

Patterns of geophyte diversity and storage organ size in the winter-rainfall region of southern Africa

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ABSTRACT

The winter-rainfall region of southern Africa, covered largely by the fynbos and succulent karoo biomes, harbours the world's greatest concentration of geophyte species. Species diversity is greatest in the south-west, where more than 500 species co-occur in one quarter-degree square; in the south-east the values are generally around 100, and in the arid north-west, always less than 50 (more often less than 10). In at least three species-rich genera (*Moraea*, *Eriospermum* and *Oxalis*), the size of storage organs (bulbs, corms, tubers) varies inversely, with the largest average values occurring in the species-poorer areas — both in the north-western, and in the south-eastern parts of the region. This negative correlation between average storage organ size and species diversity is, however, only observed at relatively large spatial scales, which suggests that there is no direct relationship between storage organ size and species diversity. More likely, both these measures are driven by winter rainfall amount and reliability, both of which peak in the south-western Cape. We suggest that reliable winter rainfall makes large storage organs unnecessary and depresses extinction rates, thus leading to the accumulation of species.

Key words

Bulbs, Cape Floristic Region, geophytes, Namaqualand, southern Africa, species diversity.

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INTRODUCTION

A large proportion of the bulbs cultivated worldwide originated in the Cape; such are the genera *Amaryllis*, *Clivia*, *Freesia* and many other commonly potted or garden plants. Indeed the diversity of bulbous, cormous, and tuberous plants growing in the winter-rainfall region (WRR) of southern Africa is unparalleled (Manning *et al.*, 2002; Parsons & Hopper, 2003; Procheş *et al.*, 2005).

The WRR, loosely defined as the area where more than 50% of the total annual precipitation falls during the six winter months (Bayer, 1984; Jürgens, 1991; see Fig. 1), stretches over large portions of three South African provinces, and south-western Namibia. The vegetation is predominantly fynbos and succulent karoo. In the Cape Floristic Region alone (excluding most of the succulent karoo in the north-west of the WRR), geophytes are represented by 1552 species, accounting for 17% of the total flora (Goldblatt & Manning, 2000), while the entire WRR totals 2096 (20%) (Procheş *et al.*, 2005).

There is a dearth of comprehensive information on the geographical patterns of species diversity in these plants, and a

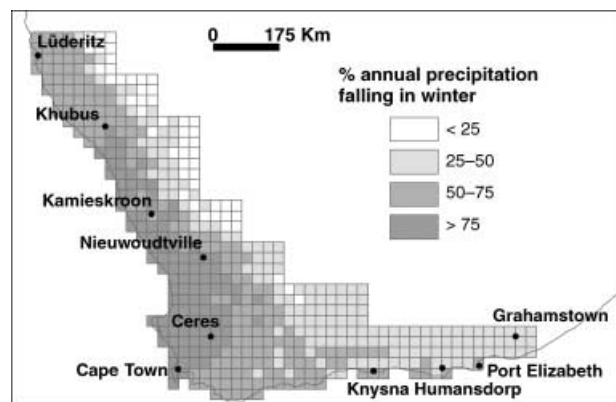


Figure 1 The winter-rainfall region (WRR) of southern Africa is defined here as the area where at least 50% of the annual precipitation falls during the six winter months (April to October). All adjacent areas divided into quarter-degree squares in this figure were considered in the species counts. Data courtesy of the South African Weather Bureau.

poor understanding of the factors potentially determining these patterns. The only available multigeneric analysis (Ruiters, 2001) is limited to the south-western WRR; this area includes only a subset of the environmental conditions found in the WRR and therefore inferences drawn from analyses conducted here will only provide a part of the overall picture (see Procheş *et al.*, 2005).

Given that the size of the storage organs in geophytes can be readily quantified (for bulbs, corms, tubers, but not for rhizomes), these plants offer important opportunities for analysing relationships between plant size and other variables. Body size studies are one of the latest trends in animal research, and have recently had a strong impact on both biogeographical and community ecology theory (e.g. Cushman *et al.*, 1993; Gaston *et al.*, 2001). Relationships between plant growth form (or stature) and geographical distribution have also been shown in plants (e.g. Cowling & McDonald, 1998); plant body size, however, is more difficult to quantify. Nevertheless, in geophytes, due to the limited capacity of the storage organ, an ecologically and biogeographically significant body-size characteristic is easily measurable and species-specific. To simplify terminology, the size of the storage organ will be further referred to as bulb size.

The main purpose of our study was to illustrate the broad patterns of geophyte diversity in the WRR at the relatively coarse scale of quarter-degree squares (QDS) (634–671 km²). Secondly, we looked at bulb size patterns for various parts of the WRR. Given the variety of rainfall conditions across the region, we expected bulb size to vary from one area to another in a consistent manner across unrelated geophyte lineages.

