PC 5) is roughly half the size of the Hottentots-W Kleinrivier Centre and has nearly half the number of endemics: 10 versus 21. Therefore, it appears that the relationship between area, diversity and endemism is fairly constant between these two PCs in the SWPP, with both displaying remarkable biodiversity and endemism. The RZE PC (6) also performs relatively well, compared to the other datasets that I analysed. The distribution of Proteaceae PC (Figure 89) and habitat properties of Proteaceae endemics (Table 52), indicates a strong preference for temperate, montane, TMS and Mediterranean type habitats in the SWPP.

The remaining mountain centre, the Stellenbosch-Bainskloof Mountains (PC 13), has very high diversity (135 taxa), but only two endemics. Similarly, there are relatively few taxa with half their ranges restricted to the Stellenbosch-Bainskloof Mountains (PC 13).

(Table 51). This high diversity and low endemism may indicate that my floristic boundaries for the Sandveld-Stellenbosch Mountains Centre (PC 18) are inappropriate and that the Stellenbosch-Bainskloof Mountains (PC 13) should possibly be a sub-centre of one of the other PCs. Alternatively, it could be that the Sandveld-Stellenbosch Mountains Centre (PC 18) is an area of overlap between different floristic elements, which may boost diversity, but results in few endemics. A similar pattern is observed in the RDL Dataset.

The Malmesbury Centre (PC 12) forms an independent centre and is separate from the NWPP Sandveld Centre (PC 14). Rebelo and Siegfried (1990), and Weimarck also retrieved a Malmesbury Centre. Its endemic taxa occur on granite and shale (Table 52), which makes the absence of granite Saldanha Peninsula endemics unusual. The two QDSs that are not assigned to phytogeographical units in the Malmesbury Centre occur in a similar unassigned area in the study of Rebelo and Siegfried (1990). There are at least three near endemics (*Leucospermum parile* (6), *Leucodendron verticillatum* (5) and *Protea odorata* (5)) that overlap marginally in 3318DD and 3418BB.

### 13.2.2 The Northwest Phytogeographical Province

The core of the NWPP consists of the Northwestern Mountains (PC 2). In Proteaceae, the Northwestern Mountains is the second largest PC by area (16 QDSs, Table 51), and consolidates much of the NWPP into a single PC. The Northwestern Mountains comprises two sub-centres, one of which is centred on the Cedarberg Mountain range (PSC 2.2). The other is slightly further north, combining the Pakhuis-Gifberg-Nieuwoudtville areas (PSC 2.1). The other major centre of the NWPP is the Groot Winterhoek Centre (PC 8), which is also well defined.

The remaining centres have low numbers of endemics. The Piketberg-Swartberg Centre (PC 14) includes the northern Sandveld Fynbos and is fairly large geographically, with many taxa, but relatively few endemics. The Kamiesberg PC (16) consists of a single QDS, with only three taxa, remarkably, two of which are endemic. The Swartruggens and Swartrugberge/Baviaansberg, which are much drier, are not assigned to any PC, and this further indicates the preference of CFR Proteeae endemics for mesic conditions. The NE Hexrivier-Wabooms-West Langeberg PC (PC 15) is located mostly in the south-eastern NWPP (as defined by my Combined Dataset). It extends into the western KMPP and this hints at a high altitude mountain corridor (Table 52) located in this arid area, as noted in Restionaceae and Rutaceae. Although it has high diversity, it contains few endemics. This can most likely be attributed to the subdivision of the Western Hex River Mountains between other PCs, the RZE (PC 6) and the Groot Winterhoek (PC 8), rather than forming a consolidated Hex River PC, as occurs in the Combined Dataset.

### 13.2.3 The Langeberg Phytogeographical Province

Proteaceae floristic patterns in the Langeberg and surrounds share a number of floristic similarities with my Combined Dataset, particularly in the west and north. In my Proteaceae Dataset, the Langeberg PC (7) deviates from patterns in the Combined Dataset by expanding east into the SEPP and south into the APPP. There are two principal PCs in the LBPP, the West and Central Langeberg (PC 10), and the E Langeberg-Outeniqua (7), which divides the LBPP in the region of Tradoupas.

Aside from a single QDS, the West and Central Langeberg (PC 10) is exclusively montane (Figure 89, Table 52), with a conspicuous absence of taxa from the Central Langeberg Plains, as seen in many other datasets, such as Asteraceae, Bruniaceae, Fabaceae and Restionaceae. Although diversity in some of these QDSs are reasonably high on the Central Langeberg Plains (Figure 90), Inverse Weighting illustrates that there are not many range-restricted taxa here (Figure 91), possibly explaining why the QDSs have not been assigned to a PC. This "gap" is also observed in the floristic units of Rebelo and Siegfried (1990) (Figure 88).

The East Langeberg-West Outeniqua Centre (PC 7) includes the eastern portion of the Langeberg Mountains, East Langeberg Plains and extends into the East and Far East Agulhas Plains (of my Combined Dataset). The eastern Langeberg (PC 7) contains a very extensive lowland (plains) area due to *Leucospermum praecox* (10). The remaining more range-restricted endemics are montane, as in the West and Central Langeberg Centre (10). Thus, sub-centre development (the majority of the endemics, see Table 52) is restricted to the mountains.

There is a slight decrease in the number of Proteaceae endemics towards the centre of the Langeberg mountain range (PC 10). Endemism rises further east in the Outeniqua PSC (7.1), a much smaller area (two QDS) that has only one less endemic than the West and Central Langeberg Centre (PC 10, five QDS). In Proteaceae, the East Langeberg Sub-Centre (PSC 7.2) has the lowest number of endemics of its surrounding floristic units and is bordered by the West and Central Langeberg (PC 10) and the West Outeniqua (PSC 7.1). This is slightly anomalous, as diversity usually drops fairly uniformly to the east and north in the CFR (Levyns, 1964), but also occurs in the Combined Dataset. It may indicate less mesic habitat area in the LBPP QDS compared to the Outeniqua QDS.

### 13.2.4 The Agulhas Plains Phytogeographical Province

The Agulhas Plains are divided into two PCs, and as with most clade datasets form the equivalent of sub-centres in the Combined Dataset. There is a strong Bredasdorp (PC 4) component and a weaker Potberg (PC 11) component as well. The Bredasdorp PC (PC 4) is larger and extends further north than that of the Combined Taxa Dataset, including the eastern parts of the Kleinrivierberge. It has more in common with Weimarck's (1941) Bredasdorp Sub-Centre and Rebelo and Siegfried's (1990) Bredasdorp District, than Goldblatt and Manning's (2000) APPP Phytogeographical Centre, geographically and ecologically. Only one endemic is recorded on limestone, while two occur on clay; thus I favour the Bredasdorp name over the Agulhas name. The East and Far East Agulhas Plains of my Combined Taxa Dataset have been incorporated into the East Langeberg-West Outeniqua PC (PC 7) in Proteaceae. Although geographically small, the Potberg Centre (11) contains four endemic taxa, highlighting the conservation importance of the area.

### 13.2.5 The Karoo Mountains Phytogeographical Province

The KMPP is relatively well-developed, with strong PC development in the Witteberg (PC 18), and Klein Swartberg (PC 9). The Klein Swartberg (PC 9) extends eastward to include the western Groot Swartberg and southward to include the Rooiberg and part of the Little Karoo. The combining of the western portion of the Groot Swartberg with the Klein Swartberg is unusual (see Goldblatt and Manning (2000); Rebelo and Siegfried (1990); and Weimarck (1941)). More frequently, floristic boundaries are observed in the region of the Seweweekspoort, which divides the Klein Swartberg and Groot Swartberg (Rebelo and Siegfried, 1990), rather than in the region of the Swartberg Pass, as displayed in my Proteaceae Dataset (Figure 89). This seems well supported in my study, however, as many of the endemic taxa in this PC occupy large areas of the Klein Swartberg Centre (9) and this does not allow for further sub-division of this floristic unit. Despite the eastern Groot Swartberg forming part of another floristic unit, there are taxa that link the Klein Swartberg and Groot Swartberg-Kammanassie Mountains into a single floristic unit. This is observed in my Combined Dataset where the Klein and Groot Swartberg form a single floristic unit, due to *Protea montana* (8) and *Protea prunosa* (4). Other Proteaceae taxa highlight KMPP PC affinities, but overlap marginally into neighbouring PCs, include *Protea venusta* (11) and *Leucodendron dregei* (12); while *Leucodendron osbornei* (6) indicates affinities between the Swartberg to the Witteberg.

Rebelo (1995) also notes a peculiar form of *Paranomus spathulatus* from the Gamkaberg and states that *P. spathulatus form gamka* (1) may in fact be an as yet an undescribed species. The Gamka Mountains (PC 17), to the east of the Rooiberg, have not been identified as containing endemic taxa in my other datasets.

### 13.2.6 The Southeast Phytogeographical Province

The SEPP (Figure 89, Table 51) is a relatively expansive PC (37 QDSs), covering most of the central and eastern SEPP and eastern KMPP of Weimarck, and Goldblatt and Manning (2000), although the western Outeniqua Mountains form part of the Greater Langeberg floristic unit (PSC 7.1). Cluster analysis resulted in fairly impoverished, disjunct PCs due to the absence of range-restricted taxa and subsequent GIS investigation produced the current consolidated floristic unit.

The eastern part of the KMPP, from the central Groot Swartberg (Swartberg Pass) and Kammanassieberg merges with the higher northern mountains of the SEPP (Baviaanskloof and Kouga). This forms a geographically large sub-centre (PSC 3.1), which contains three relatively widespread endemic taxa. *Protea intonsa* (14) and *Leucodendron singulare* (4) are concentrated in the northern and western portions of this centre, while *Leucodendron rourkei* (8) is found predominantly in the south and east. The Groot-Winterhoekberge-Elandsberge PSC (3.2) contains a single endemic and is situated in the far eastern part of the SEPP.

## 13.3 Non-CFR Phytogeographical Centres

The Proteeae are fairly well-represented in high altitude habitats outside the CFR, by *Protea* and particularly by the genus *Faurea*, the latter with 14 of its 15 taxa occurring outside the CFR, in Africa and Madagascar. Only *Faurea macnaughtonii* is represented in the CFR. The extra-CFR Proteeae were not included in this analysis, so comment is not made on their potential for PC formation, although they may contribute to PC formation in higher altitude summer rainfall areas.

## 13.4 Summary

Proteaceae is a near classic montane TMS Cape Clade (Linder, 2003), but it also shows floristic development on the lower altitude areas of the SWPP, LBPP and Bredasdorp/APPP. However, PC development is largely absent from the Rûens area (southwest of Swellendam). Taxa outside the CFR did not form part of my dataset. Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, NWPP, SEPP-East KMPP, Bredasdorp/APPP, LBPP and central KMPP.

# Chapter 14: Red Data List Taxa (Table 53, Figure 93)

## 14.1 Introduction

### 14.1.1 General

The purpose of Red Data Listing (RDL) is to identify taxa that are naturally rare, currently threatened, or predisposed to threat (Hilton-Taylor, 1996). Many RDL Taxa are naturally rare and have small distributional ranges (Hilton-Taylor, 1996). If they occur over wide geographic areas, they usually have disjunctions, which can result in conflict when trying to establish PC. However, these types of taxa are relatively few in number in the CFR, and conflict from them was deemed negligible. The RDL Dataset is thus an ideal dataset to undertake analyses, which accentuates range-restricted taxa to identify PC.

It is useful analyse the RDL Dataset as a distinct dataset as it comprises mostly range-restricted taxa from a number of diverse lineages and it most likely presents a good surrogate of overall PC patterns in all taxa in the CFR, as it is not disproportionately biased to Cape Clades (listed Linder, 2003), as some of my other datasets. In the CFR, the RDL Dataset may be more inclusive of non-TMS Taxa, relative to my other datasets, because CFR Taxa that are under the greatest anthropological threats, occur mostly in lowland areas with nutrient rich shale derived soils, which are desirable for agriculture, and coastal areas due to urbanisation. This is in contrast to overall CFR diversity patterns, where 70% of taxa occur in montane TMS Substrates (Cowling and Proches, 2005). I try to determine whether this lack of TMS bias in the RDL Dataset produces noticeably different PC patterns to montane TMS Fynbos Clades.

The RDL Dataset is frequently used in Conservation Planning as by definition, RDL Taxa are in need of special conservation consideration. In using RDL Taxa to determine priority diversity areas for protection in the Succulent Karoo, Lombard et al., (1999) found as much as 40% incongruence between ecological guilds (succulents, bushes) of the RDL Taxa that they analysed at the QDS geographical level. Aside from my Combined Dataset, the Red Data List Dataset is the most phylogenetically heterogeneous dataset analysed in this study. It may thus be a good dataset to indicate congruence, or the lack there of in different biotic elements that form PCs in the CFR, both within the RDL Taxa Dataset and when comparing the RDL Taxa Dataset to others in my study. The aim of Conservation Planning is to conserve both pattern (distribution of diversity and endemism) and process (mechanisms that facilitate, or inhibit gene transfer). Therefore, I briefly compare the RDL Taxon patterns of endemism of the other datasets that I analysed. This may give an indication of how much pattern and process is being conserved in my other datasets, from conservation efforts focussing on RDL Taxa.

### 14.1.2 Comparison between the RDL Dataset PCs and PCs of my other datasets

Cowling and Proches (2005) found that 70% of CFR Taxa occur on montane TMS Substrates. Analysis of the frequencies of my RDL endemics on different substrates revealed that 62.8% occurred on TMS Substrates (Table 54), less than the 70% calculated for the entire flora (Cowling and Proches, 2005). This may be due to the bias towards threatened taxa that are generally more abundant in lowland areas. It is also important to note that Cowling and Proches (2005) focused on the frequencies of all taxa in the CFR (total diversity), while my results refer exclusively to frequencies of RDL Dataset PC endemics. It is unknown whether their ratio of 70% is constant in derivative datasets, such as CFR endemic taxa, or RDL Taxa, whether CFR or PC endemic or not. Whatever the exact ratios, my recording of lower frequency PC endemic RDL Taxa on TMS Substrates, may help explain some of the conflict I observed in the process of constructing PCs within the RDL Dataset. This may be due to the lower dominance of TMS Taxa and patterns, and may also explain some of the lack of congruence between the RDL Dataset and my other data sets. This is particularly applicable to those groups or datasets that contain higher numbers of montane TMS Fynbos Taxa (listed in descending TMS percentage), for example, Bruniaceae, Rosaceae, Polygalaceae, Asteraceae, Proteaceae and Restionaceae. I could not find sufficient data on my *Erica* PC endemics, though *Erica* certainly belongs here.

I found that although there are some notable departures in the phytogeographical boundaries of the RDL Taxa, in comparison to TMS Cape Clades, there are still discernable similarities to phytogeographical patterns of my Combined Dataset and to the literature (Weimarck; Goldblatt and Manning, 2000). For example, the Agulhas Plains, Klein and Groot Swartberge, and the Southeast Centres all show similarities to TMS Cape Clades. One obvious exception is the Nieuwoudtville Escarpment, due to the high abundance of Geophytes in the RDL Dataset (Table 56), which usually performs less well in purely montane TMS Cape Clades. However, RDL shrubs and shrublets are still underrepresented in the Nieuwoudtville Escarpment and Nieuwoudtville Surrounds PC. Other areas that are slightly overrepresented by RDL Taxa include the Agulhas Plains, especially the Western Agulhas Plains and in the extreme east, the Port Elizabeth QDS,

Table 53: Taxonomic properties of the Centres identified for the Red Data List Taxa (Figure 93).

| Label | Centres<br>Sub-Centres | Area | Families | Genera | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | South Southwest Mtns | 9 | 38 | 127 | 330 | 196 | 92 | 196 | 0.24 | 0.23 |
| 1.1 | Hottentots-Kleinrivierberge | 6 | | | 260 | 127 | 51 | 97 | 0.32 | 0.30 |
| 1.2 | South RZE | 3 | | | 144 | 53 | 26 | 39 | 0.50 | 0.48 |
| 2 | Northern NWPP | 13 | 37 | 94 | 204 | 124 | 68 | 136 | 0.15 | 0.14 |
| 2.1 | Pakhuis Mtns | 5 | | | 131 | 75 | 35 | 55 | 0.31 | 0.29 |
| 2.2 | Piketberg-N Sandveld | 7 | | | 91 | 43 | 24 | 44 | 0.26 | 0.23 |
| 2.3 | Remainder | 1 | | | 10 | 1 | 1 | 1 | 1.00 | - |
| 3 | Nieuwoudtville Escarpment | 4 | 31 | 64 | 117 | 90 | 66 | 80 | 0.30 | 0.29 |
| 4 | South Northwest Centre | 13 | 40 | 108 | 237 | 123 | 61 | 94 | 0.12 | 0.10 |
| 4.1 | Southern Northwest Core | 9 | | | 197 | 95 | 46 | 69 | 0.17 | 0.15 |
| 4.2 | Swartrugberge-NE Hexrivier | 3 | | | 59 | 18 | 10 | 12 | 0.40 | 0.33 |
| 4.3 | Remainder | 1 | | | 16 | 2 | 1 | 1 | 1.00 | - |
| 5 | East KMPP-West SEPP | 23 | 32 | 78 | 158 | 89 | 58 | 110 | 0.08 | 0.07 |
| 5.1 | Groot Swartberg | 4 | | | 59 | 30 | 17 | 25 | 0.37 | 0.33 |
| 5.2 | Outeniqua | 6 | | | 66 | 25 | 15 | 22 | 0.24 | 0.19 |
| 5.3 | Plettenberg Bay | 5 | | | 26 | 11 | 5 | 10 | 0.40 | 0.25 |
| 5.4 | Kammanassie | 2 | | | 24 | 6 | 5 | 6 | 0.60 | 0.50 |
| 5.5 | Dwyka | 3 | | | 17 | 5 | 2 | 4 | 0.67 | 0.33 |
| 5.6 | Remainder | 3 | | | 22 | 2 | 1 | 1 | 0.33 | - |
| 6 | Nieuwoudtville Surrounds | 10 | 31 | 67 | 122 | 88 | 51 | 75 | 0.15 | 0.13 |
| 6.1 | Gifberg | 4 | | | 100 | 67 | 36 | 52 | 0.36 | 0.34 |
| 6.2 | Boegoeberg-Soutpansberg-Hantamsberg | 3 | | | 19 | 7 | 7 | 10 | 0.48 | 0.39 |
| 6.3 | Remainder | 3 | | | 18 | 11 | 5 | 5 | 0.33 | 0.17 |
| 7 | Central LBPP Mtns and Plains | 8 | 34 | 83 | 152 | 81 | 50 | 86 | 0.22 | 0.20 |
| 7.1 | East Central LBPP Mtns | 3 | | | 82 | 34 | 20 | 26 | 0.43 | 0.40 |
| 7.2 | West Central LBPP | 4 | | | 99 | 45 | 17 | 24 | 0.35 | 0.31 |
| 7.3 | Remainder | 1 | | | 16 | 1 | 1 | 1 | 1.00 | - |
| 8 | Peninsula | 3 | 27 | 84 | 180 | 73 | 44 | 71 | 0.54 | 0.53 |
| 9 | APPP/LBPP Plains | 14 | 38 | 86 | 169 | 88 | 43 | 79 | 0.13 | 0.11 |
| 9.1 | Potberg-West Agulhas Plains | 6 | | | 105 | 39 | 21 | 36 | 0.29 | 0.25 |
| 9.2 | East APPP/LBPP Plains | 7 | | | 95 | 35 | 17 | 22 | 0.18 | 0.13 |
| 9.3 | Remainder | 1 | | | 5 | 0 | 0 | 0 | - | 1.00 |
| 10 | East Southeast Centre | 14 | 25 | 51 | 71 | 50 | 38 | 57 | 0.11 | 0.08 |
| 10.1 | Vanstadens-Coastal | 7 | | | 49 | 30 | 22 | 30 | 0.19 | 0.16 |
| 10.2 | Steytlerville-Kirkwood PSC | 6 | | | 27 | 16 | 12 | 18 | 0.25 | 0.18 |
| 10.3 | Remainder | 1 | | | 7 | 1 | 1 | 1 | 1.00 | - |
| 11 | NW Karoo | 11 | 30 | 64 | 90 | 51 | 33 | 50 | 0.14 | 0.11 |
| 12 | West Agulhas Plains | 9 | 24 | 70 | 144 | 72 | 30 | 56 | 0.21 | 0.18 |
| 12.1 | West Agulhas Plains Core | 6 | | | 119 | 55 | 23 | 41 | 0.30 | 0.27 |
| 12.2 | Remainder | 3 | | | 54 | 13 | 1 | 1 | 0.33 | - |
| 13 | Saldanha Peninsula and West Coast | 12 | 29 | 62 | 88 | 45 | 30 | 60 | 0.17 | 0.14 |
| 13.1 | Saldanha-South West Coast | 9 | | | 75 | 34 | 24 | 50 | 0.23 | 0.20 |
| 13.2 | North West Coast | 3 | | | 15 | 11 | 6 | 10 | 0.56 | 0.47 |
| 14 | Vanrhynsdorp Lowlands | 3 | 16 | 29 | 47 | 38 | 29 | 40 | 0.46 | 0.44 |
| 15 | Klein Swartberg-Rooiberg | 8 | 29 | 65 | 104 | 57 | 26 | 46 | 0.22 | 0.19 |
| 15.1 | Klein Swartberg | 4 | | | 74 | 30 | 15 | 28 | 0.47 | 0.43 |
| 15.2 | Rooiberg | 2 | | | 39 | 15 | 8 | 9 | 0.56 | 0.50 |
| 15.3 | Remainder | 2 | | | 21 | 2 | 1 | 1 | 0.50 | - |
| 16 | Worcester Valley | 4 | 30 | 74 | 127 | 53 | 24 | 30 | 0.31 | 0.28 |
| 17 | South Sandveld | 6 | 24 | 67 | 146 | 63 | 23 | 44 | 0.32 | 0.29 |
| 17.1 | South Sandveld Core | 4 | | | 109 | 38 | 16 | 30 | 0.47 | 0.43 |
| 17.2 | Remainder | 2 | | | 89 | 12 | 3 | 3 | 0.50 | 0.25 |

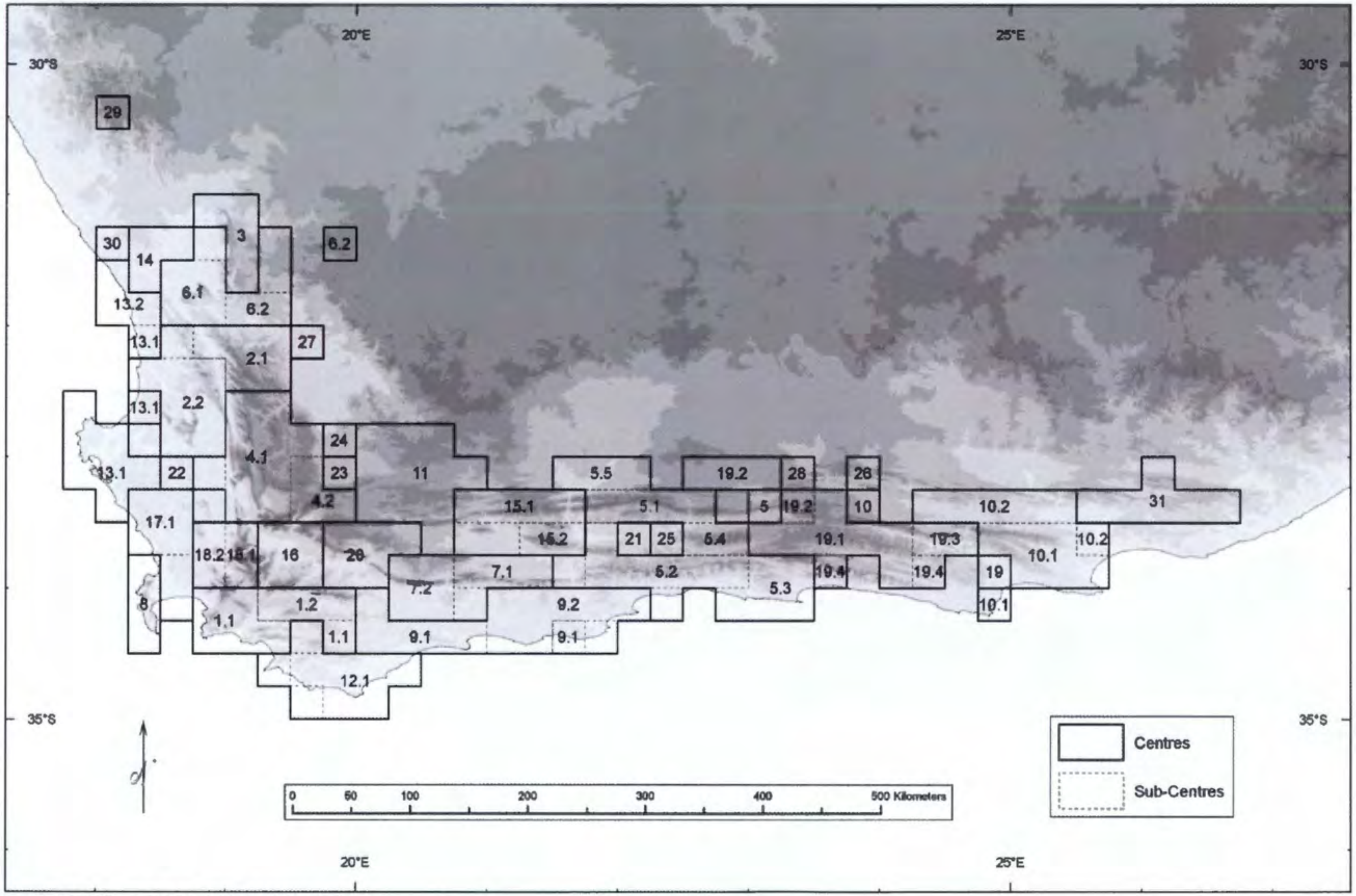


Figure 93: PC and PSC for the RDL Dataset.

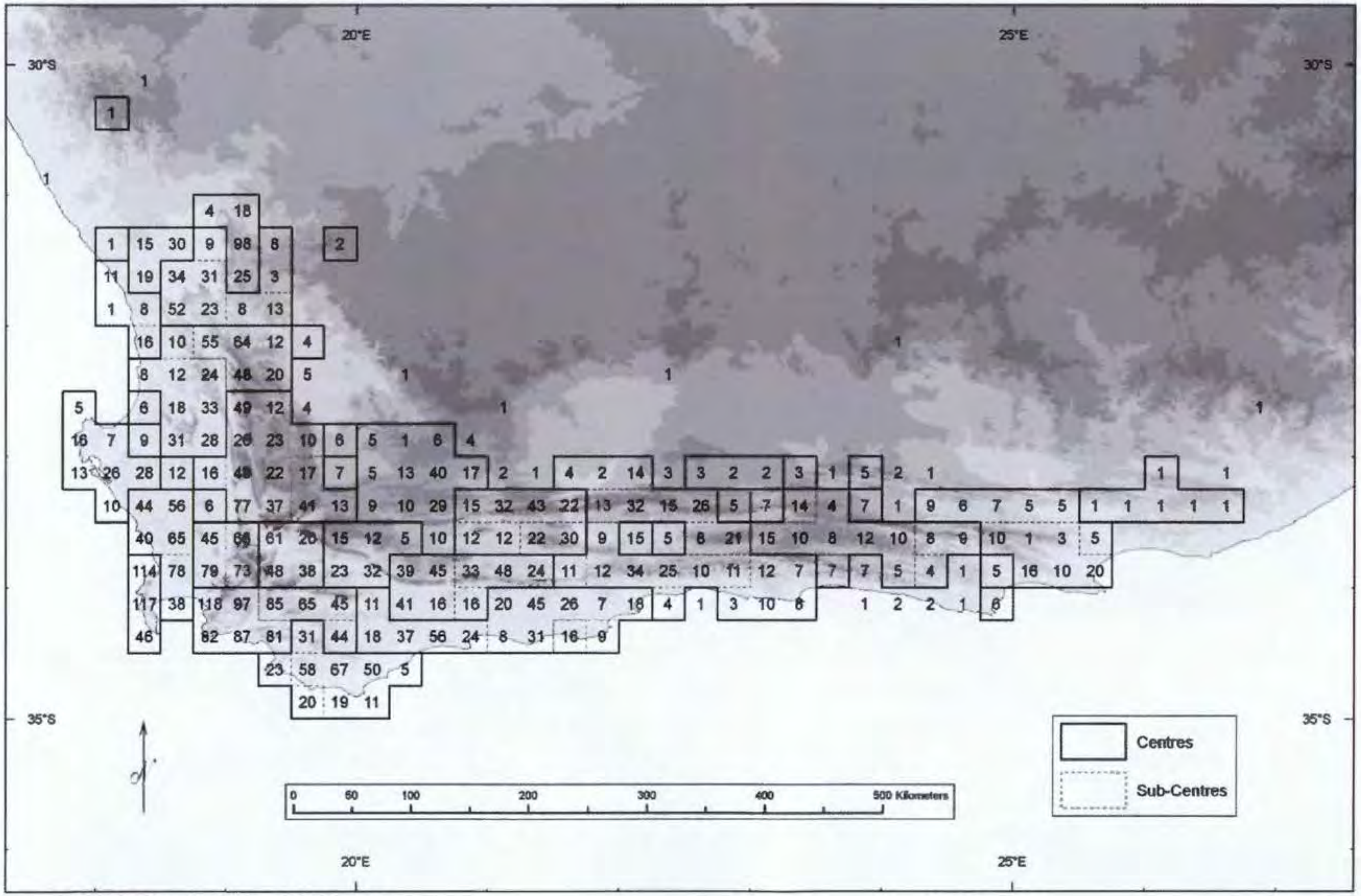


Figure 94: QDS Diversity for the RDL Dataset.

