

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/279896152>

Extraordinary high regional-scale plant diversity in southern African arid lands: Subcontinental and global comparisons

Article in *Diversity and Distributions* · January 1998

CITATIONS

90

READS

232

4 authors:



Richard M Cowling

Nelson Mandela University

484 PUBLICATIONS 24,576 CITATIONS

[SEE PROFILE](#)



Philip W. Rundel

University of California, Los Angeles

371 PUBLICATIONS 13,301 CITATIONS

[SEE PROFILE](#)



Philip George Desmet

ECOSOL GIS and Nelson Mandela University

46 PUBLICATIONS 1,615 CITATIONS

[SEE PROFILE](#)



Karen Esler

Stellenbosch University

267 PUBLICATIONS 4,770 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Spatial Biodiversity Planning [View project](#)



Factors Influencing Invasion of Giant Reed (*Arundo donax*) in Riparian Ecosystems of Mediterranean-type Climate Regions [View project](#)



Extraordinary high regional-scale plant diversity in southern African arid lands: subcontinental and global comparisons

R. M. COWLING^{1*}, P. W. RUNDEL², P. G. DESMET¹ and K. J. ESLER³ ¹*Institute for Plant Conservation, University of Cape Town, Rondebosch 7701, South Africa, ²Department of Biology, University of California, Los Angeles, CA 90024-1768, U.S.A. ³Department of Botany, University of Stellenbosch, Stellenbosch 7600, South Africa.*

Abstract. The Karoo-Namib Region, comprising the arid lands of southern Africa, supports an extraordinarily rich and compositionally unusual flora. This region includes the winter-rainfall Succulent Karoo (part of the Greater Cape Flora), the summer-rainfall Nama Karoo, and incorporates the Namib Desert. The Succulent Karoo is home to the world's largest succulent flora and is very rich in geophytes.

Species-area patterns at the regional scale (10^1 – 10^6 km²) show that the Succulent Karoo had 2.6 times as many species per unit area than the Nama Karoo. The Succulent Karoo was also richer than other winter-rainfall, semi-arid (100–400 mmyr⁻¹) regions of the world, having, for example, nearly four times as many species than equivalent-sized North American regions. Similarly, southern African winter-rainfall desert (<100 mmyr⁻¹) regions were exceptionally species-rich: here 331 species have been recorded in an area of 1.3 km². The Namib Desert, which spans the Succulent and Nama Karoo regions, has up to 200 times the number of species that similar-sized areas of

the Saharan Desert. On the other hand, the Nama Karoo does not appear to be unusually rich at the regional scale.

The Succulent Karoo represents a major extra-tropical centre of plant biodiversity. Reasons for its high diversity include unusually predictable seasonal rainfall and relatively mild summers. The climatic regime has selected for short-lived and drought-sensitive shrub lifestyles, largely associated with dwarf to low leaf succulents. A combination of short generation times and limited gene flow has resulted in massive diversification within certain lineages (especially the Mesembryanthema), leading to the fine-scale discrimination of habitat and geographic space. Plant-pollinator coevolution appears to have played some role in the diversification of the region's large geophyte flora.

Key words. Arid lands, diversification, global comparisons, plant diversity, regional scale, southern Africa, Succulent Karoo.

INTRODUCTION

For a largely warm temperate area, southern Africa has a remarkably rich flora of vascular plants, with 23,404 species and infraspecific taxa recorded from the region, of which some 80% are endemic (Cowling & Hilton-Taylor, 1994). Most research has focused on describing and explaining patterns of diversity in the predominantly fynbos flora of the Cape Floristic

Region (e.g. Cowling, Holmes & Rebelo, 1992). The extraordinary plant diversity and floristic peculiarity of southern Africa's arid lands is less well known. While Cape fynbos has its analogue in the kwongan of mediterranean southwestern Australia (Cowling *et al.*, 1996), the flora of southern Africa's winter-rainfall karoo, with its unrivalled diversity of succulent species (Van Jaarsveld, 1987; Ihlenfeldt, 1994, Hilton-Taylor, 1996), is in a league of its own.

In this paper we describe and compare patterns of regional plant diversity at a subcontinental (southern Africa) and global scale. We also attempt to explain

*Corresponding author; e-mail: rmc@botzoo.uct.ac.za.

