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Biogeography

Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa

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Key words: dune, gravel pavement, growth form diversity, leaf-succulent plants, rock outcrop, Succulent Karoo

Abstract

We examined patterns of richness and endemism in relation to phylogeny (family membership), growth form and habitat in the flora of an arid (<60 mm annual rainfall), sandy coastal belt between Port Nolloth and Alexander Bay on the north-west coast of Namaqualand, South Africa. This region forms part of the species-rich Succulent Karoo biome. In an area of 750 km^2, 300 plant species were recorded with 24% endemnicity. This level of diversity and endemism is exceptionally high for a desert region. Plant distribution is strongly influenced by habitat type. Diversity, especially of endemic species, was concentrated on rocky or unusual (lag-gravel pavements) habitats. Endemics were not random phylogenetic nor biological assemblages. Dwarf leaf-succulent shrubs, especially Mesembryanthemaceae, were significantly over-represented amongst the endemic component. The results are discussed in terms of a model for plant diversification in an arid environment with relatively predictable sources of moisture.

Introduction

Namaqualand, a winter-rainfall desert region of north-western South Africa (Cowling et al. 1999), forms part of the Namaqualand-Namib phytogeographically Domain of the Greater Cape Flora (Jürgens 1991). At the biome scale, it is included in the Succulent Karoo, a region characterized by low but predictable winter rain, and the dominance among growth forms of dwarf to low, leaf-succulent shrubs (Rutherford & Westfall 1986; Milton et al. 1997; Desmet & Cowling 1998). In comparison to other arid lands of the world, the Succulent Karoo is exceptionally species-rich, both at the local and regional scales (Cowling et al. 1989; 1999). The region includes some 4849 species of vascular plants (40% endemic) in an area of 112 212 km^2 (Hilton-Taylor 1996). At the regional scale (10^1–10^6 km^2), the Succulent Karoo supports nearly four times as many species as the winter-rainfall deserts of North America (Cowling et al. 1998).

The Succulent Karoo has an unusual flora, both in terms of taxonomic composition and growth form mix (Cowling & Hilton-Taylor 1994; in press; Hilton-Taylor 1996). Flora attributes not shared with other desert regions include: the low numbers of tall shrubs and grasses; the large numbers of leaf-succulent species, especially in the Mesembryanthemaceae or Mesembryanthema (Aizoaceae, sensu Bittrich & Hartmann 1988) (ca. 850 spp. in 100 genera) and Crassulaceae (171 spp. in 4 genera); and a great diversity of geophytes, especially in the Iridaceae (334 spp. in 28 genera), Hyacinthaceae (163 spp. in 23 genera), and Oxalidaceae (114 spp. in *Oxalis*). Some genera with these growth forms have undergone spectacular diversification, e.g. for leaf succulents: *Conophytum* (116 spp., Mesembryanthemaceae), *Ruschia* (ca. 100 spp., Mesembryanthemaceae), and *Crassula* (110 spp., Crassulaceae); and for geophytes: *Oxalis* (114 spp., Oxalidaceae) and *Eriospermum* (65 spp., Eriospermaceae). The area also supports about 700 species of dwarf, contracted succulents or stone plants (especially Mesembryanthemaceae) (Milton et al. 1997), a growth form unique to the Succulent Karoo. Ihlenfeldt (1994) describes the recent and ex-

plosive diversification in the Mesembryanthemaceae as an event unrivalled among flowering plants.

The Succulent Karoo, and Namaqualand in particular, includes many recently evolved, locally endemic or range-restricted plant species (Cowling & Hilton-Taylor 1994; in press; Hilton-Taylor 1996). Species endemic to the biome are over-represented among families that are either predominantly succulent (Mesembryanthemaceae, Crassulaceae, Asclepiadaceae, Aloaceae) or predominantly geophytic (Iridaceae, Eriospermaceae, Amaryllidaceae and Oxalidaceae) (Hilton-Taylor 1996). There is some evidence that most endemics are habitat (chiefly edaphic) specialists, and that diversification has been strongly associated with edaphic specialization (Manning & Goldblatt 1996; Cowling et al. 1998a). However, more data are required on the composition and characteristics of floras, correlates of range size and patterns of diversity in relation to habitats, before meaningful generalizations can be made.

This study comprises an analysis of the flora in an arid (<60 mm yr^{-1}) area of north-western Namaqualand. Owing to restrictions imposed by the diamond-mining industry, areas such as this have not been thourghly explored by botanists, let alone studied in any detail. Since this area represents the extreme-arid part of the strongly winter-rainfall Namaqualand-Namib Domain, such an analysis can provide novel insights regarding the biodiversity patterns in the Succulent Karoo. We asked the following questions:

- How large is the flora in relation to other areas with similar environments?
- What is the family-level and growth form composition of the flora?
- What are the phylogenetic, habitat and growth form correlates of restricted range size?
- What are the patterns of diversity on the major habitats?