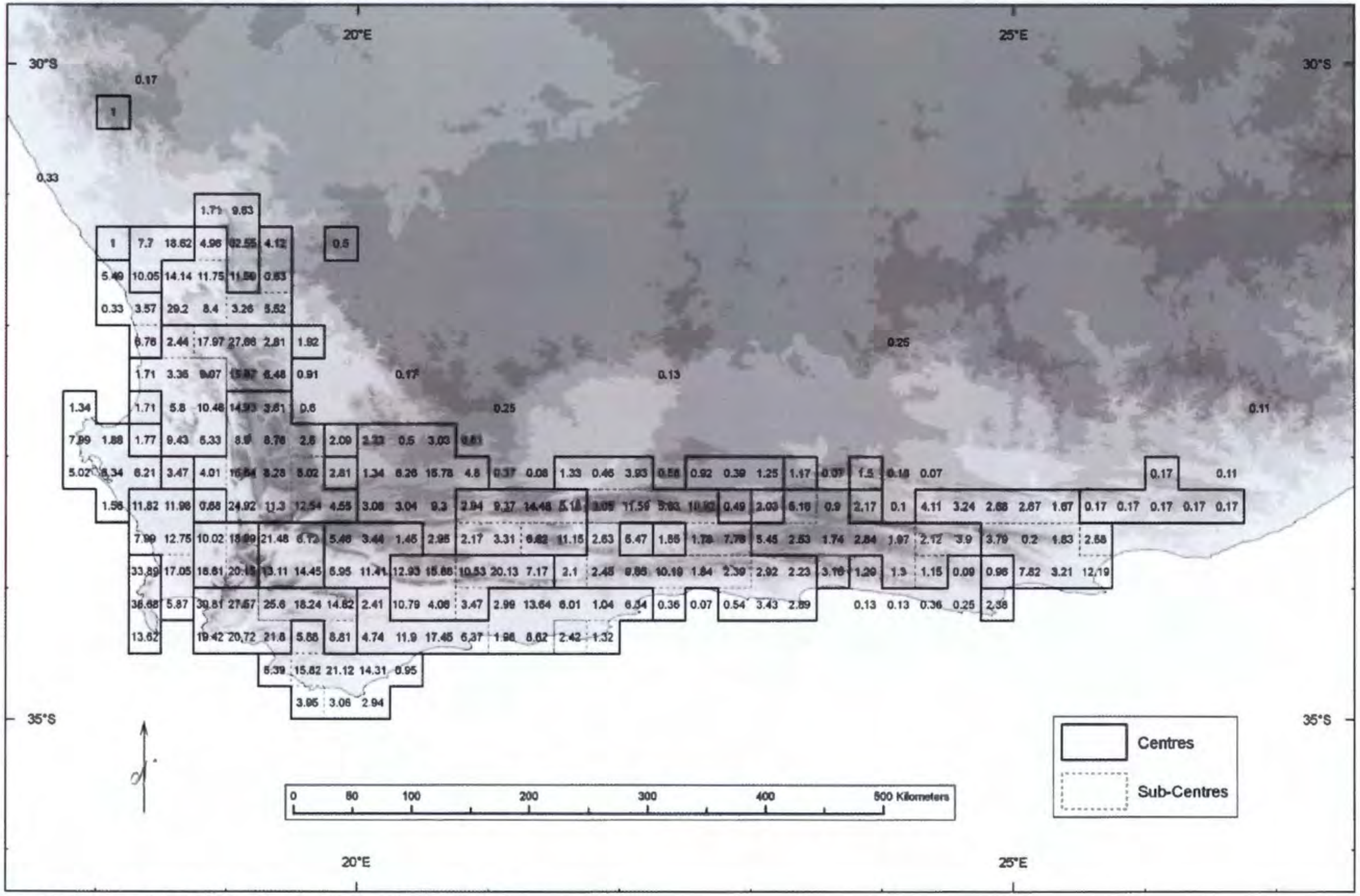


Figure 95: Sum of the Inverse Taxon Ranges for the RDL Dataset.

| Label | Centres<br>Sub-Centres | Area | Families | Genera | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|---|---|
| 18 | Sandveld-Stellenbosch Mtns | 4 | 29 | 83 | 182 | 50 | 22 | 28 | 0.32 | 0.29 |
| 18.1 | Stellenbosch Mtns | 2 | | | 115 | 28 | 12 | 12 | 0.50 | 0.45 |
| 18.2 | Sandveld | 2 | | | 103 | 17 | 6 | 8 | 0.67 | 0.60 |
| 19 | Central Southeast Centre | 16 | 25 | 46 | 65 | 33 | 21 | 38 | 0.11 | 0.07 |
| 19.1 | Kouga | 7 | | | 36 | 15 | 7 | 12 | 0.24 | 0.12 |
| 19.2 | Southern Groot Karoo | 4 | | | 17 | 8 | 4 | 7 | 0.44 | 0.25 |
| 19.3 | East Baviaanskloofberg | 2 | | | 14 | 5 | 4 | 4 | 0.50 | 0.33 |
| 19.4 | Tsitsikamma | 2 | | | 10 | 3 | 3 | 4 | 0.67 | 0.50 |
| 19.5 | Remainder | 1 | | | 5 | 0 | 0 | 0 | - | 1.00 |
| 20 | West Langeberg-Kwadouwsberg-Waboomsberg | 5 | 25 | 50 | 65 | 23 | 13 | 18 | 0.28 | 0.22 |
| 21 | Oudtshoorn | 1 | 9 | 14 | 15 | 5 | 3 | 3 | 1.00 | 1.00 |
| 22 | NE South Sandveld | 1 | 7 | 10 | 12 | 2 | 2 | 2 | 1.00 | 1.00 |
| 23 | South Ceres Karoo | 1 | 6 | 7 | 7 | 2 | 2 | 2 | 1.00 | 1.00 |
| 24 | North Ceres Karoo | 1 | 4 | 6 | 6 | 1 | 1 | 1 | 1.00 | - |
| 25 | Dysseldorp | 1 | 4 | 4 | 5 | 1 | 1 | 1 | 1.00 | - |
| 26 | North Grootrivierberge | 1 | 5 | 5 | 5 | 1 | 1 | 1 | 1.00 | - |
| 27 | West Tankwa | 1 | 3 | 4 | 4 | 1 | 1 | 1 | 1.00 | - |
| 28 | Boesmanspoortberg | 1 | 3 | 3 | 3 | 1 | 1 | 1 | 1.00 | - |
| 29 | Kamiesberg | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 30 | North West Coast | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 31 | Zuurberg | 6 | 1 | 1 | 1 | 1 | 1 | 6 | 1.00 | - |
| 32 | Outside | 30 | 18 | 40 | 57 | 2 | 0 | 0 | - | 1.00 |

and the Gamtoos River Mouth QDS. Comparison of the RDL QDS Diversity Map (Figure 94) with others seems to indicate relatively good congruence to QDSs that are usually found to contain high diversity in montane TMS Cape Clades. Whether this correlation is as strong, or as congruent at finer ecological (especially substrate) or geographical scales within QDSs, requires further investigation.

It seems possible that the phytogeographical patterns of the RDL Dataset that differ from montane TMS Cape Clades, or the Combined Dataset, may be due to conflict between different biotic elements in the RDL Taxa Dataset. Examples of where these differences occur include the PSC sub-division of the South Southwest Mountains Centre (PC 1), the PC sub-division of the NWPP, especially into northern (PC 2) and southern (PC 4) Cedarberg PC; and the formation of the Worcester Valley Centre (PC 16). Much the same affect may occur when combining a dataset that emphasises the importance of mountains or sandstone (for example, Ericaceae, Proteaceae and Restionaceae) with a dataset that also contains taxa in the lowlands and on shale (for example, Fabaceae and Geophytes). Although the RDL Taxa Dataset is dominated by sandstone endemics on slopes, there is an increase in the number of endemics on other lower altitude substrates, like limestone, clay and shale; and in lower altitude vegetation types like Renosterveld and

Table 54: Habitat Data for the RDL Taxa Dataset Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Label | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliffs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats/Dunes | Other | Unknown |
| 1 | South Southwest Mtns | 8 | 4 | 13 | 6 | 4 | 2 | 1 | 1 | 30 | 3 | 7 | 2 | | | 1 | 1 | 3 | 55 | 5 | 3 | 2 | 16 | 3 | | 22 | 1 | 4 | 3 | | | | | | | |
| 2 | Central NWC | 1 | 1 | 5 | 1 | 5 | 4 | 1 | | 27 | | 2 | | | | | 1 | 1 | 36 | 4 | | 2 | | 2 | 2 | 23 | 8 | 5 | 1 | | 1 | | | | | |
| 3 | Nieuwoudtville Escarpment | 1 | | | | 5 | 2 | 1 | | 17 | | 12 | | | | | 2 | 2 | 9 | 2 | | 7 | 2 | 1 | 1 | 12 | 3 | 4 | 6 | | 1 | | | | | |
| 4 | South Northwest Centre | | | | 3 | 4 | 5 | 1 | | 28 | 2 | 3 | 1 | | | | | 3 | 30 | 1 | | 3 | 3 | 1 | 1 | 10 | 4 | 10 | 4 | | | | | 1 | | |
| 5 | East KMC-West SEC | 5 | 3 | 9 | 2 | 6 | 1 | | | 13 | | 2 | | | | | 1 | | 30 | 1 | 3 | 1 | 6 | 2 | 4 | 12 | 1 | 4 | 3 | 1 | 3 | | | | | |
| 6 | Nieuwoudtville Surrounds | 2 | | | 1 | 4 | | | | 12 | | 1 | | | | 1 | | | 17 | 2 | | 6 | 1 | 1 | 2 | 16 | 4 | 2 | | | 3 | | | | | |
| 7 | Central LBC Mtns and Plains | 4 | 3 | 8 | 3 | 1 | 1 | | | 17 | 2 | 3 | 1 | | | 2 | 1 | 1 | 34 | 1 | | | 4 | 2 | | 11 | 3 | 3 | 4 | 1 | | 1 | | | | |
| 8 | Peninsula | 5 | 1 | 2 | 2 | 1 | | | | 8 | | 2 | 1 | 1 | | | | 3 | 15 | 2 | | 8 | 5 | 1 | 1 | 12 | 6 | 3 | | | | | | 4 | | |
| 9 | APC/LBC Plains | 4 | | | 6 | | | | | 4 | 1 | 2 | | 12 | | | | 1 | 7 | | 6 | 6 | | | | 5 | 7 | 4 | 6 | | 1 | 1 | 1 | 6 | | |
| 10 | East Southeast Centre | 1 | | | 3 | 1 | 1 | | | 9 | | | | 1 | 1 | | | 1 | 14 | | 1 | 3 | 2 | 1 | 1 | 7 | 4 | 2 | | | 4 | 2 | 1 | 1 | | |
| 11 | NW Karoo | | | | | 1 | 1 | | | 4 | | | | | | | 1 | | 4 | 1 | | 1 | | | 2 | 4 | | | | | 3 | | | | | |
| 12 | West Agulhas Plains | 6 | | | 1 | | | | | 5 | | 2 | | 9 | | 1 | | | 7 | | 4 | 6 | 3 | | | 2 | 1 | 2 | 1 | | | | | 10 | | |
| 13 | Saldanha Peninsula and West Coast | 1 | | | 1 | | | | | | | | 8 | 6 | | | | | 3 | 6 | 2 | 2 | | | | 10 | 10 | | | | | | | 10 | | |
| 14 | Vanrhynsdorp? | | | | | | | | | | 1 | | 1 | 1 | | | 1 | | | | | | | | | 1 | | | | | | | | | | |
| 15 | Klein Swartberg-Rooiberg | 1 | | 2 | 1 | 5 | 1 | | | 6 | 2 | | | | | | | 2 | 9 | 1 | 1 | | 2 | 1 | 2 | 6 | | 2 | 2 | | 1 | | | | | |
| 16 | Worcester Valley | | | | | | | | | 4 | 1 | 1 | | | | | 1 | | 8 | 1 | 1 | 3 | 1 | | 1 | 9 | 2 | 3 | 3 | | 1 | | | | | |
| 17 | South Sandveld | | | | 2 | | | | | 2 | 1 | | 4 | | | | | | 2 | | 1 | 11 | 3 | | | 4 | 8 | 2 | 3 | | 1 | | | 2 | | |
| 18 | Sandveld-Stellenbosch Mtns | 2 | 2 | 7 | | 1 | 1 | | | 5 | | | 1 | | | | 1 | 2 | 10 | 1 | | 2 | 3 | | | 6 | 1 | | | 1 | | | | | | |
| 19 | Central Southeast Centre | 1 | 1 | 3 | | | 1 | | | 5 | | | | | | | | 1 | 7 | 3 | | | | | 1 | 9 | | 1 | | | | 1 | | | | |
| 20 | West Langeberg-Kwadousberg-Waboomsberg | | | 1 | 4 | 2 | 2 | | | 3 | | 1 | | | | | | | 4 | 1 | | 1 | | | 2 | 3 | 1 | 1 | 2 | | | | | 1 | | |
| 21 | Oudtshoorn | | | | | | | | | | | | | | 1 | | | | 1 | | 1 | | | | | 1 | | | | | | | | | | |
| 22 | NE South Sandveld | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 23 | South Ceres Karoo | | | | | | | | | | 1 | | | | | | | | | 1 | | | | | | 1 | | | | | 1 | | | | | |
| 24 | North Ceres Karoo | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 25 | Dysseldorp | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | 1 | | | | | |
| 26 | North Grootrivierberge | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| 27 | West Tankwa | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 28 | Boesmanspoortberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 29 | Kamiesberg | | | 1 | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| 30 | North West Coast | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | | | | | | | | | | |
| 31 | Zuurberg | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | 42 | 15 | 51 | 38 | 40 | 22 | 4 | 1 | 199 | 14 | 38 | 19 | 30 | 2 | 5 | 10 | 20 | 303 | 34 | 23 | 64 | 51 | 15 | 20 | 187 | 65 | 52 | 38 | 3 | 22 | 5 | 2 | 35 | 0 | 0 |

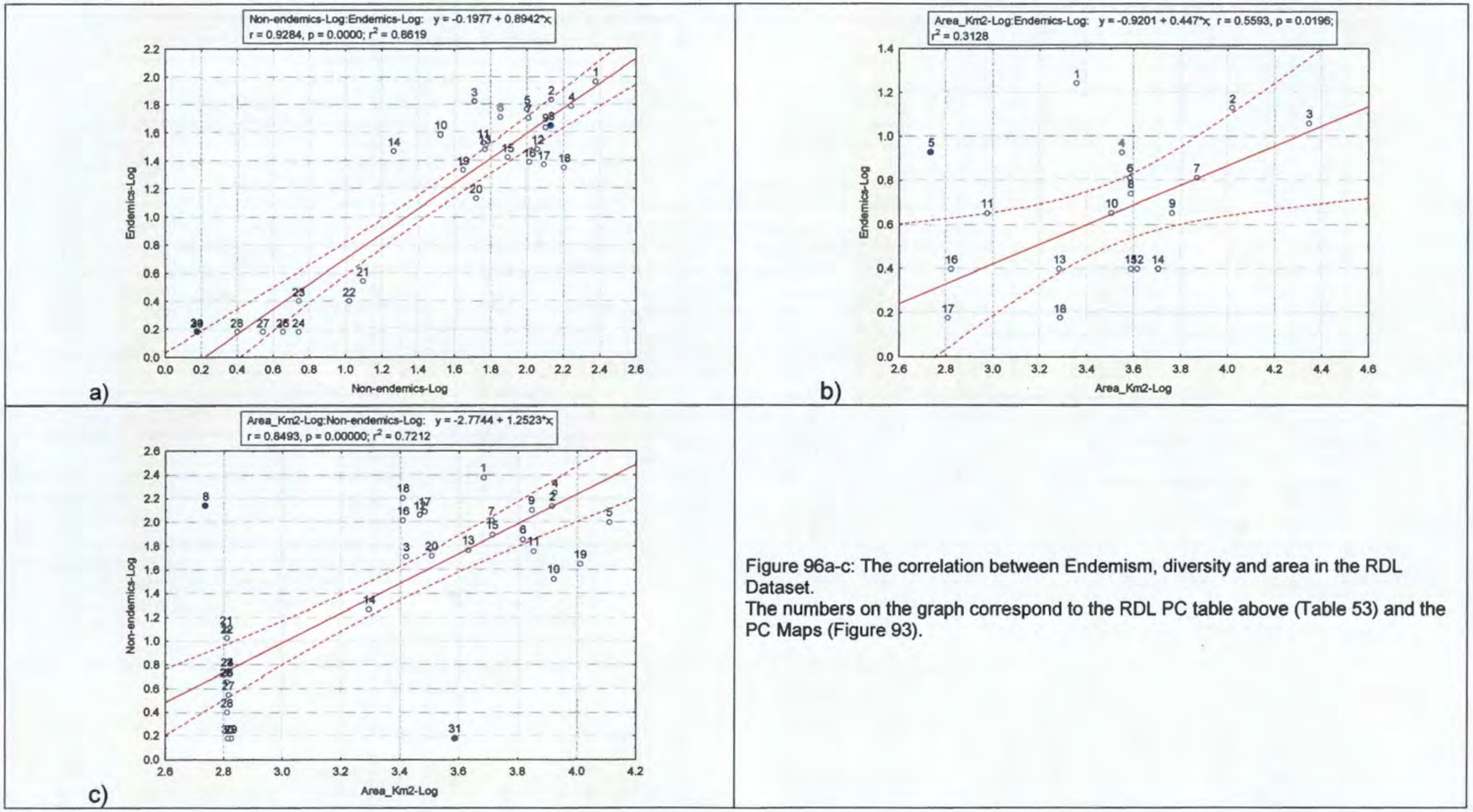


Figure 96a-c: The correlation between Endemism, diversity and area in the RDL Dataset.
The numbers on the graph correspond to the RDL PC table above (Table 53) and the PC Maps (Figure 93).

Karooveld (Table 54). However, sandstone taxa still dominant the RDL Taxa Dataset (Table 54), which may overwhelm the patterns of biotic elements on other substrates, as observed in the Combined Taxa Dataset. In general, the PCs of the RDL Taxa Dataset are largely centred on mountains. It may be more informative to analyse the RDL Taxa Dataset at a finer spatial resolution, which would likely result in less overlap between the different biotic elements that may contribute conflicting information to cluster analysis and PC formation. Moline and Linder (2005) obtained slightly more resolved cluster results when using the Broad Habitat Units (BHUs) of Cowling and Heijnis (2001) rather than QDSs.

Aside from differences in the spatial boundaries of RDL PCs, another notable departure from the more typical montane TMS Fynbos Clade patterns are the differences in the frequencies of endemic taxa between the various PCs, and thus, the rankings of the PCs. This is probably the most notable departure from TMS Fynbos Datasets I analysed. Although the RDL PCs with the highest number of endemics are still centred in the Hottentots Holland-Kogelberg-Kleinriviersberge region, the remainder of the RDL SWPP PCs perform relatively poorly. The second (Northern NWPP, PC 2) and fourth (South Northwest Centre, PC 4) ranked RDL PCs are from the core NWPP, while the third (Nieuwoudtville Escarpment, PC 3) and sixth (Nieuwoudtville Surrounds, PC 6) ranked RDL PCs are from further north, in the southern Succulent Karoo (sSK), as defined by my Combined Dataset (Table 56). The Gifberg is retrieved in most of the datasets that I analysed, due to the presence of a few high altitude fynbos TMS elements, but perform exceptionally well in the RDL Dataset, due to the high numbers of Geophytes (Table 56). These non-montane non-fynbos elements contribute to the Gifberg being included into the Nieuwoudtville Surrounds PC (6), which surrounds the Nieuwoudtville Escarpment (PC 3) (Figure 93). However, the Gifberg does form a distinct phytogeographic area at the PSC level (Figure 93).

The Peninsula (PC 8) performs relatively poorly in the RDL Dataset, possibly due to the emphasis of the RDL Taxa Dataset on threatened taxa. The majority of Peninsula endemics occur on TMS. In the RDL Dataset 67% of Peninsula endemics with known substrate preferences are on TMS (Table 54), less than the 85.7% of Peninsula endemics from my Combined Dataset (Table 9). Sandstone (montane) substrates are not generally in the more anthropogenically threatened areas (Helme and Trinder-Smith, 2006), which may reduce the number of sandstone RDL Taxa on the Peninsula. This may explain why the Peninsula PC (8) is relatively underrepresented by endemic RDL Taxa. I recorded 44 RDL Peninsula endemics, while Helme and Trinder-Smith (2006) recorded 66 RDL Peninsula endemics from a total of 158 Peninsula endemics using a more updated dataset. Thus, only 41.8% of the Helme and Trinder-Smith (2006) Peninsula endemics are classified as RDL Taxa. In addition, much of the montane TMS area of the Peninsula forms part of the Table Mountain National Park protected area, which conserves 80% of the mountain chain (Helme and Trinder Smith, 2006). This is predominantly TMS, relieving the pressure on the TMS Taxa, which may result in their exclusion from the Red Data List. Therefore, Peninsula sandstone endemics and ultimately Peninsula endemics as a whole are likely to be underrepresented in the RDL Dataset. This underrepresentation of sandstone taxa may be a more general pattern in the RDL Taxon Dataset.

To compare the properties of the NWPP and SWPP at the phytogeographical province level (one hierarchical level higher than PCs according to my definition, see Chapter 2, Section 2.3.5), a cursory analysis was undertaken, superficially combining the NWPP and SWPP PCs (Table 55) into areas largely congruent to phytogeographical provinces, as defined by my Combined Dataset and the literature (Goldblatt and Manning, 2000; Weimarck, 1941). I delimited a core NWPP, and a NWPP that included the south and north Succulent Karoo PC to the north. The SWPP out performs the core NWPP in absolute numbers of taxon diversity, endemism and in concentrations of diversity and endemism (Table 55). However, the enlarged NWPP (with sSK and nSK PCs) contains a higher diversity and a higher number of endemics. However, when taking into account the geographical area of the phytogeographical provinces, one can see that the SWPP has a proportionately higher number of taxa and endemics (Table 55). This once again highlights the extraordinary concentration of diversity and endemism in the SWPP of the CFR.

Table 55: Comparisons of the diversity and endemism values of the traditional SW and NW phytogeographical provinces for the RDL Taxa Dataset. PCs which are contentious for placement in either the NWPP or SWPP are underlined.

| Province | Centre/Sub-Centre Labels | Area | # Taxa | Taxa >= 0.5 | # Endemics |
|---|---|---|---|---|---|
| SWPP | 1; 8; 13.1; 16; 17; 18 | 37 | 656 | 527 | 349 |
| Core NWPP | 2; 4 | 26 | 381 | 256 | 155 |
| NWPP and sSK/nSK | 2; 3; 4; 6; 13.2; 27; 29 | 65 | 708 | 570 | 444 |

Other RDL Dataset PCs that perform relatively poorly when compared to the Combined Dataset include the Sandveld-Stellenbosch Mountains Centre (PC 18) and the West Langeberg-Kwadouwsberg-Waboomsberg Centre (PC 20); while the Worcester Valley Centre (PC 16) is not retrieved in the Combined Dataset, only in the Fabaceae and Geophytes Datasets. The floristic boundaries between these three PCs (16, 18 and 20), and between them and the PCs to the north and south is tenuous, with many alternative combinations of clustering QDSs, together offering similarly optimal results. The PC boundaries in these areas are not robust. The Worcester Valley Centre (PC 16) and the West Langeberg-Kwadouwsberg-Waboomsberg Centre (PC 20) contain low altitude Renosterveld endemics, which may create conflict. In addition, these three PCs (16, 18, and 20) are situated on the boundary between the NWPP and SWPP, and may contain overlapping taxa from these two phytogeographical provinces, producing additional conflict.

Although there are notable differences between the phytogeographical patterns in the RDL Taxa and some of the other datasets that I analysed (mostly montane, TMS Fynbos Clades), the similarities to the Combined Dataset and the Geophyte Datasets are not surprising, as the RDL Taxa Dataset is one of the most numerous contributors of data to both the Combined Dataset and Geophyte Datasets. In addition, many (62.8%) of the endemic RDL Taxa occur in montane sandstone habitats (Table 54). In conclusion, the RDL Dataset is a reasonably good surrogate of floristic patterns and processes when compared to my Combined Dataset, with the recognition that the lower altitude choria slightly better developed in the RDL Dataset, occasionally at the expense of the montane PCs of my Combined Dataset. The RDL Dataset combines PC features and patterns observed in more montane TMS Fynbos Clades (Ericaceae, Polygalaceae, Proteaceae, Restionaceae and Rutaceae), and those in lesser montane TMS Clades (Fabaceae and Geophytes). They may be a better surrogate of overall PC patterns than either of these individual biotic groups, or any of my individual datasets, or a single family or clade. As a proxy for overall biodiversity pattern and process, the RDL Taxa seems adequate, although it is advised that its particular biases and limitations are taken into consideration, such as the relative underrepresentation of numbers of endemic taxa on the Peninsula. Thus, it does not display pure, unfiltered natural biodiversity patterns alone, though it no doubt better indicates the frequencies of PC endemic taxa under threat.

### 14.1.3 The relationship between endemism, diversity, and area in the RDL Dataset PCs

In my RDL Taxon Dataset, a highly significant and strong positive relationship ($r^2 = 0.86$, $p<0.001$) exists between: (1) the number of endemic species (endemism) and the number of non-endemic species found within PCs (Figure 96a). A highly significant but weak relationship was found between the number of endemics and the geographic size of PC ($r^2 = 0.39$, $p<0.001$) (Figure 96b), and the number of non-endemics and the geographic size of the PC ($r^2 = 0.20$, $p=0.001$) (Figure 96c). The Peninsula PC (8) and the Zuurberg PC (31) constituted extreme outliers in my dataset, being over and underrepresented respectively with regards to PC area, in endemic (Figure 96b) and non-endemic taxa (Figure 96c). Although all regression analyses produced significant statistical relationships, diverse phylogenetic relationships (Table 53) and growth forms

(Table 56) in the RDL Taxa Dataset impose additional levels of complexity on the interpretation of the results.

Endemism (Figure 96a) and Diversity (Figure 96c) are still highest in the South Southwest Mountains (PC 1), although the number of endemic taxa predicted by non-endemic taxa (Figure 96a) does not fall outside the 95% confidence interval. However, a remarkable feature of the Southwest Mountains (1) is the number of endemic (Figure 96b) and non-endemic (Figure 96c) taxa in relation to PC area.

The Nieuwoudtville Escarpment (3) and the Nieuwoudtville Surrounds PC (6) have more endemic taxa than either of the numbers of non-endemic taxa (Figure 96a) would predict. However, the Nieuwoudtville Escarpment (PC 3) has far more endemics than predicted by the PC area (Figure 96b) and also more non-endemic taxa than expected (Figure 96c). This is in contrast to most Cape Clades that show a decrease in diversity and endemism in a northerly and/or easterly direction from the Caledon District (Levyns, 1964). Closer inspection of the taxa that are endemic to the Nieuwoudtville Escarpment (3) and the Nieuwoudtville Surrounds PC (6) reveals that there is an overrepresentation of Geophytes, and an underrepresentation of shrubs and shrublets (Table 56). Shrubs and shrublets make up the bulk of the numbers of TMS montane (fynbos) clade diversity and endemism and Levyns' pattern (1964) is maintained in the shrub/shrublet growth form categories.

In the Central Southeast Centre (19), the numbers of endemic and non-endemic taxa correlate well with each other (Figure 96a), but there are fewer endemic (Figure 96b) and non-endemic taxa (Figure 96c) than predicted by the large PC size. The large geographic size of the East KMPP-West SEPP (PC 5) allows a high proportion of the taxa represented there to be endemic (Figure 96a). This is despite the fact that there is a general underrepresentation of both endemic (Figure 96b) and non-endemic (Figure 96c) taxa predicted by PC size.

The East Southeast Centre (10) has a high proportion of taxa that are endemic (Figure 96a), with endemism predicted by PC area (Figure 96b), with the result that non-endemic taxa are underrepresented (Figure 96c). Although the Vanrhynsdorp Lowlands Centre (PC 14) has high levels of endemism (Figure 96a and b), non-endemic taxon numbers are as predicted (Figure 96c). Both these PCs (10 and 14) are overrepresented by succulent taxa (Table 56), while the Vanrhynsdorp Lowlands PC (14) also contains higher than expected Geophytes (Table 56).

The West Agulhas Plains (12), the Worcester Valley (16), the South Sandveld (17), and the Sandveld-Stellenbosch Mountains (18) have less endemism than predicted by non-endemic taxa (Figure 96a). However, because their PCs are small, numbers of endemic (Figure 96b) and non-endemic taxa (Figure 96c) exceed values predicted by PC area. The

West Agulhas Plains (12) and South Sandveld (17), comprise mainly low latitude taxa, while the Worcester Valley (16), and to a lesser extent, the Sandveld-Stellenbosch Mountains (18) have some lower altitude representatives.

## 14.1.4 Frequencies of growth forms of the PC endemic RDL Taxa

Although the growth forms in most of my other datasets are not identical, they are much less heterogeneous than the growth forms present in my RDL Dataset. Montane TMS Fynbos has a fairly uniform growth form, most frequently comprising shrubs or shrublets. However, the RDL Dataset consists of a far greater variety of growth forms and phylogenetic diversity, prompting an investigation into growth form spatial distribution. In order to identify whether there are any statistically significant differences in the distributional patterns of RDL endemic growth forms between the different PCs that I identified, an $\chi^2$ analysis was undertaken on the RDL PC endemic growth forms (Table 56).