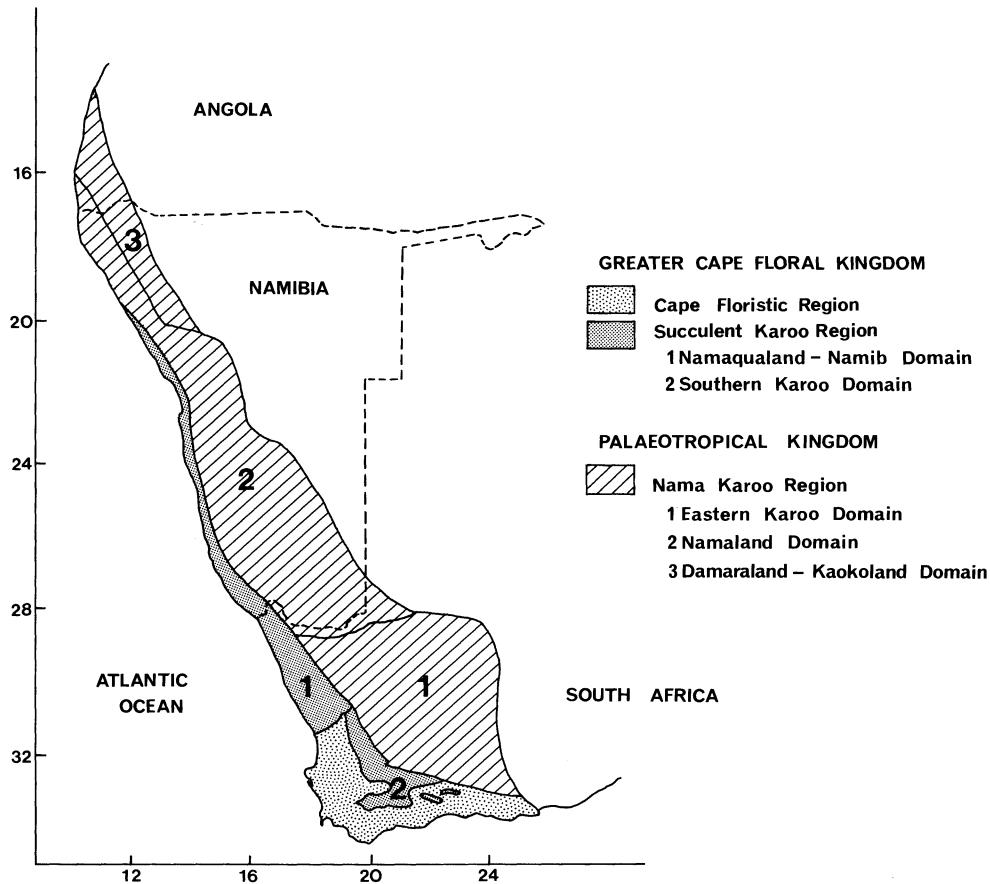


Fig. 1. Phytogeographical map of south-western Africa. Redrawn from Jürgens' (1991).

these patterns in terms of differences in selective regimes, plant life histories, and differential rates of diversification (Rosenzweig, 1995).

It is necessary to clarify the use of some terms in this paper. Firstly, we use the term 'Karoo-Namib Region' to describe, in a phytogeographical context, the semi-arid shrubland and desert areas of southern Africa (Werger, 1978a). Although Jürgens (1991) provides the necessary justification for dividing this region into two phytochoria of equal rank, namely the Succulent Karoo Region and the Nama Karoo Region (Fig. 1), we retain the term as a matter of convenience. Secondly, our species counts always refer to vascular plants only. Thirdly, we use the terms 'species' instead of the more long-winded 'species and infraspecific taxa'.

STUDY AREA

Biogeographical background

Our area of interest is the Karoo-Namib Region of southern Africa (Werger, 1978a,b), an arid to semi-arid phytochorion distinct from other arid lands of sub-Saharan Africa. Werger (1978a,b) followed White (1976, 1983) in recognizing a Karoo-Namib phytochorion and agreed with earlier workers that this unit forms part of the Palaeotropical Kingdom as opposed to the Cape Kingdom. He did, however, emphasize the transitional nature of the region's flora, with strong Sudano-Zambeian affinities towards its northern and eastern boundaries, and strong Cape affinities towards the south-west.

Using distribution data for 1700 species, Jürgens (1991) developed a new phytogeographical subdivision of southern Africa's arid lands (Fig. 1). Rather than tinkering with boundaries, his proposals have far-reaching implications for African biogeography. The fundamentals of his scheme are summarized below.

- The division of the Karoo-Namib Region into two phytochoria of equal rank, namely the *Succulent Karoo Region* (more-or-less coincident with Werger's (1978a) Western Cape Domain) and the *Nama Karoo Region*.
- The recognition that the Succulent Karoo Region forms part of a greater Cape Flora rather than part of the Palaeotropical Kingdom (also see Hilton-Taylor, 1987).
- The recognition of a new system of domains in both regions, delimited on the basis of the distribution of species from zonal vegetation complexes. Thus, the Namaqualand-Namib Domain (strongly winter rainfall) and the Southern Karoo Domain (winter to non-seasonal rainfall) are recognized for the Succulent Karoo Region; and the Namaland Domain (including most of Werger's (1987a) Namaqualand and Namib Domains), Damaraland-Kaokoland Domain (see also Nordenstam, 1974; Hilton-Taylor, 1994), and the Eastern Karoo Domain (corresponding to Werger's (1978a) Karoo Domain) are recognized for the Nama Karoo Region.
- The division of the Namib Desert (as a geographic entity) into two phytochoria: a south-central coastal portion as part of the Succulent Karoo (Namaqualand-Namib Domain); and a northern and inland zone as part of the Nama Karoo (Namib Subdomain of the Namaland Domain) (see also Robinson, 1978).

In this paper we refer exclusively to Jürgens' (1991) scheme of regions and domains.

Floras

The flora of southern Africa's arid lands is unusually rich and compositionally interesting (Cowling & Hilton-Taylor, in press). The entire flora of the Karoo-Namib Region probably exceeds 7000 species of which up to 50% are endemic (Hilton-Taylor & Le Roux, 1989). There are 4849 species in the Succulent Karoo (40.3% endemic) (Hilton-Taylor, 1996) and 1427 species (34.5% endemic) in the Namibian part of the Namib Desert (partly Namaqualand-Namib Domain and

partly Namib Subdomain of the Namaland Domain) (Robinson, 1978). There are no reliable estimates of the size of the Nama Karoo flora: Gibbs Russell (1987) provides a value of 2147 species in a 'core area' of 198,500 km², about 30% of the region.

Floras from the Succulent Karoo differ compositionally from Nama Karoo floras and those from other arid lands (Cowling & Hilton-Taylor, in press). They are uniquely characterized by high numbers of Aizoaceae (especially Mesembryanthema) (Hartmann, 1991), and relatively high numbers of Iridaceae and Geraniaceae. The last two-mentioned families are well represented in all fynbos floras of the Cape Region, and Aizoaceae rank highly in lowland fynbos and renosterveld floras (Cowling & Holmes, 1992). Succulents are extremely well represented in Succulent Karoo floras and are associated with many of the larger families (Aizoaceae, Asteraceae, Liliaceae, Crassulaceae, Geraniaceae, Euphorbiaceae and Asclepiadaceae). Indeed, the Succulent Karoo probably harbours about one third of the world's approximately 10,000 succulent species (Van Jaarsveld, 1987; Smith *et al.*, 1993).