We discuss the results in terms of a descriptive model of diversification in the Succulent Karoo (Cowling et al. 1998).

The study area

Physiography

The study site is located on the north-west coast of South Africa (Figure 1). It covers a narrow band approximately 10 km wide and 80 km long on the coast between Port Nolloth (29°15′ S, 16°53′ E) in the south, and Alexander Bay (28° 36′ S, 16°29′ E) in the north, an area of approximately 750 km^2. For the most part, the area is a featureless, gently undulating and dune-covered expanse generally referred to as the Sandveld (Le Roux & Schelpe 1988). Halfway between Alexander Bay and Port Nolloth the Sandveld is bisected by the 'canyon' of the Holgat River, which has its catchment in the south-western mountains of the Richtersveld. This canyon, and the Buchu Twins (162 m), a pair of inselbergs (referred to locally as koppies) 30 km south of Alexander Bay, are the only major topographic relief in this coastal region. To the north of the koppies, on the southern bank of the lower Orange River valley, the dunes are reduced to a thin transgressive sand sheet over the underlying schistose bedrock. Here, the landscape comprises low, exposed bedrock ridges and koppies with a rudimentary pebble pavement or lag-gravel pavement in places. To the south-east of Alexander Bay, there is a small lichen field (ca. 120 ha.). It owes its existence to the unique combination of gypsum soils, relief-induced high incidence of fog, and most importantly, its location in a gap in the wind channels and resultant mobile sand sheets that otherwise characterize the local environment (Jürgens & Niebel 1991, 1995; Desmet 1996).

The coastline of the study area lacks any significant embayments or estuaries. Low-lying pans along the coast are evidence of palaeo-estuarine systems. South-east of the Buchu Twins, lies a group of low granite outcrops which, except for their very tops, are covered with sand and are barely discernible. The coastal belt south of the Holgat River is devoid of any significant topographic features and comprises gently undulating red dunes and low, dune covered ridges. Port Nolloth itself is located on a filled late-Quaternary palaeo-estuary. Consequently, there are a number of saline seeps and pans in the dune landscape around the town. A notable feature of this stretch of coast is the diamond mining activity and a large white, active dune field some 5 km to the north-east of Port Nolloth.

Climate

The area is located within a region that experiences a relatively cool desert climate with frequent fog. The low incidence of rainfall is controlled by the South Atlantic Ocean Anticyclone. The predominantly southerly winds associated with this high-pressure cell cause upwelling of the cold Benguela Current. This, in turn, cools and stabilizes the near surface air mass, re-