The SWPP is well represented by endemic RDL shrubs and shrublets. Interestingly, the Peninsula is significantly underrepresented in endemic RDL shrubs over a metre in size, but very well represented in shrubs up to and including a metre in size. The stunted stature of Cape Peninsula endemics may be on account of one or more of the harsh environmental conditions on the Peninsula, including shallow and/or nutrient poor soils (Simmons and Cowling, 1996), combined with frequent burning, which may preclude substantial biomass accumulation. In addition, the strong wind regime may further suppress plant height. The Cape Peninsula is battered by winter north-westerly winds, which frequently exceed gale force; and summer southerly and south-easterly winds that may blow at gale force for a week or more, although there are sheltered areas (Simmons and Cowling, 1996). The summer winds may exacerbate the summer aridity of the area, further stunting growth. There is also a higher than expected number of endemic RDL perennial herbs on the Peninsula and in the East SEPP PC, for unknown reasons. The South Southwest Mountains (PC 1) are relatively poorly represented by RDL Geophyte endemics and are dominated by shrubs and shrublets, and a relatively high number of Graminoids (particularly Restionaceae). When considering the life history frequencies of the Saldanha Peninsula and West Coast Centre (PC 13) RDL endemics, it is apparent why the Saldanha Peninsula and West Coast Centre does not display strong Cape Clade affinities in my study. Typical CFR growth forms are either underrepresented (shrublets), or significantly underrepresented (shrubs) here. Instead, annuals (very significant) and Geophytes (overrepresented) dominate, which explains why the area is not included in the CFR Core cluster in my Hierarchical Analysis (Chapter 2, Section 2.4.1.1). The Saldanha Peninsula and West Coast PC (13) is dominated by endemics with different frequencies of growth forms (Table 56), substrate (Table 54) and phylogenetic affinities (Table 53) to endemics that occur in the core CFR PC.

Table 56: $\chi^2$ Analysis of the Frequencies of the different Endemic RDL Life Forms in the various Phytogeographical Centres identified in this study. ($\chi^2$=5.52×$10^{-25}$, df=210, p=1).
Caution should be exercised in not extrapolating these values for the entire CFR flora. Categories utilised here are those identified by Goldblatt and Manning (2000). Shrubs comprise plants greater than 1 metre, while shrublets are plants up to and including 1 metre. Geophytes comprise rhizomatous, cormous, and bulbous plants. Succulents include leaf and stem succulents. The frequencies of certain less well known taxa that could not be classified are recorded, and probably mostly comprise annuals and succulents.

| Province | PC | Geophytes | Shrubs | Shrublets | Succulents | Perennials | Annuals | Graminoids | Trees | Unclassified | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|
| SWPP | NE South Sandveld | 2 | | | | | | | | | 2 |
| SWPP | Peninsula | 9 | 3 | 17 | 1 | 6 | 2 | 3 | | 3 | 44 |
| SWPP | Sandveld-Stellenbosch Mtns | 4 | 8 | 7 | | 2 | | | | 1 | 22 |
| SWPP | South Sandveld | 10 | 2 | 6 | 1 | | 2 | 1 | | 1 | 23 |
| SWPP | South Southwest Mtns | 11 | 33 | 36 | | 3 | 2 | 5 | | 2 | 92 |
| SWPP-NWPP | Worcester Valley | 8 | 4 | 6 | 4 | 1 | | 1 | | | 24 |
| NWPP | Northern NWPP | 26 | 18 | 10 | 4 | 3 | 4 | | | 3 | 68 |
| NWPP | South Northwest Centre | 14 | 26 | 13 | 1 | 2 | 1 | 3 | | 1 | 61 |
| NWPP | West Tankwa | | | | 1 | | | | | | 1 |
| NWPP-LBPP | West Langeberg-Kwadouwsberg-Waboomsberg | 8 | 3 | | 1 | 1 | | | | | 13 |
| LBPP | APPP/LBPP Plains | 3 | 14 | 18 | 6 | 2 | | | | | 43 |
| LBPP | Central LBPP Mtns and Plains | 7 | 16 | 17 | 4 | 2 | 1 | 3 | | | 50 |
| APPP | West Agulhas Plains | 5 | 9 | 14 | 1 | | | 1 | | | 30 |
| KMPP | Dysseldorp | | | | | | 1 | | | | 1 |
| KMPP | NW Karoo | 9 | 7 | 4 | 7 | 1 | 2 | | | 3 | 33 |
| KMPP | Oudtshoorn | 2 | | | | 1 | | | | | 3 |
| KMPP-NWPP | North Ceres Karoo | | 1 | | | | | | | | 1 |
| KMPP-NWPP | South Ceres Karoo | 2 | | | | | | | | | 2 |
| KMPP-SEPP | Boesmanspoortberg | | | | | | | | | 1 | 1 |
| KMPP-SEPP | East KMPP-West SEPP | 17 | 17 | 11 | 5 | 1 | 1 | 3 | 1 | 2 | 58 |
| KMPP-SEPP | Klein Swartberg-Rooiberg | 5 | 7 | 8 | 1 | 2 | | 1 | | 2 | 26 |
| KMPP-SEPP | North Grootrivierberge | | | | | | | | 1 | | 1 |
| SEPP | Central Southeast Centre | 4 | 6 | 3 | 4 | 1 | | | 1 | 2 | 21 |
| SEPP | East Southeast Centre | 8 | 6 | 4 | 8 | 3 | 1 | | 1 | 7 | 38 |
| SEPP | Zuurberg | | | 1 | | | | | | | 1 |
| WC-Succ | Saldanha Peninsula and West Coast | 15 | 1 | 4 | 4 | 1 | 4 | | | 1 | 30 |
| WC-Succ | North West Coast | | | | | 1 | | | | | 1 |
| sSK | Nieuwoudtville Escarpment | 35 | 11 | 3 | 5 | 3 | 3 | | 1 | 5 | 66 |
| sSK | Nieuwoudtville Surrounds | 26 | 3 | 6 | 6 | 3 | 2 | | | 5 | 51 |
| sSK | Vanrhynsdorp Lowlands | 15 | | 1 | 7 | | 1 | | | 4 | 28 |
| nSK | Kamiesberg | | | 1 | | | | | | | 1 |
| | Totals | 245 | 195 | 190 | 71 | 39 | 27 | 21 | 5 | 43 | 836 |

Table Colour Key: The $\chi^2$ Expected Values were calculated and compared to the Observed Values. Where observed values were divided into six categories. Three categories for underrepresented taxa: those that were less than half the expected, approximately half the expected, and those that were underrepresented. For overrepresented taxa: slightly overrepresented, approximately double the expected, and more than double the expected values. These categories have been colour coded for ease of reference below.

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 🟧 | < Half | 🟨 | ≈ Half | ⬜ | =Under-Represented | 🟩 | = Over-Represented | 🟦 | ≈ Double | 🟦 | > Double |

The RDL PC in the traditional LBPP is overrepresented with endemic shrubs and shrublets, and relatively underrepresented in endemic Geophytes. Endemic RDL succulents perform well in the APPP/LBPP Plains (PC 9), and endemic RDL graminoids perform well in the Central LBPP Mountains and Plains (PC 7).

In the NWPP, the two core CFR PCs (2 and 4) and the peripheral Kamiesberg (PC 29) contain expected numbers of RDL shrub endemics, while the remaining peripheral PCs (3, 6 and 14) are underrepresented with regards to this growth form. The changes in the dominance of life histories along this northerly gradient (PCs 4, 2, 6, 3 and 14) generally correspond with decreasing moisture availability and quantity. In the south (PC 4), endemic RDL shrubs are significantly overrepresented, while in the north (PC 2) they decrease in frequency, still being overrepresented, but to a lesser degree. Similarly, in the south, endemic RDL graminoids feature, but disappear to the north, where endemic RDL annuals and Geophytes become more dominant. In the remaining peripheral NWPP PCs, where endemic RDL shrubs or shrublets are either underrepresented to varying degrees, Geophytes are usually one of the more dominant groups. Endemic RDL succulents are significantly overrepresented in more xeric PCs, such as the Vanrhynsdorp Lowlands Centre (PC 14), and less so in other PCs with Succulent Karoo affinities, as are perennials and annuals. These growth forms are proportionately less well-represented among endemics in the core CFR PC.

In the West Agulhas Plains Centre (PC 12), RDL endemic shrublets, shrubs and graminoids are significantly overrepresented. Its extreme southerly position, in the west of the CFR, well within the winter rainfall season region, may facilitate the dominance of Cape elements.

In the more montane RDL PCs of the KMPP, such as the East KMPP-West SEPP Centre (PC 5) and Klein Swartberg-Rooiberg (PC 15), endemic RDL shrubs and shrublets are slightly overrepresented. In more arid, less topographically heterogeneous areas, such as the NW Karoo Centre (PC 11), endemic RDL succulents become more dominant (Table 56).

The life form frequencies of RDL taxa endemic to SEPP PCs (PC 5 in part, 10 and 19) once again reflect the importance of topography and geographic position, and how these factors affect life form frequencies. In the more westerly Central Southeast Centre (PC 19), shrubs are more dominant, due to higher winter rainfall abundance, mainly due to the Kouga Mountain Range, and to a lesser extent, the Tsitsikamma Mountains to the south. As one proceeds further east, both the geographically larger PCs here, the East Southeast Centre (PC 10) and the Central Southeast Centre (PC 19), have a lower representation of shrubs/shrublets. However, a very large endemic succulent component is also present, which is very significant in the more easterly East Southeast Centre (PC 10), mainly in its lower altitude areas. The perennial component is also important and is overrepresented in the easterly East Southeast Centre (PC 10).

In conclusion, topography, geography and precipitation have a significant effect on growth form frequencies of RDL PC endemics. Where topography is more extreme and/or winter rainfall more abundant, endemic RDL shrubs and shrublets are usually overrepresented. Coastal PCs such as the Peninsula (PC 8) and the West Agulhas Plains (PC 12) seem to have a better representation of endemic RDL shrublets rather than shrubs, possibly due to wind exposure and/or shallow soils (Cowling et al., 1996). As one travels north and east in the CFR from the Hottentots Holland-Kogelberg area and concomitantly, as absolute (and winter) rainfall decreases, endemic RDL Geophytes and succulents become increasingly well-represented in the RDL Dataset (Table 56). In general, the numbers of endemic RDL succulents may be underrepresented in my analysis, as many of the unclassified taxa are from Euphorbiaceae and are likely to be succulents, thus increasing the numbers of endemic RDL succulents further. This indicates a correlation between the frequencies of the growth forms of endemics and moisture availability, particularly winter rainfall. Due to the rarity of endemic RDL graminoids in PCs and trees in general, whenever they are endemic to a PC they are overrepresented. Similarly, annuals are not a very common life form in the CFR (Goldblatt and Manning, 2000), and endemic annuals were usually overrepresented when recorded as endemic to PCs.

## 14.2 CFR Phytogeographical Centres

### 14.2.1 The Southwest Phytogeographical Province

There are numerous differences between the RDL Taxa Dataset PCs and the montane TMS Cape Clades that I analysed. This was both in terms of phytogeographical boundaries and the relative number of endemics in the PCs, and consequently, their rankings. The Southern Mountains Centre (PC 1) contains the largest diversity of RDL Taxa and the largest number of endemics (Table 53) of all my RDL PCs. Although endemism and diversity is highest in the Hottentots-Kleinrivierberge Sub-Centre (PSC 1.1), which is common for most montane TMS Fynbos Clades; the density of diversity and endemism is fairly similar in both sub-centres (PSC 1.1 and 1.2) (Table 53). In the Combined Dataset, the South RZE Sub-Centre (PSC 1.2) is larger, extending one QDS to the east and also including two northerly QDSs, which groups the south and north sides of the RZE Mountains into a single geographical unit. The division of the RDL Taxa RZE Mountains between the South RZE Sub-Centre (PSC 1.2) and Worcester Valley Centre (PC 16) may indicate higher ratios of lower altitude fynbos and renosterveld elements

(Table 54), combining the lower lying areas. Due to conflict and spatial incongruence, various equally optimal combinations of QDSs in Centres 16, 18 and 20 are possible. Thus, floristic boundaries in this area are not very robust in my study, which indicates that this may be an area of floristic overlap.

The Cape Peninsula (PC 8) contains a reasonable number of RDL Endemic Taxa, but not as many as when compared with montane TMS Fynbos Clades that I analysed. This may be due to montane TMS Taxa being less threatened, resulting in a slight decrease in numbers of these taxa in the RDL Dataset, when compared to more threatened taxa on other lower altitude substrates. This is slightly anomalous when considering that two of the three QDSs on the Peninsula contain the second and third highest RDL QDS inverse diversity scores (Figure 95), and that the Peninsula PC has high diversity (Figure 94). Low altitude biotic elements on the Peninsula may overlap with the South Sandveld and Malmesbury phytogeographical elements, producing conflict and reducing endemism. A recent analysis of diversity and endemism on the Peninsula (Helme and Trinder-Smith, 2006) indicates that my dataset is dated, only recording 44 of a possible 66 RDL Peninsula endemics

The South Sandveld Centre (PC 17) and NE South Sandveld Centre (PC 22) are congruent with areas usually identified as floristically important, in earlier biogeographical studies on CFR Taxa (Moline and Linder, 2005; Linder, 2001; Linder and Mann, 1998; Weimarck, 1941). This area mostly contains low altitude, sandy flats flora, on littoral sand, granite, or on TMS Substrates (Table 54). It contains relatively high numbers of taxa from Cape Clades, when compared to other low altitude PCs in the RDL Taxon Dataset, for example, the Saldanha Peninsula (PC 13).

The Sandveld-Stellenbosch Mountains Centre (PC 18) has relatively few endemic taxa in the RDL Taxa Dataset, but has the third highest diversity. The same phenomenon is observed in my Proteaceae Dataset, where the Sandveld-Stellenbosch Mountains Centre forms an independent PC. Apart from high/low altitudinal and TMS/littoral/shale conflict, there may also be conflict within the TMS flora due to the complex topographic nature of the area. The affinities of the mountains to the lower altitude areas may be more due to spatial resolution rather than floristic patterns, caused by interdigitisation of habitats in the QDSs. This high diversity and low endemism may indicate that my floristic boundaries for the Sandveld-Stellenbosch Mountains Centre (PC 18) are inappropriate and that the area may need to merge with a neighbouring floristic area. Alternatively, this could be an area of overlap between different floristic elements, which may boost diversity, but have few endemics.

The Worcester Valley Centre (PC 16) is not usually retrieved in montane TMS Cape Clades, although it was recovered in Fabaceae (*Aspalathus*), Polygalaceae (*Muraltia*), and the Geophyte Datasets. This is likely due to the presence of appreciable numbers RDL non-montane biotic elements in the PC (Table 54), such as geophytes and succulents (Table 56), with the result that low altitude biotic elements cause QDSs to cluster together into PCs, in preference to montane taxa causing clustering. However, even in the Geophyte Dataset, the Berg River seems to be a floristic boundary below the QDS scale of resolution. Although most of the RDL Worcester Valley endemic taxa seem to have TMS fynbos affinities, there are numerous records of Renosterveld RDL endemics (Table 54).

### 14.2.2 The Northwestern Phytogeographical Province

There are a number of notable departures in the RDL Dataset NWPP PC from the results of the Combined Dataset, and traditional NWPP phytogeographical patterns in the literature (Weimarck; Goldblatt and Manning, 2000). The most obvious is the sub-division of the Cedarberg Mountain Range into distinct northern (PC 2) and southern (PC 4) components. Further anomalies within the context of this split, are the association of the northern Cedarberg (Pakhuis Mountains) component (PSC 2.1) with the northern Sandveld/Piketberg area (PSC 2.2), and the association of the southern Cedarberg (PSC 4.1) with the Groot Winterhoek (PSC 4.1) and the northwest Hexrivierberge (PSC 4.1). While in the former case, the phytogeographical sub-division of the North Sandveld/Piketberg and North Cedarberg into separate PSCs occurs along traditional high/low altitude floristic boundaries. The lack of apparent sub-division of the three usually distinct mountain ranges into separate PSCs in the southern area (PC 4) is puzzling. This may be due to conflict between the endemic taxa in the floristic unit (PSC 4.1). Whether this conflict is between, or within biotic elements is unclear. The southern part of the Hexriver Mountains is grouped with the Worcester Valley PC (16), which may erode the distinctiveness of the Hexriver Mountains as a discrete floristic unit. There is evidence of an easterly floristic unit (PSC 4.2), which combines the Swartrugberge, northeast Hexrivier and Bontberg QDSs. However, as anticipated, this area has a much lower level of diversity and endemism values compared to the more mesic western sub-centre. The Swartruggensberge, combine with the more mesic Southern Northwest Core Sub-Centre (PSC 4.1) in the west. In the RDL Taxa Dataset, the Swartruggensberge does not combine with the more arid Swartrugberge-Northeast Hex River Sub-Centre (PSC 4.2) to the south, as occurs in the Combined Dataset.

There is some conflict in assigning QDS 3319BC to either the Swartrugberge-Northeast Hex River Sub-Centre (PSC 4.2), as it is at present, or with the Worcester Valley (PC 16) to the south. QDS 3319BC has five single QDS RDL endemics and this adds an additional four endemic taxa when either combined with the Swartrugberge-Northeast Hexrivier Sub-

Centre (PSC 4.2), or with the Worcester Valley (PC 16). This conflict may also have influenced the lack of floristic differentiation on the usually discreet phytogeographical areas of the Southern Cedarberg, Groot Winterhoek and Hex River Mountains.

### 14.2.3 The Langeberg Phytogeographical Province

The Central Langeberg Mountains and Plains PC (PC 7) is centred on the Middle and East Langeberg Mountains, and extend southward slightly to include a portion of the Central Langeberg Plains. The western Langeberg Mountains form part of the more depauperate West Langeberg-Kwadouwsberg-Waboomsberg Centre (PC 20); while the low altitude areas to the south of the East Langeberg Mountains (PSC 9.2) are more strongly associated with the Central and East APPP/LBPP Plains Centre (PC 9). The Potberg-Central Agulhas Plains (PSC 9.1) and East Langeberg Plains (PSC 9.2) are more strongly associated with the APPP Plains, rather than with the mountainous areas of the LBPP, and the APPP/LBPP Plains (PC 9) has relatively high numbers of limestone endemics (Table 54). There is conflict concerning the affiliations of 3421AB between two alternative PCs (7 and 9). The QDS itself has five endemic taxa and this adds an additional five endemic taxa when combined with the mountains (PSC 7.1), or four endemics when maintained in the plains (PSC 9.2). Although the absolute number of endemics is increased by combining QDS 3421AB with the mountains, when combined with the plains PC (9) it results in a higher relative ratio of endemism for the PC, and is classified there. In reality, there is hardly any conflict in the distribution of these taxa below the QDS scale of resolution, with the potential endemic taxa occupying different habitats, different altitudes, or different vegetation types. In the Combined Dataset, 3421AB is more closely associated with the montane area at the QDS scale of resolution. This is expected, as montane TMS Fynbos Taxa contribute 70% of taxa in the CFR, overwhelming other biotic elements.

In the west, the low altitude areas south of the West Langeberg (part of the southeast SWPP) are incorporated into the Potberg-Central Agulhas Plains Sub-Centre (PSC 9.1). The Central Langeberg Mountains and Plains Centre (PC 7) contain relatively high numbers of perennial, shrubby CFR Clade Taxa (Table 56), on TMS slopes (Table 54), and this PC (7) contains areas of high altitude habitats (Figure 93).

Although there was some justification for the establishment of East (PSC 7.1) and West (PSC 7.2) sub-centres, divided in the Tradouwspas region, there is much overlap of taxa, particularly in the western QDS of the East Central Langeberg Mountains Sub-Centre (3320DD of PSC 7.1). The favouring of this QDS in the East Central Langeberg Mountains Sub-Centre (PSC 7.1) has resulted in more endemics being recorded from this sub-centre, although there is a higher diversity of taxa in the West Central Langeberg Sub-

Centre (7.2). Similarly, there are more taxa with at least half their ranges in the western sub-centre and this lack of conversion into more endemic taxa is also affected somewhat by the classification of 3320DD to the east sub-centre (7.1). Merging 3320DD to the western sub-centre results in one more absolute endemic, but once again, the relative increase in endemism is slightly lower (47% versus 50%), so the current classification is maintained.

### 14.2.4 The Agulhas Plains Phytogeographical Province

The APPP PC (9 and 12) are extremely well developed in the RDL Taxa Dataset, relative to many other datasets I analysed, which may once again reflect inherent bias in the RDL Taxa Dataset to include slightly higher numbers of taxa found in low altitude, non-TMS habitats, which are more predisposed to threat from human utilisation, particularly coastal urban development, and agriculture. This is especially noticeable in the east (PSC 9.2), where the borders of the APPP are further north than in my Combined Dataset, and the literature (Weimarck; Goldblatt and Manning, 2000), sequesting QDSs to the south of the East Langeberg and West Outeniqua Mountains. Further, the Potberg-Central Agulhas Plains (PSC 9.1) extends west into the Rûens area, and contains shale/renosterveld endemics (Appendix II).

In the RDL Taxa, the Potberg floristic unit (PSC 9.1) is more strongly associated with the Central and Eastern APPP, rather than to the West. This phenomenon is weakly displayed in a few other datasets, such as Asteraceae, *Erica* and Fabaceae, where the Potberg shows slightly greater, but not necessarily exclusive affinities to the east APPP, rather than to the west APPP. More frequently in my datasets, the Potberg has stronger affinities to the west APPP, as observed in the Combined Dataset and in the literature (Weimarck). In my RDL Dataset, the Potberg is closely associated to the Central and Eastern APPP/LBPP Plains Centre (PC 9) and it is worth noting that the eastern APPP PC (9) contains more RDL Endemic Taxa than the West Agulhas Plains Centre (PC 12), which was the opposite of what was observed in most of my other datasets. However, the more easterly APPP/LBPP Plains Centre (PC 9) is 55.56% larger by area than the West Agulhas Plains Centre (PC 12) and it contains about 43.33% more endemic taxa, displaying fairly similar ratios of endemism and area. However, there is only a marginal increase in diversity (17.36%) and near endemism (22.22%), indicating that the Western APPP contains a greater diversity of RDL Taxa and near endemics relative to area, although a slightly smaller proportion of them are endemic, based on my current phytogeographical boundaries. This is presumably because high numbers of taxa, especially near endemic taxa, are shared with the Potberg floristic unit (PSC 9.1), which is classified in another PC. If the Potberg were classified with the West Agulhas Plains

Centre (PC 12), it would have a net gain of 26 endemic taxa, while the Central and Eastern APPP/LBPP Plains Centre (PC 9) would have a net loss of 26 endemic taxa. The present classification is maintained due to the relative increase in endemism in the Central and Eastern APPP/LBPP Plains Centre (PC 9). Thus, there appears to be conflict between the endemic taxa of the floristic units from the eastern APPP and potential endemics from the western APPP. Comparisons of the numbers of endemic taxa at the sub-centre level (between 9.1, 9.2 and 12.1) indicate that the West Agulhas Core Sub-Centre (PSC 12.1) contains slightly higher numbers of endemism and diversity, but much higher numbers of near endemic taxa, in a similar sized area to the sub-centres of the APPP/LBPP sub-centres (PC 9.1) (Table 53), indicating much higher densities of range restricted taxa in the western APPP Sub-Centres. Thus, finer scale distributional taxa may result in an increase in endemism in the West Agulhas Plains (PC 12).

### 14.2.5 The Karoo Mountain Phytogeographical Province

In the RDL Taxa Dataset, the KMPP is divided into three major PCs. From west to east, these are: the Northwest Karoo Centre (PC 11), the Klein Swartberg-Rooiberg Centre (PC 15) and the East KMPP-West SEPP Centre (PC 5). The Northwest Karoo Centre (PC 11) is centred on the Witteberg and Klein Roggeveld Mountains, and the intervening lower altitude areas, overlapping parts of the Ceres Karoo and Moordenaars Karoo. There is much overlap in the distributions and taxa and no sub-centre patterns are discernable. The Klein Swartberg-Rooiberg Centre (PC 15) includes the Klein Swartberg and Rooiberg Mountain Ranges, which are in separate PSCs; and the Anysberg and Touwsberg to the southwest.

Interestingly, the Groot Swartberg Mountains (PSC 5.1) has greater affinities to the Outeniqua Mountains (PSC 5.2), which are combined into a single PC (5), rather than to the Klein Swartberg (PSC 15.1), as in the Combined Dataset. The Groot Swartberg Mountains (PSC 5.1) are usually placed in the KMPP, while the Outeniqua Mountains (PSC 5.2) are usually placed in the SEPP (Combined Dataset; Weimarck; Goldblatt and Manning, 2000). However, although the East KMPP-West SEPP Centre (PC 5) combines the parts of the eastern KMPP and western SEPP, the sub-centre boundaries of the East KMPP-West SEPP Centre (PC 5) still largely follow the floristic boundaries between the KMPP and SEPP as defined by my Combined Dataset and the literature (Goldblatt and Manning; 2000; Weimarck). However, the Outeniqua Sub-Centre (PSC 5.2) extends one QDS further westward than in my Combined Dataset and two QDSs further westwards than that of Goldblatt and Manning (2000), up to the Gouritz River (QDS 3321DC) (Figure 93). The East KMPP-West SEPP Centre (PC 5) contains mostly TMS/fynbos endemics, but the lower altitude elements (Fynbos, Renosterveld and Succulent Karoo) (Table 54) may cause the higher altitude TMS areas of the East KMPP and the West SEPP to combine together in the RDL Taxa Dataset. This is unusual, as the Groot Swartberg usually clusters with the Klein Swartberg, especially in montane TMS Cape Clades, with the possible exception of Proteaceae Dataset (Figure 89). Where there are PC endemic taxa that occur in the Groot Swartberg (PSC 5.1) and the Outeniqua Mountains (PSC 5.2), they all occur on the Kammanassieberge rather than the Rooiberg, as a stepping-stone between the Groot Swartberg and Outeniqua Mountains. These endemics include both sandstone fynbos elements and clay Renosterveld/karooid elements. *Mimetes chrysantha* (2) links the Rooiberg to the Outeniquaberge and occurs on sandstone slopes.

Apart from the Northwest Karoo Centre (PC 11) that has no subdivisions, the sub-centres of the other two centres (PC 5 and 15) almost always coincide with specific mountain ranges and are named after these mountains. The Dwyka Sub-Centre (PSC 5.5) is another exception, situated on the incised river valleys just north of the Dwyka-Gouritz River Valley, separating the Klein and Groot Swartberg Mountain Ranges, and contains non-montane non-CFR taxa.

### 14.2.6 The Southeast Phytogeographical Province

There are three major RDL PCs associated with the SEPP as defined by my Combined Dataset and Goldblatt and Manning (2000), two are restricted to the SEPP (PCs 10 and 19), while the East KMPP-West SEPP Centre (PC 5) overlaps into the KMPP. The Outeniqua Sub-Centre (PSC 5.2) and the Plettenberg Bay Sub-Centre (PSC 5.3) are essentially restricted to the West SEPP of my Combined Dataset, and Weimarck's Knysna interval. The Central Southeast Centre (PC 19) occurs in the centre of the SEPP, and is congruent with Weimarck's (1941) Zitzikamma Sub-Centre; while the East Southeast Centre (PC 10) is in the east, of which part (PSC 10.1) is congruent with Weimarck's (1941) Cockscomb Sub-Centre. Unusually, the more westerly PC (19) has fewer RDL Endemics than the more easterly PC (10), which is two QDSs smaller (Table 53). Furthermore, the Vanstadens-Coastal Sub-Centre (PSC 10.1) has more RDL endemics than the entire Central Southeast Centre (PC 19), in a much smaller area. This is an exception to the trend of decreasing diversity and endemism along south-north and west-east gradients (Levyns, 1964). The East Southeast Centre (PC 10) has nearly double the number of montane TMS elements when compared to the Central Southeast Centre (PC 19), as well as having significantly higher numbers of other endemic biotic elements (Table 54), and is due to the inclusion of the more sub-tropical summer rainfall flora from the east. Similar patterns are observed in the Combined Dataset, at the PSC level in the Combined Dataset South-eastern Centre (PC 5). Weimarck (1941) mentions rich diversity and endemism in his Zitzikamma and Cockscomb Sub-Centres, and lists four and five endemics respectively, but did not observe the discrepancy in endemism levels that I encountered. The Central Southeast Centre (PC 19) excludes nearly all lower altitude coastal QDSs, unlike the East Southeast Centre (PC 10), which groups together many coastal QDSs containing taxa (Figure 93 and Figure 94) in close proximity to it.

Sub-Centres of the Central Southeast Centre (PC 19) are found mainly in mountainous QDSs (Figure 93; Table 54), except for the Southern Groot Karoo Sub-Centre (PSC 19.2). Although the backbone of the Central Southeast Centre (PC 19) is along the Kouga Mountain Range (PSC 19.1), there are no RDL Taxa that occupy the entire area. Instead, there is overlap from five endemic RDL Taxa, each of which occupies two QDSs. Both sub-centres of the East Southeast Centre (PC 10) contain relatively high numbers of RDL Endemics, especially the Vanstadens-Coastal Sub-Centre (PSC 10.1).

Further east, outside the area of the core CFR, is the Zuurberg Centre (PC 31), situated in the northern montane parts of the Zuurberg Sub-Centre of Weimarck (1941). It contains a single RDL representative, a small tree-like asterid, *Oldenburgia grandis* (6).