METHODS

A species database was compiled for the distribution in the WRR of 1024 geophyte species belonging to eight families (48.9% of the total number; for sources used, see Table 1) at the quarter-degree square (QDS) scale. The WRR, as defined here, contains 505 QDSs. Since large parts of the WRR are under-collected, land

classifications (Hilton-Taylor, 1987; Cowling & Hejnis, 2001; Driver *et al.*, 2003) were used to interpolate missing localities. Thus, a species was considered present in a QDS where it was not recorded, if: (1) it was recorded in QDSs both west-east, and north–south of that QDS, and (2) there was at least one land class (corresponding to the ecological requirements of the species) in common with at least one such QDS. A spatial database was derived from the species database, containing total species diversity for all geophytes, as well as for each genus, and for WRR non-endemics, broad and narrow endemics, in each QDS (narrow endemics were defined as those with a distribution range of 25 QDSs or less). Although only 48.9% of the species known to occur in the region were included in the database, the range of taxa analysed means that the resulting patterns are likely to be representative for the entire WRR geophyte flora. We tested our method by comparing data from local floras (at spatial scales close to QDS) with our figures.

Additionally, the average size of the storage organ for each species was recorded in the largest genera (most often measured during the flowering season; see Table 1), and plotted (box-whisker plots, showing the medians, ranges, and central 50% of the values) at generic level, for several different localities in the WRR (Lüderitz, Kamieskroon, Ceres, Cape Town, Knysna, Humansdorp, Grahamstown; see Fig. 1 for their location in the WRR). In this analysis, a species was considered present at a given locality if occurring within one degree (four QDSs) from it. Rainfall data were derived from actual weather station data provided by the South African Weather Bureau, and models from Dent *et al.* (1988) and Schultze (1997).

RESULTS AND DISCUSSION

Patterns of species diversity

The diversity map for the 1024 species considered (Fig. 2a) showed WRR geophytes to be most diverse in the Hottentots

Table 1 Geophyte taxa for which distributions were recorded. The numbers under ‘species’ represent distributions recorded/total number of species in the winter-rainfall region (WRR) of southern Africa. For the genera marked with an asterisk, bulb size information was also recorded

Family	Species	Genera	Source
Orchidaceae	192/230	<i>Bartholina, Holothrix, Habenaria, Pachites, Satyrium, Schizodium, Disa, Brownleea, Pterygodium, Disperis, Corycium</i>	Linder & Kurzweil, 1999
Tecophileaceae	7/9	<i>Cyanella</i>	Scott, 1991
Iridaceae	429/767	<i>Ferraria, Freesia, Geissorhiza, Gladiolus*, Lapeirousia, Moraea*, Romulea, Syringodea, Watsonia</i>	de Vos, 1979, 1983; Goldblatt, 1972, 1985, 1986, 1989; Goldblatt & Manning, 1998
Ruscaceae	76/76	<i>Eriospermum*</i>	Perry, 1994
Hyacinthaceae	29/285	<i>Daubenya, Lachenalia</i>	Duncan, 1993, 1997a, 1997b, 1998, 1999a, 1999b, 2001, 2002; Manning & van der Merwe, 2002
Amaryllidaceae	84/147	<i>Carpolyza, Clivia, Cyrtanthus, Haemanthus, Hessea, Strumaria</i>	Reid & Dyer, 1984; Rourke, 2002; Snijman, 1984, 1994
Oxalidaceae	181/181	<i>Oxalis*</i>	Oberlander <i>et al.</i> , 2002
Geraniaceae	26/98	<i>Pelargonium</i>	van der Walt, 1977; van der Walt & Vorster, 1981, 1988
Total	1024/2096		