The Succulent Karoo flora includes 730 genera of which sixty-seven (9.2%) are endemic (Hilton-Taylor, 1996). This is more than three times the number of endemic genera in the Sahara-Arabian and North American arid lands (Shmida, 1985), which are orders of magnitude larger than the Succulent Karoo. Another unusual feature of the flora is the high species to genus ratio of 6.9. The region includes several unusually large genera for an arid land flora, including *Ruschia* (Aizoaceae: 136 spp.), *Conophytum* (Aizoaceae: 116 spp.), *Oxalis* (Oxalidaceae: 114 spp.), *Euphorbia* (Euphorbiaceae: 77 spp.), *Pelargonium* (Geraniaceae: 72 spp.), *Senecio* (Asteraceae: 72 spp.), *Eriospermum* (Liliaceae: 65 spp.), *Othonna* (Asteraceae: 61 spp.), and *Drosanthemum* (Aizoaceae: 55 spp.) (Hilton-Taylor, 1996). Most of these large genera are comprised entirely of either succulent shrubs or geophytes.

The Nama Karoo flora is not as well known as the flora of the Succulent Karoo. Generally, regional floras are more typical of those from other arid lands (Cowling & Hilton-Taylor, in press) where Asteraceae, Poaceae and Fabaceae are the most frequent top-ranking families (Shmida, 1985). As with the Succulent Karoo, Nama Karoo floras are unusual among arid land floras in the low importance of Chenopodiaceae. Interestingly, the Damaraland-Kaokoland Domain flora (Robinson, 1978; Nordenstam, 1974; Hilton-Taylor, 1994) bears a strong resemblance to Thar

(Indian) Desert floras in the relative importance of Acanthaceae, Capparaceae and Cucurbitaceae (Shmida, 1985). Although no data have been published, there are certainly fewer genera endemic to the Nama Karoo than the Succulent Karoo. However, the former region is home to the only exclusively desert family—the Welwitschiaceae (Shmida, 1985).

Selective regimes

The Succulent Karoo and Nama Karoo differ fundamentally in their climatic, and hence, selective regimes (Desmet & Cowling, in press). These differences, which have profound implications for diversity and rates of diversification, are summarized as follows.

- The Succulent Karoo derives most of its rainfall from depressions associated with the circumpolar westerly belt (Schulze & McGee, 1978). Most rain falls during winter (May–September) (Werger, 1978a, 1986; Rutherford & Westfall, 1986) and, even at low annual totals, rainfall is remarkably predictable when compared to other winter-rainfall arid lands (Desmet & Cowling, in press; Elser, Rundel & Cowling, in press).
- Nama Karoo rainfall is derived from a number of sources to the east and north of the region (Desmet & Cowling, in press). Most rain falls during the late summer months (or with strong autumn and weak spring peaks in the Eastern Karoo) and, for a given annual total, rainfall is much less predictable than in the Succulent Karoo (Hoffman & Cowling 1987).
- In the Succulent Karoo, rainfall events are widespread, of long duration and are mostly gentle showers; rainfall events in the Nama Karoo are invariably highly localized, short, intense thundershowers (Desmet & Cowling, in press).
- Temperature extremes in the Succulent Karoo are ameliorated by proximity to the ocean and the high incidence, in the Namaqualand-Namib Domain, of fog during the summer months (Schulze & McGee, 1978; Olivier, 1995; Desmet, 1996). Frosts are rarely, if ever experienced over most of the area (Rutherford & Westfall, 1986; Werger, 1986). In the Nama Karoo, continentality is more pronounced: temperature extremes (including freezing conditions in winter) prevail.
- In the Succulent Karoo, high humidity (especially at night and in the early morning) and frequent fog (at least in the Namaqualand-Namib Domain)

provide additional sources of moisture during the dry summer months (Walker, 1986; Von Willert *et al.*, 1992; Desmet, 1996). In the Nama Karoo, violent rainfall events are the principle source of precipitation (Werger, 1986).

Thus, the Succulent Karoo has a warm temperate and oceanic climate characterized by relatively mild winters with low but reliable winter rainfall, and relatively mild summers where drought is ameliorated by heavy dew and frequent fog. The Nama Karoo has a more continental climate, characterized by hot summers with low and unreliable rainfall, and very dry, mild to cool winters with frequent night frosts. It is important to emphasize that the environmental conditions in the Southern Karoo Domain of the Succulent Karoo are in many respects transitional between those in the Namaqualand-Namib Domain and the Nama Karoo.

METHODS

We compiled species–area data at a regional scale (10^1 – 10^6 km²) for warm temperate and subtropical arid lands from throughout the world. We divided our data set into different categories: Nama Karoo sites; Succulent Karoo sites; summer rainfall, semi-arid (100–400 mmyr⁻¹) sites; winter rainfall, semi-arid sites; and desert (<100 mmyr⁻¹) sites. We had difficulty in locating data from the New World, summer rainfall regions and from Australia. The double logarithmic form of the species–area curve provided the best fit for all data sets (Williamson, 1988; Rosenzweig, 1995).

We used *F* tests to compare whether the slopes and intercepts of species–area regressions for different data sets were significantly different (Zar, 1984). In cases where we could not reject the null hypothesis that slopes were identical in the overall populations, i.e. they were homogeneous, we compared the intercept- or k-ratio of the two curves. This ratio provided an overall estimate of the difference in regional diversity between the two data sets (Gould, 1979).