## 14.3 Non-CFR Phytogeographical Centres

### 14.3.1 The Succulent Karoo Cluster

There is a close floristic association between the Nieuwoudtville Escarpment (PC 3), the Nieuwoudtville Surrounds (PC 6), and the Vanrhynsdorp Lowlands PC (14). These cluster together to form the southern Succulent Karoo Cluster (sSK), in the hierarchical analysis of the Combined Dataset PCs (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). A further indication of this close association in the RDL Taxa Dataset is that QDS 3118BD can be added to either the Vanrhynsdorp Lowlands Centre (14), or the Nieuwoudtville Surrounds Centre (PC 6) with equal optimality. The QDS itself contains three endemic RDL taxa, and adds a further RDL endemic when combined with either of the two centres (PC 6 or 14) mentioned above. Although the Nieuwoudtville Escarpment (PC 3) and the Nieuwoudtville Surrounds (PC 6) do contain endemic montane TMS fynbos elements, they are included in the Succulent Karoo discussion, due to the overrepresentation of Geophytes and succulents, and underrepresentation of shrubs/shrublets (Table 56). The remaining northern PC, the Kamiesberg (PC 29), forms part of the northern Succulent Karoo (nSK), in the hierarchical analysis of the Combined Dataset PCs (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26).

The Vanrhynsdorp Lowlands Centre (PC 14) is a low altitude PC in a very xeric environment, outside the core CFR (Chapter 2, Section 2.4.1.1). It is therefore unsurprising that it contains no perennial shrubs (Table 56), or montane TMS fynbos elements (Table 54), or Cape Clade Endemics (Appendix II). It also consists almost exclusively of geophyte and succulent endemics.

In the RDL Dataset, the Nieuwoudtville Escarpment Centre (PC 3) performs significantly better than in most other datasets that I analysed. In the RDL Taxa Dataset, it performs even better than the Peninsula (PC 8). The Nieuwoudtville Escarpment (PC 3) averages 16.5 endemics per QDS, while the Peninsula averages 14.67. Similarly, in the RDL Taxa Dataset, the Nieuwoudtville Surrounds Centre (PC 6) contains many more endemics than the same area in many of the other datasets that I analysed. And similarly, it also ranks higher than the RDL Peninsula PC, although this is not as pronounced as the Nieuwoudtville Escarpment Centre. The Gifberg (South of Nieuwoudtville) is phytogeographically important in the RDL Taxa, primarily due to its endemic geophytes, but it is also retrieved in many of my other datasets due to a scattering of montane TMS Fynbos Endemics.

My RDL Dataset only includes a single taxon in the Kamiesberg (PC 29), *Felicia diffusa ssp khamiesbergensis* (1), which is also endemic to the Kamiesberg. There should be more, as Helme and Desmet (2006) report as many as 57 strict Kamiesberg Endemics. Thirty-nine of these have RDL Status listings, but the RDL Taxa Dataset that I used, was mostly restricted to the geographic confines of the CFR.

### 14.3.2 The West Coast Cluster

There are two RDL Dataset PCs on the West Coast, the Saldanha Peninsula (PC 13), and the North West Coast Centre (30). In the RDL Dataset, the Saldanha Peninsula (PC 13) is quite distinct and well-developed, and extends northwards along the coast into the NWPP, as far as Olifantsrivier Mouth, crossing the floristic boundary of the SWPP and NWPP. This configuration may have influenced the clustering of the Saldanha Peninsula into the south Succulent Karoo Cluster in the Combined Dataset (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26). The RDL Taxa Dataset of the Saldanha Peninsula Centre (13) is reminiscent of Acock's (1953) classification of these areas into his Strandveld Vegetation Unit.

The Saldanha Peninsula (PC 13) contains a number of diverse phylogenetic and biotic elements, but has relatively few fynbos elements (Table 54 and Appendix II). Most of the taxa are granite or limestone endemics (Table 54). My RDL Taxa Dataset has a relatively high number of Saldanha Peninsula Endemics, placing it much higher in the PC rankings than in my Combined Dataset, where it is ranked 20th (Table 9). Although there may be fewer PCs in the RDL Taxa Dataset, this elevation in ranking may be due to the proportionately higher numbers of geophytes. Of the 30 RDL Endemic Taxa in the

Saldanha Peninsula Centre (PC 13), 15 are Geophytes, one is a perennial, four are succulents and four are annuals. Five of the taxa are shrub/shrublets (Table 56), while there are no montane TMS fynbos element endemics (Table 54).

The more southerly sub-centre (PSC 13.1) has many more RDL Endemics and a much higher RDL diversity than the remaining sub-centre (PSC 13.2); and it is mostly situated in the traditional SWPP (Weimarck; Goldblatt and Manning, 2000). There are two QDSs in the NWPP that clustered with it, one of which is disjunct and is centred on Lambert's Bay (QDS 3218AB, Figure 93). Three RDL Taxa are endemic to the Saldanha Peninsula-South West Coast (PSC 13.1) and are recorded from the disjunct QDS (3218AB), *Aloe arenicola* (2), *Aloe distans* (3), and *Empodium occidentale* (5), which may indicate under collection in the area. The low QDS diversity scores (Figure 94) support this view. The North West Coast Sub-Centre (PSC 13.2) occurs entirely within the NWPP and displays even fewer links to its large southerly PC area. The remaining PC, the North West Coast Centre (30), contains a single endemic, *Crassula multiceps* (1).

## 14.4 Summary

The RDL Taxa Dataset comprises a heterogeneous phylogenetic assortment of taxa, which are considered rare and predisposed to threat, or are already threatened. As such, they comprise both montane and lowland taxa, possibly with a slight bias towards the latter, relative to most of my other datasets. The RDL Taxa Dataset comprises the largest single dataset in my analysis, so it is no surprise that some of the patterns here are apparent in the Combined Dataset.

However, the use of the RDL Dataset allows for a unique opportunity to compare a fairly representative sub-dataset of the flora of the CFR, comprising a heterogeneous group of taxa from many different lineages, and from many different habitats. Thus, RDL Taxa may be more representative of CFR endemism than my more taxonomically natural datasets. It includes patterns of all biotic elements, not just those that may be limited to particular clades. CFR clades can be very large (Goldblatt and Manning, 2000; Linder, 2003) and fairly homogenous (both in growth form and general habitat preferences). If anything, the RDL Dataset overcompensates, with a slight underrepresentation of the usually dominant sandstone taxa. This results in certain PCs having slightly less endemics (proportionately) than they do in fynbos clades, thus lowering their ranking, while other PCs become more prominent, due to an increase in non-sandstone endemics. This results in an increase in endemics from non-fynbos clades, notably succulents and geophytes.

Inclusion of higher numbers of non-sandstone taxa causes some conflict and realignment of floristic boundaries, with montane areas featuring slightly less strongly.

Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, NWPP east KMPP-southwest SEPP, LBPP, APPP, east SEPP, west KMPP and central SEPP.

Recent work on the Peninsula (Helme and Trinder-Smith, 2006) and in the Kamiesberg (Helme and Desmet, 2006) indicates that my RDL Taxa data is dated and under-representative.

# Chapter 15: Restionaceae (Table 57, Figure 97, Figure 98)

## 15.1 Introduction

The African Restionaceae (Linder et al., 2003; Linder, 1991) is a typical montane TMS Cape Clade (Levyns, 1964; Linder, 2003), and display characteristic phytogeographical patterns of montane TMS Cape Clades (Linder and Mann, 1998; Linder, 2001; Moline and Linder, 2005). In the western areas of the CFR, where the Mediterranean climate is most strongly developed and on the Langeberg Mountains, Restionaceae PCs form large consolidated units.

Compared to other taxa in the CFR, the African Restionaceae has been relatively well investigated phytogeographically (Moline and Linder, 2005; Linder, 2001; Linder and Mann, 1998; Oliver et al., 1983). All of these studies undertook multiple analyses on their respective datasets. These studies used either different weighting techniques, or different clustering algorithms to identify phytogeographically distinct areas. Although the results of these different studies are not identical, there is little notable conflict. This relative conformity may be due to the mostly uniform ecological and distributional properties of the different Restionaceae Taxa that were analysed, in part (by Moline and Linder, 2005, and Linder and Mann, 1998), and as a whole (by Linder, 2001). It may also be due to the overwhelming dominance of certain biotic elements, such as endemics on sandstone slopes. Furthermore, where there are different biotic elements, spatial differences may be in less conflict than in the other datasets that I analysed. Of the Restionaceae Endemics that were recorded on shale (Table 58), only one endemic occurs exclusively in shale-renosterveld, one occurs on both sandstone and shale, while the remaining two are recorded from shale bands. This indicates that these floristic patterns are more similar to sandstone taxa. Thus, one of the most likely sources of conflict in creating PCs is very much reduced in Restionaceae. Moline and Linder (2005) reported slight improvements to the retrieval of PCs when using eco-geographical regions, which are more spatially refined to areas of similar habitat, compared to grid cells, which are more random, spatially. With eco-geographical regions, greater improvement could be realised in taxa with more disparate biotic elements. However, caution should be exercised when considering that improvements measured from increasing endemism are proxies of success and do not necessarily indicate better areas for testing historical hypotheses.

Table 57: Taxonomic properties of the Centres identified for the group Restionaceae (Figure 97, Figure 98).

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Southwestern Centre | 32 | 265 | 158 | 71 | 302 | 0.13 | 0.12 |
| 1.1 | Hottentots Holland | 6 | 204 | 45 | 15 | 38 | 0.42 | 0.38 |
| 1.2 | Peninsula | 3 | 121 | 7 | 7 | 12 | 0.57 | 0.50 |
| 1.3 | RZE | 5 | 141 | 11 | 5 | 8 | 0.32 | 0.15 |
| 1.4 | Franschhoek-Bainskloof-Elandskloof Mtns | 3 | 153 | 10 | 5 | 8 | 0.53 | 0.42 |
| 1.5 | Sandveld | 3 | 57 | 2 | 1 | 3 | 1.00 | - |
| 1.6 | Remainder | 12 | 97 | 1 | 0 | 0 | - | 1.00 |
| 2 | Northwestern Centre | 23 | 162 | 61 | 26 | 104 | 0.17 | 0.14 |
| 2.1 | Hexrivier | 3 | 113 | 11 | 3 | 4 | 0.44 | 0.17 |
| 2.2 | Swartruggens-Baviaansberg-N Wabooms-Witteberg | 7 | 71 | 9 | 3 | 11 | 0.52 | 0.29 |
| 2.3 | N and SE Cedarberg | 5 | 88 | 6 | 2 | 7 | 0.70 | 0.40 |
| 2.4 | SW Cedarberg-Groot Winterhoek | 4 | 98 | 5 | 2 | 6 | 0.75 | 0.50 |
| 2.5 | Remainder | 4 | 69 | 0 | 0 | 0 | - | 1.00 |
| 3 | Greater Langeberg-West Outeniqua | 10 | 113 | 22 | 17 | 32 | 0.19 | 0.14 |
| 3.1 | W Central and W East Langeberg | 3 | 93 | 14 | 11 | 14 | 0.42 | 0.37 |
| 3.2 | E Central Langeberg | 1 | 39 | 2 | 2 | 2 | 1.00 | 1.00 |
| 3.3 | West Outeniqua | 2 | 33 | 1 | 1 | 2 | 1.00 | - |
| 3.4 | Remainder | 4 | 45 | 1 | 0 | 0 | - | 1.00 |
| 4 | Agulhas Plains | 15 | 107 | 18 | 8 | 35 | 0.29 | 0.19 |
| 4.1 | West and W East Agulhas Plains/E Potberg | 8 | 98 | 14 | 6 | 16 | 0.33 | 0.20 |
| 4.2 | Remainder | 7 | 37 | 1 | 0 | 0 | - | 1.00 |
| 5 | Klein Swartberg | 3 | 47 | 4 | 3 | 6 | 0.67 | 0.50 |
| 6 | E West Outeniqua-Tsitsikamma | 7 | 50 | 2 | 2 | 12 | 0.86 | 0.71 |
| 7 | E Kammanassie | 1 | 18 | 2 | 2 | 2 | 1.00 | 1.00 |
| 8 | Groot Swartberg | 2 | 38 | 1 | 1 | 2 | 1.00 | - |
| 9 | South Gifberg-Nieuwoudtville | 3 | 29 | 1 | 1 | 3 | 1.00 | - |
| 10 | Kamiesberg | 2 | 14 | 1 | 1 | 2 | 1.00 | - |
| 11 | Boesmanspoortberg-Uniondale | 2 | 12 | 1 | 1 | 2 | 1.00 | - |
| 12 | W Kammanassie | 1 | 5 | 1 | 1 | 1 | 1.00 | - |
| 13 | Tropical East Coast | 1 | 1 | 1 | 1 | 1 | 1.00 | - |
| 14 | Drakensberg | 5 | 5 | 1 | 1 | 5 | 1.00 | - |
| 15 | Outside | 129 | 124 | 3 | 0 | 0 | - | 1.00 |

## 15.1.1 The relationship between endemism, diversity and area in the Restionaceae PCs

A highly significant and positive relationship ($r^2 = 0.61$, $p<0.001$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 101a). A highly significant and strong positive relationship is also found between the number of endemics and the geographic size of the PC ($r^2 = 0.82$, $p<0.001$) (Figure 101b), and between the number of non-endemics and the geographic size of the PC ($r^2 = 0.78$, $p<0.001$) (Figure 101c). The Drakensberg PC (14) constituted an outlier and was excluded from my regression, and has fewer endemic (Figure 101a) and non-endemic taxa (Figure 101c) than predicted from the PC area. Restionaceae diversity and endemism drops off sharply outside the core CFR.

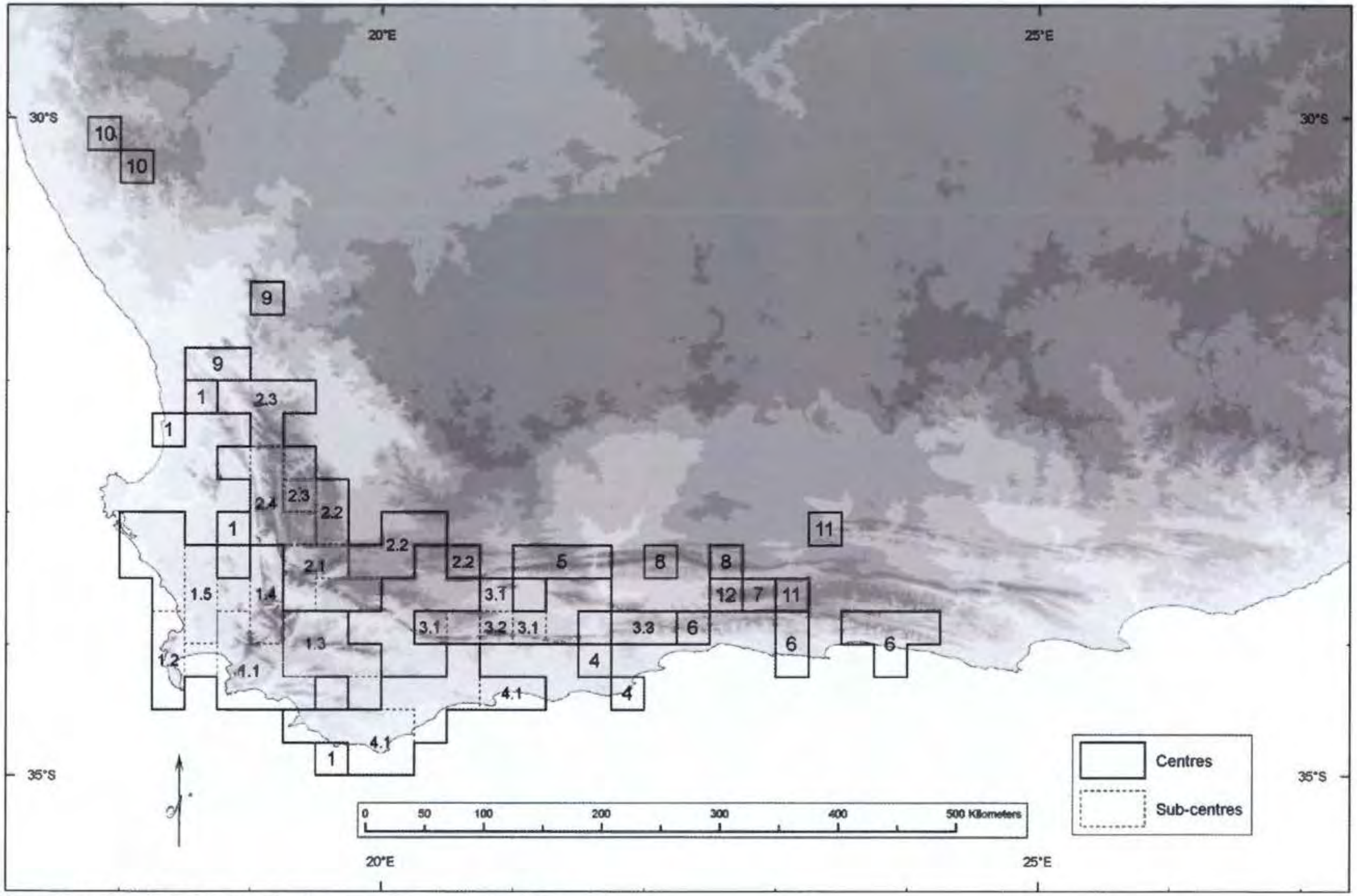


Figure 97: PC and PSC for the Restionaceae Dataset in the CFR.

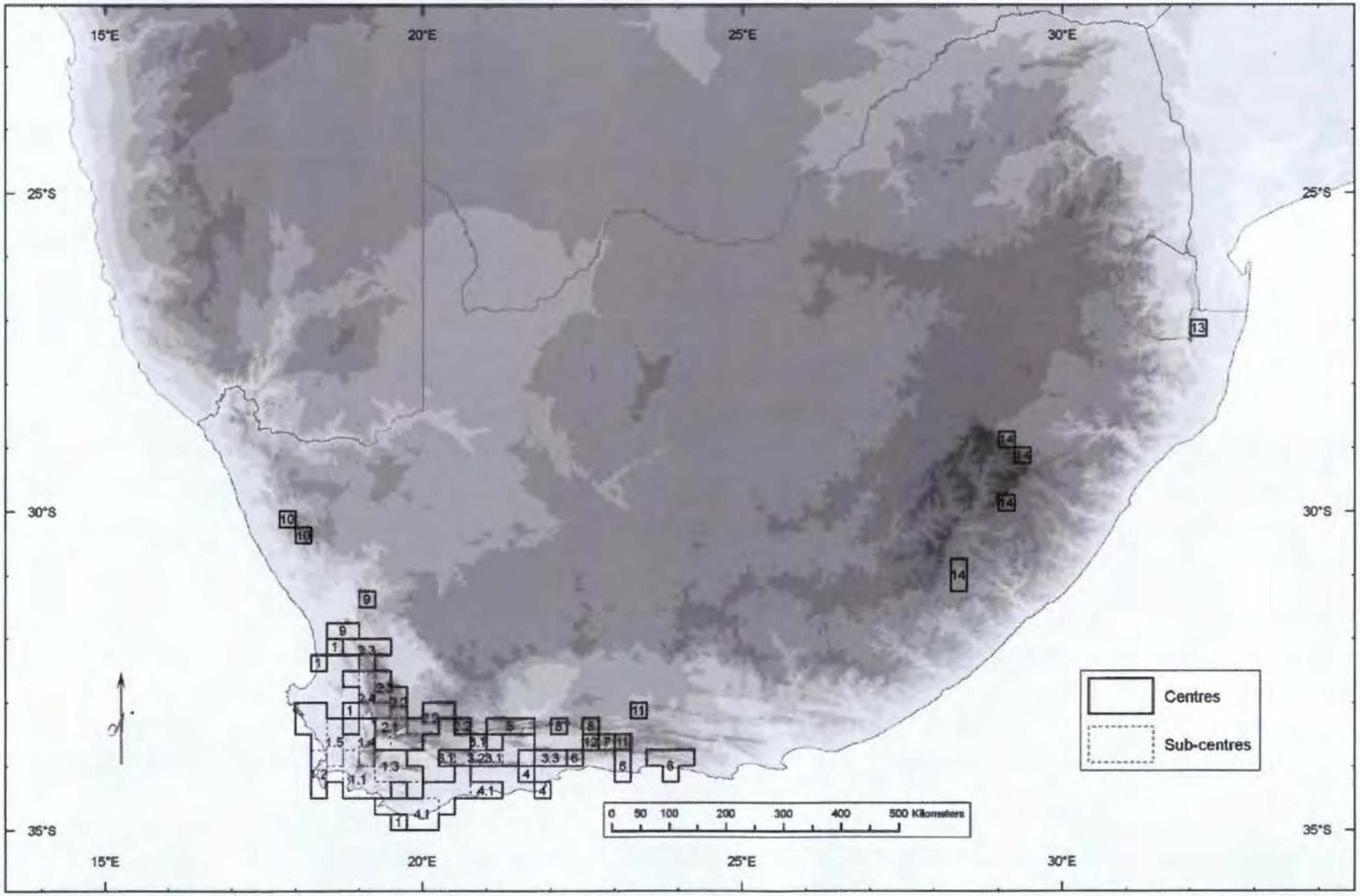


Figure 98: PC and PSC for the Restionaceae Dataset in Southern Africa.

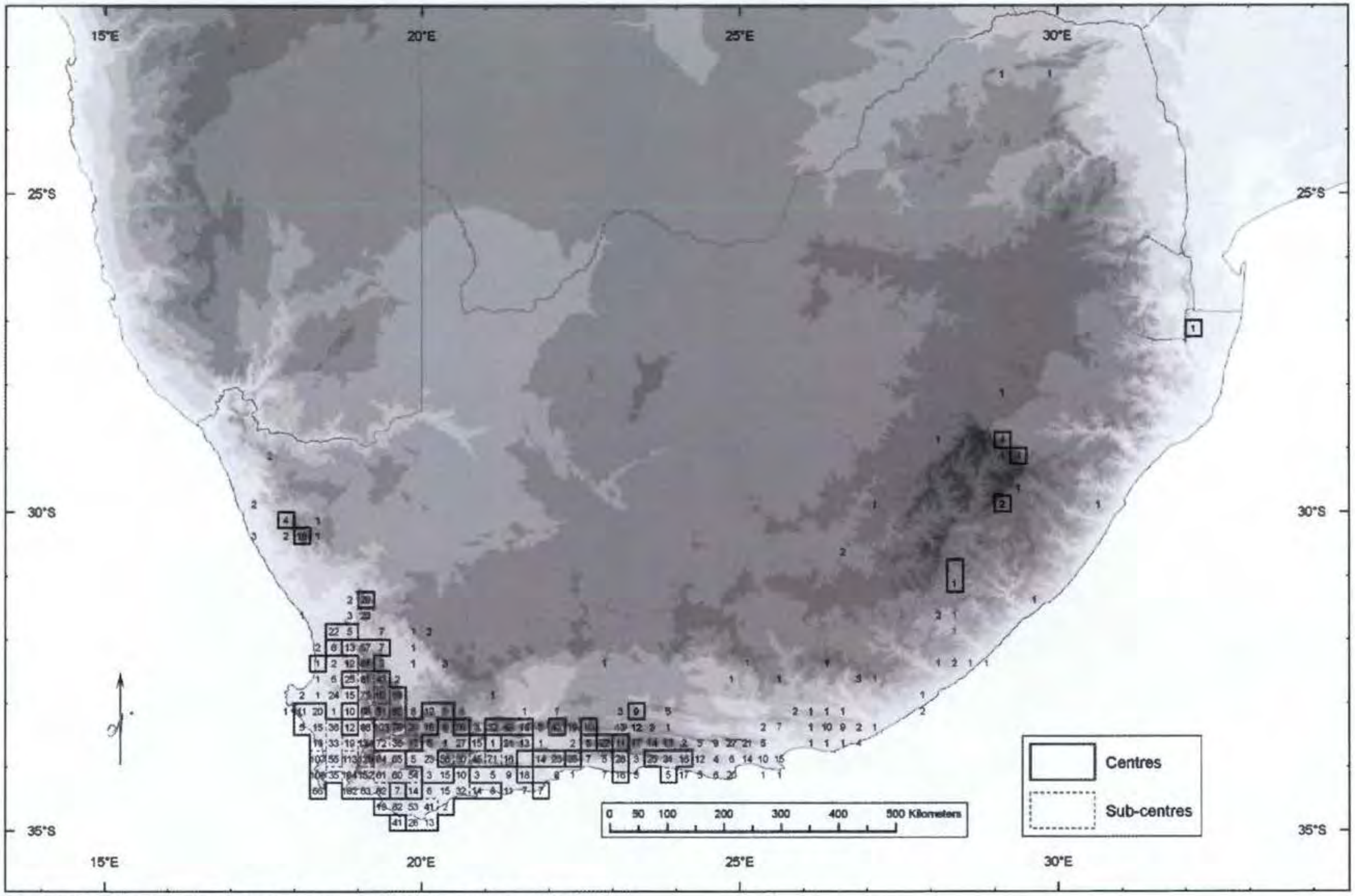


Figure 99: QDS Diversity for the Restionaceae Dataset in Southern Africa.

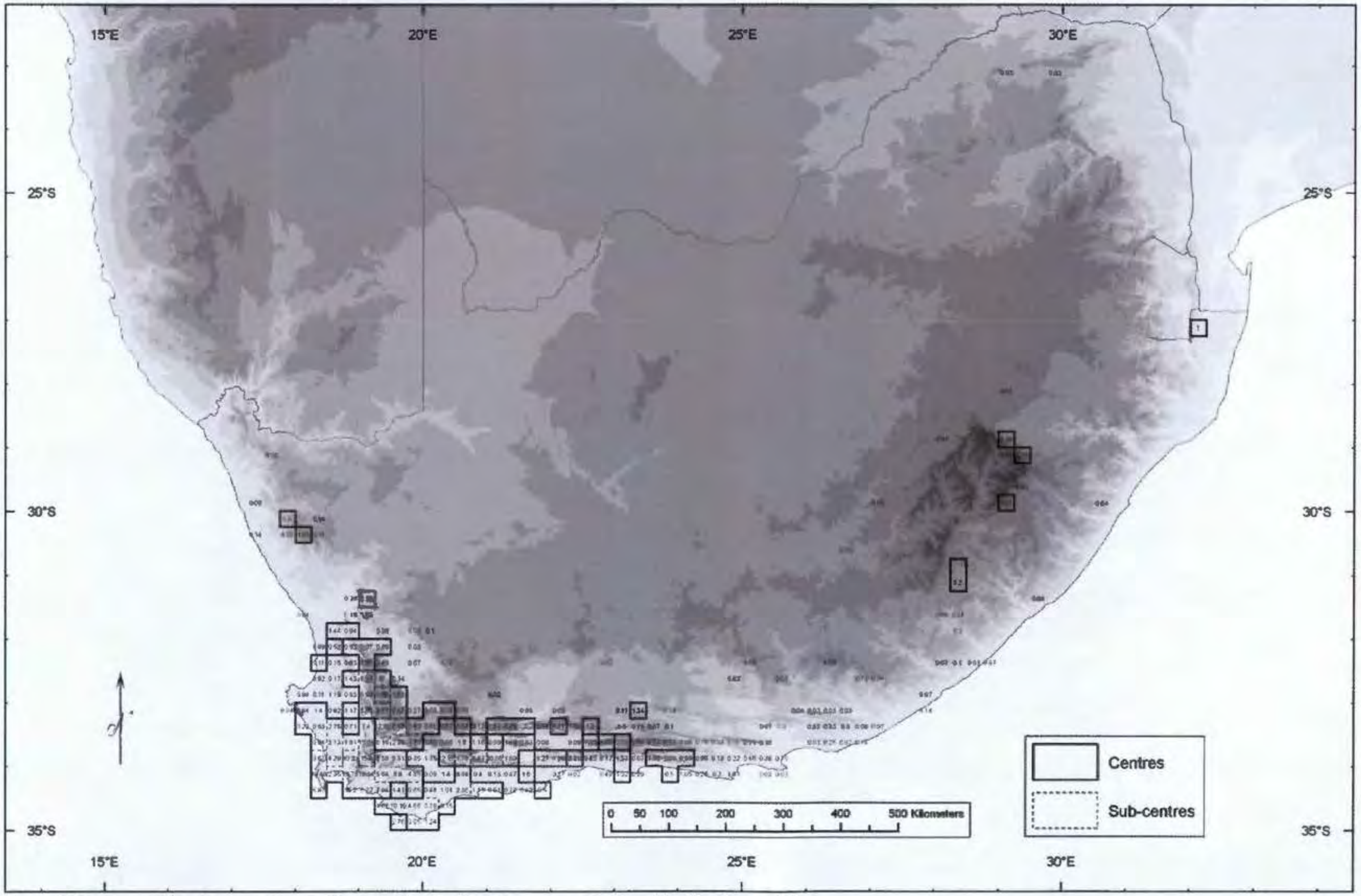


Figure 100: Sum of the Inverse Taxon Ranges for the Restionaceae Dataset in Southern Africa.