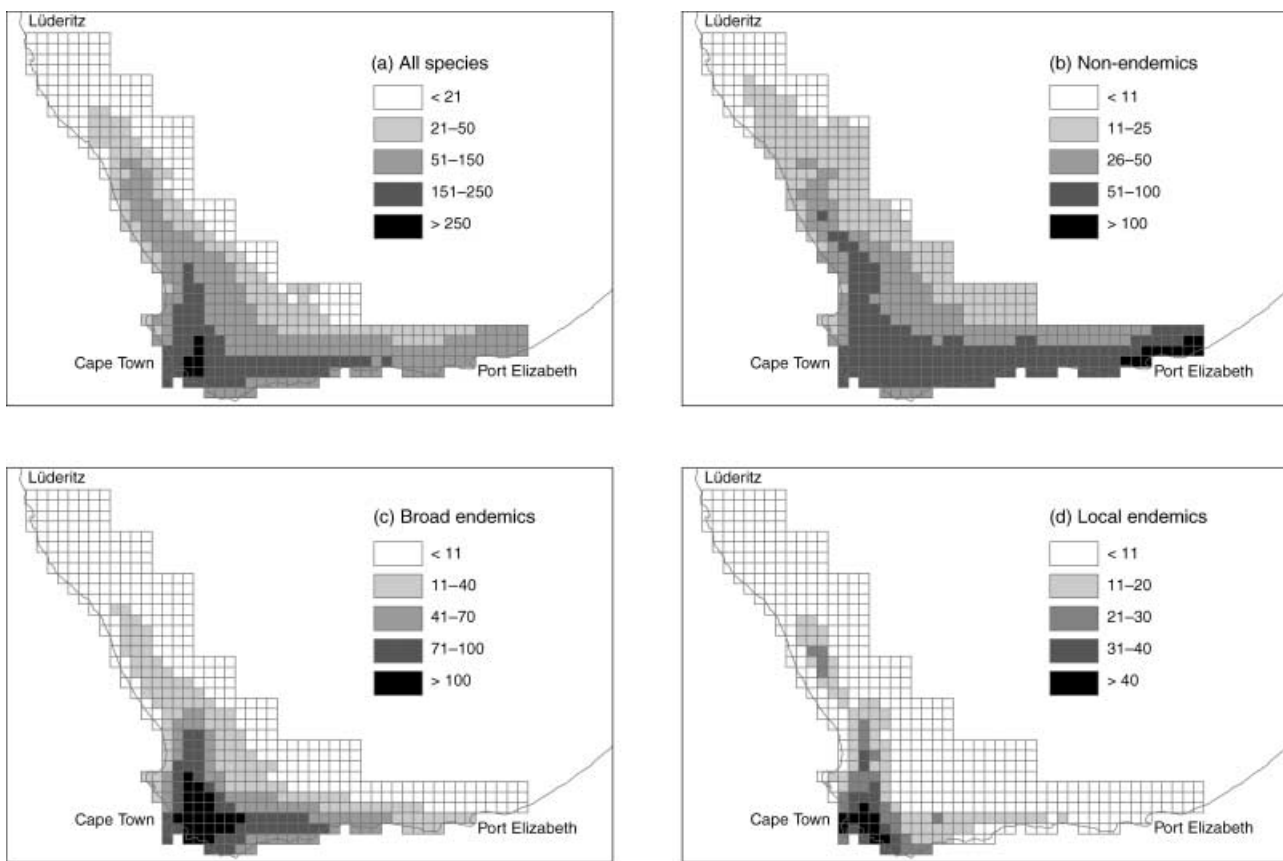


Figure 2 Diversity patterns for (a) all geophytes considered (numbers of species out of a total of 1024, representing 48.9% of the total geophytic flora of the region); (b) the species not endemic to the WRR; (c) broad endemics (present in more than 25 quarter-degree squares); (d) narrow endemics (present in fewer than 25 quarter-degree squares).

Table 2 In the present study, distributions were recorded for only 48.9% of the geophyte species known to occur in the WRR. To test whether the diversity patterns thus mapped are reliable, geophyte richness values for local floras are compared to those recorded here for the overlapping QDSs. The resulting values are always close to 50%, indicating a representative sampling of the taxa

Geographic area	Geophyte flora	Flora reference	Overlapping QDSs	Geophytes included here	% included
Cederberg Range	327	Taylor, 1996	3	175	54%
Cape Peninsula	408	Adamson & Salter, 1950	3	208	51%
George District	347	Fourcade, 1940	12	202	58%
Knysna District	373	Fourcade, 1940	7	179	48%
Uniondale District	162	Fourcade, 1940	11	171	59%
Humansdorp District	394	Fourcade, 1940	18	95	43%

Holland Mountains (near Cape Town), with 272 species occurring in the most species-rich QDS. A broad area of high diversity (> 150 species/QDS) was documented throughout the south-western WRR, including the Cape Peninsula, and extending northwards to the Cederberg, and thence in the Bokkeveld Mountains, in the vicinity of Nieuwoudtville. This area of high richness also extended eastwards along the Cape Fold Mountains to the vicinity of Knysna. Moderate diversity (50–150 species/QDS) was found throughout the southern and south-eastern coastal forelands of the WRR and along the eastern reaches of the folded belt, extending as far as Grahamstown. Also included in

this category were the north-western uplands (Namaqualand, beyond Kamieskroon). Relatively low diversity values, below 20 species/QDS, were recorded in the extreme north-west (including south-western Namibia), as well as along the transition to the summer-rainfall Nama-karoo, on the north-eastern border of the WRR.

Our data (for 48.9% of the total number of species) appear to be representative of the entire geophyte flora, with local floras always equalling close to twice the numbers. Thus, our numbers approximated 43–59% of the complete local floras (Tables 2, e.g. for the Cape Peninsula (Adamson & Salter, 1950) listed 408

species, while our three QDSs covering this area jointly contained 208). Appropriate floral checklists were not available from every part of the WRR, therefore some geographical biases are not excluded; also, as our figures are based on species ranges, they may represent overestimates of the present-day floras in heavily transformed QDSs. Nevertheless, we suggest that, generally, by multiplying the numbers in Fig. 2 by a factor of two, diversity values very close to the actual numbers of geophytes occurring within each QDS will be obtained. This would result in an astonishing 544 species in the most species-rich QDS, and values close to 10 in the poorest areas.