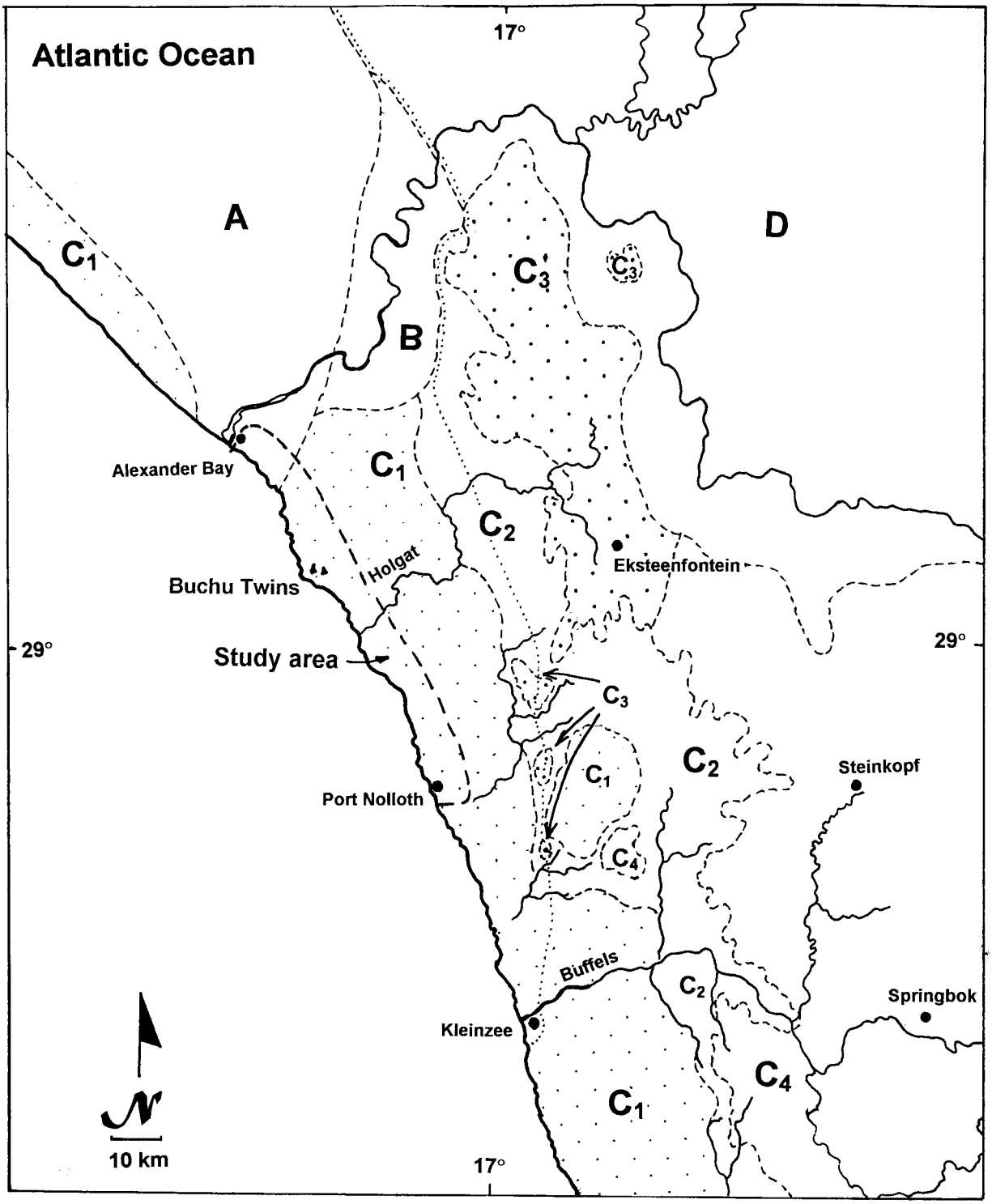

Figure 1. Map showing the geographical and phtyogeographical location of the study area. Phytogeographic zones adapted from Jürgens (1991) are: (A) Southern Namib Domain. (B) Western Gariep Centre of the Southern Namib Domain. (C) Namaqualand Domain comprising: (C1) Sandveld District; (C2) Lowland Succulent Karoo District; (C3) Richtersveld District or Gariep Centre; and, (C4) Namaqualand Rocky Hills District. (D) Eastern Gariep Centre of the Namib Subdomain within the Namaqualand Domain. Boundary of the coastal fog zone of endemism represented by dotted line.

duces the potential for rainfall and maintains an almost isothermal atmosphere over the Namaqualand coast (Preston-Whyte & Tyson 1988).

The mean total annual rainfall measured at Port Nolloth and Alexander Bay is 63 mm and 41 mm, respectively (Schultze 1965). Rainfall events tend to be distributed between April and August and peak during May, June and July for all stations, and generally arrive as soft, gentle rains. The highest mean monthly rainfall does not exceed 10 mm. Rainfall decreases from south to north. Rainfall variability is such that there is never a year without some rainfall. Thus, the occurrence of severe drought (i.e. years with no rainfall) is a very rare phenomenon. Extreme events such as thunder-showers, cloud-bursts, snow and hail are non-existent.

The low rainfall is offset by frequent advective sea fog. The average total number of days per annum during which fog is recorded at Port Nolloth is 148, or 41% of the total. As a result, the sunshine duration averages less than 70% of the possible total and this has an ameliorating effect on the climate (Burns 1994). Alexander Bay airport, 10 km inland from the coast, experiences on average 67.1 days of fog a year or 18% of total days. The difference in fog days at both stations is due to the location of the recording stations relative to the coast rather than higher or lower fog incidence due to latitudinal variation in fog intensity. Fog occurrence at both stations peaks in late summer to autumn. Fog is a significant source of water in the desert environment (Schultze & McGee 1978), and also a far more predictable source of moisture than rainfall (Pietruszka & Seely 1985; Desmet & Cowling 1998). Frequent, heavy dews also characterize this coastal area. This is also a potentially significant source of moisture (Noy-Meir 1973; Desmet 1996; Desmet & Cowling 1998).