RESULTS

Southern African comparisons

The log–log species–area curves were significant for both the Succulent Karoo ($P < 0.001$) and the Nama Karoo ($P < 0.05$) (Fig. 2). Since the slopes of these two curves were homogeneous ($F = 0.026$; $df = 18$; $P = 0.87$),

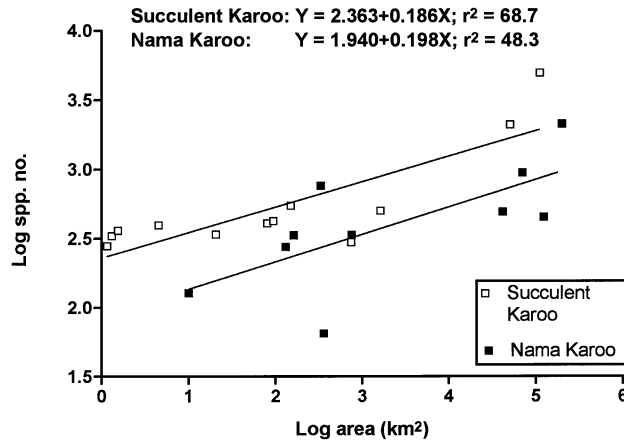


Fig. 2. Species-area relations for Succulent Karoo and Nama Karoo sites in southern Africa. $Y = \log$ spp. no. and $X = \log$ area. Data from Nordenstam (1974), Gibbs Russell (1987), Hilton-Taylor (1994, 1996), Desmet (1996), Cowling *et al.* (1997) and N. Jürgens (pers. comm.).

and the intercepts were significantly different ($F=9.709$; $df=19$; $P=0.006$), we computed their k - or intercept-ratio. This value was 2.65, indicating that for any given region within the range of areas in Fig. 2, Succulent Karoo has more than 2.5 times the number of species as the Nama Karoo.

Global comparisons

When compared to other winter rainfall, semi-arid zones of the world, the Succulent Karoo emerged as having the highest regional diversity over the full range of areas (Fig. 3a). There were sufficient and appropriate data for comparative analyses of the species-area relations of the Succulent Karoo and North American winter-rainfall semi-arid regions. The regression statistics were as follows:

Succulent Karoo:

$$Y = 2.350 + 0.221X; r^2 = 87.7\%; P < 0.001; n = 9$$

North America:

$$Y = 1.770 + 0.301X; r^2 = 75.3\%; P < 0.001; n = 21,$$

Where $Y = \log$ species number and $X = \log$ area. The overall slopes of these curves were not significantly different ($F=2.506$; $df=26$; $P=0.13$) but the intercepts were ($F=31.439$; $df=27$; $P<0.0001$). The resultant intercept-ratio was 3.79, indicating that within the range of areas for the two data sets (Fig. 3a), the

Succulent Karoo has nearly four times as many species as North American winter-rainfall semi-arid regions.

Regional diversity in the Nama Karoo did not appear to be substantially higher than that in other summer rainfall, semi-arid areas (Fig. 3b), although more data would enable more meaningful comparisons. Certainly, Australian regions were considerably poorer than those from southern Africa, but the Sonoran Desert (the only North American site) had similar richness to an equivalent area of the Nama Karoo.

Species richness in desert regions, defined here as both summer and winter rainfall areas with an annual rainfall of less than 100 mm, showed a non-significant relationship with area (Fig. 3c). Nonetheless, desert regions in southern Africa generally had more species when compared to similar-sized desert regions in North Africa, including the topographically complex uplands of the central Sahara. For example, the Namib Desert has between four and 200 times as many species as equivalent-sized areas of the Saharan Desert. The desert zone of the Namaqualand-Namib domain of the Succulent Karoo is especially rich: in the mountain desert region of South Africa's Richtersveld, 331 species have been recorded in an area of 1.3 km²! (Von Willert *et al.*, 1992).

Interestingly, the trend for winter-rainfall arid lands to be richer than those from summer rainfall regions holds at a global scale. A comparison of the two

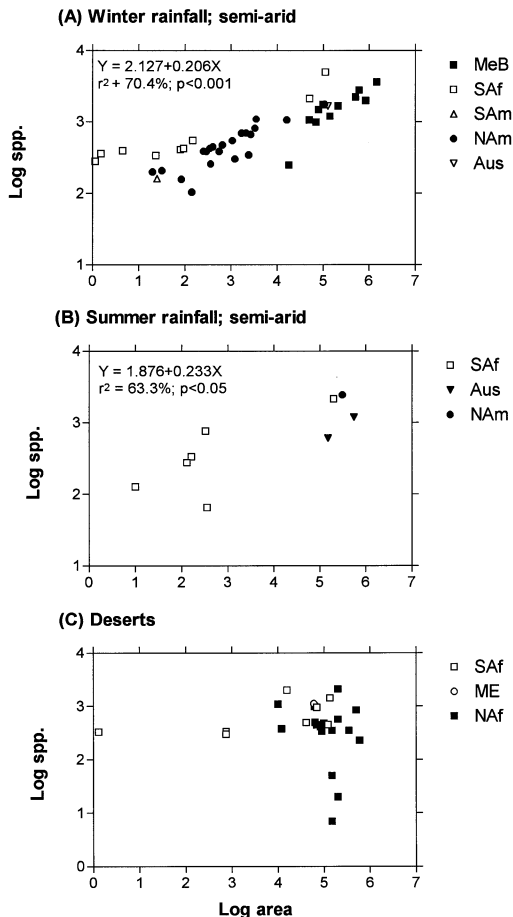


Fig. 3. Species-area relations for warm-temperate to subtropical semi-arid shrublands and deserts of the world: (a) winter-rainfall, semi-arid; (b) summer rainfall, semi-arid ($100\text{--}400\text{ mm yr}^{-1}$); and (c) desert ($<100\text{ mm yr}^{-1}$) regions. $Y = \log$ spp. no. and $X = \log$ area. Data for southern Africa (SAf) from Robinson (1978), Nordenstam (1974), Gibbs Russell (1987), Cowling & Hilton-Taylor (1994), Hilton-Taylor (1994; 1996), Desmet (1996) and Cowling *et al.* (1997). Data for Australia (Aus) from Williams & Calaby (1985) and J.S. Beard (pers. comm.). Data for North America (NAf) from Raven & Axelrod (1978), Mulroy, Rundel & Bowler (1979), Rundel & Gibson (1996) and P.W. Rundel (unpublished data). Data for South America (SAm) from Armesto & Vidiella (1993). Data for the Mediterranean Basin (MeB) from Le Hou  rou & Boulos (1991). Data for the Middle East (ME) from Danin (1983). Data for North Africa (NAf) from Le Hou  rou (1986, 1992).

species-area curves (Fig. 3a and b) revealed that the slopes were not significantly different ($F = 0.276$; $df = 48$; $P = 0.60$), but the intercepts were ($F = 3.061$; $df = 49$; $P = 0.09$). The corresponding k -ratio was 1.78,

indicating that winter-rainfall regions were more than one-and-a-half times richer than equivalent sized summer-rainfall regions. The analysis was constrained by the lack of data from summer-rainfall areas outside southern Africa.