A similar diversity pattern with the one presented in Fig. 2(a), at least within the Cape Floristic Region (more-or-less equivalent to the fynbos biome; southern part of the WRR) has been recorded for many non-geophytic genera centred in the WRR (e.g. Proteaceae, Ericaceae; see Levyns, 1964; Oliver *et al.*, 1983; Ojeda, 1998). However, in geophytes, diversity patterns along the western escarpment are more continuous. This can be explained by the fact that typical fynbos plants are limited in their distribution by rainfall values, which are low through most of Namaqualand, but sufficiently high in several patches of mountainous habitat, thus leading to the occurrence of fynbos enclaves in a succulent karoo matrix. On the other hand, the existence of a storage organ allows geophytes to also occur in the drier areas. Thus, from a geophyte point of view, the recognition of the Cape Floristic Region as a fynbos-centred unit is unnecessary, the WRR (fynbos and succulent karoo) being a more appropriate study area.

When analysing species diversity patterns according to distribution ranges, WRR non-endemic species were most diverse in the south-east, gradually becoming fewer towards the western and north-western parts of the WRR (as many of the geophyte species from the coastal and montane grasslands of the eastern seaboard extend into the eastern WRR, but fewer further west) (Fig. 2b). Broad endemics were centred in the south-west, but also fairly numerous in the west and south (Fig. 2c), while narrow endemics were almost entirely confined to the south-west, with a second diversity centre in the west, in the vicinity of Kamieskroon (Fig. 2d). These patterns indicate that the diversity centre in the south-west largely owes its existence to WRR endemics, both broadly and narrowly distributed.

Most of the genera considered showed diversity patterns remarkably similar to those for all species, although some differences were noted (Fig. 3). Thus, in the case of orchids (such as *Disa*, Fig. 3a) besides the south-western peak, there was an additional high-diversity band in the south, while most of the arid areas were completely devoid of species. The four genera of Iridaceae presented very similar diversity patterns, all showing distinct peaks in the south-western WRR (Kogelberg and Hottentots Holland Mountains) (Fig. 3b–e). All four are genera centred in the WRR, although only *Geissorhiza* is actually endemic (and presents the most typical patterns for a WRR endemic genus; Fig. 3b, cf. Oliver *et al.*, 1983). *Gladiolus* and *Watsonia*, on the other hand, have secondary peaks in the east, indicating enrichment from summer-rainfall species for these two genera that have wide distributions outside of the WRR

(Fig. 3c,e; cf. Goldblatt, 1989; Goldblatt & Manning, 1998). *Moraea* extends deeper into the semiarid north-west (Fig. 3d).

Slightly different patterns were noted in the Amaryllidaceae and *Eriospermum* (Ruscaceae) (Fig. 3f–h). *Eriospermum*, an ancient and isolated African genus (Lu, 1985), showed multiple centres of diversity in the succulent karoo, but also fairly high diversity across the entire fynbos biome (Fig. 3f). Similar patterns have already been noted in *Oxalis* (Oberlander *et al.*, 2002) — both *Eriospermum* and *Oxalis* (at least in the WRR) are plants of low stature, although often with large storage organs, which may explain their penetration into the semi-arid north-west.

In Amaryllidaceae, two distinct high diversity areas were recorded: one in the north-west and the other in the east, between Humansdorp and Port Elizabeth (Fig. 3g–h). These nodes correspond to the centres of diversity for the Haemantheae and Amaryllideae (north-west, similar to *Eriospermum*), and *Cyrtanthus* (Cyrtantheae; east). Outside the WRR, the Amaryllidaceae are mainly found in areas receiving high summer rain (Snijman, 1999). Interestingly, relatively few Amaryllidaceae are endemic to the mesic south-western WRR. Including all the Amaryllidaceae genera not considered here is likely to further strengthen this bimodal pattern (see distributions in Goldblatt & Manning, 2000), rather than change it.

Bulb size patterns

Bulb sizes in three large genera showed very similar patterns across the WRR (Fig. 4). The corms of *Moraea* (Iridaceae), hypocotyledonary tubers of *Eriospermum* (Ruscaceae), and bulbs of *Oxalis* (Oxalidaceae), although having different morphological origins, and associated with distantly related lineages, all showed a trend of decreasing average size from the north-western (Lüderitz, Kamieskroon, Ceres) and eastern (Grahamstown, Humansdorp, Knysna) parts of the WRR, towards the south-west (Cape Town area). However, in none of the cases was this variation statistically significant. Given the large amount of microhabitat variation in each of the sample regions, which is likely to influence bulb size through fine-scale variation in soil moisture, this was not unexpected.

