An overview of the Cape geophytes

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The Cape Region (here treated as the winter rainfall region of southern Africa, thus including fynbos, renosterveld and succulent karoo vegetation) is the world's foremost centre of geophyte diversity. Some 2100 species in 20 families have been recorded from this area, 84% of them endemic. The most important families, with more than a hundred geophyte species each, are Iridaceae, Oxalidaceae, Hyacinthaceae, Orchidaceae, Amaryllidaceae and Asphodelaceae. Although southern Africa does not appear to have been the main diversification centre for the plant orders with highest geophyte representation (Asparagales and Liliales), it represents an active centre of transition to geophytism, such transitions having occurred independently in numerous plant groups, often followed by rapid speciation. Several Cape geophyte groups have consequently expanded across Africa to the Mediterranean Basin, and possibly to other winter rainfall regions. Remarkably high local species diversity in renosterveld vegetation, even in relatively homogeneous environments, suggests that pollinator specificity and phenology play an important role in niche partitioning. However, character diversity is also high in storage organs and leaves, and this could account for the high species diversity values recorded at larger spatial scales, especially across environmental gradients. Long-term climatic stability, combined with topoclimatic and edaphic diversity and regular fire occurrence, is likely to be responsible for the remarkable geophyte diversity of the Cape, as compared to other mediterranean-climate regions.   © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, **87**, 27–43.

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INTRODUCTION

Mediterranean climates are well known for their remarkable plant diversity (Cowling *et al.*, 1996), and the high numbers of geophytes they harbour have long been noted (Raunkiaer, 1934). The geophyte floras of some of these regions have been the subject of taxonomic and ecological reviews (e.g. south-western Australia: Pate & Dixon, 1982; Parsons & Hopper, 2003; California: Rundel, 1996; Chile: Hoffmann, Liberona & Hoffmann, 1998). The Cape Flora of South Africa is, however, by far the richest in geophyte species (Fig. 1),

and while Cape petaloid monocots have recently received a popular review (Manning, Goldblatt & Snijman, 2002), a comprehensive taxonomic, ecological and evolutionary assessment for the Cape geophytes is still lacking.

A number of recent monographs (e.g. Goldblatt, 1986, 1989; Marais, 1994; Perry, 1994; Goldblatt & Manning, 1998; Linder & Kurzweil, 1999) clearly indicate that good taxonomic information has been accumulated, at least as far as some large genera are concerned. These are mainly genera of horticultural importance, with many species now being cultivated worldwide. However, significant discoveries continue to be made even in such groups, including the recent discovery of a new *Clivia* near Nieuwoudtville, hundreds of kilometres from the closest previously

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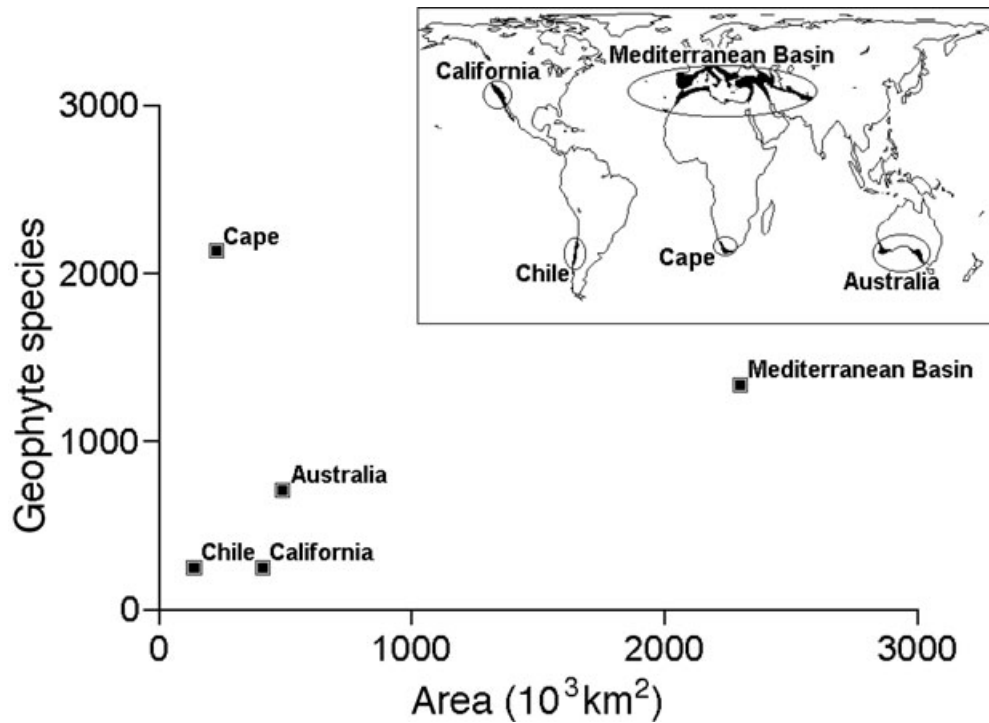
Figure 1. Geophyte diversity in the five mediterranean-climate regions of the world. Data from Cowling *et al.* (1996) and Parsons & Hopper (2003), with an additional estimate of 1335 species for the Mediterranean Basin (Ş. Procheş, unpubl. data). Data for the Cape, as compiled in this paper.