Table 58: Habitat Data for the Restionaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliifs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats/Dunes | Other | Unknown |
| 1 | Southwestern Centre | | 1 | 6 | 11 | 16 | 19 | 3 | | 16 | 3 | | | 1 | | | | 2 | 26 | 3 | 2 | 5 | 26 | 4 | 4 | 11 | 8 | | | | | | | 7 | | |
| 2 | Northwestern Centre | | | 2 | | 2 | 10 | 6 | 1 | 11 | | | | | | | 1 | | 17 | 3 | 1 | 2 | 5 | 3 | 7 | 12 | 3 | | | | | | | | | |
| 3 | Greater Langeberg-West Outeniqua | 3 | | 1 | | 1 | 6 | 3 | | 5 | 1 | | | | | | | 3 | 11 | | | | 5 | | 1 | 5 | | | | | | | | | | |
| 4 | Agulhas Plains | | | | 2 | | | | | 2 | | | | 6 | 1 | | | | 2 | | | 3 | | | | 1 | 1 | | | | | | | 6 | | |
| 5 | Klein Swartberg | | | | | | | 3 | | 2 | | | | | | | | | 2 | 1 | | | | | | 2 | | | | | | | | | | |
| 6 | E West Outeniqua-Tsitsikamma | | | | 1 | 1 | 1 | | | | | | | | | | | | 1 | | | | 1 | 1 | | | 1 | | | 1 | | | | | | |
| 7 | E Kammanassie | | | | | | | | | 1 | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | |
| 8 | Groot Swartberg | | | 1 | | | | 1 | 1 | | | | | | | | | | 1 | | | | 1 | | | 1 | | | | | | | | | | |
| 9 | South Gifberg-Nieuwoudtville | | | | | 1 | | | | 1 | | | | | | | | | 1 | | | | 1 | | | 1 | 1 | | | | | | | | | |
| 10 | Kammiesberg | | | 1 | | | | 1 | | | | | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | |
| 11 | Boesmanspoortberg-Uniondale | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 12 | W Kammanassie | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 13 | Tropical East Coast | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 14 | Drakensberg | | | | | | | | 1 | | | | | | | | 1 | | 1 | | | | | | | | | | | | | 1 | | | | |
| 15 | Outside | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Totals | 3 | 1 | 11 | 14 | 21 | 36 | 17 | 3 | 38 | 4 | 0 | 1 | 7 | 1 | 0 | 2 | 6 | 63 | 7 | 3 | 10 | 39 | 8 | 12 | 34 | 14 | 0 | 0 | 1 | 0 | 1 | 0 | 13 | 0 | 0 |

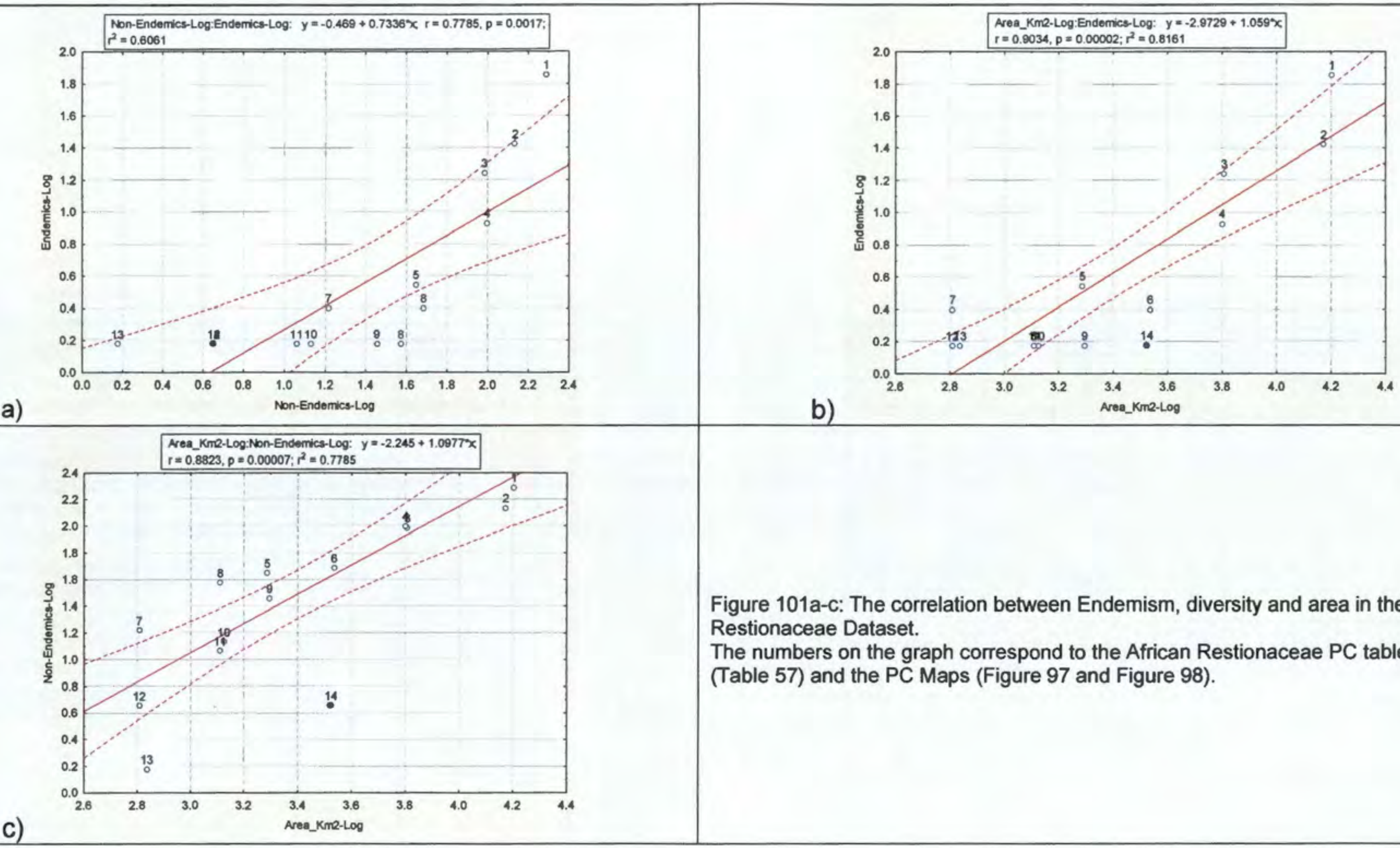


Figure 101a-c: The correlation between Endemism, diversity and area in the African Restionaceae Dataset.
The numbers on the graph correspond to the African Restionaceae PC table above (Table 57) and the PC Maps (Figure 97 and Figure 98).

In Restionaceae, the Southwest Centre (1) has higher than expected endemism levels, when compared to both its non-endemic taxa (Figure 101a) and its PC area (Figure 101b). Conversely, endemism is underrepresented in both the more arid eastern West Outeniqua-Tsitsikamma (6) and the South Gifberg-Nieuwoudtville (9) PC (Figure 101a and b). On the other hand, the Swartberg (PC 8) has a low proportion of endemic taxa (Figure 101a and c), likely due to its small PC size. The Kammanassieberg PC (7) has more endemic (Figure 101b) and non-endemic (Figure 101c) taxa than its small size predicts.

## 15.2 CFR Phytogeographical Centres

### 15.2.1 The Southwest Phytogeographical Province

The Restionaceae Dataset shows a very structured and comprehensive clustering of QDSs in the SWPP, with all the phytogeographical units of my Combined Dataset clustering into a single PC. The sub-centres correspond largely with the PCs of the Combined Dataset and the Proteaceae Dataset, another TMS Cape Clade. The Southwest Centre (PC 1) is strongly congruent with the SWPP of Weimarck (but excludes his Bredasdorp Sub-Centre) and with the SWPP of Goldblatt and Manning (2000), but does not extend as far to the southeast, terminating at Riviersonderend. The eastern boundary of my RZE PSC (1.3) is similar to the eastern boundary of Linder and Mann's (1998) Tulbagh-Bredasdorpberg unit. However, Linder and Mann (1998) included the western portion of the APPP (extending to the coast), as part of the SWPP, while I do not. The Southern Mountains Centre, of Moline and Linder (2005), is confined to the southern mountainous areas of the SWPP, and represent an accurate depiction of where the majority of endemism and diversity is concentrated (Figure 97 and Figure 98). Moline and Linder's (2005) Southern Mountains and Cape Flats Centres coincide with the Hottentots Holland (PSC 1.1) and South Sandveld (PSC 1.5) Sub-Centres of my study respectively.

In my analysis of Restionaceae, most of the QDSs, in the traditional SWPP, form a very neat and almost continuous centre (PC 1) (Figure 97, Figure 98). This PC is concentrated mostly in the southwest Cape Mountains, but spreads northwest into the southern Sandveld Fynbos. There are two disjunct taxa in the NWPP Sandveld, namely *Calopsis impolita* (10) in 3218BA and *Restio quinquefaris* (8) in 3218AD, which both occur on sandy, coastal flats, which highlights low altitude floristic development and dispersal in Restionaceae. There is also a smaller, more frequently observed disjunction (Combined Dataset, Bruniaceae, Ericaceae, Fabaceae and Proteaceae) across the West Agulhas

Plains (PSC 4.1) to Quoin Point (3419DC). This is due to *Elegia cuspidata* (9), *Nevillea obtusissima* (6) and *Restio purpurascens* (10), all Southwestern Centre (PC 1) endemics.

Sub-centre boundaries, diversity and endemism largely correspond with traditional CFR phytogeographical patterns. The richest sub-centre corresponds to the area traditionally considered the heart of the fynbos biome, the Hottentots Holland-Kleinrivier PC (PSC 1.1) or Kogelberg (Levyns, 1964) followed by the Peninsula (PSC 1.2) and the RZE (PSC 1.3). These choria are all largely congruent to my Combined Dataset. The Wemmershoek-Elandsberg PC (PSC 1.4) is slightly incongruent, joining the Elandsberg QDS with the Wemmershoek-Bainskloof PC (PSC 1.4) rather than with the Groot Winterhoek to the north. The clustering of the Elandsberg QDS into the SWPP is very similar to the classifications of Goldblatt and Manning (2000), and Weimarck, but differs from my Combined Dataset, which clusters the Elandsberg QDS with the NWPP. This southern grouping of the Elandsberg QDS further emphasises the strong southern (SWPP) affinities of Restionaceae. Lastly, there is a southern Sandveld Fynbos PC (PSC 1.5), with a single endemic.

The uniqueness of the Cape Peninsula, as an independent phytogeographical unit, is beyond dispute, both in my study and in the literature (Linder, 2001; Oliver et al., 1983; Weimarck, 1941). Apart from its lower altitude affinities, it also displays disjunct higher altitude TMS affinities to both northern and southern mountains within the SWPP. The Peninsula has stronger affinities to the southern mountains, mostly the Hottentots Holland-Kogelberg Mountains (indicated via *Willdenowia rugosa* (4); *Anthocortus laxiflorus* (5)), as retrieved by Moline and Linder (2005). There also appears to be less range-restricted, but distinctly southerly taxa (*Ischyrolepis cincinnata* (7), *Restio festuciformis* (8), *Restio harveyi* (8) and *Restio ambiguous* (9)) that enhance these affinities. A few taxa seem to have more northerly SWPP Mountain affinities, to the Stellenbosch Mountains-Bainskloof Mountains (*Ischyrolepis pratensis* (5) and *Restio micans* (5)).

At the QDS scale, montane, lower and higher altitude taxa are combined in QDSs. Subsequently the Peninsula also shows affinities to the lower lying Cape Flats and West Coast regions (Linder and Mann, 1998). The study of Moline and Linder (2005) is unique in that it identifies separate West Coast and Cape Flats PCs, possibly because of their use of eco-geographical regions, which make a distinction between areas occupied by different biotic elements.

### 15.2.2 The Northwest Phytogeographical Province

As with the SWPP PC, the Northwestern Centre (PC 2) merges most of the mountain areas of the NWPP (Weimarck; Goldblatt and Manning, 2000), including the Cedarberg and Groot Winterhoek Mountains into a single PC. However, excluded are the Gifberg and

Nieuwoudtville Escarpment, which unite to form their own separate centre (PC 9). There is no PC development on the Piketberg Mountains.

The boundary between the NWPP and SWPP varies slightly between different phytogeographical studies on Restionaceae taxa. Moline and Linder (2005) extend their Northern Mountains Centre southwards, to include the Hawequas Mountain Fynbos BHU complex (Cowling and Heijnis, 2001); while the Tulbagh-Bredasdorpberg Centre of Linder and Mann (1998) extends northwards, to include the southwest Hex River Mountains. This study conforms to the majority of others (Linder, 2001; Goldblatt and Manning, 2000; and Weimarck, 1941), and reiterates that the Berg River Valley is the major divide between the NWPP and SWPP, most particularly for montane TMS taxa (biotic elements). This does not mean that the results of Moline and Linder (2005), or Linder and Mann (1998) are incorrect. On the contrary, their results may indicate that the correct classifications of the areas are based on the taxa they analysed. This conflict lends further support to the notion that floras/taxa overlap in this area, resulting in difficulties in assigning QDSs.

The subdivision of the largest PC of the NWPP, the Northwest Centre (PC 2), does not follow boundaries in my Combined Dataset, or sub-divisions of previous studies for this area (Weimarck; Goldblatt and Manning, 2000). The sub-centres all have similar levels of endemism, differing only by a single endemic. The Hex River Mountains form a continuous sub-centre (PSC 2.1), and have the greatest similarities to phytogeographical boundaries of other datasets and studies. The second highest number of endemics is found in the Swartruggens-Baviaansberg-N Wabooms-Witteberg Sub-Centre (PSC 2.2). This is an unusual sub-centre pattern that is well-developed in Restionaceae; Moline and Linder (2005) and Linder and Mann (1998) depict a similar phytogeographical pattern for *Elegia* and *Thamnochortus* respectively. However, their areas extended further east to include the Klein Swartberg. Interestingly, my Rutaceae Dataset also features a similar eastward extension of the NWPP. I found the Klein Swartberg to form a distinct PC, independent of the NWPP extension onto the Witteberg. This corridor sub-centre (2.2) combines a number of QDSs that are grouped together in the Greater Witteberg Centre (PC 12) of the Combined Taxa Dataset. The QDSs of this region in my Restionaceae Dataset cluster together, although in some of my other datasets, these QDSs can be classified in up to three different PCs and in two different phytogeographical provinces (NWPP or KMPP). My Restionaceae extension to the Witteberg bears striking resemblance to Weimarck's delimitation of his Northwest Centre. The presence of NWPP elements on the Greater Witteberg may explain why it clusters with the NWPP in the Combined Dataset.

Interestingly, three taxa in Restionaceae (all from separate genera), occur in this potential corridor, to varying degrees (Figure 97 and Appendix II), but all taxa are recorded from

3319BD. *Hypodiscus sulcatus* (5) shows the most conventional pattern, occurring almost entirely in the Goldblatt and Manning's KMPP portion of my sub-centre (PCS 2.2). *Ischyrolepis karooica* (2) occurs on the mountains around Karoopoort and on the Bontberg, the latter being on the boundary of the NWPP and the KMPP of Goldblatt and Manning. *Thamnochortus scabridus* (4) is fairly widespread in my sub-centre (PSC 2.2), but is restricted to the Northwest Centre of Weimarck. The affinities of the Swartruggens and Baviaansberg area (PSC 2.2 in part) are ambiguous, and may belong either in the NWPP, or in the west KMPP. H.P. Linder (personal communication, 2003) has observed that there is a near continuous high altitude corridor linking the Swartruggens and Baviaansberg areas to the Witteberg. The corridor may be north of Touwsberg, from the Baviaansberg over the Karoopoort to the Saalberg, and the Bonteberg, finally stretching to the Voetpadsberg before reaching the Witteberg. Alternatively, there are mountains to the south of Touwsberg and the N1, such as the Suurberg, the Perdegang and Pramkop, which could provide a montane corridor. This may also explain why the Greater Witteberg Centre (PC 12) from my Combined Dataset, shows greater affinities to the NWPP than to the KMPP, in the hierarchical analyses that I performed (Figure 22, Figure 23, Figure 24, Figure 25 and Figure 26).

The Cedarberg Mountains are divided into a northern (Pakhuis) (PSC 2.3) and a southern region (PSC 2.4). The southern region combines the southern Cedarberg and Groot Winterhoek Mountains (PSC 2.4) (Figure 97) into an area similar to that seen in Orchidaceae and Poaceae. This differs from other traditional CFR Clades such as Proteaceae, where the Cedarberg and Groot Winterhoek form discreet phytogeographic areas.

In Restionaceae, the northern boundary of the Northwest Centre (PC 2) occurs south of the Gifberg, or Olifants River, and is congruent with previous analyses (Weimarck; Linder and Mann, 1998; Linder, 2001; Moline and Linder, 2005), which all largely concentrated on montane TMS Cape Clades, or Restionaceae. In Restionaceae, the South Gifberg-Nieuwoudtville Centre (PC 9) is distinct from the other NWPP PCs, as in the Proteaceae Dataset, although in Restionaceae it is not as geographically continuous. Linder (2001) also retrieved this disjunction on a very similar dataset. As Restionaceae is a montane TMS Cape Clade, it is absent from the lower altitude areas surrounding the South Gifberg-Nieuwoudtville Centre (PC 9), and shows no affinities to the south Succulent Karoo flora (sSK) (Chapter 2, Section 2.4.2.1.2.2). Thus for Restionaceae, the South Gifberg-Nieuwoudtville Centre (PC 9) is almost certainly nested within the greater NWPP, which is similar to the classification of Goldblatt and Manning (2000), but differing from the hierarchical analysis of my Combined Dataset, which place this area in the sSK. Both classifications are correct, and depend on the biotic elements being analysed.

Restionaceae endemics in the Gifberg-Nieuwoudtville Centre (PC 9) occupy a very small high altitude archipelago portion of the QDS, which I refer to as the northern NWPP, while the lower altitude areas have south Succulent Karoo affinities. The remaining minor PC in the Restionaceae NWPP is an outlier in the Kamiesberg Mountains (PSC 10).

Interestingly, my study did not identify any phytogeographical development on the Piketberg. Moline and Linder's (2005) study on Restionaceae is the only study to identify the Piketberg Mountain as floristically distinct from the surrounding flats, and to indicate its relationship to the Northern Mountains.

### 15.2.3 The Agulhas Plains Phytogeographical Province

The APPP is a fairly well-delimited, nearly continuous centre (PC 4), consolidating much of the lower lying areas around Bredasdorp, stretching from Gansbaai in the west, to the Gouritz River in the east. However, this PC lacks some definition at the sub-centre level. Most of the endemic taxa (six of eight) occur on limestone, except for *Ischyrolepis anomala* (2) and *Calopsis pluchra* (4), which do not occur exclusively on limestone.

Although Weimarck identified the presence of a Bredasdorp/Agulhas phytogeographical unit, it is only recently that it has been elevated to equal status with other phytogeographical provinces (Linder, 2001; Goldblatt and Manning, 2000; Linder and Mann, 1998; Oliver et al., 1983). The position and extent of the APPP/Bredasdorp floristic unit varies in the literature, from being very disjunct (Oliver et al., 1983), or to how far east it extends (Linder and Mann, 1998); or to whether it includes areas north of the Kleinriviersberge, or not (Weimarck). My Restionaceae Dataset, as with many other studies (Linder and Mann, 1998; Goldblatt and Manning, 2000; Linder 2001; Moline and Linder, 2005) indicates a fairly continuous centre, south of the Kleinrivierberge in the west, and reaching as far east as Gouritz River, although sometimes it extends further east (Linder and Mann, 1998). In the eastern areas of the APPP, the Restionaceae Agulhas Plains PC (4) extends sporadically to the base of the Langeberg on the low-lying areas around Riversdale and Albertinia, which is congruent with other studies (Linder and Mann, 1998; Moline and Linder, 2005).

There is only a single core sub-centre (PSC 4.1), rather than differentiation into west, east and Potberg floristic areas. There are a number of disjunctions in the East Agulhas Plains, while the Far East Agulhas Plains are not retrieved. The Potberg does not form a distinct phytogeographical unit, nor is it part of the core Agulhas Plains Centre (PSC 4.1). This is atypical, as many of my datasets contain Potberg endemics (Combined Dataset, Asteraceae, Geophytes, Polygalaceae, Proteaceae, RDL Taxa, Rosaceae and Rutaceae). However, two QDSs east of the Potberg form part of the disjunct core sub-centre that is centred in the Western APPP.

### 15.2.4 The Langeberg Phytogeographical Province

The Langeberg also clusters into a single PC in Restionaceae, mostly restricted to the Langeberg Mountains, but also includes the West Outeniqua Mountains (PSC 3.3). The LBPP consists mostly of mountainous flora (Figure 97), although there are some low altitude endemics (Table 58). The Greater Langeberg Mountains-West Outeniqua (PC 3) excludes QDSs from the West, Central and East Langeberg Plains, making it very similar to the PC identified by Linder (2001). The LBPP also includes parts of both the Touwsberg to the north (PSC 3.1) and the Rooiberg (PC 3 in part), due to *Elegia galpinii* (6). Usually the Rooiberg is combined with the Klein Swartberg (Combined Taxa Dataset).

Other studies on endemism in Restionaceae have also identified the importance of the Langeberg for endemic taxa (Moline and Linder, 2005; Linder, 2001; Goldblatt and Manning, 2000; Linder and Mann, 1998; Oliver et al., 1983; Weimarck, 1941). However, not all of these delimit the Langeberg as an independent centre (Linder, 2001; Goldblatt and Manning, 2000; Linder and Mann, 1998). Moline and Linder (2005) and Oliver et al., (1983) combine elements of the KMPP, LBPP and SEPP into a single large centre, probably due to a paucity of range-restricted taxa in these three eastern phytogeographical provinces of their datasets.

The inclusion of the Western Outeniqua Mountains (PSC 3.3), west of the Outeniqua Pass into the LBPP of Restionaceae, is a curious pattern, but is supported by *Elegia galpinii* (6) and *Thamnochortus karooica* (4). However, the boundary between the Western Outeniqua Mountains Sub-Centre (PSC 3.3) and the remainder of the LBPP occurs in the same area as recorded in my Combined Taxa Dataset, indicating at least some similarities to the Combined Dataset.

In my study *Thamnochortus glaber* (14) was not used in PC identification, although it potentially could have been without conflict. *T. glaber* (14) is a fairly widespread taxon, occurring principally in the summer rainfall region, extending east to the Zuurberg Sub-Centre of Weimarck (1941), along the coastal edge of the Albany Centre, as defined by van Wyk and Smith (2001). GIS analysis indicated that *T. glaber* (14) has one record in the Langeberg PC (4), with no recorded conflict with other PCs. This suggests a possible extension of the Langeberg, but I do not uphold this, as it crosses the SEPP, and greater sampling will probably result in conflict, reducing the validity of this extension.

### 15.2.5 The Karoo Mountain Phytogeographical Province

The Karoo Mountain Centre contains a number of smaller disjunct PCs (four to five), which do not currently consolidate into a single PC. This fragmentation may be because a portion of the KMPP (Combined Dataset) seems to have been incorporated into surrounding centres, namely, the Witteberg (PSC 2.2) in the NWPP, and the Rooiberg (PC 3 in part) in the LBPP, causing conflict with more widespread KMPP Taxa. The Klein Swartberg (PC 5) is fairly well developed, while the Groot Swartberg (PC 8) is less so. Curiously, the Kammanassieberg is divided into two minor centres (PC 7 and 12), which may indicate under collection, while the Boesmanspoort-Uniondale Centre (PC 11) is a disjunct PC in the east.

Geographically, Restionaceae PCs are not very well developed in areas of the CFR that do not receive appreciable winter rainfall (> 200 mm/year). It seems that in these more arid areas (especially in the KMPP), montane habitats compensate for the less temperate climate, with endemic taxa in the KMPP and LBPP being restricted to more montane habitats (Table 58). My PC delimitation for Restionaceae in the KMPP east of the Witteberg is largely congruent with other studies (Linder, 2001; Goldblatt and Manning, 2000; Oliver et al., 1983; and Weimarck, 1941), indicating robust patterns.

### 15.2.6 The Southeast Phytogeographical Province

As with the KMPP, the SEPP is poorly developed in Restionaceae, with only a single, southerly centre (PC 6), containing two endemic taxa, with largely congruent distributions. The PC is very fragmented and scattered throughout the western and central SEPP. I found that Restionaceae PC development in the CFR does not extend beyond the eastern Tsitsikamma Mountains. My SEPP patterns are largely congruent with Linder (2001). Other studies have also produced results that indicate fragmented and disjunct distributions of endemic taxa in the SEPP, but have also found PCs further east, on the Vanstadens-Groot Winterhoek Mountains (Moline and Linder, 2005; Oliver et al., 1983). Generally, studies that make use of more taxonomically diverse and extensive datasets, for example, my Combined Dataset, and studies by Goldblatt and Manning (2000), and Weimarck (1941), are able to demarcate more geographically continuous centres in the SEPP.

## 15.3 Phytogeographical Centres outside the CFR

### 15.3.1 The Tropical East Coast Phytogeographical Centre

A fairly range-restricted taxon, *Restio zuluensis* (1) occurs in the northeast part of the country. Surprisingly, this taxon is not found at high altitudes, but in low altitude swamps (Linder, 1985). Its taxonomic affinities are unclear (Linder, 1985).

### 15.3.2 The Drakensberg Phytogeographical Centre

As with other montane TMS Cape Clades (for example, *Erica,* Proteaceae and *Cliffortia*), Restionaceae has a PC in the Drakensberg. However, Restionaceae differs from these other clades in that it is only represented by a single endemic species, *Restio galpinii* (5). Furthermore, *R. galpinii* is not strictly endemic to the northeast Drakensberg, but extends southwest disjunctly, nearly as far as Maclear (3128AB) in the Underberg.

## 15.4 Summary

Restionaceae is another classic CFR group (Linder, 2003) that is mostly montane and restricted to nutrient poor, coarse-grained soils, principally sandstone (Table 58). PC development is best in the western and southerly phytogeographical provinces, especially the SWPP, and weakest in the SEPP and KMPP, congruent with Levyns' (1964) Cape Clade diversity gradient. PC formation is well-developed in the lowlands of the SWPP and APPP, but is comparatively poor in the lowland areas of the NWPP, LBPP and especially the SEPP and KMPP, where endemics are mostly montane (Table 58). This is presumably due to increased aridity and low winter precipitation. There is evidence of an NWPP-KMPP high altitude corridor. Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, NWPP, LBPP, APPP, KMPP and SEPP.

# Chapter 16: Rosaceae: *Cliffortia* (Table 59, Figure 102, Figure 103)

## 16.1 Introduction

Within Rosaceae, *Cliffortia* is the best-represented clade in the CFR and is largely centred there, although there are a few widespread taxa, which extend outside the CFR. *Cliffortia* is usually considered to be a Cape Clade (Levyns, 1964; Linder, 2003), with 114 of the global total of 120 species represented in the CFR, of which 104 are endemic to the CFR (Goldblatt and Manning, 2000). Thus, endemism at the regional level is extremely high, with 86.7% of all *Cliffortia* endemic to the CFR. However, when one investigates the patterns of endemism of *Cliffortia* at finer phytogeographical scales (PC level) levels of endemism drop off sharply, especially in comparison to other Cape Clades, for example, Ericaceae, Proteaceae, Restionaceae and Rutaceae. Thus, I found that my *Cliffortia* PC had relatively low numbers of endemics, which is unusual for a Cape Clade. The PC with the highest numbers of endemics, the Central Southwestern Mountains (PC 1), only contains nine endemic species. Furthermore, this low local endemism appears to be the case at intermediate phytogeographical scales for *Cliffortia* (between PC and the region), such as at the phytogeographical province level (Combined Dataset; Appendix of Goldblatt and Manning, 2000). In Goldblatt and Manning's (2000), Appendix, entitled: 'Statistics for the families of the Cape Flora'; the SWPP is the only phytogeographical province that performs moderately well by CFR standards, with 35 of 78 species endemic (44.9%). The other Rosaceae phytogeographical provinces have relatively low numbers of taxa and/or endemics (NWPP: 35 taxa, 5 endemics; KMPP: 32 taxa, 12 endemics; LBPP: 29 taxa, 5 endemics; SEPP: 24 taxa, 2 endemics; APPP: 11 taxa, 3 endemics).

The reasons for this lack of local/PC endemism are unclear and may involve the genetic dispersal capabilities of the genus. It seems that within the CFR barriers (local) to gene dispersal are not as acute as the regional barriers (perhaps climate, such as winter rainfall) between the CFR and other phytogeographical regions. *Cliffortia* may not make extensive use of serotiny of myrmecochory, as do other Cape Clades. Alternatively, the age of residency/persistence in CFR PCs may play a role, or whether the taxa are re-sprouters, or re-seeders. For the most part, PCs are generally reduced in size, but often have disjunctions, and PC development is mostly restricted to more mountainous QDSs, increasingly so in more arid areas of the CFR, which receive low winter rainfall. Analysing the hierarchical relationships of the PCs identified may also prove interesting. The frequent disjunctions indicate either widespread under collection, or alternatively, habitat/niche specificity.

Table 59: Taxonomic properties of the Centres identified for the group Rosaceae (Figure 102, Figure 103).