The Atlantic Ocean has a significant moderating effect on the coastal temperature regime. Minimum temperatures are particularly stable and tend to follow ocean surface temperatures. In contrast, the diurnal maxima can vary considerably and occasionally can rise to extremely high values ($>30\,^{\circ}$C), primarily as a result of berg or föhn-like winds. Diurnal temperature variation is greatest in winter when nocturnal offshore air movement is dominant. Alexander Bay affords an almost perfect example of land-sea breezes in winter (Schultze 1965). Wind is a very important controlling variable in determining plant life history strategies, adaptations and distribution along the coast of the Namaqualand-Namib Domain (Desmet 1996). High-energy southerly winds during the arid summer months determine the direction of sand movement along the coast

Phytogeography

The study area straddles two floral districts (Jürgens 1991) (Figure 1). These are: Diamond Area No. 1 of southern Namibia or the Southern Namib District (previously the winter rainfall area of the Namib Domain (Werger 1978)); and the Namaqualand Sandveld District (previously the north-western portion of the Western Cape Domain (Werger 1978)). To the east of these two districts lies the East Gariep Center of endemism (Jürgens 1991). This region, centered on the Richtersveld mountains, supports an extremely diverse and endemic-rich flora (Cowling & Hilton-Taylor 1994; Hilton-Taylor 1996).

Methods

A plant species list for the study area was compiled based on collections made by the primary author over a two-year period. Only higher plants were collected. Voucher specimens of Mesembryanthemaceae *incertae* reside in the Bolus Herbarium (PGD collection numbers). Nomenclature is according to Arnold & De Wet (1993). Nomenclature of the Mesembryanthemaceae follows the Bolus Herbarium.

Plant growth forms were classified into seven broadly-defined categories: (1) dwarf (<0.3 m) leaf-succulent shrubs; (2) non-dwarf leaf-succulent shrubs; (3) stem succulents including pachycauls; (4) non-succulent shrubs; (5) graminoids including all grass-like growth forms; (6) annuals and forbs; and, (7) geophytes. All species were classified according to their occurrence on seven broadly-defined habitat types or combinations thereof: (1) disturbed sites (e.g. road verges); (2) dunes only; (3) dunes and koppies/rock outcrops combined; (4) dunes and lag-gravel pavements combined; (5) saline habitats (conductivity >2 mS); (6) koppies/rock outcrops only; and, (7) lag-gravel pavements only. Lag-gravel pavements (desert pavement) are common geological phenomena in deserts. In the context of the Succulent Karoo, however, lag-gravel pavements must be considered unusual or azonal habitat. Here lag-gravel pavements, formed either through aeolean or fluvial erosion, are a rare habitat type with respect to total area covered relative to other broad habitat types although they

are encountered across the biome. The soil conditions in this habitat can differ significantly from those for the surrounding habitats (e.g. Von Willert et al. 1992; Schmiedel & Jürgens 1999). Most interestingly, though, throughout the Succulent Karoo this habitat supports a diverse and unique flora restricted to only this habitat (Schmiedel & Jürgens 1999; P. Desmet unpublished data). This flora is characterized by a diversity of extremely contracted succulent growth form types amongst the endemic component (P. Desmet unpublished data).

Species were also classified as being either endemic or non-endemic. A species was considered endemic if its known distribution was restricted to the area between Kleinzee, in the south, Lüderitz, in the north, and to the west of the western Richtersveld Mountains, in the east. This region comprises the southern Namib coastal fog zone. Chi-squared tests were used to test the null hypothesis that endemic and non-endemic species are distributed in the same frequency with respect to categories of phylogeny (family membership), growth form, and habitat.

Results

Three-hundered species from 40 families were recorded in the study area (Table 1), 24% of which are endemic according to the criterion given above. The Asteraceae, Mesembryanthemaceae and Crassulaceae dominate the flora of the study area. The Mesembryanthemaceae are significantly over-represented in terms of their endemic species component (50%, Table 2). However, the Asteraceae (14%), Poaceae (6%) and Aizoaceae *sensu stricto* (13%) are significantly under-represented. Crassulaceae (37%) also show high levels of endemism; however, this value is not significantly different from that of the flora as a whole, excluding Crassulaceae.

Succulent growth forms dominate the flora of the study area (Table 3), both in terms of composition (44%) and also the endemic component (Figures 2a and 3a). By comparison, non-succulent shrubs comprise only 19% of the flora. Succulent growth forms are also over-represented among endemics, whereas the reverse holds for other growth forms (Figure 2). Within the succulent growth form group, dwarf leaf-succulents show very high levels of endemism (Figure 3b). These dwarf leaf-succulents are located primarily on hard (viz. koppies and rocky outcrops) or unusual (lag-gravel pavements) substrata (Figures 2b and 3c). Tree growth forms or phanerophytes are entirely absent from the flora. These growth forms are restricted to riparian habitats along the banks of the Orange River, which were not included in the study area.