recorded species (Rourke, 2002). The current state of knowledge of other Cape geophytes (e.g. *Bulbine, Ornithogalum*) is, however, comparatively poor.

Among the major Cape geophyte families, the Iridaceae and Orchidaceae have probably received the most extensive taxonomic coverage (Linder & Kurzweil, 1999; Manning *et al.*, 2002). In the Hyacinthaceae, a new generic-level organization is emerging from molecular studies, resulting in numerous genera being merged under *Drimia, Daubenya, Lachenalia*, and *Ornithogalum* (Goldblatt & Manning, 2000a; Manning & van der Merwe, 2002; Manning, Goldblatt & Fay, 2004). The discovery of new species continues at a significant rate in these families, with 11 new species of *Lachenalia* (Hyacinthaceae) described since 1993 (e.g. Duncan, 1998). For the Oxalidaceae, an extensive, if outdated, review is available (Salter, 1944), and the geophytic Asphodelaceae are likewise in need of modern taxonomic study. Phylogenetic studies are underway for numerous geophytic taxa (Cape clades included), making use of the taxonomic information accumulated for the better-known groups and helping to clarify the status of the lesser-known ones (e.g. Fay *et al.*, 2000; Vinnersten & Bremer, 2001; Manning *et al.*, 2004).

One field in which geophyte research has been particularly productive is pollination biology. It is apparent that pollinator specificity plays an important role in the maintenance of Cape geophyte diversity, and the Cape has become an important area for pollination research (Johnson, 1996; Goldblatt & Manning, 2000b; Johnson & Steiner, 2000). Progress has also been made in geophyte ecophysiology, with an emphasis on the importance of morphology and life cycles for adaptation to local environmental conditions (Johnson, 1992; Le Maitre & Brown, 1992; Ruiters & McKenzie, 1994; Esler, Rundel & Vorster, 1999; Rossa & von Willert, 1999).

Despite this impressive progress in our understanding of Cape geophyte taxonomy and ecology, a comprehensive picture is still lacking concerning the actual extent of geophytism in the Cape. In particular, there is a need for integrating phylogenetic information in the study of geophytism (Parsons & Hopper, 2003). Here we review the literature on Cape geophytes in order to determine the main factors responsible for geophyte diversification in the Cape, from a macrophylogenetic as well as ecological perspective.

WHAT IS THE APPROPRIATE STUDY AREA?