Gladiolus (Iridaceae) showed no obvious geographical pattern in bulb size (data not presented), which could be explained by the association of component species with relatively moist conditions locally (see Goldblatt & Manning, 1998). The three genera in Fig. 4 all have members that grow in both dry and mesic habitats, hence the broad range of bulb sizes. Data for the other two of the top six largest geophytic genera in the WRR (*Disa*, Orchidaceae, and *Lachenalia*, Hyacinthaceae) were not available. One can expect little variation in *Disa*, which is generally associated with even moister sites than *Gladiolus* (Linder & Kurzweil, 1999), whereas *Lachenalia* spans a broader range of climatic and microclimatic conditions (Manning *et al.*, 2002), and could show a pattern similar to those presented in Fig. 4, although the fact that this latter genus often inhabits rock crevices may impose limitations on bulb size.

Given the geographical patterns of bulb size in the three genera in Fig. 4, it is reasonable to expect a negative correlation, albeit a

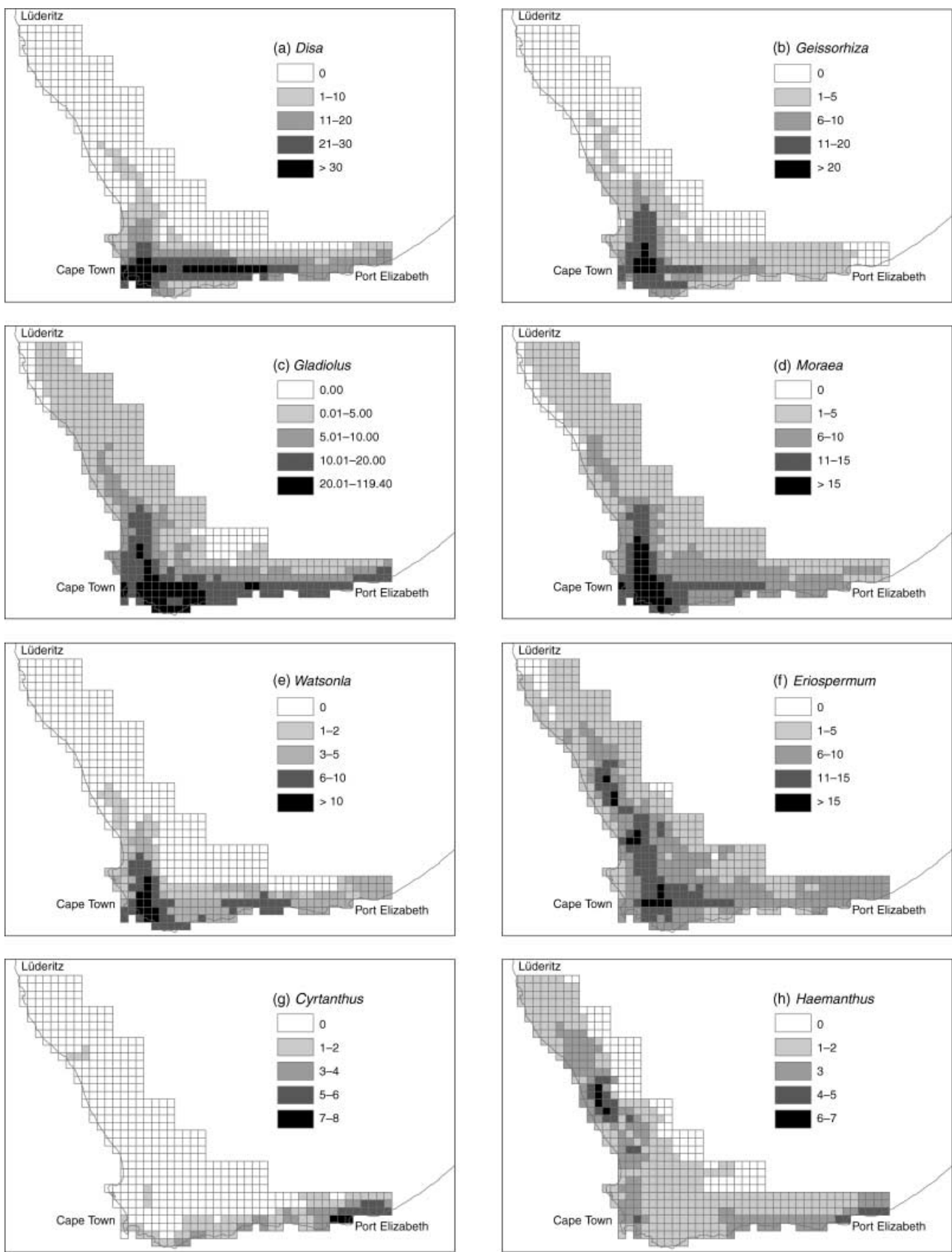


Figure 3 Diversity patterns for (a) *Disa* (Orchidaceae); (b) *Geissorhiza*; (c) *Gladiolus*; (d) *Moraea*; (e) *Watsonia* (all four, Iridaceae); (f) *Eriospermum* (Ruscaceae); (g) *Cyrtanthus*; (h) *Haemanthus* (both Amaryllidaceae).