DISCUSSION

Southern African comparisons

When compared with the Nama Karoo, the Succulent Karoo has higher levels of local endemism (Cowling & Hilton-Taylor, in press), higher local diversity (Cowling *et al.*, 1989; 1994), and higher differentiation (beta and gamma) diversity (Cowling *et al.*, 1989; Cowling & Hilton-Taylor, in press). Therefore, it is not surprising that considerably more species are packed into Succulent Karoo landscapes. What explains these differences?

The answer may lie in the unique climatic regime of the Succulent Karoo. Mild, oceanic and fog-ameliorated conditions, combined with predictable (albeit low) winter showers have selected for relatively short-lived (3–10 yr) shrub lifestyles. The overwhelming majority of these species are leaf succulents (largely Mesembryanthema) with limited water storage capacity and shallow root systems (Von Willert *et al.*, 1992). This relatively benign environment enables regular germination and seedling establishment of perennials, thereby obviating the need for great longevity. The predictability of the moisture regime (Desmet & Cowling, in press) also enables succulents to maintain very small water storage capacity, leading to the widespread development of minutism (Midgley & van der Heyden, in press). The occasional years of lower-than-average rainfall cause widespread mortality (J  rgens *et al.*, 1997; R.M. Cowling, unpublished data) of these drought-intolerant plants (Von Willert *et al.*, 1985), and ensure that there is usually sufficient space for seedling recruitment. The result is rapid, at least for an arid land, population turnover and weakly structured, species-rich communities (Cowling *et al.*, 1994). But what is the link between regional diversity and these local-scale processes?

A possible explanation invokes differential rates of diversification. Lineages with the traits described above (the majority of Succulent Karoo species), have high numbers of sexually produced generations—attributes that would invariably lead to high rates of genetic recombination and rapid speciation (Rosenzweig,

1995). Moreover, for the Mesembryanthema at least, limited gene flow (in terms of seed and pollen dispersal) (Ihlenfeldt, 1994), peculiar genetic controls on morphology (Ihlenfeldt, 1994), and weakly persistent seed banks (Esler, in press), would enhance diversification. The rapid accumulation of taxa would result in a very fine-scale discrimination of habitats, such as Ihlenfeldt (1994) describes for *Argyroderma* and Hammer (1993) for *Conophytum* (both Mesembryanthema) in the Namaqualand-Namib Domain. The result is very species-rich landscapes with numerous highly localized habitat specialists, often capable of existing in small and isolated populations (Hammer, 1993; Ihlenfeldt, 1994; Cowling & Hilton-Taylor, in press). Clearly, landscapes with greater heterogeneity will support more species (Cowling *et al.*, 1997), but the capacity for fine-scale habitat discrimination of explosively diversifying lineages lends support to Rosenzweig's (1992, 1995) argument that habitat diversity is a co-evolved property of species diversity.

Predictable winter rain of the Succulent Karoo would also favour seasonally active geophytes, dependent as they are on regular moisture inputs to sustain storage organs and promote flowering. Recent research suggests that diversification of Namaqualand-Namib Domain geophytes has been promoted by pollinator-flower coevolution, e.g. Iridaceae and Geraniaceae with long-tongued flies, (Nemestrinidae) (Goldblatt, Manning & Bernhardt, 1995; Manning & Goldblatt, 1996), and Iridaceae, Liliaceae (*sensu lato*) and Orchidaceae with monkey beetles (Scarabaeidae: Hoplinii) (Picker & Midgley, 1996). Goldblatt & Manning (1996) suggest that edaphic specialization provided the initial impetus for genetic differentiation between founder and parent populations of the predominantly Succulent Karoo irid genus, *Lapeirousia*. Specialization to different pollinators (long-tongued flies) is invariably associated with parapatric species pairs in this genus.

In the Nama Karoo, community structure, diversity patterns and rates of diversification are not unusual for an arid land (Cowling & Hilton-Taylor, in press). Shrubs are mainly long-lived and well-dispersed and the short-lived component is comprised almost entirely of widespread, wind-pollinated, and wind- or animal-dispersed grasses with persistent seed banks (Hoffman & Cowling, 1987; Esler, in press). Shrub community structure is relatively stable and competition from this long-lived component (Yeaton & Esler, 1990) limits recruitment (Milton, 1995; Wiegand, Milton & Wissel,

1995). These factors would militate against rapid diversification and habitat specialization. Even in the environmentally heterogeneous escarpment zones, beta diversity is very low (Palmer & Cowling, 1994).

Global comparisons

Here we ask the question: is regional diversity and composition of growth forms in the Succulent Karoo unique when compared to other winter rainfall arid lands of the world? The following conclusions can be made.

- In the Succulent Karoo, total diversity and the diversity of leaf succulents shrubs at the regional scale, is without parallel. The only other part of the world with an even moderate concentration of non-halophytic leaf succulents is the Canary Islands (Jürgens, 1986). Interestingly, these species are concentrated in foggy, coastal environments which receive low but predictable rainfall (Shmida & Werger, 1992).
- The explosive diversification of certain Succulent Karoo genera, resulting in large species flocks, and the high level of generic endemism (Hilton-Taylor, 1996), is unique among the world's arid lands.