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | Central Southwestern Mtns | 7 | 67 | 17 | 9 | 23 | 0.37 | 0.29 |
| 1.1 | Hottentots-Stellenbosch-Franschhoek Mtns | 4 | 62 | 11 | 5 | 10 | 0.50 | 0.38 |
| 1.2 | W Kleinrivier Mtns | 1 | 18 | 1 | 1 | 1 | 1.00 | - |
| 1.3 | Remainder | 2 | 33 | 0 | 0 | 0 | - | 1.00 |
| 2 | S Northwestern Mtns | 8 | 48 | 9 | 8 | 16 | 0.25 | 0.14 |
| 2.1 | Bainskloof | 1 | 25 | 4 | 4 | 4 | 1.00 | 1.00 |
| 2.2 | Hexriver-NW Langeberg | 4 | 35 | 3 | 2 | 5 | 0.63 | 0.25 |
| 2.3 | Remainder | 3 | 22 | 2 | 0 | 0 | - | 1.00 |
| 3 | Greater Swartberg | 8 | 34 | 6 | 6 | 18 | 0.38 | 0.25 |
| 3.1 | Groot Swartberg | 4 | 25 | 4 | 2 | 5 | 0.63 | 0.25 |
| 3.2 | Klein Swartberg | 1 | 15 | 1 | 1 | 1 | 1.00 | - |
| 3.3 | Remainder | 3 | 15 | 0 | 0 | 0 | - | 1.00 |
| 4 | Greater Langeberg-West Outeniqua | 15 | 39 | 6 | 5 | 26 | 0.35 | 0.18 |
| 4.1 | Central Langeberg-Central and East Plains | 6 | 25 | 1 | 1 | 6 | 1.00 | - |
| 4.2 | East Langeberg-E Central Langeberg | 3 | 21 | 2 | 1 | 3 | 1.00 | - |
| 4.3 | Remainder | 6 | 22 | 1 | 0 | 0 | - | 1.00 |
| 5 | Eastern Escarpment | 55 | 19 | 4 | 4 | 74 | 0.34 | 0.12 |
| 6 | Peninsula and Sandveld | 7 | 44 | 4 | 3 | 12 | 0.57 | 0.36 |
| 6.1 | N Peninsula | 1 | 33 | 1 | 1 | 1 | 1.00 | - |
| 6.2 | Remainder | 6 | 37 | 3 | 0 | 0 | - | 1.00 |
| 7 | RZE and Outliers | 7 | 29 | 2 | 2 | 8 | 0.57 | 0.14 |
| 7.1 | RZE | 4 | 27 | 1 | 1 | 4 | 1.00 | - |
| 7.2 | Remainder | 3 | 5 | 1 | 0 | 0 | - | 1.00 |
| 8 | Potberg | 3 | 16 | 2 | 2 | 4 | 0.67 | 0.33 |
| 9 | Arid Interior | 11 | 16 | 2 | 2 | 13 | 0.59 | 0.18 |
| 10 | SE Mountains | 12 | 26 | 2 | 1 | 12 | 1.00 | - |
| 11 | West Agulhas Plains | 2 | 21 | 2 | 1 | 2 | 1.00 | - |
| 12 | Perdeberg-Paarlberg and E Caledon Swartberg | 2 | 33 | 1 | 1 | 2 | 1.00 | - |
| 13 | Witteberg | 1 | 16 | 1 | 1 | 1 | 1.00 | - |
| 14 | Rooiberg | 2 | 8 | 1 | 1 | 2 | 1.00 | - |
| 15 | Outside | 236 | 63 | 14 | 0 | 0 | - | 1.00 |

On the whole, the QDS Taxon Diversity (Figure 104) is typical for CFR Taxa, having its highest value in the Hottentots Holland QDS, and decreasing to the north and east (Levyns, 1938, 1964). The QDS inverse weighting (Figure 100) reflects the uniqueness of the Bainskloof QDS, which registers the highest value, indicating many range restricted taxa, followed by the Hottentots Holland QDS. It is also apparent that there is considerable collector bias, with QDSs being within easy access from roads, thus having much higher values.

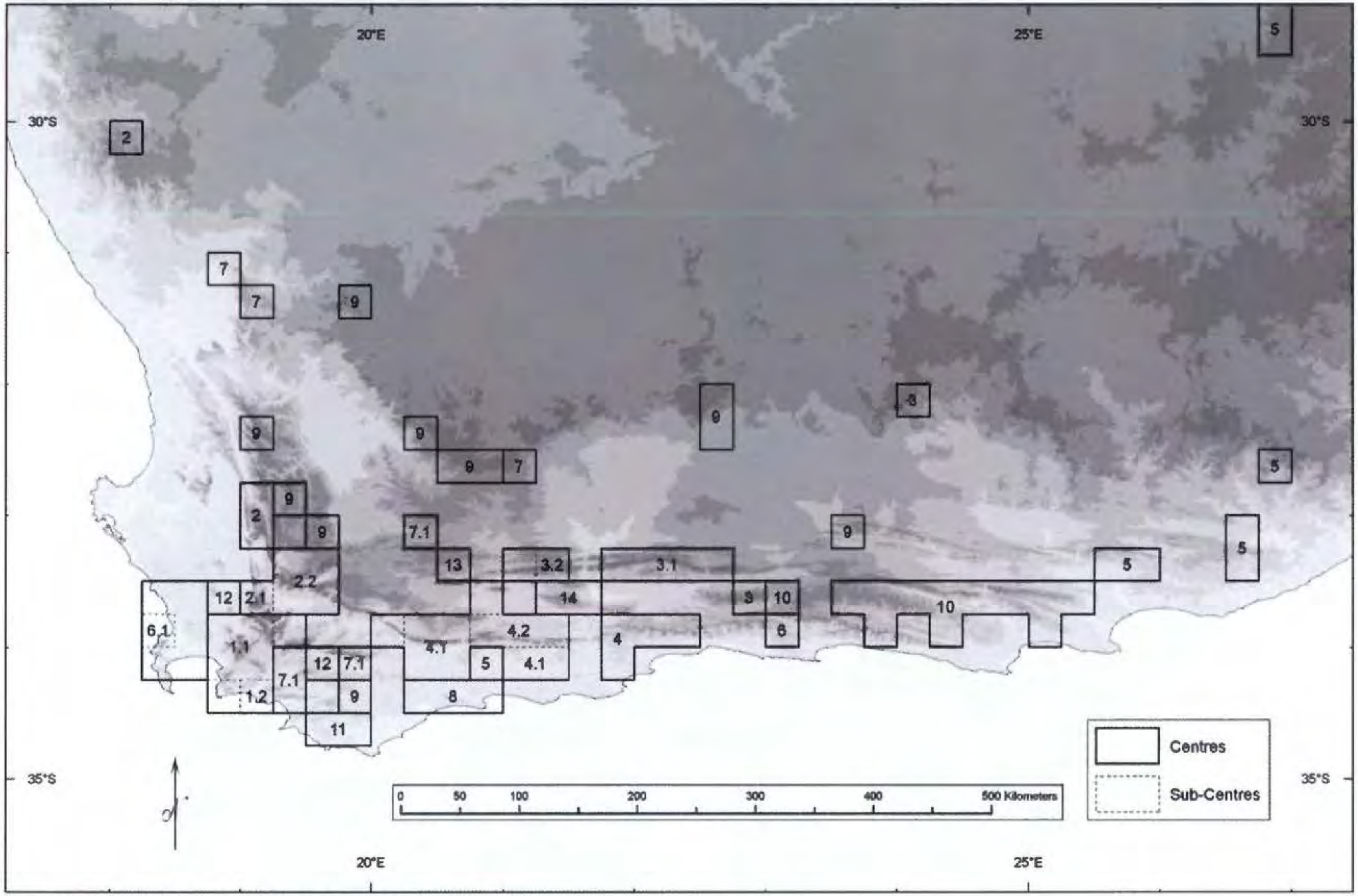


Figure 102: PC and PSC for the Rosaceae Dataset in the CFR.

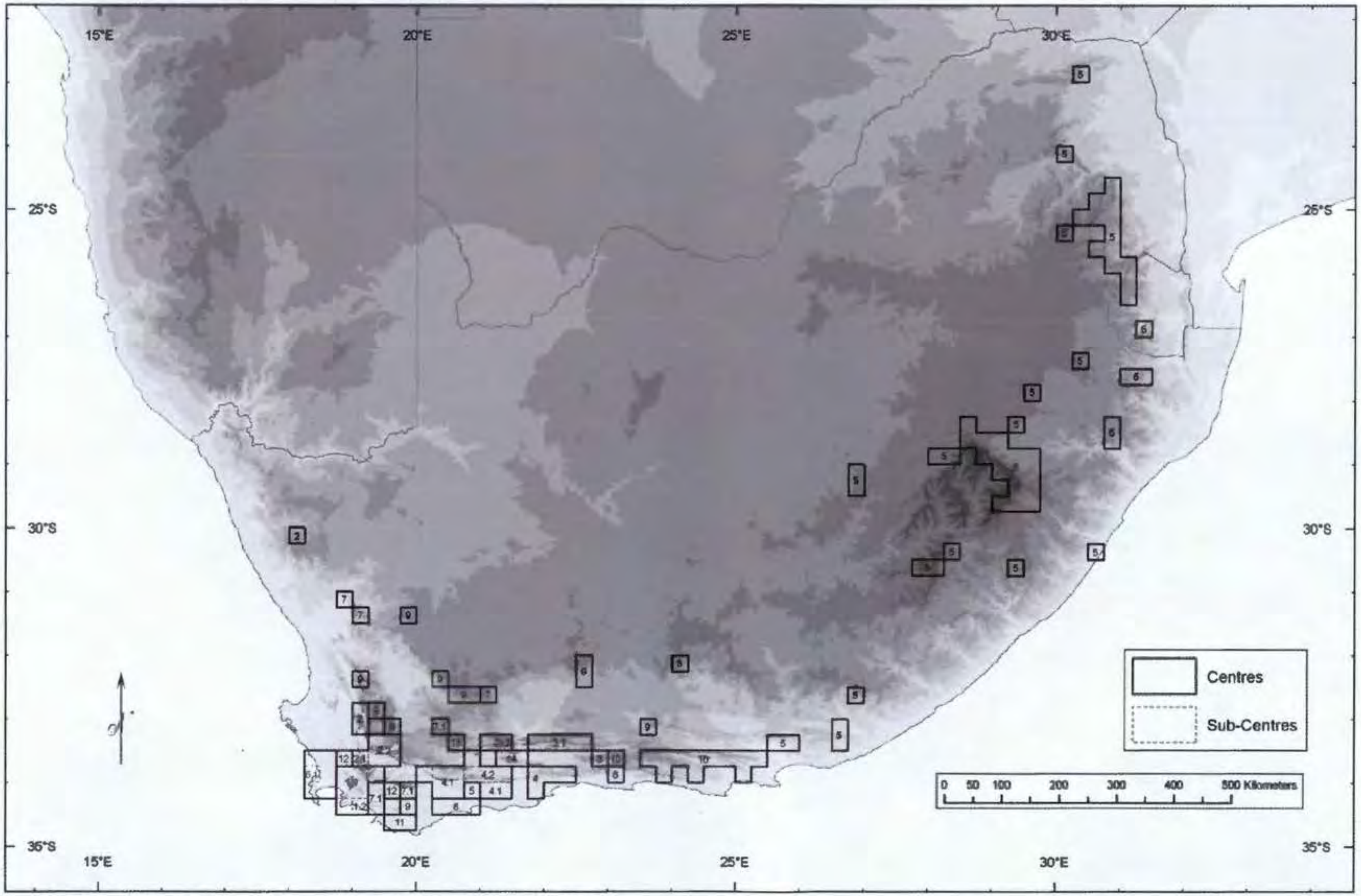


Figure 103: PC and PSC for the Rosaceae Dataset in Southern Africa.

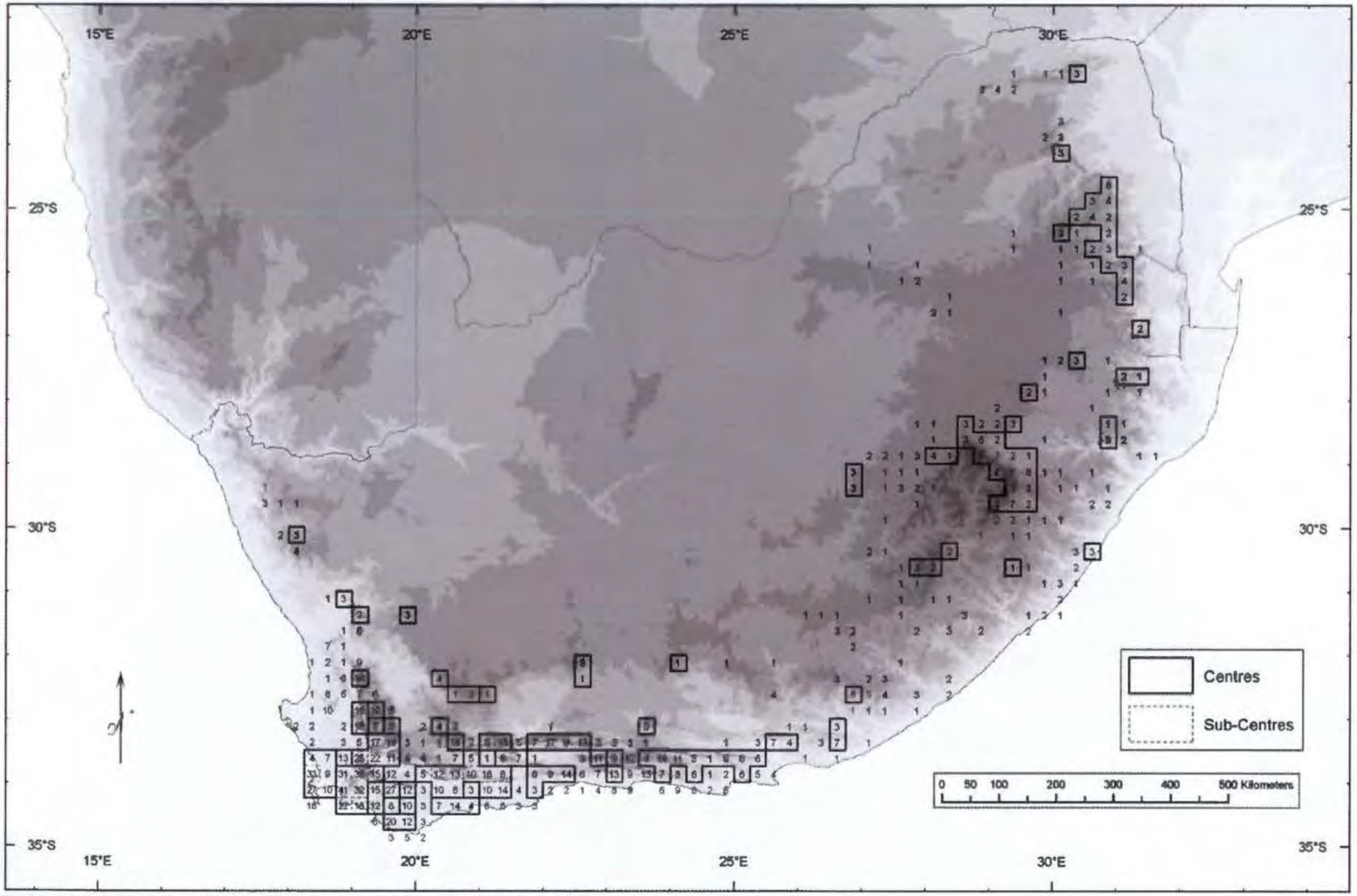


Figure 104: QDS Diversity for the Rosaceae Dataset in Southern Africa.

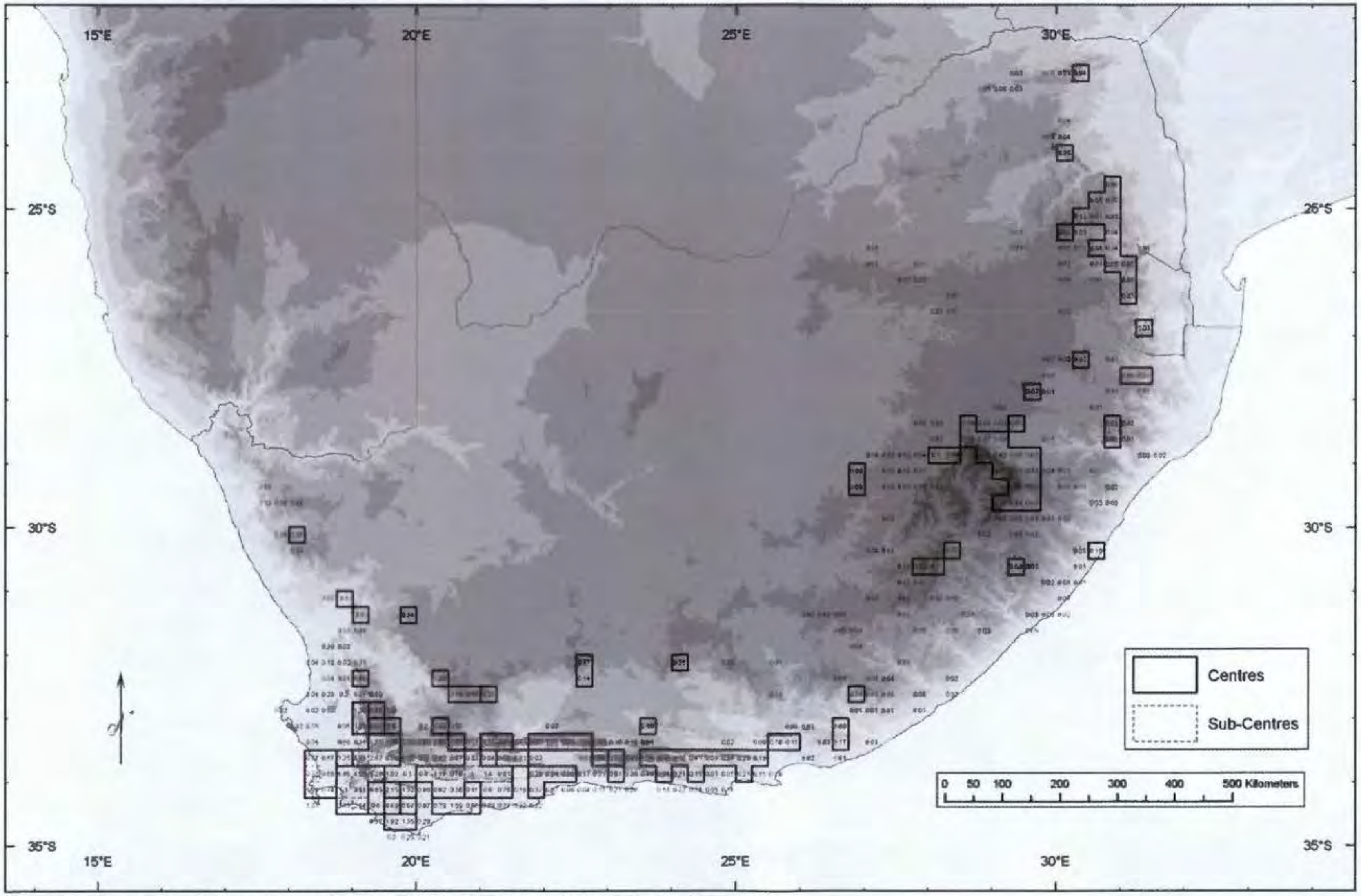


Figure 105: Sum of the Inverse Taxon Ranges for the Rosaceae Dataset in Southern Africa.

Table 60: Habitat Data for the Rosaceae Endemics

|  |  | Altitude |  |  | Altitude |  |  |  |  | Rock Type |  |  |  |  |  |  |  | Topography |  |  |  |  | Habitat |  |  |  |  | Vegetation |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliifs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats | Other | Unknown |
| 1 | Central Southwestern Mtns | 2 |  | 1 |  |  |  |  |  | 3 |  |  |  |  |  |  |  |  | 9 |  |  |  | 3 |  |  | 1 |  |  |  | 1 |  |  |  |  |  |  |
| 2 | S Northwestern Mtns |  | 1 | 6 |  |  |  |  |  | 2 |  |  |  |  |  |  |  |  | 7 |  |  |  |  | 1 |  | 2 |  |  |  |  |  |  |  |  |  |  |
| 3 | Greater Swartberg |  |  | 4 |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  | 5 | 1 |  |  | 1 | 1 |  | 3 |  |  |  |  |  |  |  |  |  |  |
| 4 | Greater Langeberg-West Outeniqua | 1 |  | 2 |  |  |  |  |  | 3 |  |  |  |  |  |  |  |  | 5 |  |  |  |  |  |  | 2 |  |  |  |  |  |  |  |  |  |  |
| 5 | Eastern Escarpment |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 6 | Peninsula & Sandveld | 2 |  | 1 |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  | 3 |  |  | 1 |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |
| 7 | RZE & Outliers |  |  |  |  |  |  |  |  | 2 |  |  |  |  |  |  |  |  | 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 8 | Potberg |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  | 1 |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |
| 9 | Arid Interior | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 10 | SE Mountains |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 11 | West Agulhas Plains | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 12 | Perdeberg-Paarlberg & E Caledon Swartberg |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 13 | Witteberg |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  | 1 | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 14 | Rooiberg |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |
|  | Totals | 7 | 1 | 15 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 37 | 1 | 1 | 3 | 4 | 2 | 0 | 10 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |

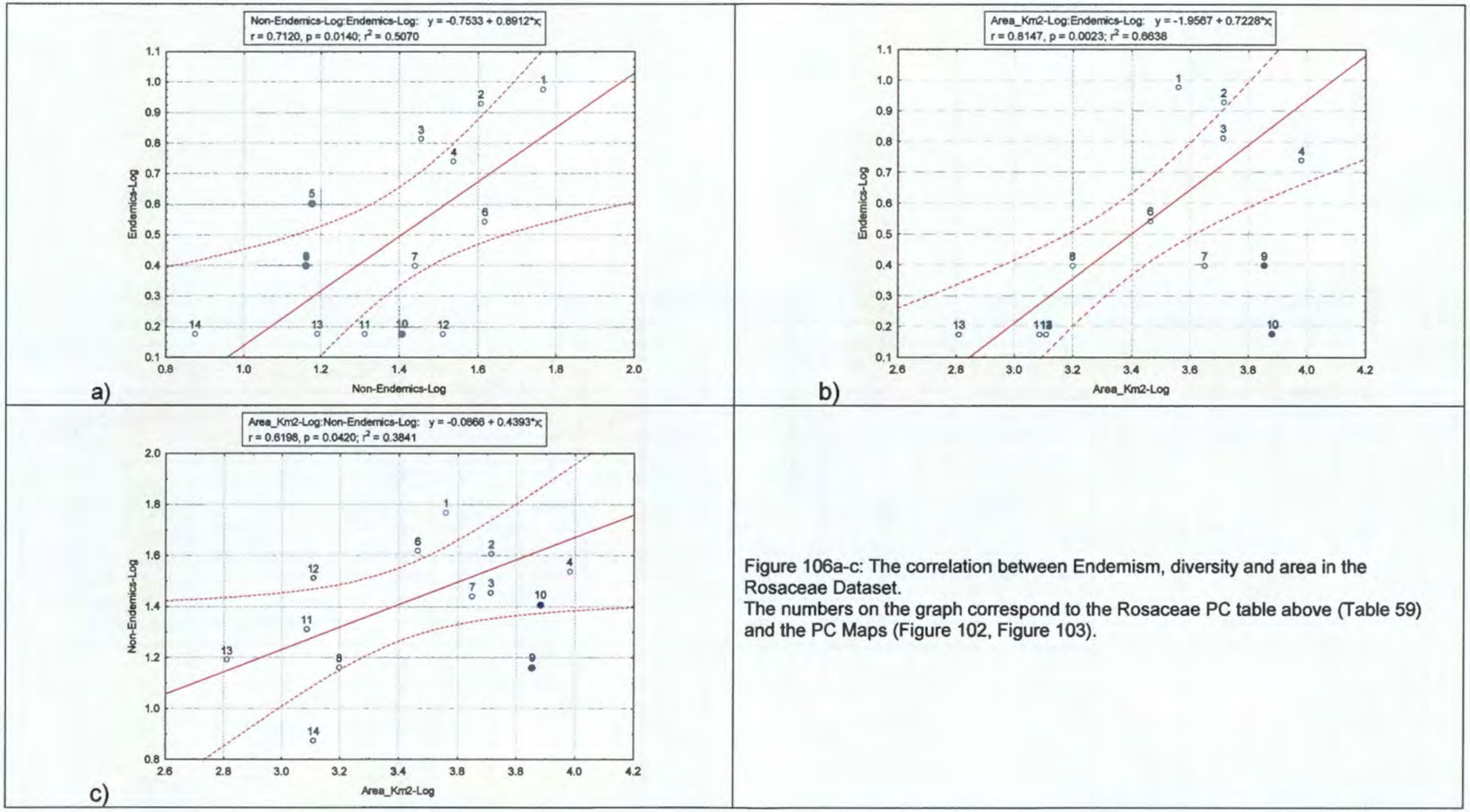


Figure 106a-c: The correlation between Endemism, diversity and area in the Rosaceae Dataset.
The numbers on the graph correspond to the Rosaceae PC table above (Table 59) and the PC Maps (Figure 102, Figure 103).

### 16.1.1 The relationship between endemism, diversity, and area in the Rosaceae (*Cliffortia*) PCs

The inclusion of all Rosaceae PCs in my regression analyses resulted in very poor correlations between endemism, diversity and area in the PCs. It was necessary to exclude three PCs: the Eastern Escarpment (PC 5), the Arid Interior (PC 9), and the Southeast Mountains (PC 10), to obtain a statistically significant correlation. All three are situated outside the mesic winter rainfall area. These PCs are usually large and disjunct, skewing the correlation. With the exclusion of these three PCs, I found a significant and positive relationship ($r^2 = 0.51$, $p=0.014$) between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 106a). A significant relationship was also found between the number of endemics and the geographic size of the PC ($r^2 = 0.66$, $p=0.0023$) (Figure 106b) which was strong, and between the number of non-endemics and the geographic size of the PC ($r^2 = 0.38$, $p<0.042$) (Figure 106c), which was weak. My Rosaceae regression results may change with further collection effort.

The Southern Northwestern Mountains (PC 2) are overrepresented with regards to endemism (Figure 106a and Figure 106b), but contain predicted levels of non-endemic taxa (Figure 106c), indicating a high level of endemism and diversity in a relatively small area. Although the Central Southwestern Mountains (PC 1) contains higher numbers of endemic and non-endemic taxa when compared to PC area, endemism does not exceed the value predicted by non-endemic taxa (Figure 106a), as both values are high. However, as the Central Southwestern Mountains (PC 1) contains higher numbers of endemic and non-endemic taxa in a smaller geographic area, the residuals of endemism to area (Figure 106b), and non-endemic taxa to area (Figure 106c) are the highest of all Rosaceae PCs.

In the Greater Swartberg PC (3), endemism is higher than the numbers of non-endemic taxa would predict (Figure 106a). Conversely, in the Southeastern Mountains (PC 10), there are less than expected numbers of endemic taxa, as predicted by both the non-endemic taxa (Figure 106a) and the PC area (Figure 106b), and it was necessary to exclude this point, due to its large area.

The boundaries of the Greater Peninsula (PC 6) (Figure 102) are atypical in Rosaceae and include large amounts of the lower altitude Cape Flats. While this increases diversity, it also increases the numbers of non-endemic taxa in the PC (Figure 106c), but endemism is not increased in the same proportion and is underrepresented (Figure 106a). Endemism is also underrepresented in the Perdeberg-Paarlberg and E Caledon Swartberg PC (12), probably due to the fragmented nature of the PC, which is disjunct across a number of catchments. This may indicate under collection of one or more of its endemic taxa. The numbers of non-endemic taxa are underrepresented in another of the more arid PCs, namely the Rooiberg (PC 14). Similarly, the large area and fragmented nature of the RZE and Outliers PC (7), which also has an large arid inland component, would have contributed to its lower than predicted endemism (Figure 106b).

The Eastern Escarpment Centre (PC 5) does contain higher numbers of endemic taxa than are expected from its non-endemic taxa (Figure 106a), but this is largely on account of its large area, which encompasses the majority of its taxon ranges. The large PC area (55 QDSs) of the Eastern Escarpment (PC 5) is due to the absence of conflict between range-restricted taxa in the area in my dataset, and the lack of differentiation of the area into multiple PCs.

## 16.2 CFR Phytogeographical Centres

### 16.2.1 The Southwest Phytogeographical Province

The greatest number of Rosaceae endemics are found in the central Southwest Mountains (PC 1), centred on the Stellenbosch-Hottentots Holland area, unusually not the more southerly Hottentots Holland-W Kleinrivier area (PC 1 in part, or PSC 1.2), or the Kogelberg area. The Kogelberg is not even included in a sub-centre, indicating low levels of highly range restricted taxa here, although the area to the east forms the West Kleinrivier Mountains (PSC 1.2). There is some centre development on the Peninsula (PSC 6.1), extending onto the surrounding Cape Flats (PC 6), due to the low altitude habitats of *Cliffortia ericifolia* (5) and *C. hirta* (6).

The remaining PCs of the SWPP contain a number of disjunctions, possibly due to under-sampling, and are thus relatively weakly defined. The Perdeberg-Paarlberg and E Caledon Swartberg PC (PC 12) contains a single endemic, *Cliffortia polygonifolia var pubescens* (2), which occurs on the flats on either side of the Limietberg-RZE mountain range.

The RZE and Outliers PC (PC 7) only contain two endemics. The core area of the RZE and Outliers Centre is on the RZE Mountains (PSC 7.1), but even this core area has an outlier on the Witteberg (PSC 7.1). The entire centre is very disjunct, having outliers as far away as in the Klein-Roggeveldberge (PC 7 in part) and on the Nieuwoudtville Plateau (PC 7 in part). The disjunct nature of the RZE and Outliers PC (PC 7) due to *C. acutifolia* (4) make the PC unstable, and it is likely to collapse with increasing collections.

## 16.2.2 The Northwest Phytogeographical Province

The SWPP is followed closely in richness by the southern Northwest Mountains (PC 2), which extend southwards over the traditional SWPP-NWPP boundary of the Berg River to include the Bainskloof Mountains (PSC 2.1). PC development in the NWPP is very localised, and essentially restricted to the Groot Winterhoek and Hex River Mountains, There is no additional independent PC development further north in the NWPP, in the Cedarberg, Gifberg, or on the Nieuwoudtville Escarpment, which is very unusual for a CFR Clade. This indicates that most of the range restricted taxa occur further south.

No analysis performed in this study combined the Bainskloof Mountains (PSC 2.1) (3319CA) to the southern parts of the traditional Southwestern Centre. The Bell-Analysis recognised the Bainskloof Mountains (PSC 2.1) and Hex River-NW Langeberg (PSC 2.2) as separate PCs. However, the integration weighting (Int and MInt) combined the Bainskloof Mountains (PSC 2.1) and the south-western Hex River Mountains (south-western corner of Hexriver-NW Langeberg, PSC 2.2), which are part of the NWPP of Weimarck (1941) and Goldblatt and Manning (2000). Thus, these two areas were combined into the S Northwestern Mountains (PC 2). However, as there are four endemics only occupying the single QDS PSC 2.1, a new collection of one of these taxa in a neighbouring QDS may alter this floristic classification. This PC delimitation is therefore also unstable.