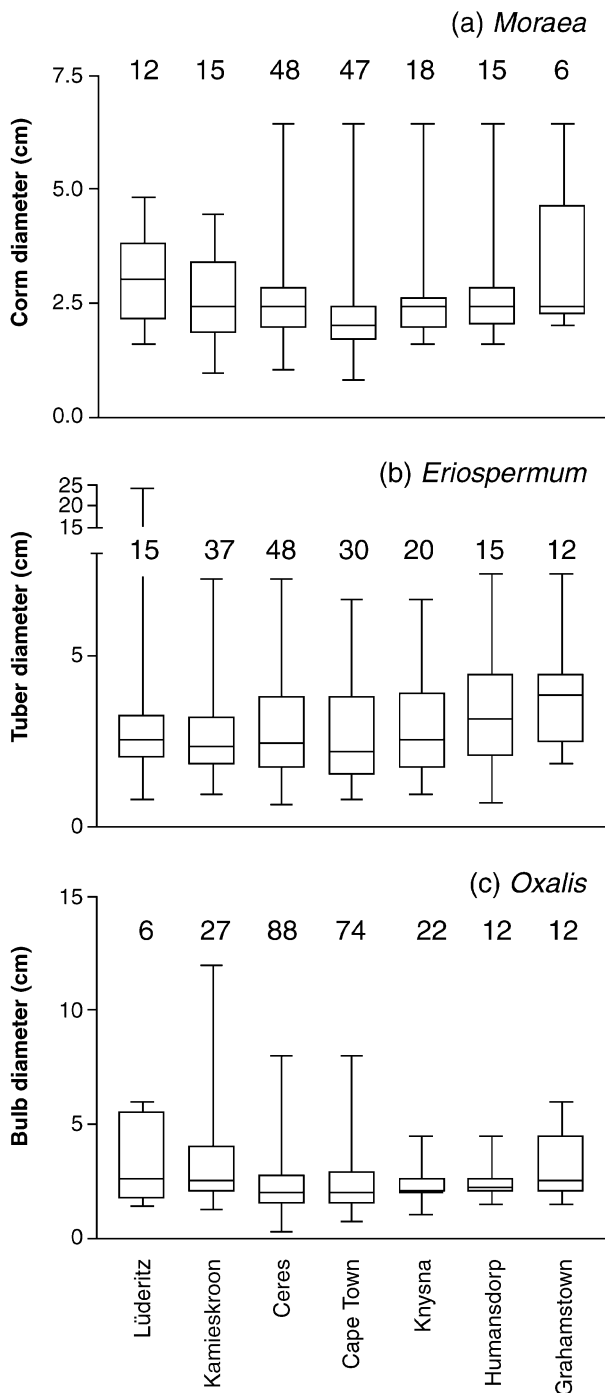


Figure 4 Storage organ sizes for three geophytic genera at five localities across the winter-rainfall region (WRR) of southern Africa. Shown are the medians, central 50% of the values, and ranges. The numbers of species for each genus at each site are shown above the range bars. A species was considered present at a given locality if occurring within one degree (four QDSs) from it. (a) *Moraea* subg. *Moraea* (Iridaceae); (b) *Eriospermum* (Ruscaceae); (c) *Oxalis* (Oxalidaceae). See Figure 1 for the location of the localities.

weak one, between species diversity and bulb size. Indeed, this is the case: $r = -0.77$, $P = 0.048$ for *Moraea*, $r = -0.85$, $P = 0.024$ for *Eriospermum*, and $r = -0.41$, $P = 0.354$ for *Oxalis*. The scale considered in this analysis is larger than the QDS scale used for the diversity patterns (areas of 8×8 QDSs (two by two degrees), centred in the localities listed in Fig. 3). The relationships between bulb size and diversity are not obvious at the QDS scale (in fact, at this scale, in *Moraea* there is a positive correlation!). Also, there are different responses in each genus to the east–west and north–west to south–east gradients (variation along the former being low in *Eriospermum*, but high in *Oxalis*). This suggests that the relationship between bulb size and species diversity is not a direct one, but rather one mediated by broad-scale environmental factors, which vary locally, resulting in relationships at the broader, but not the finer scale.

Geophytes and the rainfall gradients in the WRR

An environmental factor that varies in tune with both the species diversity patterns and the bulb size patterns presented here, is the rainfall regime. Although the WRR is characterized — by definition — by most precipitation occurring in the cooler months, the proportion of winter rainfall varies widely across the region, barely (and only patchily) exceeding 50% in the eastern parts, but exceeding 75% in the west and north–west. The amount of winter precipitation also varies, with the north–western areas being extremely arid ($< 100 \text{ mm yr}^{-1}$), while parts of the south–west and south have annual totals in excess of 2000 mm.