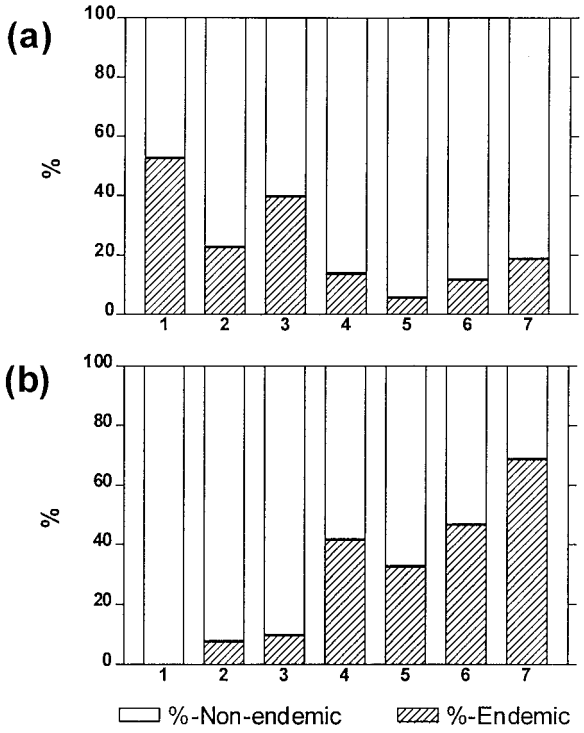

Figure 2. Composition of endemics according to: (a) growth form as follows: (1) dwarf leaf-succulents; (2) non-dwarf leaf-succulent shrubs (>0.3 m high); (3) stem succulents including pachycauls; (4) non-succulent shrubs; (5) graminoids including all grass-like growth forms; (6) annuals and forbs; and, (7) geophytes. (b) Habitat type as follows: (1) disturbed sites (e.g. road verges); (2) dunes only; (3) dunes and koppies/rock outcrops; (4) dunes and lag-gravel pavements; (5) saline habitats; (6) koppies/rock outcrops only; and, (7) lag-gravel pavements only.

High species density (Table 4) and high levels of endemism (Figure 3b) are concentrated on hard, stable substrata (e.g. rock outcrops). Dune habitats occupy the largest proportion of the study area and consequently, have the largest number of species (Table 4). This habitat type, however, has the lowest species to area ratio and endemics are significantly under-represented. Koppies and rocky outcrops support the greatest diversity of plants when expressed in terms of species per unit area (Table 4). These habitats are rich in species restricted to these habitats (Figure 3b). Also, they share a significant number of species with the surrounding general matrix or dune habitat (Table 4), whereas the reverse does not hold for the dune

Table 1. A list of plant families and the number of species represented within the study area.

	Family	Species		Family	Species
1	Asteraceae	53	22	Colchicaceae	3
2	Mesembryanthemaceae	47	23	Neuradaceae	3
3	Crassulaceae	28	24	Sterculiaceae	3
4	Poaceae	17	25	Oxalidaceae	2
5	Aizoaceae (sensu stricto)	15	26	Acanthaceae	1
6	Scrophulariaceae	14	27	Anacardiaceae	1
7	Geraniaceae	11	28	Boraginaceae	1
8	Fabaceae	10	29	Campanulaceae	1
9	Euphorbiaceae	9	30	Caryophyllaceae	1
10	Selaginaceae	9	31	Curcurbitaceae	1
11	Asclepiadaceae	7	32	Illecebraceae	1
12	Asparagaceae	7	33	Labiatae	1
13	Asphodelaceae	7	34	Plumbaginaceae	1
14	Chenopodiaceae	7	35	Polygalaceae	1
15	Iridaceae	7	36	Portulacaceae	1
16	Hyacinthaceae	6	37	Rubiaceae	1
17	Zygophyllaceae	5	38	Santalaceae	1
18	Amaryllidaceae.	4	39	Tecophilaeaceae	1
19	Solanaceae	4	40	Thymelaeaceae	1
20	Apiaceae	3	41	unknown	4
21	Brassicaceae	3			

Table 2. The ten largest families in the flora with the percentage of each family endemic to the region. Chi-squared Test poses the null hypothesis that the frequency of endemic species per family is similar to that for the entire flora minus that family (independent sample).

Position	Family	Number of species	% endemic	χ^2
	Total flora	299	24	
1	Asteraceae	51	14	11.09^{**}
2	Mesembryanthemaceae	46	50	26.10^{***}
3	Crassulaceae	27	37	3.21^{NS}
4	Poaceae	17	6	5.57^{*}
5	Aizoaceae (sensu stricto)	15	13	0.93^{NS}
6	Scrophulariaceae	14	14	0.73^{NS}
7	Geraniaceae	11	45	–
8	Fabaceae	9	30	–
9	Euphorbiaceae	9	22	–
10	Selaginaceae	9	11	–

Significance levels with Yates correction: *** <0.001, ** <0.01, NS not significant, – sample too small for analysis.