So far, the best coverage of the Cape geophytes is that provided by Goldblatt & Manning (2000a) for the Cape Floristic Region (CFR), which coincides largely with

the fynbos biome (comprising the fire-prone fynbos and renosterveld shrublands), but also includes enclaves of other biomes, such as Afromontane forest, succulent karoo and subtropical thicket. The review of Manning *et al*. (2002) includes, in addition to the CFR, the Roggeveld (a relatively small area of the winter-rainfall part of the Great Escarpment) as well as the extensive and arid basin of the Tanqua Karoo. It is, however, clear that high geophyte diversity is not strictly associated with typical CFR vegetation (fynbos and renosterveld); the succulent karoo (a sparse, succulent-rich, fire-free biome) also harbours a remarkable number of geophytes (Cowling *et al*., 1998, 1999b; Esler *et al*., 1999). Therefore, a review of Cape geophytes should ideally include both the fynbos and succulent karoo biomes. This area has already been defined as one biogeographical unit, namely the extended 'Capensis' region (Bayer, 1984; Jürgens, 1991) though its definition as a phytochorion has yet to be upheld by a comprehensive analysis. Geophytes could be an excellent group for studying 'Capensis' distributions, since they include fynbos-centred genera, succulent karoo-centred genera, and genera equally prevalent in both biomes.

For the present study, the Cape region of geophyte endemism is therefore defined as that covered by the fynbos and succulent karoo biomes, and broadly equivalent to the winter rainfall region of southern Africa (the area where at least 50% of the annual precipitation falls in winter). This region stretches from Lüderitz on the Namibian coast to about 150 km east of Port Elizabeth in the Eastern Cape, and 100–300 km inland (Fig. 2). It has long been noted that the Drakensberg grasslands are also rich in geophytes (Bews, 1925). However, the inclusion of summer-rainfall areas would raise a problem regarding the northern limits of the study area, with the east African highlands also being fairly species-rich. Therefore, all species counts and estimates to follow refer to the area illustrated in Figure 2.

DEFINING GEOPHYTISM

Geophytes were defined by Raunkiaer (1934) as plants with an underground perennation organ (bulb, corm, tuber, or rhizome) and leaves that die back annually. Several changes have since been made to that definition. However, in most parts of the world, no evergreen plants are considered to be geophytes (Parsons, 2000). In southern Africa, the transition from evergreen to seasonally green can be seen in numerous genera, and it is sometimes difficult to draw a firm distinction between the two, as even plants belonging to the same species may behave differently depending on local climatic conditions. Given this continuous range of phenologies, the most convenient approach is to consider as geophytes all plants with an underground perennation organ, as long as it also fulfils a storage function. This definition includes plants with pachymorphic (thick), but not leptomorphic (thin) rhizomes.

Nevertheless, one still has to explore the limits of geophytism, in order to cover all types of transitions
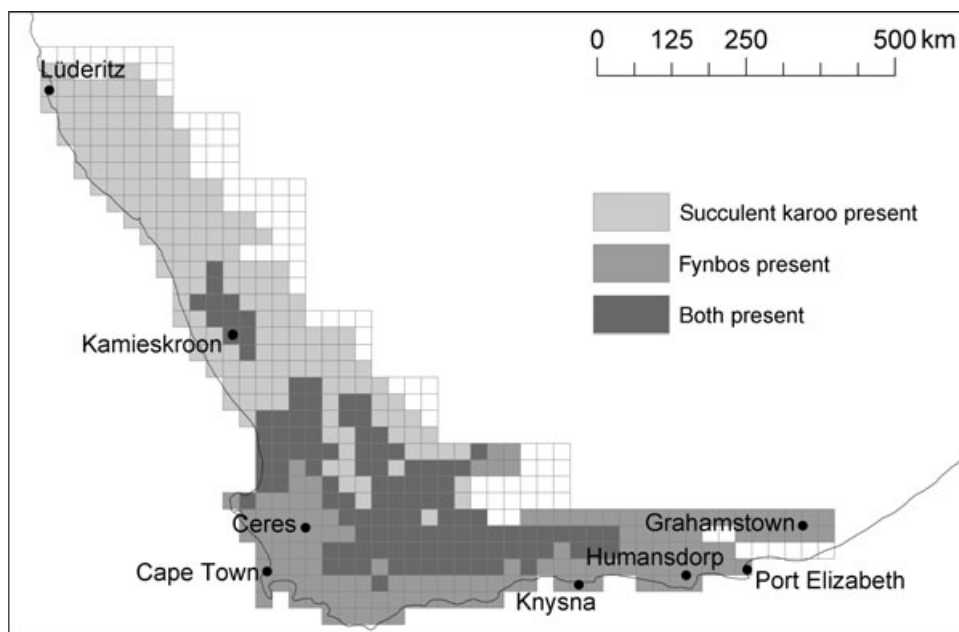