However, it is of interest that globally, winter-rainfall semi-arid regions are richer than those that receive summer rainfall. Cowling *et al.* (1992) showed that regions in the strongly winter-rainfall part of the fynbos biome have more than double the number of species than those that receive a substantial amount of summer rain. A similar pattern exists for the heath (kwongan) areas of southern Australia (Fox, 1994). In semi-arid areas, winter rainfall is more predictable and effective than summer rainfall (Noy-Meir, 1985; Hoffman & Cowling, 1987). These conditions may favour the persistence and diversification plants with short-lived lifestyles—leaf succulents in the Succulent Karoo, and annuals elsewhere (Shmida & Whittaker, 1979; Armesto & Vidiella, 1993; Rundel & Gibson, 1996). The low diversity and low local endemism of annuals in the Succulent Karoo (Desmet, 1996; Hilton-Taylor, 1996) remains a puzzling enigma.

Diversification in an arid world: is the Succulent Karoo unique?

There are two extra-tropical areas that are recognized as extraordinary centres of plant diversity and endemism: the mediterranean-climate regions of South

Africa and south-western Australia (Cowling *et al.*, 1996). Clearly, the Succulent Karoo is a third such region. Interestingly, the patterns and determinants of diversity in the Succulent Karoo bear a striking resemblance to those in the mediterranean-climate regions, even though the predominant vegetation (fynbos in South Africa and kwongan in Australia) is a dense, sclerophyllous and fire-prone shrubland. Both regions have very species-rich landscapes with high differentiation diversity and large numbers of habitat-specific, local endemics associated with a limited number of genera (Cowling *et al.*, 1996). Diversification is largely associated with fire-sensitive lineages (short generation times) that have limited gene flow. Thus, fire plays a key role in promoting diversification and the fine-scale partitioning of habitat space. We suggest that occasional droughts that interrupt the otherwise remarkably predictable rainfall regimes of the Succulent Karoo (Esler, Rundel & Cowling, in press), are analogous to fire in these mediterranean-climate shrublands in that they also promote generation turnover and population fragmentation.

There is no evidence that the massive diversification of the Succulent Karoo flora is the result of an unusually long and stable history. Like mediterranean shrublands, karroid vegetation became a widespread formation in south-western Africa only fairly recently, probably in the Pliocene (Deacon, Hendey & Lamprechts, 1983; Scott, Anderson & Anderson, 1997). As was the case globally, arid-adapted lineages occupied azonally dry sites since the late Cretaceous, and especially after the Oligocene (Axelrod, 1972; Smida, 1985), and many have persisted as paleoendemics (e.g. *Welwitschia mirabilis*). However, the explosive speciation of the Mesembryanthema in southern Africa (2000 species, 116 genera), largely concentrated in the Succulent Karoo, is a relatively recent phenomenon, and is probably unrivalled in angiosperms (Ihlenfeldt, 1994).

ACKNOWLEDGMENTS

Aspects of the research for this paper were funded by the Foundation for Research Development (Pretoria) and the Institute for Plant Conservation. We thank Steve Hammer, Craig Hilton-Taylor, Timm Hoffman, Norbert Jürgens, Sue Milton, Shirley Pierce, Mike Rosenzweig, Ernst van Jaarsveld, Jan Vlok and Graham Williamson for valuable discussion.

REFERENCES

- Armesto, J.J. & Vidiella, P.E. (1993) Plant life-forms and biogeographic relations in the flora of Lagunillas (30°S) in the fog-free Pacific coastal desert. *Ann. Mo. Bot. Gdns.* **80**, 499–511.
- Axelrod, D.I. (1972) Edaphic aridity as a factor in angiosperm evolution. *Am. Nat.* **106**, 311–320.
- Cowling, R.M., Esler, K.J., Midgley, G.F. & Honig, M.A. (1994) Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *J. Arid Environ.* **27**, 141–58.
- Cowling, R.M., Gibbs Russell, G.E., Hoffman, M.T. & Hilton-Taylor, C. (1989) Patterns of plant species diversity in southern Africa. *Biotic diversity in southern Africa. Concepts and conservation* (ed. by B.J. Huntley), pp. 19–50. Oxford University Press, Cape Town.
- Cowling, R.M. & Hilton-Taylor, C. (1994) Patterns of plant diversity and endemism in southern Africa: an overview. *Strelitzia*, **1**, 31–52.
- Cowling, R.M. & Hilton-Taylor, C. (in press) Plant biogeography, endemism and diversity. *The Karoo: ecological patterns and processes* (ed. by W.R.J. Dean and S.J. Milton). Cambridge University Press, Cambridge.
- Cowling, R.M. & Holmes, P.M. (1992) Flora and vegetation. *The ecology of fynbos. Nutrients, fire and diversity* (ed. by R.M. Cowling), pp. 23–61. Oxford University Press, Cape Town.
- Cowling, R.M., Holmes, P.M. & Rebelo, A.G. (1992) Plant diversity and endemism. *The ecology of fynbos. Nutrients, fire and diversity* (ed. by R.M. Cowling), pp. 62–112. Oxford University Press, Cape Town.
- Cowling, R.M., Richardson, D.M., Schulze, R.E., Hoffman, M.T., Midgley, J.J. & Hilton-Taylor, C. (1997) Species diversity at the regional scale. *Vegetation of southern Africa* (ed. by R.M. Cowling, D.M. Richardson and S.M. Pierce), pp. 447–473. Cambridge University Press, Cambridge.
- Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K. & Arianoutsou, M. (1966) Plant diversity in mediterranean-climate regions. *Trends Ecol. Evol.* **11**, 362–366.
- Danin, A. (1983) *Desert vegetation of Israel and Sinai*. Cana Publishing House, Jerusalem.
- Deacon, H.J., Hendey, Q.B. & Lamprechts, J.J.N. (eds) (1983) *Fynbos palaeoecology: a preliminary synthesis. South African National Scientific Programmes Report 75*. CSIR, Pretoria.
- Desmet, P.G. (1996) *Vegetation and restoration potential of the arid coastal belt between Port Nolloth and Alexander Bay, Namaqualand, South Africa*. MSc thesis, University of Cape Town.
- Desmet, P.G. & Cowling, R.M. (in press) The climate of the Karoo—a functional approach. *The Karoo: ecological patterns and processes* (ed. by W.R.J. Dean and S.J. Milton). Cambridge University Press, Cambridge.
- Esler, K.J. (in press) Plant reproductive ecology. *The Karoo: ecological patterns and processes* (ed. by W.R.J.