Table 3. Distribution of species between different growth form types.

	Growth form description	Number of species	% of flora
1.	Dwarf leaf-succulent	49	17
2.	Shrub leaf-succulent (non-dwarf)	58	19
3.	Stem succulent	25	8
	All succulent growth forms	132	44
4.	Non-succulent shrub	58	19
5.	Graminoid	17	6
6.	Annual/forb	51	17
7.	Geophyte	42	14

matrix. The lag-gravel pavements have disproportionately high numbers of endemic species (Figure 3b), but share an expected proportion of species with the dune flora to the south (Table 4).

A comparison of the proportional representation of the seven growth-forms in each of the three major habitat types (Figure 3a) shows that dwarf leaf-succulents tend to be concentrated on the hard substrata. This trend explains the observed patterns in endemism between habitats (Figure 3b). All three habitats have similar proportions of non-dwarf leaf-succulent and non-succulent shrubs. However, dune habitats have proportionately more annuals, forbs and geophytes. A comparison of the endemic component in each habitat (Figure 4) highlights an interesting pattern in the flora of the lag-gravel pavements. Endemics are more evenly distributed between growth form types and do not show the disproportionate over-representation in the dwarf leaf-succulent component characteristic of the flora as a whole.

Discussion

Owing to the lack of data from environmentally similar areas, it was not possible to assess the relative richness of the study area in terms of a species-area relationship. The only foggy desert area suitable for comparison with regards to regional diversity is the 70 000 km^2 winter-rainfall desert of North Africa's Atlantic seaboard. This area, which comprises a narrow (25–50 km wide) and mainly sandy, fog-affected desert, supports 450 species of vascular plants (Le Houèrou 1992). The fact that the study area supports two-thirds the number of species recorded in this region – an area 100 times its size – gives some idea of its relative diversity. It must be borne in mind that this diversity is packed into an area of low environmental heterogeneity where heterogeneity is expressed in terms of standard environmental correlates of diversity such as topographical range, aspect and soil-type diversity (Desmet 1996). Similarly, the Namibian portion of the Namib Desert has almost 200 times as many species as similar-sized areas of the Saharan Desert (Cowling et al. 1998). The relatively high diversity of both the study area and the Namibian Namib is largely the result of massive radiation, in the winter-rainfall zone, of leaf-succulent lineages, namely the Mesembryanthemaceae, Crassulaceae and Asteraceae (*Senecio* and *Othonna*) (see also Robinson 1978). The endemic component of the flora, characterized by dwarf leaf-succulents in the Mesembryanthemaceae and to a lesser extent, Crassulaceae, epitomizes this radiation. The dominance (Desmet 1996) and high diversity of leaf succulents is a unique feature of southern African winter-rainfall desert regions (Jürgens 1986).

The flora of the study area is typical of the Succulent Karoo's Namaqualand-Namib Domain (Cowling & Hilton-Taylor 1994; 1998; Hilton-Taylor 1996). Members of the Asteraceae, Mesembryanthemaceae and Crassulaceae dominate the flora. The family-level composition of the flora shows a strong affinity with that of the Cape Floristic Region (Bond & Goldblatt 1984; Cowling & Holmes 1992). The high rank in the flora of Mesembryanthemaceae, Scrophulariaceae, Geraniaceae, Selaginaceae and Iridaceae supports the currently held view (Jürgens 1991) that the flora of the Succulent Karoo forms part of a Greater Cape Flora rather than part of the Palaeotropical Kingdom. Very few species encountered in the study area occur outside the winter rainfall boundaries of the Greater Cape

Table 4. The number of species encountered in each of the three major habitat types. Number of species represents all species restricted to each habitat plus those shared (% shared) with the other major habitat types. Chi-squared Test poses the null hypothesis that the frequency of species in a specific habitat shared with other habitats is the same for all habitats. Species: area is expressed as on a log-log basis.

	Habitat type	Area (km^2)	Number of Species (%)	χ^2	Spp./area
1.	Dunes	683	198 (21)	5.501 NS	0.81
2.	Lag-gravel pavements	58	61 (20)	1.067 NS	1.01
3.	Koppies & rocky outcrops	3	63 (46)	15.653***	3.77
4.	Total	744	281 (15)	–	0.85

***: $p < 0.0001$, NS: not significant.

Floral Region. Species that do, however, are nearly all associated with disturbed or saline habitats.