Thus, there are two major rainfall gradients in the WRR (see also Campbell, 1983; Deacon *et al.*, 1992). From the extreme south–west eastwards, the amount of rain declines rapidly to the east of the south–north trending folded belt (see also Deacon *et al.*, 1992), but increases again when the transect intersects the coastal section of the folded belt (Fig. 5a). However, the most significant trend along this gradient is the eastwards decline in the proportion of winter rain, especially east of 21°E (Fig. 5b). From there to the eastern boundary of the WRR, rain may fall at any time of the year, although equinoctial peaks are evident. This gradient represents a spatially large transition from strongly winter to strongly summer rainfall regimes, a globally unique phenomenon. Rainfall reliability for the winter months, when WRR geophytes are photosynthetically active (Rossa & von Willert, 1999), expressed as coefficients of variation of monthly totals, also declines eastwards along this gradient (Fig. 6).

Along the north–south gradient, total rainfall increases dramatically where the transect coincides with the Cederberg portion of the folded belt (Fig. 5c). However, in terms of seasonality, the entire gradient experiences winter dominance (Fig. 5d). The reliability of this winter rain is extremely high, both within the fynbos and succulent karoo biome parts (Desmet & Cowling, 1999; Cowling *et al.*, 2005). Of all the subregions in the WRR, the south–west is the only one that receives both plentiful and reliable winter rainfall.

The advantage of the geophytic habit is the ability to persist short-term drought and respond rapidly to improved moisture conditions (Dafni *et al.*, 1981; Rees, 1989). In the WRR, most

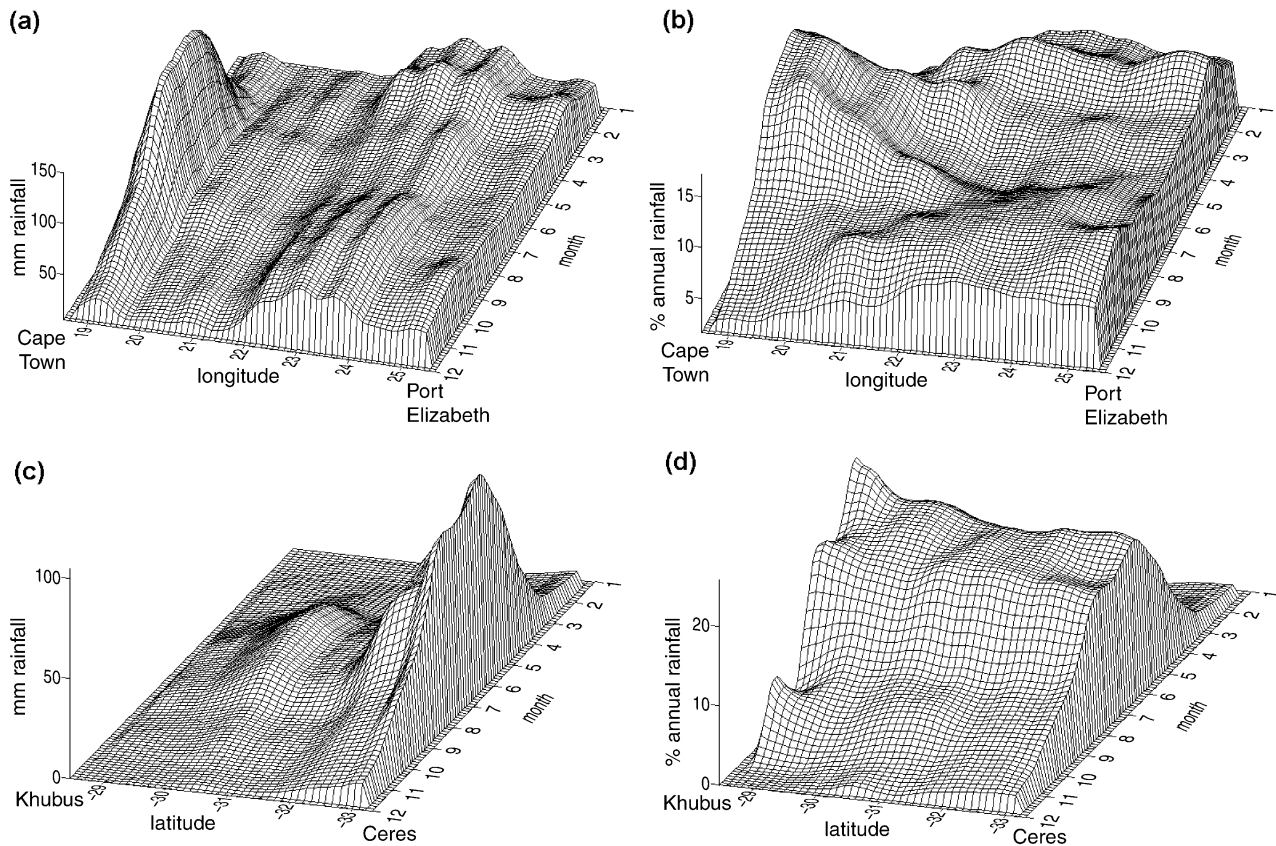


Figure 5 Rainfall regimes in the winter-rainfall region (WRR) of southern Africa. The west–east (Cape Town to Port Elizabeth) gradient showing (a) total annual rainfall and (b) % winter rainfall, and the north–south (Khubus to Ceres) gradient showing (c) total annual rainfall and (d) % winter rainfall. See Figure 1 for the location of the localities; rainfall data from Dent *et al.* (1988) and Schultze (1997).