- Dean and S.J. Milton). Cambridge University Press, Cambridge.
- Esler, K.J., Rundel, P.W., and Cowling, R.M. (in press) The succulent karoo in a global context: plant structural and functional comparison with North American winter-rainfall deserts. *The Karoo: ecological patterns and processes*. (ed. by W.R.J. Dean and S.J. Milton). Cambridge University Press, Cambridge.
- Fox, M.D. (1994) Australian mediterranean vegetation: intra- and intercontinental comparisons. *Ecology and biogeography of mediterranean ecosystems in Chile, California and Australia* (ed. by M.T.K. Arroyo, M.D. Fox and P.H. Zedler), pp. 137–159. Springer-Verlag, Heidelberg.
- Gibbs Russell, G.E. (1987) Preliminary floristic analysis of the major biomes in southern Africa. *Bothalia*, **17**, 213–227.
- Goldblatt, P., Manning, J.C. & Bernhardt, P. (1995) Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa; floral divergence and adaptation for long-tongue fly pollination. *Ann. Mo. Bot. Gdns*, **82**, 517–534.
- Goldblatt, P. & Manning, J.C. (1996) Phylogeny and speciation in *Lapeirousia* subgenus *Lapeirousia* (Iridaceae: Izioidae). *Ann. Mo. Bot. Gdns*, **83**, 346–361.
- Gould, S.J. (1979) An allometric interpretation of species–area curves: the meaning of the coefficient. *Am. Nat.*, **114**, 335–43.
- Hammer, S.A. (1993) The genus *Conophytum*. Succulent Plant Publications, Pretoria.
- Hartmann, H. (1991) Mesembryanthema. *Contrib. Bol. Herb.*, **13**, 75–157.
- Hilton-Taylor, C. (1987) Phytogeography and origins of the Karoo flora. *The karoo biome: a preliminary synthesis. Part 2. Vegetation and history* (ed. by R.M. Cowling and P.W. Roux), pp. 70–95. *South African National Programmes Report* **142**. CSIR, Pretoria.
- Hilton-Taylor, C. (1994) The Kaokoveld. Namibia and Angola. *Centres of plant diversity. A guide and strategy for their conservation. Vol. 1: Europe, Africa, South West Asia and the Middle East*. (ed. by S.D. Davis, V.H. Heywood and A.C. Hamilton), pp. 201–203. IUCN Publications Unit, Cambridge.
- Hilton-Taylor, C. (1996) Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. *The biodiversity of African plants*. (ed. by L.J.E. van der Maesen, X.M. van der Burght and J.M. van Medenbach de Rooy), pp. 58–72. Kluwer, Dordrecht.
- Hilton-Taylor, C. & Le Roux, A. (1989) Conservation status of the fynbos and karoo biomes. *Biotic diversity in southern Africa. Concepts and conservation* (ed. by B.J. Huntley), pp. 202–223. Oxford University Press, Cape Town.
- Hoffman, M.T. & Cowling, R.M. (1987) Plant physiognomy, phenology and demography. *The karoo biome: a preliminary synthesis. Part 2. Vegetation and history* (ed. by R.M. Cowling and P.W. Roux), pp. 1–34. *South African National Programmes Report*, **142**. CSIR, Pretoria.
- Ihlenfeldt, H-D. (1994) Diversification in an arid world: the Mesembryanthemaceae. *Ann. Rev. Ecol. Syst.*, **25**, 521–546.
- Jürgens, N. (1986) Untersuchungen zur ökologie sukkulenter pflanzen des südlichen Afrika. *Mitt. Inst. Allgem. Bot., Hamb.*, **21**, 139–365.
- Jürgens, N. (1991) A new approach to the Namib Region. I: Phytogeographic subdivision. *Vegetatio*, **97**, 21–38.
- Jürgens, N., Gunster, A., Seely, M.K. & Jacobsen, K.M. (1997) Desert. *Vegetation of southern Africa*. (ed. by R.M. Cowling, D.M. Richardson and S.M. Pierce), pp. 189–215 Cambridge University Press, Cambridge.
- Le Houërou, H.J. (1986) The desert and arid zones of North Africa. *Hot deserts and arid shrublands. Vol. B*. (ed. by M. Evenari, I. Noy-Meir and D.W. Goodall), pp. 101–148. Elsevier, Amsterdam.
- Le Houërou, H.N. (1992) Outline of the biological history of the Sahara. *J. Arid Environ.*, **22**, 3–30.
- Le Houërou, H.N. & Boulos, L. (1991) Bioclimatic and phytogeographic characteristics of the arid rangelands of northern Africa and the Near East. *Proceedings of the IVth International Rangeland Congress*, Montpellier, France, pp. 536–543.
- Manning, J.C. & Goldblatt, P. (1996) The *Proseca peringuyei* (Diptera: Nemenstrinidae) pollination guild in southern Africa: long-tongued flies and their tubular flowers. *Ann. Mo. Bot. Gdns*, **83**, 67–86.
- Midgley, G. & van der Heyden, F. (in press) Form and function in perennial plants. *The Karoo: ecological patterns and processes* (ed. by W.R.J. Dean and S.J. Milton). Cambridge University Press, Cambridge.
- Milton, S.J. (1995) Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *J. appl. Ecol.*, **32**, 145–156.
- Mulroy, T.W., Rundel, P.W. & Bowler, P.A. (1979) The vascular flora of Punta Banda, Baja California Norte, Mexico. *Madrono*, **26**, 69–90.
- Nordenstam, B. (1974) The flora of the Brandberg. *Dinteria*, **11**, 3–67.
- Noy-Meir, I. (1985) Desert ecosystem structure and function. *Hot deserts and arid shrublands. Vol. A* (ed. by M. Evenari, I. Noy-Meir and D.W. Goodall), pp. 93–104 Elsevier, Amsterdam.
- Olivier, J. (1995) Spatial distribution of fog in the Namib. *J. Arid Environ.*, **29**, 129–138.
- Palmer, A.R. & Cowling, R.M. (1994) An investigation of topo-moisture gradients in the eastern Karoo, South Africa, and the identification of factors responsible for species turnover. *J. Arid Environ.*, **26**, 135–147.
- Picker, M.D. & Midgley, J.J. (1996) Pollination by monkey beetles (Coleoptera: Scarabaeidae: Hopliini): flower and colour preferences. *Afr. Entomol.*, **4**, 7–14.
- Raven, P.H. & Axelrod, D.I. (1978) Origin and relationships of the California flora. *Univ. Calif. Publ. Bot.*, **72**, 1–134.
- Robinson, E.R. (1978) Phytogeography of the Namib Desert of South West Africa (Namibia) and its significance to discussions of the age and uniqueness of this desert. *Palaeoecology of Africa*, **10**, 67–74.