Diversity in the study area shows strong patterns in relation to the examined variables. As is the case for the entire Succulent Karoo flora (Hilton-Taylor 1996), the Mesembryanthemaceae are massively over-represented in terms of their endemic component. Likewise, rocky or unusual habitats support the majority of the endemic flora, and within this endemic flora the dwarf leaf-succulent growth form dominates. Species that are encountered in both the lag-gravel pavements and/or rocky habitats, as well as in the dune habitat are generally widespread, non-endemic species. Rocky and lag-gravel pavement habitats support a unique flora restricted to these habitats plus species which also grow in the surrounding matrix (dune) habitat. However, the reverse does not hold for the matrix. These patterns are not restricted to the study area; anecdotal evidence suggests similar patterns for the Knersvlakte endemic centre to the south of the study area (Jürgens 1986), the Gariep region to the east (Jürgens 1991), and the winter-rainfall Namib Desert in Namibia, to the north (Williamson 1997). Therefore, we generalize that for the Namaqualand-Namib Domain, an endemic species will most likely be restricted to stable, rocky or unusual (e.g., lag-gravel pavement) substrata. The odds are also high that these species will be dwarf succulent members of the Mesembryanthemaceae. The under-representation of geophytes among endemics within the study area differs from the pattern recorded for the Succulent Karoo as a whole (Cowling & Hilton-Taylor 1994), and probably reflects the extreme aridity of the region.

Species are not distributed uniformly or randomly between habitats. Diversity is concentrated on stable substrata, namely the rock habitats, and unusual or azonal habitats such as lag-gravel pavements. Why is this so? These habitats comprise plant niches that are fundamentally different from those of the surrounding dunes (Shmida 1985). Rocky substrata are more resistant to aeolian and fluvial erosion and provide protection against sand abrasion and sun. Furthermore, owing to high runoff, plants growing amongst rocks may receive more rain-fed, but especially more fog- and dew-fed moisture than dune habitats; however, the skeletal soils on rocky outcrops are edaphically xeric habitats due to shallow rooting depth and poor soil water-holding capacity (Porembski et al. 1996). Thus, in arid areas rocky sites are stable, protective habitats, but prone to extremes of water availability being waterlogged during precipitation events and drought-prone otherwise. Substratum stability is partly the reason why dwarf succulents are concentrated in rocky areas. Small perennials with small rooting systems cannot survive in 'mobile' (erosionally active) landscapes (e.g., dune habitat). High species diversity in desert rocks is discussed in more detail by Danin (1978, 1996, 1997).

The lag-gravel pavement endemics of the western Gariep Centre are restricted to this habitat in the Lower Orange River Valley. None of these plants are encountered on rocky habitats to the south such as the Buchu Twins or the Holgat River Canyon. Lag-gravel pavements are an ecologically extreme and unusual habitat in the Succulent Karoo, supporting many range-restricted and specialized species (Jürgens 1986; Schmiedel & Jürgens 1999; P. Desmet unpublished data).

Our results are consistent with the model of diversification in the Succulent Karoo proposed by Desmet et al. (1998). Dwarf and relatively short-lived succulent lineages, which are also prone to drought-induced