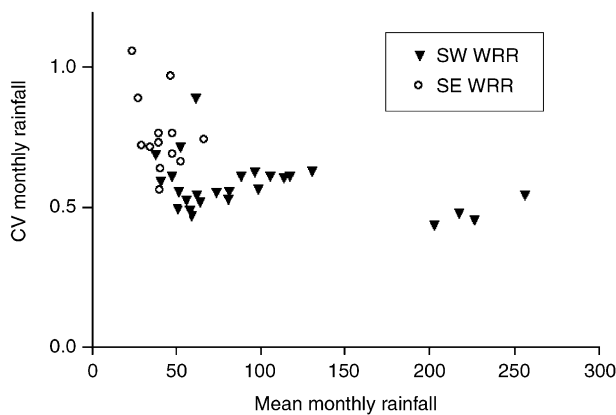


Figure 6 The relationship between mean and coefficient of variation in monthly rainfall (July) for localities in the south-western and south-eastern parts of the winter-rainfall region (WRR) of southern Africa.

geophytes are photosynthetically active in the cooler months (Rossa & von Willert, 1999). Therefore, ample and reliable winter rain — as experienced in the south-western WRR — will promote the persistence of geophytes, and enable the evolution of small bulbs, since opportunities for the replenishment of storage organs occur every year. In the east, however, unreliable winter

rains impose constraints on winter-growing geophytes since prolonged dry spells may limit organ replenishment and compromise flowering, ultimately leading to the local extinction of populations. There are two ways to overcome this: first, leafing and flowering can occur opportunistically, in response to rainfall events, as is the case for some species of *Cyrtanthus* (Amaryllidaceae) and *Tritonia* (Iridaceae) (R.M.C., pers. obs.); second, larger storage organs can buffer plants against unpredictable winter rains. In the drier, north-western parts of the WRR, the uniquely reliable winter-rainfall regime has enabled the extraordinary diversification of geophytes in a wide range of lineages. Here, the diversification of species with below-ground water storage parallels the diversification of those with above-ground water storage, namely the dwarf and low succulent shrubs in the Aizoaceae ('core' Ruschiodeae) (Klak *et al.*, 2004), Asteraceae and Crassulaceae. Both of these habits are characterized by relatively small storage organs for a desert ecosystem, a feature most likely explained by the uniquely reliable rainfall regime experienced there (Cowling *et al.*, 1999). However, the low rainfall regime of this region may also have placed a constraint on storage organ size: larger bulbs would be required to ensure that sufficient reserves are maintained, at least relative to the high rainfall zone of the south-west.

The patterns in bulb size along the climatic gradient in the WRR are consistent with the rainfall regime-based hypotheses

presented above. For a geophyte, life gets tougher towards the two ends of the WRR, and extinction risks are probably higher there, especially for small-bulbed species (although this hypothesis would need to be experimentally tested). On the other hand, in the south-west extinction risks are likely to be minimal — due to both reliable and abundant winter rainfall. Therefore, the higher diversity of bulbs in the south-west is likely to be a consequence of low extinction rates. In the east and north, higher extinction rates — owing to lower and less reliable rain, respectively — would depress overall diversity.

CONCLUSIONS

This paper presents broad patterns for geophyte species diversity and bulb size in the WRR, suggesting that both of these variables may be dependent on climatic factors, and especially on rainfall quantity and reliability. A few additional analyses can be conducted using this dataset, and these are likely to shed further light on the topic. However, the scale used here (quarter-degree to two degrees), while ideal for illustrating patterns for the entire WRR, becomes relatively coarse when it comes to the most species-rich areas, such as the south-west. Many of the environmental variables influencing geophyte diversity and morphology are also likely to be best measured at finer scales. Of great interest would be studies looking at within-region variation in bulb size in relation to microhabitats (deep sandy soils, clayey soils, gravel plains, rock outcrops, etc.), as well as community-level analyses of bulb size patterns across climatic gradients. Also, at the scale of the entire WRR, phenological observations in relation to bulb size over several years, conducted in the different regions (north-west, south-west, east) would be needed to test the hypotheses we advanced. Ultimately, experimental manipulation of soil moisture and its impact on growth and flowering in related species with different bulb sizes and reciprocal transplant studies of sister taxa in different parts of the climatic gradients would provide at least some of the answers sought here.

So far, geophyte below-ground organs remain very poorly studied, although they certainly represent an essential feature for understanding the remarkable success of this group in the winter-rainfall region of southern Africa.

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