- Rosenzweig, M.L. (1992) Species diversity gradients: we know more and less than we thought. *J. Mammology*, **73**, 715–30.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rundel, P.W. & Gibson, A.C. (1996) *Ecological communities and processes in a Mohave Desert ecosystem: Rock Valley, Nevada*. Cambridge University Press, Cambridge.
- Rutherford, M.C. & Westfall, R.H. (1986) Biomes of southern Africa—an objective categorization. *Mem. Bot. Surv. S. Afr.* **54**, 1–98.
- Schulze, R.E. & McGee, O.S. (1978) Climatic indices and classifications in relation to the biogeography of southern Africa. *Biogeography and ecology of southern Africa* (ed. by M.J.A. Werger), pp. 11–52. Junk, The Hague.
- Scott, L., Anderson, H.M. & Anderson, J.M. (1997) Vegetation history. *Vegetation of southern Africa* (ed. by R.M. Cowling, D.M. Richardson and S.M. Pierce), pp. 62–84. Cambridge University Press, Cambridge.
- Shmida, A. (1985) Biogeography of the desert flora. *Hot deserts and arid shrublands. Vol. A* (ed. by M. Evenari, I. Noy-Meir and D.W. Goodall), pp. 23–78. Elsevier, Amsterdam.
- Shmida, A. & Whittaker, R.H. (1979) Convergent evolution of deserts in the Old and New Worlds. *Werden und Vergehen von Pflanzengesellschaften* (ed. by O. Wilmanns & R. Tuxen), pp. 437–450. J. Kramer, Vaduz.
- Shmida, A. & Werger, M.J.A. (1992) Growth form diversity on the Canary Islands. *Vegetatio*, **102**, 183–199.
- Smith, G.F., Hobson, S.R., Meyer, N.L., Chesselet, P., Archer, R.H., Burgoyne, P.M., Glen, H.F., Herman, P.P.J., Retief, E., Smithies, S.J., van Jaarsveld, E.J. & Welman, W.G. (1993) Southern African succulent plants—an updated synopsis. *Aloe*, **30**, 32–74.
- Van Jaarsveld, E. (1987) The succulent riches of South Africa and Namibia. *Aloe*, **24**, 45–92.
- Von Willert, D.J., Brinckmann, E., Schleiter, B. & Eller, M.B. (1985) Availability of water controls crassulacean acid metabolism in succulents of the Richtersveld (Namib desert, South Africa). *Planta*, **164**, 45–55.
- Von Willert, D.J., Werger, M.J.A., Brinckmann, E., Ihlenfeldt, H-D. & Eller, B.M. (1992) *Life strategies of succulents in deserts: with special reference to the Namib Desert*. Cambridge University Press, Cambridge.
- Walter, H. (1986) The Namib Desert. *Hot deserts and arid shrublands. Vol. B* (ed. by M. Evenari, I. Noy-Meir and D.W. Goodall), pp. 245–282. Elsevier, Amsterdam.
- Werger, M.J.A. (1978a) The Karoo-Namib Region. *Biogeography and ecology of southern Africa* (ed. by M.J.A. Werger), pp. 231–299. Junk, The Hague.
- Werger, M.J.A. (1978b) Biogeographical divisions of southern Africa. *Biogeography and ecology of southern Africa* (ed. by M.J.A. Werger) pp. 145–170. Junk, The Hague.
- Werger, M.J.A. (1986) The Karoo and Southern Kalahari. *Hot deserts and arid shrublands. Vol. B* (ed. by M. Evenari, I. Noy-Meir and D.W. Goodall), pp. 283–360. Elsevier, Amsterdam.
- White, F. (1976) The vegetation map of Africa—the history of a completed project. *Boissiera*, **24**, 659–666.
- White, F. (1983) *The vegetation of Africa*. UNESCO, Paris.
- Wiegand, T., Milton, S.J. & Wissel, C. (1995) A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. *Ecology*, **76**, 2005–2221.
- Williams, O.B. & Calaby, J.H. (1985) The hot deserts of Australia. *Hot deserts and arid shrublands. Vol. A* (ed. by M. Evenari, I. Noy-Meir and D.W. Goodall), pp. 269–312. Elsevier, Amsterdam.
- Williamson, M. (1988) Relationship of species number to area, distance and other variables. *Analytical biogeography. An integrated approach to the study of animal and plant distributions* (ed. by A.A. Myers and P.S. Giller), pp. 91–115. Chapman & Hall, London.
- Yeaton, R.I. & Esler, K.J. (1990) The dynamics of a succulent karoo vegetation, a study of species association and recruitment. *Vegetatio*, **88**, 103–113.
- Zar, J.H. (1984) *Biostatistical analysis*. Prentice-Hall, New York.