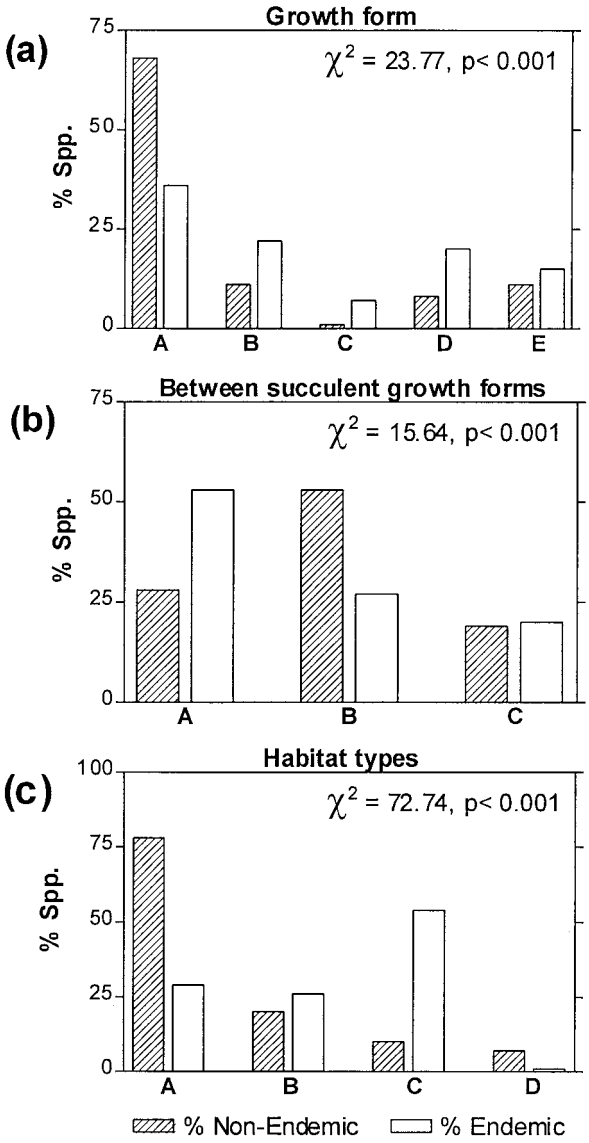

Figure 3. Percentage endemism within different growth forms and habitat types expressed as% endemism relative to the entire endemic flora. (a) Growth form vs. endemism: A all succulent growth-forms, B non-succulent shrubs, C graminoids, D forbs and annuals, E geophytes. (b) Within succulent growth forms: A dwarf leaf-succulents, B leaf-succulents, C stem succulents. (c) Across major habitat types: A dunes, B koppies and rock outcrops, C lag-gravel pavements, D others (viz. disturbed and halophytic habitats). Chi-squared Test poses the null hypothesis that endemics occur in the same frequency as non-endemics across the different categories.

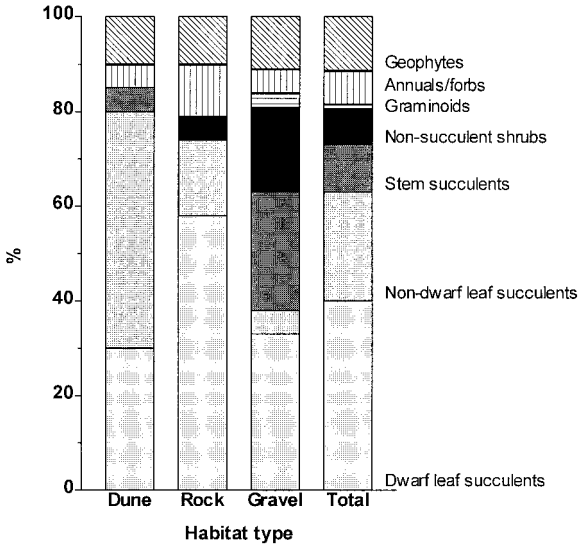

Figure 4. Proportional representation of the seven growth form types within the endemic component of the three major habitat types: Dunes; Rock – koppies and rocky outcrops; Gravel – lag-gravel pavements; and, total flora.

population crashes, have subdivided the landscape at a very fine-scale. Poorly dispersed lineages in the Mesembryanthemaceae (Ihlenfeldt 1994) have undergone a greater degree of ecological diversification, leading to more pronounced habitat specialization, than better dispersed lineages in, for example, the Crassulaceae and Asteraceae. Short-lifespan, the unusual feature of Succulent Karoo succulent lineages (Von Willert et al. 1992; Jürgens et al. 1999) is probably a response to the region's relatively predictable rainfall. There has been selection for gap replacement by sexual reproduction rather than persistence (Cowling et al. 1998). Owing to short generation times and, especially in the poorly dispersed and insect-pollinated Mesembryanthemaceae (Esler in press), limited gene flow, there has been rapid diversification (Ihlenfeldt 1994; Cowling et al. 1998). We add a further observation here. The small body size of many of these habitat-specialist succulents ensures that they can sustain large populations in a small area. Since large populations are capable of accumulating genetic diveristy, they are more likely to develop into new species than are small, genetically conservative populations (Rosenzweig 1995). Small populations can experience genetic drift. However, they are unlikely to accumulate novel traits. What this means is that isolated populations of dwarf succulents are probably sufficiently large to undergo further diversification and

to continue to subdivide habitat space more finely. Examples of such rapidly diversifying lineages of dwarf succulents include *Conophytum* (Hammer 1993) and *Argyroderma* (Hartmann 1975; Ihlenfeldt 1994), both in the Mesembryanthemaceae. Diversification in the Mesembryanthemaceae is discussed in more detail in Desmet et al. (1998).

Finally, the patterns in plant diversity in the study area have important implications for conservation strategies aimed at protecting the regional flora. These efforts should concentrate on conserving koppie and other rocky habitats as well as the lag-gravel pavements. Koppies and rock habitats show high species diversity; are home to the majority of the endemic flora (dwarf leaf-succulents); and have many species in common with non-rocky substrata. Lag-gravel pavements have a lower overall diversity, however, they are home to a unique flora rich in narrow endemics. The added challenge to conservationists is to incorporate an evolutionary understanding of these patterns of diversity into their reserve design.

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