The Bainskloof Mountains (PSC 2.1) contain an impressive four endemics, restricted to a single QDS, making it the second richest of all Rosaceae sub-centre. The Hottentots-Stellenbosch-Franschhoek Mountains Sub-Centre (PSC 1.1) has one more endemic in an area four times the size. Furthermore, the Bainskloof Sub-Centre (SC 2.1) contains more endemics than nine of the other Rosaceae PCs (Table 59). The only other sub-centre of the NWPP is the Hex River-Northwestern Langeberg Sub-Centre (PSC 2.2). Unusually, the Groot Winterhoek does not have any endemics of its own, thus it does not form a distinct sub-centre. There is a large disjunction of the Northwest Mountains (PC 2) to the Kamiesberg, which may indicate a large area of under collection. The Kamiesberg, like the Groot Winterhoek, does not have any endemic *Cliffortia* taxa of its own.

The remaining PC (9) is debatable, and very fragmented. It consists of a QDS in the Cedarberg, a QDS in the Skurweberg and a QDS in the Swartrugberge/Baviaansberg, grouped together into a very disjunct and widely distributed centre, which I call the Arid Interior Centre (PC 9). Much of the remainder of the PC occurs along the Great Escarpment, in the Hantam-Roggeveld area and as far east as the Molteno Pass, near Beaufort West. From the distribution of the Arid Interior Centre (PC 9), one could speculate on how Weimarck (1941) may have identified the affinities of the Hantam-Roggeveld Sub-Centre to the NWPP, after the completion of his revision of the genus

*Cliffortia* (Weimarck, 1934), a few years before his phytogeographical study (1941). At that stage, *Cliffortia aborea* (7), *Cliffortia hantamensis* (6) were only known from the Hantamsberge and Roggeveld, but later collections (the earliest by E. E. Esterhuysen, in 1940, near Beaufort West) revealed a much wider distribution pattern, making these taxa less range-restricted and therefore downgrading their importance in forming PCs. However, these taxa are still important for determining floristic affinities between the different floristic areas. *Cliffortia aborea* (7) and *Cliffortia hantamensis* (6) both show the Doorn River Interval of Weimarck (1941), across the Doorn and Tankwa River lowlands. This disjunction occurs in other clades to, such as Orchidaceae. Even though similar patterns are observed in Orchidaceae (which Weimarck may or may not have been aware of), I do not propose that the Hantamsberge and the Roggeveld be upheld presently as sub-centres of the NWPP. That the rest of Southern Africa, or at least large parts of it, were somehow nested within the CFR was an idea that permeated the mindset of early CFR biogeographers (Goldblatt, 1978). The Hantam-Roggeveld areas form at least a centre in their own right, as proposed by Goldblatt and Manning (2002), and van Wyk and Smith (2001). The fact that the Hantam-Roggeveld contains members of the genus *Cliffortia,* which is largely centred in the CFR, may be of historical interest.

### 16.2.3 The Karoo Mountain Phytogeographical Province

One surprise of *Cliffortia* is how well the Swartberg performed. The Greater Swartberg (PC 3) includes the Klein (PSC 3.2) and Groot Swartberg (PSC 3.1), and Kammanassieberg (PC 3 in part). It is the third richest PC, even outperforming the LBPP. The only other time the Greater Swartberg outperforms the Greater Langeberg in my study was in my Fabaceae Dataset. What makes this even more remarkable is that in *Cliffortia*, the Greater Langeberg (PC 4) consists of nearly twice the number of QDSs than the Greater Swartberg (PC 3) (8 QDSs versus 15 QDSs), while in Fabaceae the Swartberg occupies double the area of the Langeberg (14 QDSs versus 7 QDSs), with the Swartberg including the Witteberg. In Rosaceae, the Witteberg is independent (PC 13) and is represented by a single taxon in a single QDS. The Rooiberg (PC 14) is also independent and contains a single taxon occupying two QDSs.

### 16.2.4 The Agulhas Plains Phytogeographical Province

The West and Potberg areas of the APPP are comparatively well defined geographically in Rosaceae, each with a distinct PC. There is a definite West Agulhas Plains Centre (PC 11) with one endemic and a Potberg Centre (PC 8) with two endemics.

There is no PC development in the East Agulhas Plains or in the Far East Agulhas Plains areas.

### 16.2.5 The Langeberg Phytogeographical Province

The LBPP has a good representation of endemics and is well defined spatially, having Central (PSC 4.1) and East (PSC 4.2) sub-centres, and a well-demarcated plains region (PSC 4.1). Interestingly, the East Langeberg Plains (PSC 4.1) are more strongly affiliated with the Central Langeberg Mountains (PSC 4.1) and Central Langeberg Plains (PSC 4.1), rather than the East Langeberg Mountains (PSC 4.2). In *Cliffortia*, the LBPP extends eastwards to occupy parts of the West Outeniqua (PC 4 in part), as also observed in the Combined Dataset, Proteaceae and Restionaceae.

### 16.2.6 The Southeast Phytogeographical Province

The Southeast Mountains PC (PC 10) is situated on the Kouga and Baviaanskloof Mountains. Although geographically large, it is not well-supported taxonomically, having only one endemic, *Cliffortia drepanoides* (12), which is not particularly range-restricted.

## 16.3 Non-CFR Phytogeographical Centres

Further east is an East Escarpment Centre (PC 5), comprising the Drakensberg and the Northeastern Escarpment. This centre is by far the largest in size (55 QDSs) and covers an area extending from the Zuurberg in the southwest, to the Soutpansberg in the northeast. Fragments of this centre are represented in many areas of the eastern high altitude corridor in the summer rainfall region of the country. Although it has rather low diversity, a high numbers of the represented taxa are endemic due to its large size. Once again, this PC may be only of historical significance for *Cliffortia* and is unlikely to be maintained when Drakensberg centred clades are analysed, or combined in analyses.

## 16.4 Summary

The *Cliffortia* Dataset differs notably from the other datasets that I analysed. I found that local endemism at the PC and phytogeographical province levels was low. Goldblatt and Manning (2000) record very high CFR (regional) endemism, but low endemism to their phytogeographical centres, indicating that although *Cliffortia* Taxa are mostly restricted to the CFR, there are relatively low numbers of very range-restricted taxa. Endemism is largely concentrated in montane areas, although there is some PC development on the APPP and lowland LBPP. Local endemism is poor in the northern NWPP and most of the SEPP. There also appear to be examples of widely disjunct taxa, resulting in disjunct PCs, indicating instability of these choria. Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: SWPP, southern NWPP, KMPP, LBPP and in a widespread Eastern Escarpment PC. Endemism on the APPP is relatively poor, exacerbated by the fragmented nature of PCs here in *Cliffortia*.

# Chapter 17: Rutaceae: Diosmeae (Table 61, Figure 107)

## 17.1 Introduction

Within Rutaceae, Diosmeae is considered a Cape Clade (Levyns, 1964; Linder, 2003), and is almost entirely endemic to the CFR. Upon closer investigation, a number of phytogeographical patterns atypical of Cape Clades are apparent. In studying Diosmeae QDS taxon richness (Figure 108), it is obvious that there are two major centres of diversity. The highest value is recorded from the northwest Cedarberg, closely followed by a high value in the Hottentots Holland. This is antithetical of the pattern described by Levyns (1938, 1962, 1964), where diversity is centred in the southwest of the CFR, tapering off to the north and east in the Cape Clades. The Cedarberg area has three of the four highest QDS diversity scores (Figure 108), indicating the importance of this region for Diosmeae. The QDS Inverse weighting scores (Figure 109) further highlight the importance of the Cedarberg for range-restricted Diosmeae Taxa. Three Cedarberg QDSs have higher inverse weighting values than even the Hottentots Holland-Stellenbosch Mountains QDSs. From these diversity patterns at the QDS level, it is not too surprising that these trends are repeated at the PC floristic level. The North Northwestern Mountains (PC 1) has a greater number of endemics than the Central Southwestern-South Northwestern Mtns (PC 3), but interestingly, the SWPP PC has slightly higher taxon diversity in a smaller area (Table 61). It may be that the SWPP covers a greater diversity of habitats, especially when considering the eastward extension of the Central Southwestern-S Northwestern Mountains (PC 3), through the NWPP into the KMPP, which may increase the diversity of taxa (biotic elements) represented. By contrast, the N Northwestern Mountains (PC 1) is centred on the Cedarberg and is largely restricted to the central and northern NWPP, and may cover a more uniform, compact area, which is largely congruent with a number of previous phytogeographical studies (Weimarck, 1941; Goldblatt and Manning, 2000; Linder, 2003). Thus, although diversity may be lower in the N Northwestern Mountains (PC 1), many more of the taxa represented there are endemic to the PC, approximately 55.6%. Conversely, only 26.2% of taxa present in the Central Southwestern-S Northwestern Mountains (PC 3) are endemic to it.

The Central Southwestern-South Northwestern Mountains (PC 3) and the Rooiberg-West Outeniqua (PC 8) display ambiguous patterns for the development of higher-level phytogeographical provinces in Diosmeae. This may be due to overlapping between different floristic elements, leading to conflict, which may also reduce PC endemism.

Table 61: Taxonomic properties of the Centres identified for the group Rutaceae (Figure 107).

| Label | Centres<br>Sub-Centres | Area | Diversity | Spp >=0.5 | # Endems | r | con | CON |
|---|---|---|---|---|---|---|---|---|
| 1 | N Northwestern Mtns | 26 | 81 | 60 | 45 | 136 | 0.12 | 0.10 |
| 1.1 | Cedarberg-N Kouebokkeveld | 10 | 69 | 39 | 25 | 55 | 0.22 | 0.19 |
| 1.2 | S Piketberg-SW Cedarberg-Swartberg | 6 | 38 | 10 | 4 | 8 | 0.33 | 0.11 |
| 1.3 | W South Gifberg-N Olifant's River Valley | 2 | 22 | 3 | 2 | 3 | 0.75 | 0.50 |
| 1.4 | Remainder | 8 | 21 | 2 | 0 | 0 | - | 1.00 |
| 2 | Western Agulhas Plains | 16 | 78 | 43 | 31 | 93 | 0.19 | 0.16 |
| 2.1 | SE Western Agulhas Plains | 5 | 42 | 16 | 6 | 13 | 0.43 | 0.32 |
| 2.2 | Potberg | 3 | 37 | 10 | 5 | 8 | 0.53 | 0.42 |
| 2.3 | W Western Agulhas Plains | 2 | 29 | 6 | 4 | 7 | 0.88 | 0.83 |
| 2.4 | Central Langeberg Plain | 2 | 11 | 2 | 2 | 3 | 0.75 | 0.50 |
| 2.5 | Kleinrivierberge | 2 | 25 | 1 | 1 | 2 | 1.00 | - |
| 2.6 | Remainder | 4 | 30 | 0 | 0 | 0 | - | 1.00 |
| 3 | Central Southwestern-S Northwestern Mtns | 15 | 84 | 34 | 22 | 48 | 0.15 | 0.10 |
| 3.1 | Bainskloof-Hexriver-N Waboomsberge | 6 | 47 | 13 | 9 | 15 | 0.28 | 0.19 |
| 3.2 | Hottentots-Stellenbosch-Wemmershoek Mtns | 5 | 48 | 15 | 8 | 15 | 0.38 | 0.29 |
| 3.3 | S Waboomsberge-W Langeberg | 2 | 13 | 1 | 1 | 2 | 1.00 | - |
| 3.4 | Remainder | 2 | 19 | 1 | 0 | 0 | - | 1.00 |
| 4 | Central and East Langeberg | 5 | 35 | 15 | 12 | 22 | 0.37 | 0.31 |
| 5 | East and Far East Agulhas Plains | 9 | 35 | 13 | 8 | 17 | 0.24 | 0.13 |
| 5.1 | Central East Agulhas Plain | 3 | 26 | 4 | 4 | 6 | 0.50 | 0.33 |
| 5.2 | Far East Agulhas Plain | 1 | 9 | 1 | 1 | 1 | 1.00 | - |
| 5.3 | W Central East Agulhas Plain | 1 | 13 | 1 | 1 | 1 | 1.00 | - |
| 5.4 | Remainder | 4 | 18 | 2 | 0 | 0 | - | 1.00 |
| 6 | RZE | 5 | 36 | 9 | 7 | 13 | 0.37 | 0.27 |
| 6.1 | SE RZE | 2 | 28 | 3 | 3 | 4 | 0.67 | 0.50 |
| 6.2 | NW RZE | 2 | 25 | 3 | 2 | 3 | 0.75 | 0.50 |
| 6.3 | Remainder | 1 | 5 | 0 | 0 | 0 | - | 1.00 |
| 7 | Witteberg-Swartberg Mtns | 11 | 32 | 9 | 6 | 17 | 0.26 | 0.11 |
| 7.1 | Witteberg-Anysberg | 3 | 14 | 3 | 2 | 4 | 0.67 | 0.33 |
| 7.2 | Groot Swartberg-W Kammanassie | 6 | 20 | 4 | 2 | 8 | 0.67 | 0.33 |
| 7.3 | Remainder | 2 | 17 | 2 | 0 | 0 | - | 1.00 |
| 8 | Rooiberg-West Outeniqua | 5 | 24 | 6 | 5 | 12 | 0.48 | 0.35 |
| 8.1 | Rooiberg-West Outeniqua Core | 3 | 21 | 5 | 4 | 7 | 0.58 | 0.44 |
| 8.2 | Remainder | 2 | 9 | 0 | 0 | 0 | - | 1.00 |
| 9 | Groot Winterhoek | 3 | 36 | 6 | 4 | 6 | 0.50 | 0.33 |
| 9.1 | Groot Winterhoek Core | 2 | 33 | 6 | 3 | 4 | 0.67 | 0.50 |
| 9.2 | Remainder | 1 | 14 | 1 | 0 | 0 | - | 1.00 |
| 10 | Sandveld-Saldanha Peninsula | 11 | 23 | 7 | 3 | 14 | 0.42 | 0.14 |
| 11 | East Outeniqua-West Tsitsikamma-Vanstadensberge | 7 | 21 | 3 | 3 | 9 | 0.43 | 0.14 |
| 11.1 | Plettenberg | 1 | 6 | 1 | 1 | 1 | 1.00 | - |
| 11.2 | Remainder | 6 | 19 | 2 | 0 | 0 | - | 1.00 |
| 12 | Peninsula and Kogelberg | 4 | 31 | 4 | 2 | 7 | 0.88 | 0.75 |
| 13 | Port Elizabeth | 8 | 13 | 3 | 2 | 9 | 0.56 | 0.13 |
| 14 | E Kouga-SE Baviaanskloof | 3 | 21 | 2 | 2 | 5 | 0.83 | 0.67 |
| 15 | Great Winterhoek | 2 | 6 | 2 | 2 | 3 | 0.75 | 0.50 |
| 16 | E West Outeniqua | 2 | 13 | 1 | 1 | 2 | 1.00 | - |
| 17 | W Kouga-Tsitsikamma | 3 | 12 | 1 | 1 | 3 | 1.00 | - |
| 18 | E Cape | 4 | 4 | 1 | 1 | 4 | 1.00 | - |
| 19 | North Grahamstown | 2 | 3 | 1 | 1 | 2 | 1.00 | - |
| 20 | Kiwane | 1 | 2 | 1 | 1 | 1 | 1.00 | - |
| 21 | Kamiesberg | 4 | 2 | 1 | 1 | 4 | 1.00 | - |
| 22 | Outside | 95 | 79 | 4 | 0 | 0 | - | 1.00 |

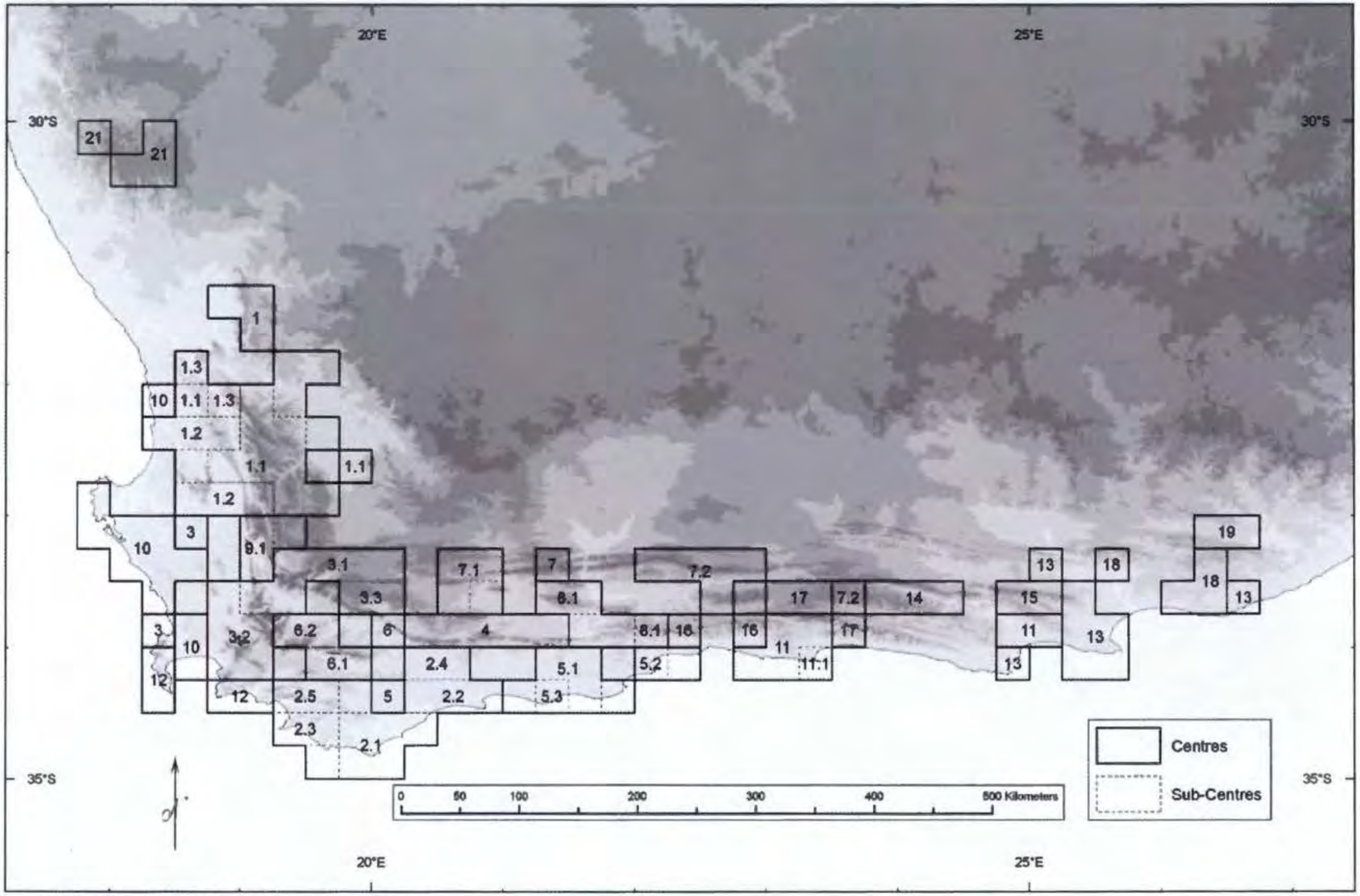


Figure 107: PC and PSC for the Rutaceae Dataset.

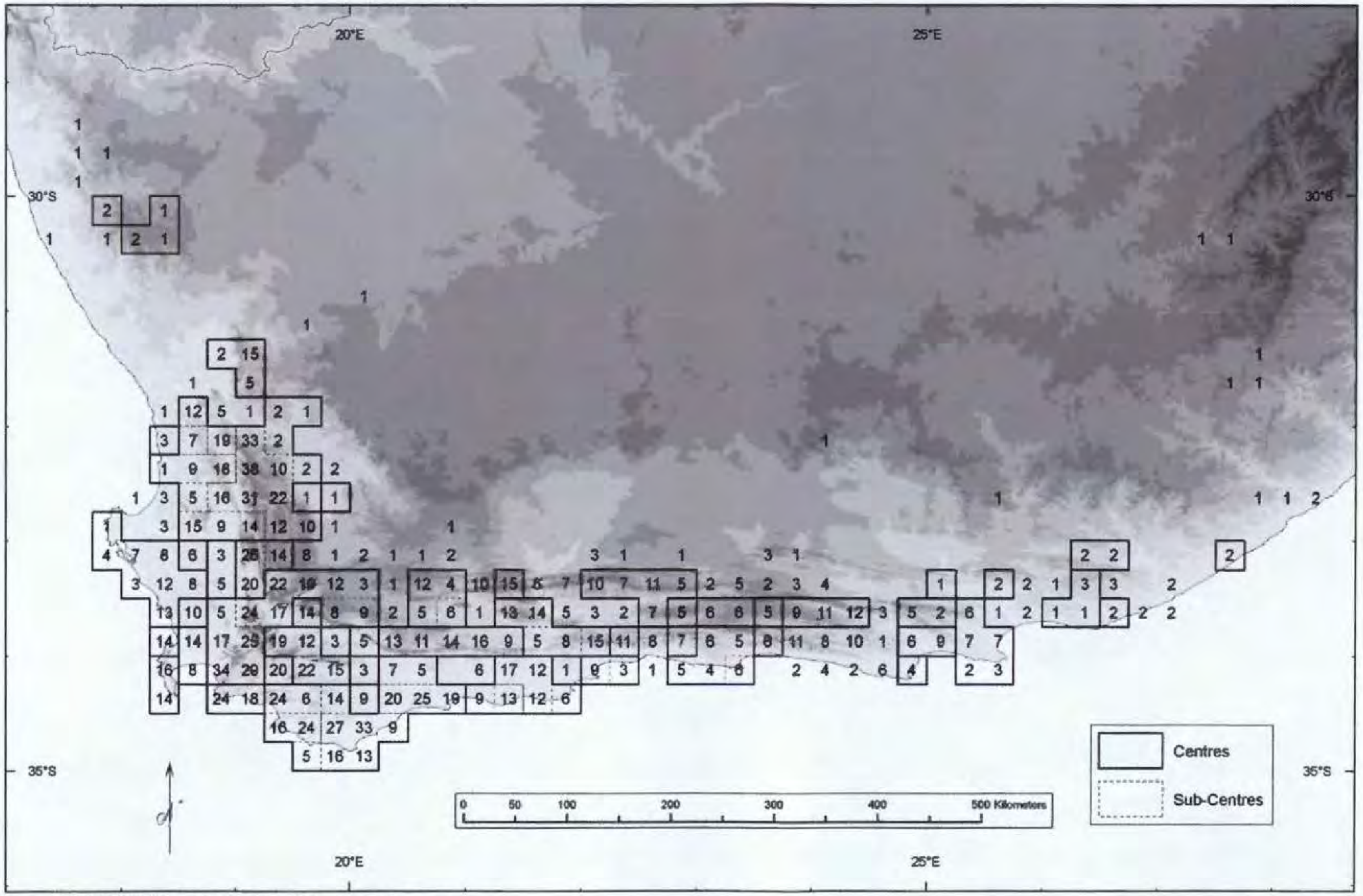


Figure 108: QDS Diversity for the Rutaceae Dataset.

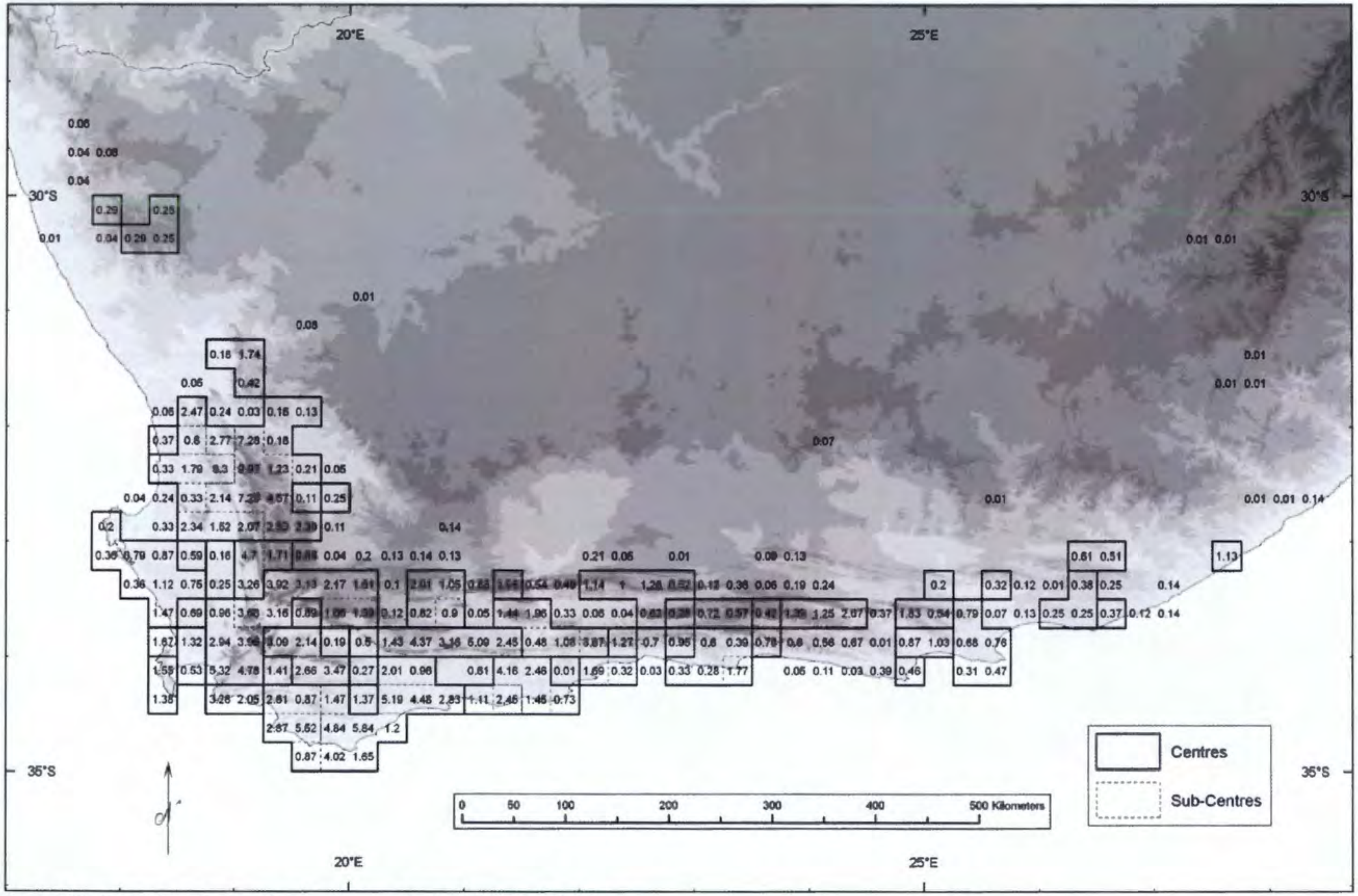
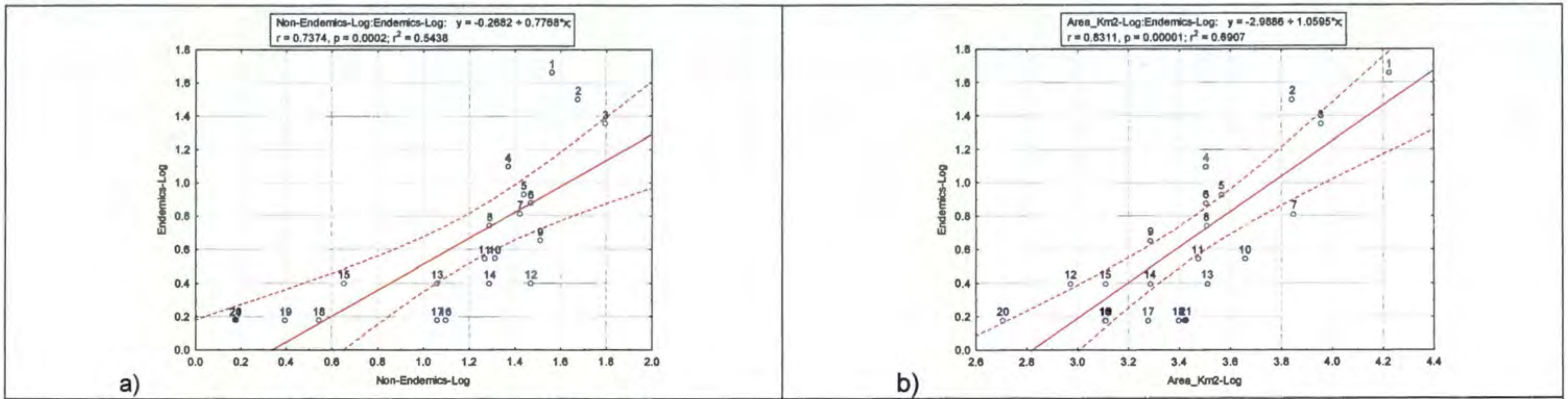


Figure 109: Sum of the Inverse Taxon Ranges for the Rutaceae Dataset.

Table 62: Habitat Data for the Rutaceae Endemics

| | | Altitude | | | Altitude | | | | | Rock Type | | | | | | | | Topography | | | | | Habitat | | | | | Vegetation | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Labels | Centre | Low | Middle | High | 0-500 | 500-1000 | 1000-1500 | 1500-2000 | >2000 | Sandstone | Shale | Clay | Granite | Limestone/Calcareous | Conglomerate | Loam | Other | Summits/Ridges/Plateaus | Slopes | Outcrops/Cliifs/Crevices | Hills | Flats | Moist Habitats | Riverine | Dry | Stony/Rocky/Gravelly | Sandy | Fynbos | Renosterveld | Forest | Karooid | Grassy Vegetation | Bushveld | Coastal Habitats/Dunes | Other | Unknown |
| 1 | N Northwestern Mtns | 3 | 6 | 13 | | | | | | 20 | 4 | | | | | | | 4 | 34 | 3 | | 2 | 7 | 1 | 2 | 9 | 11 | | | | | | | | | |
| 2 | Western Agulhas Plains | 2 | | 1 | | | | | | 6 | 2 | | | 18 | | | 2 | | 10 | | 5 | 6 | 4 | | | 6 | 5 | | | | | | | 10 | | |
| 3 | Central Southwestern-S Northwestern Mtns | | 2 | 8 | | | | | | 10 | 2 | | 1 | | | | 1 | 1 | 14 | 3 | 2 | 2 | 5 | | | 6 | 2 | | | | | | | 1 | | |
| 4 | Central & East Langeberg | | | 2 | | | | | | 6 | 1 | | | | | | | | 9 | | | | 3 | 1 | 1 | 2 | | | 1 | | | | | | | |
| 5 | East & Far East Agulhas Plains | | | | | | | | | | | 2 | | 3 | | | | | 1 | | 2 | 2 | | | | | 4 | | | | | | | 3 | | |
| 6 | RZE | | | 3 | | | | | | 6 | | | | | | | | | 7 | | | | 1 | | 2 | 2 | 1 | | | | | | | | | |
| 7 | Witteberg-Swartberg Mtns | | | 1 | | | | | | 6 | | | | | | | 1 | | 4 | | | | | | 2 | 4 | | | | | | | | | | |
| 8 | Rooiberg-West Outeniqua | | 1 | 2 | | | | | | 4 | | | | | | | | | 5 | | | | | | 1 | 3 | | | | | | | | | | |
| 9 | Groot Winterhoek | | | | | | | | | 4 | | | | | | | 1 | 1 | 3 | 1 | | | | 1 | | | | | | | | | | | | |
| 10 | Sandveld-Saldanha Peninsula | | | | | | | | | | | | | 1 | | | | | 1 | | | 1 | | | | | 3 | | | | | | | 2 | | |
| 11 | East Outeniqua-West Tsitsikamma-Vanstadensberge | 1 | | | | | | | | 1 | | | | | | | | | 1 | 1 | 1 | | | | | 1 | | | | | | | 1 | 1 | | |
| 12 | Peninsula and Kogelberg | 1 | | | | | | | | 1 | | | | | | | | | 2 | | | 1 | | | | | 1 | | | | | | | 1 | | |
| 13 | Port Elizabeth | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | 1 | | 2 | | |
| 14 | E Kouga-SE Baviaanskloof | | | | | | | | | 2 | | | | | | | | | 2 | | | | | | | 1 | | | | | | | | | | |
| 15 | Great Winterhoek | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 16 | E West Outeniqua | | | | | | | | | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| 17 | W Kouga-Tsitsikamma | | | | | | | | | 1 | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | |
| 18 | E Cape | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 19 | North Grahamstown | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 20 | Kiwane | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 21 | Kamiesberg | | | 1 | | | 1 | | | | | | 1 | | | | | 1 | 1 | 1 | | | | | | 1 | | 1 | | | | 1 | | | | |
| | Totals | 7 | 9 | 31 | 0 | 0 | 1 | 0 | 0 | 68 | 9 | 2 | 2 | 23 | 0 | 0 | 5 | 7 | 96 | 9 | 11 | 14 | 20 | 3 | 8 | 36 | 27 | 1 | 1 | 0 | 0 | 2 | 1 | 20 | 0 | 0 |



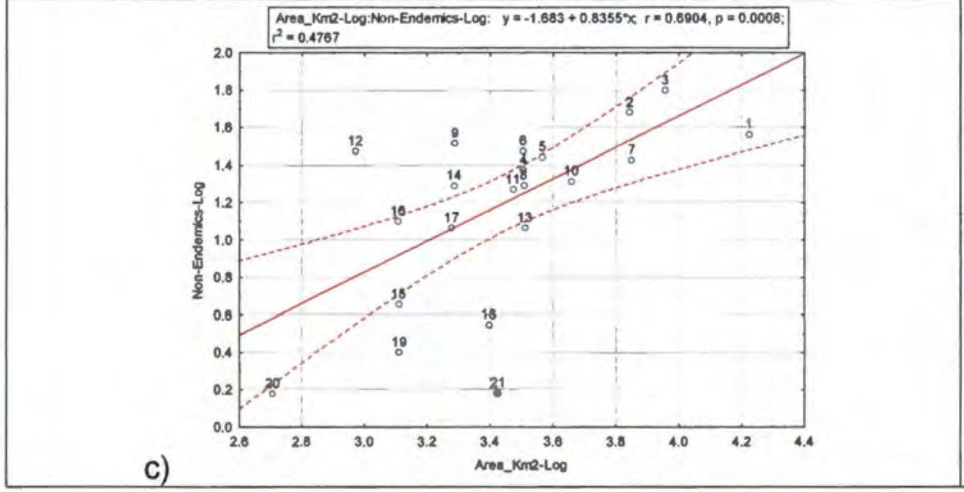


Figure 110a-c: The correlation between Endemism, diversity and area in the Rutaceae Dataset.
The numbers on the graph correspond to the Rutaceae PC table above (Table 61) and the PC Maps (Figure 107).

Investigating the hierarchical relationships of these centres would prove highly beneficial, in providing greater clarity on where the affinities of some of these centres and even sub-centres may lie. There is appreciable incorporation of low altitude QDS into choria, indicating a well developed low altitude flora.

### 17.1.1 The relationship between endemism, diversity, and area in the Rutaceae PCs

In my Rutaceae Dataset, a highly significant and positive relationship ($r^2 = 0.54$, $p<0.001$) exists between the number of endemic species (endemism) and non-endemic species found within PCs (Figure 110a). A highly significant and strong positive relationship also occurs between the number of endemics and the geographic size of the PC ($r^2 = 0.69$, $p<0.001$) (Figure 110b), and between the number of non-endemics and the geographic size of the PC ($r^2 = 0.48$, $p<0.001$) (Figure 110c),but is weaker. I excluded the Kamiesberg PC (21) outlier.

The West Agulhas Plains (PC 2) performs better in my Rutaceae Dataset than in any other dataset that I analysed and is overrepresented in endemism both with regards to non-endemic taxa (Figure 110a), and PCs area (Figure 110b), indicating the importance of the Agulhas Plains for floristic development in Diosmeae. The Central and Eastern Langeberg (PC 4) shows similar floristic patterns to the West Agulhas Plains, and is also overrepresented in endemism with regards to both non-endemic taxa (Figure 110a), and PC area (Figure 110b). The Northern Northwestern Mountains (PC 1) have significantly higher numbers of endemic taxa than predicted by its numbers of non-endemic taxa (Figure 110a). This is partly due to its large geographic area and has expected numbers of endemic (Figure 110b) and non-endemic taxa (Figure 110c) when considering PC area.

The Groot Winterhoek (9), Peninsula-Kogelberg (12) and the E Kouga-SE Baviaanskloof (14) all have higher than expected numbers of non-endemic taxa than predicted by PC area (Figure 110c), but have fewer endemic taxa than predicted by non-endemic taxa (Figure 110a). Unusually, the Peninsula does not form a consolidated area, and the Peninsula-Kogelberg portion of the PC (12) is disjunct, which may negatively affect levels of endemism.

Numbers of endemic (Figure 110b) and non-endemic (Figure 110c) taxa are under predicted by PC area, in both the Sandveld-Saldanha PC (10), and the Port Elizabeth PC (13). It is surprising that these two coastal, lower altitude PCs perform so poorly, considering how well the West Agulhas Plains PC (2) performs. The Witteberg-Swartberg (PC 7) contains fewer endemics than predicted by its PC area. A number of the more easterly-located PCs (15, 18, 19, 20 and 21), which are situated on the geographic and climatic periphery, all contain lower non-endemic taxon numbers than predicted by the PC area (Figure 110c). The easterly West Kouga-Tsitsikamma (PC 17) has low endemism (Figure 110a and b), as does the Eastern West Outeniqua (16) (Figure 110a). The Kamiesberg (PC 21) also contains lower than predicted non-endemic taxa than predicted by PC area (Figure 110c), and is geographically peripheral in the northwest.

## 17.2 CFR Phytogeographical Centres

### 17.2.1 The Northwest Phytogeographical Province

That the NWPP has much greater numbers of endemics than the SWPP is the greatest phytogeographical departure from other Cape Clades that I analysed (Table 61). Goldblatt and Manning (2000) recorded this fact at the family level in their Appendix, although it was not emphasised. In Goldblatt and Manning (2000), the NWPP has a greater absolute diversity and a greater number of endemics than the SWPP. However, their SWPP has a higher proportion of taxa endemic to it, namely, 75.4% versus 68.4% in their NWPP. This is in contrast to the results of my study (Table 63), and may either indicate that the phytogeographical centres employed by Goldblatt and Manning (2000), which are generalised for all CFR Taxa, may not be entirely congruent, or appropriate for the Diosmeae. It could also imply that the PCs identified in my study require refinement, or further evaluation. A study of the hierarchical relationships of the PCs of this study would prove highly beneficial in establishing higher-level phytogeographical boundaries and affinities.

Overall, Tribe Diosmeae has higher diversity and endemism in the NWPP (Table 63), although this is not consistent in all its genera. Genera that show significant development in the NWPP include *Macrostylis* (Williams, 1981a), and *Agathosma* (this study), *Phyllosma* and *Sheilanthera* (Williams, 1981b). Genera with nearly equal development in the north-south and east-west mountain axis include *Diosma* (Williams, 1982a), *Euchaetis* (Williams, 1981c), and *Acmadenia* (Williams, 1982b). Conversely, some taxa display their greatest development in the southern centres, namely *Adenandra* (Strid, 1972), *Coleonema* (Williams, 1981d), and *Empleurum* (Williams, 1984). These deviations from montane TMS Cape Clade patterns (Levyns, 1964) are very significant, and bear further investigation. I classified all the PCs in the SWPP and NWPP into these two higher level phytogeographical provinces, using the geographic boundaries of the Combined Dataset and the literature (Weimarck; Goldblatt and Manning, 2000), and calculated their floristic properties. I found that the NWPP still had more endemics (Table 63). Most of the endemics occur on high altitude sandstone slopes, although there are appreciable numbers of sandy soil taxa, and a minor shale component as well (Table 62).

From the table of the higher-level "potential" phytogeographical provinces (Table 63), I calculated that the NWPP contains 59.5% more QDSs than the SWPP, although it only has 18.4% higher diversity. However, the NWPP has 64.4% more endemics than the SWPP. Thus, there does not appear to be a linear correlation between area and diversity, but the ratio between endemism and QDS area between the NWPP and SWPP is similar in Diosmeae.

Table 63: Area, Taxon Diversity, and Endemicity Values for the combined Rutaceae PC which form the NWPP and SWPP of my Combined Dataset and the literature (Weimarck, 1941; Goldblatt and Manning, 2000). Higher diversity and endemism are recorded in the NWPP rather than the SWPP, contrary to what one would expect in Cape clades.

| Phytogeographical Centre | PC/PSC | # QDS | # Taxa | Taxa >=50% | # Endemics | Endemics/ # Taxa |
|---|---|---|---|---|---|---|
| NWPP | 1, 9, 21, 3.1, 3.3; one QDS of 10 | 67 | 122 | 93 | 74 | 60.6% |
| SWPP | 6, 10, 12, 3.2, 3.1 | 42 | 103 | 69 | 45 | 43.7% |

The heart of this extraordinary endemism in the NWPP is situated on the Cedarberg Mountains (PSC 1.1). This sub-centre has as many endemics as the third richest PC, although it occupies a smaller area (Table 61). This is very different from most other typical CFR Clades, which have their centres of diversity and endemism in the Kogelberg-Hottentots Holland area of the Caledon Division (Levyns, 1964). There is a radical drop in endemicity and a lesser drop in diversity, between this sub-centre and the next richest sub-centre in the Northwest Mountains, namely, the S Piketberg-SW Cedarberg-Swartberg (PSC 1.2) (Table 61). Although the areas of these PSCs are different, the ratio is not as great as the difference in endemism (Table 61). The northern Sandveld Flora (PSC 1.2) is distinct from the southern Sandveld (PC 10), and more strongly associated with the Cedarberg Flora. This possibly indicates the strength of the Cedarberg region as a centre of origin, and/or refugia for surrounding lowland areas. The Gifberg (PSC 1.3) and Nieuwoudtville Plateau (PC 1 fragment) are relatively undeveloped, particularly in terms of sub-centre development, which is perhaps surprising for a clade that is centred in the Cedarberg. The reasons for this are unclear, but may have to do with absolute rainfall amounts, which are lower in this more northerly region (Schulze, 1997), resulting in lower diversity of Diosmeae there (Figure 108), particularly range restricted taxa (Figure 109). The S Piketberg-SW Cedarberg-Swartberg (PSC 1.2) and the Gifberg (PSC 1.3) Sub-Centres are equally represented by sandstone and sandy biotic elements (Table 62), but contain none of the N Northwest Mountains (PC 1) high altitude endemics (Table 62).

The Groot Winterhoek (PC 9) also stands out as a distinct PC, though it contains relatively few endemic taxa (Table 61), compared to the other Cape Clades that I analysed. This is surprising, when considering that it is adjacent to the Cedarberg and that it contains relatively high, mesic peaks (Schulze, 1997). However, its low endemism may be due to the smaller geographic size of the three QDSs in Diosmeae, as endemism is strongly correlated with PC area (Figure 110b).

The remaining PC with NWPP affinities, the Kamiesberg (PC 21), contains two taxa, one of which, *Agathosma namaquensis* (4), is endemic, occurring at high altitudes on granite (Table 62). Furthermore, this endemic taxon is not limited to a single QDS, but four, making it relatively widespread for CFR Taxa in this particular area, possibly indicating good collection effort for this species.

In the Hex River Mountains, Diosmeae makes another departure from general Cape Clade phytogeographical patterns. Usually the Hex River Mountains show strong affinities to the Groot Winterhoek Mountains, as in the Combined Dataset. In Diosmeae, the Hex River Mountains, which are usually in the NWPP (Combined Dataset) form part of the Bainskloof-Hex River-N Waboomsberge (PSC 3.1), and thus shows affinities to the SWPP (specifically, PSC 3.2). The PC (3) also extends eastward into the KMPP, nearly reaching as far east as the Witteberg, although this eastern extension may not be as robust. This eastward extension may indicate the presence of a mountain-bridge, apparently joining the SWPP-NWPP-KMPP, or more specifically, in Diosmeae, joining the Limietberg, to the Hex River, and the Hex River to the southwest Witteberg. Although unusual, a high altitude corridor from the western phytogeographical provinces to the east is certainly not unique to Diosmeae. A similar mountain-bridge is observed in Restionaceae. However, there the Swartruggens and Swartrugberge and Baviaansberg are joined via a similar mountain-bridge to the southwest Witteberg, before the passage heads north and further east. Although the mountain bridges are similar in Diosmeae and Restionaceae, the NWPP rather than the SWPP is involved in Restionaceae. In both cases, these mountain-bridges overlap in QDSs 3319BD and 3320AC, possibly over the Saalberg, to the Bonteberg and finally to the Voetpadsberg to the Witteberg, as discussed for the Restionaceae. Interestingly, *Acmadenia matroosbergensis* (5) is nearly endemic to this corridor region (eastern portion of PC 3), but has only one disjunct locality in the Skurweberg, in the southern N Northwest Mountains Centre (PC 1). This may indicate that there is a biotic element in Diosmeae linking the more northerly NWPP to the KMPP, as in Restionaceae, in addition to the apparently more numerous biotic elements linking the SWPP-NWPP-KMPP. However, caution should be exercised in interpreting these results, until they are analysed at a finer geographical scale, as the easterly extent of the Bainskloof-Hex River-N Waboomsberge Sub-Centre (3.1) is contentious and not very strongly supported. It is possible that this eastward extension of the Bainskloof-Hex River-N Waboomsberge (PSC 3.1) may be due to the coarseness of the geographical scale of input data employed in this study. The PC was not identified by cluster analysis, but by later GIS investigation, and consists of a number of taxa that occupy two QDSs with overlapping ranges, thus extending the PC eastwards in a type of domino effect. Two of the taxa, *Agathosma mirabilis* (2), and *Agathosma foleyana* (2) occur on shale bands, while the rest occur on sandstone substrates (Table 62). Finer scale geographical investigation may prove there is altitudinal separation, or that the ranges of these taxa do not in fact overlap. Hierarchical PC analysis at the centre and sub-centre level may prove beneficial in solving some of these affinity problems. Initial analysis seems to indicate that these taxa are not sisters and that there is no stepwise speciation progression along this corridor (T.H. Trinder-Smith personal communication, 2005). The unconventional clustering of QDSs into the Bainskloof-Hex River-N Waboomsberge Sub-Centre (3.1) may have effected clustering in the rest of the SWPP and may account for its poor phytogeographical performance, and fragmented patterns.

The remaining sub-centres do not conflict as strongly with phytogeographical patterns in the Combined Dataset and are more congruent with the results of Weimarck and Goldblatt and Manning (2000). The Hottentots-Stellenbosch-Wemmershoek Mountains (PSC 3.2) is located entirely within the SWPP, although it overlaps two Combined Dataset PCs. The S Waboomsberge-W Langeberg (PSC 3.3) occurs in one PSC in the Combined Dataset (3.1) and is within the Northwest Centre of Weimarck, although the NWPP/KMPP boundary of Goldblatt and Manning (2000) bisects it.

### 17.2.2 The Southwest Phytogeographical Province

The PC boundaries for the SWPP for Diosmeae are largely incongruent with those of my Combined Dataset and the literature (Weimarck; Goldblatt and Manning, 2000). Although SWPP PC endemicity is highest in the central southwest mountains, the Hottentots-Stellenbosch-Wemmershoek Mountains Sub-Centre (PSC 3.2), situated in the SWPP, is more strongly associated with sub-centres (PSC 3.1 and 3.3) in the NWPP, rather than areas in the SWPP. Furthermore in Diosmeae, the Kogelberg-W Kleinrivier Mountains do not cluster with the Hottentots-Stellenbosch-Wemmershoek Mountains, as they do in my Combined Dataset and the literature (Weimarck). Instead the Kogelberg-W Kleinrivier Mountains forms a disjunct PC with the Peninsula (PC 12). The RZE (PC 6) forms the richest PC entirely contained in the traditional SWPP. The RZE (PC 6) is centred on the RZE Mountains and consists largely of endemics on TMS slopes (Table 62). The unusual clustering of the SWPP (PSC 3.2) with the NWPP (PSC 3.1) may be aggravated by the fact that two areas that usually form relatively rich continuous centres, namely the Peninsula (PSC 12 and a disjunct part of PC 3) and the Hottentots Holland-Kogelberg-Kleinrivier (PC 12 and 3.2) are both fragmented. The northern Peninsula forms a disjunct part of the Central Southwest-S Northwestern Mountains Centre (PC 3), separated by the southern Sandveld (PC 10), while the south Peninsula forms a disjunct

PC with the Kogelberg (PC 12). This is unusual, as the Peninsula usually preserves its integrity in most groups in the datasets that I analysed, whether they are typical CFR Clades or not, including: Asteraceae, Ericaceae, Fabaceae (single centre with two subcentres), Geophytes, RDL Taxa, Orchidaceae, Poaceae, Proteaceae and Restionaceae. The one notable exception is Bruniaceae, where the northern Peninsula is clustered with the rest of the SWPP Mountains, rather than the southern Peninsula (Figure 57). Likewise, the clustering of the Kogelberg and Hottentots QDSs into different phytogeographical units is rare, and only occurs in the Polygalaceae Dataset at the PC level (Figure 84), and in the Poaceae Dataset at the PSC level (Figure 53) (although for Poaceae they are in the same PC).

Although the Kleinrivierberge were classified within the APPP rather than the SWPP as in the Combined Dataset, there nevertheless appeared to be TMS biotic elements that overlap the current phytogeographical units of the Central Southwestern-S Northwestern Mountains Centre (PC 3), the phytogeographic units to the south (PC 12), and to a lesser extent the east (PSC 2.5), and indicate floristic affinities between them. However, due to conflict, these taxa did not form PCs. The taxa in question are: *Euchaetis elata* (5) (sandstone slope habitats), which links PCs 2 and 12; *Acmadenia nivea* (2) (high rocky slopes), *Agathosma stokoei* (4) (upper slopes), *Euchaetis glabra* (2) (sandstone slopes), which link PSC 3.2 and PC 12; and *Adenandra brachyphylla* (6) (sandstone slopes), which link PSCs 2.5, 3.2 and PC 12. There is no net gain in endemism by combining the Kleinrivierberge (PSC 2.5) to the Peninsula-Kogelberg (PC 12). However, *Agathosma geniculata* (5) combines the Kleinrivierberge (PSC 2.5) (coastal limestone) to the rest of the West Agulhas Plains, hence the current clustering, although unusual, is maintained.

The Sandveld-Saldanha Peninsula (PC 10) forms a continuous PC from the Cape Flats at False Bay all the way up to the Saldanha Peninsula, on the littoral sand and limestone of the area (Table 62). It includes most of the Sandveld and West Coast areas, but does not extend into the NWPP, indicating the distinctness of the north and south Sandveld floras in Diosmeae.

### 17.2.3 The Agulhas Plains Phytogeographical Province

The high number of endemic taxa on the Agulhas Plains Centre (PC 2) relative to other Diosmeae PCs represents another departure from other CFR Clades, particularly considering that it has many more endemic taxa than the Central Southwestern-S Northwestern Mountains Centre (PC 3), in an almost identical area. In Diosmeae, two of the five most endemically rich centres (PC 2 and 5) are found on the APPP. In general, the Diosmeae APPP is large and very well defined, although it is partitioned into two different PCs, namely the Western Agulhas Plains Centre (PC 2) in the west, and the East and Far East Agulhas Plains Centre (PC 5) in the east. This partition is in the same area as depicted in the Combined Dataset. It remains to be determined whether these PCs would combine to form a single APPP cluster in Diosmeae, as they do in some analyses in the Combined Dataset (Figure 23, Figure 24 and Figure 25), and in Goldblatt and Manning (2000).

The majority of endemic taxa are limestone endemics, although there are also appreciable numbers of sandstone endemics (Table 62). Shale endemics are not well-represented (Table 62). However, as with the North Northwest Mountains Centre (PC 1), the Western Agulhas Plains Centre (PC 2) has more endemic taxa but lower diversity than the Central Southwestern-S Northwestern Mountains Centre (PC 3), which highlights the exceptional diversity of the SWPP PC (PC 3).

The current demarcation for Diosmeae on the APPP partially resembles Weimarck's Bredasdorp Sub-Centre, which combines the Kleinrivierberge with areas to the south (APPP), rather than the mountains to the north SWPP (Hottentots-Holland) and west (Kogelberg area). However, my Combined Dataset grouped the Kleinrivierberge with the mountains of the SWPP, rather than the Agulhas Plains, in conflict with the results of Diosmeae. Both sandstone taxa (*Adenandra lasiantha* (5)), and limestone taxa (*Agathosma geniculata* (5)) support the current classification in Diosmeae. However, there are further TMS taxa that group the Kleinrivierberge (PSC 2.5) to the SWPP and are recorded in the SWPP discussion (Section 17.2.2). These taxa show conflict with neighbouring PCs, causing a cascade effect, decreasing the possible number of endemic taxa and QDSs in a phytogeographical area (see Introduction to Appendix I), resulting in the current boundary configuration.

The Western Agulhas Plains are divided into numerous sub-centres, and are very well defined. The SE Western Agulhas Plains (PSC 2.1) contains the greatest number of endemics, but is closely followed by the Potberg Sub-Centre (PSC 2.2) and the West Western Agulhas Plains (PSC 2.3). The Potberg (PSC 2.2) shows stronger affinities to the western APPP in Diosmeae, congruent with my Combined Dataset, rather than to the east APPP, as in the RDL Taxa Dataset. North of the Potberg, Diosmeae includes inland areas of the Central Langeberg Plains (as demarcated by my Combined Dataset) into the APPP, in a discrete sub-centre (PSC 2.4). The remaining sub-centre, the Kleinrivierberge (PSC 2.5) only has a single endemic, restricted to high sandstone slopes.

The East and Far East Agulhas Plains combine to form a single PC, the East and Far East Agulhas Plains (PC 5). At the sub-centre level, the PC boundaries of the Combined Taxa Dataset are vaguely apparent. Here in the east, as in the west, the APPP PC boundary has shifted north to include areas of the East Langeberg Plains (PSC 5.1) in the APPP.

## 17.2.4 The Karoo Mountain Phytogeographical Province

The KMPP is relatively poorly developed, consisting of a single, disjunct centre, the Witteberg-Swartberg Mountains (PC 7), which is restricted to the central mountainous areas of the KMPP (Figure 107; Table 62). Surprisingly, the Klein Swartberg performs relatively poorly, with no sub-centre development of its own. However, there are sub-centres on the Witteberg (PSC 7.1) and Groot Swartberg/Kammanassie Mountains (PSC 7.2). An interesting pattern is revealed linking the Rooiberg (PSC 8.1), which is a traditional KMPP region to the West Outeniqua Mountains (PSC 8.1), possibly via the Bakenskop-Attakwasberg, and is discussed below.

## 17.2.5 The Langeberg Phytogeographical Province

The Central and East Langeberg (PC 4) form a very discrete, continuous centre, restricted to the mountainous regions of the Langeberg. The centre is very much reduced in size, similar to many of my other datasets, for example, Asteraceae, Fabaceae and Restionaceae (which has no southern Langeberg plains development). There are no plains flora directly associated with the mountains, as the plains form part of the APPP. The strong development of the coastal plains flora is noteworthy and may indicate evolution in response to ocean level fluctuations, as Rourke (1972) noted for *Leucospermum*. The montane areas may also have acted as a refugium during drier periods. The phylogenetic relationships of the montane and coastal floras should also be investigated. This would be necessary in order to determine if it is possible for the montane areas of the Langeberg to act as a refugia, from which species may re-colonise the coastal shelf in response to receding ocean levels (Linder, 2003; Linder, 1995), or more favourable mesic conditions on the lowlands, and possibly then undergo divergence. Alternatively, it may be discovered that these taxa evolved on the plains, independently of the mountains. This has important conservation implications, in preserving evolutionary processes and linkages.

## 17.2.6 The Southeast Phytogeographical Province

The further East one travels, the weaker the PCs of Diosmeae become. Diosmeae is generally underrepresented in the SEPP. PC development is to be restricted to the western, central (PCs 11, 14, 16 and 17) or eastern parts (PCs 13, 15, 18 and 19) of the SEPP. There is a large area with almost no PC development, except for the East Kouga-SE Baviaanskloofberg Centre (PC 14), with two endemics, forming somewhat of a wasp's waist. The East Outeniqua-West Tsitsikamma-Vanstadensberge PC (PC 11) is disjunct across this 'gap', due to *Agathosma acutissima* (3). Whether this is a real disjunction or due to under collection requires investigation. Even within the western and eastern areas of PC development in the SEPP, there are disjunctions (PCs 13, 16 and 18), which may indicate under collection. There also appears to be centre development east of the SEPP, in Weimarck's (1941) Zuurberg Sub-Centre (PCs 13, 18 and 19).

Interestingly, the Karoo Rooiberg (PSC 8.1) merges with the West Outeniqua (PSC 8.1) and East Langeberg (PC 8), possibly over the Bakenskop-Attakwasberg. This is due to *Acmadenia baileyensis* (5) and *Agathosma roodebergensis* (3), which both occur on sandstone slopes, the latter in mid to high altitude areas. This may indicate a corridor, along which taxa could migrate, or an area of floristic overlap, between the LBPP-KMPP-SEPP. This is a curious pattern, also noted in Ericaceae (low altitude), Geophytes (low altitude) and Restionaceae (high altitude) Datasets.

## 17.3 Non-CFR Phytogeographical Centres

All but one taxon of Diosmeae occur within the CFR region as defined by Weimarck (1941). *Acmadenia kiwanensis* (1) is recorded about 55 km east of Weimarck's (1941) Zuurberg Sub-Centre, near Kiwane (PC 20). This may indicate a chance dispersal event, or perhaps a relictual relationship, as is perhaps the case with *Raspalia trigyna* (Bruniaceae).

## 17.4 Summary

Although the tribe Diosmeae is almost entirely endemic to the CFR and has long been considered a Cape Clade (Levyns, 1964; Linder, 2003), it has some very anomalous phytogeographical patterns. Its centres of peak diversity and endemism are in the Cedarberg Mountains of the NWPP, rather than in the Hottentots-Holland-Kogelberg area of the SWPP. In addition, and unusually for most taxa, especially Cape Clades, diversity and endemism are fairly poorly developed on the Peninsula. PCs are well-developed in lowland areas. The Agulhas Plains PCs, both in the west and east, are very well developed, and impinge on neighbouring PCs. Another anomaly is the extension of a PC (PC 3) in the SWPP into the southern NWPP, and western KMPP. Although weakly supported, there is some evidence of a biological pattern, but the coarse resolution of input data may have also contributed to the pattern. Levels of PC endemism (highest to lowest) in the different phytogeographical provinces are approximately as follows: NWPP, APPP, SWPP, LBPP, KMPP and SEPP.

# Appendix II: List of Taxa endemic to Phytogeographical Areas

A digital list of the taxa endemic to the phytogeographical units identified for each derivative dataset is provided in various software formats (Excel, Tab separated text, CSV). Where available, habitat data is also provided. It is not provided here in hardcopy to save both space and paper.