Figure 2. The study area, largely equivalent to the fynbos and succulent karoo biomes (the distribution at quarter-degree scale, based on Low & Rebelo, 1998).

between geophytic and non-geophytic habits (see below). First of all, it must be pointed out that some Cape plants can be classified as belonging to several morphological types, e.g. geophytes and climbers [e.g. *Kedrostis* (Cucurbitaceae)], or geophytes and succulents. Another marginal category is represented by aquatic plants with tubers or pachymorphic rhizomes, termed helophytes by Raunkiaer (1934). For example *Zantedeschia* (Araceae) and *Kniphofia* (Asphodelaceae) typically grow in temporarily inundated lands, and some species of *Aponogeton* (*Aponogeton*aceae) in temporary pools. In these cases, tubers and rhizomes fulfil a typical perennation/storage function during the dry season. In a similar way, *Isoetes* (Isoetaceae) and *Triglochin* (Juncaginaceae) could be considered geophytes.

It is difficult to classify as geophytes plants that have root enlargements deep below the ground surface [e.g. *Asparagus* (Asparagaceae)]. In some cases these are not constant features in a given species, and for other species in groups with root thickenings the underground organs are altogether unknown [e.g. in some *Annesorhiza* species (Apiaceae)].

The above transitional cases are not included on our geophyte list (Table 1; largely consistent with Germishuizen & Meyer, 2003), although they could be considered to be geophytes depending on the exact criteria used. Also excluded are several other genera of Aizoaceae, Apiaceae, Apocynaceae, Asteraceae and Campanulaceae, the 14 Cape species of *Drosera* (Droseraceae), and a few species of Crassulaceae, Cyperaceae, Lamiaceae, Polygonaceae and Ranunculaceae.

It is worth noting that, even among the species included in the list, the size of storage organs varies tremendously. In orchids (e.g. *Disa*, *Ceratandra*), root enlargements vary from clearly differentiated tubers to barely noticeable thickenings. In *Bulbine* (Asphodelaceae), the amount of water stored above ground (succulence) is often more important than that stored below ground (geophytism). Rather uncritically, these genera were included here in their entirety. However, in the dicotyledonous genera listed, the distinction between succulence and geophytism was made as far as possible, and the counts for Cape species include strictly geophytic species only.

METHODS

A geophyte list was compiled mainly from Goldblatt & Manning (2000a), Leistner (2000), Germishuizen & Meyer (2003) and Manning *et al.* (2002), while also consulting numerous generic revisions (see References in Leistner, 2000). Plant families were circumscribed according to APG II (2003). Seven large genera, for which recent and comprehensive revisions were available, were used for a few simple morphological and phenological analyses. These were *Geissorhiza* (Goldblatt, 1985), *Moraea* (subg. *Moraea*; Goldblatt, 1986), *Watsonia* (Goldblatt, 1989), and *Gladiolus* (Goldblatt & Manning, 1998) (all Iridaceae), *Eriospermum* (Ruscaceae; Perry, 1994), *Haemanthus* (Snijman, 1984) and *Cyrtanthus* (Reid & Dyer, 1984) (both Amaryllidaceae). For these genera, the phenology and average bulb size of each species were recorded. Additionally, the presence/absence of each species was recorded for five localities (one-degree squares, so selected as to cover the rainfall gradients in the Cape as much as possible; see Procheş, Cowling & du Preez, 2005), in order to compare the phenologies of their floras.

The phylogenetic discussion is based on recently published analyses, which were also used in conjunction with current distributions to infer historical distributions (Ronquist, 1997). In order to assess the relative contribution of vegetative and reproductive divergence to geophyte diversity in the Cape, characters referring to leaves/storage organs (as opposed to flowers/bracts), that were listed in genus-level dichotomous keys by Manning *et al.* (2002) were counted. For orchid genera, the natural keys in Linder & Kurzweil (1999) were used, excluding the summer-rainfall species. Local geophyte diversity values were derived from previously unpublished data of R. M. Cowling and R. H. Whittaker. Most other available data sets (based on once-off vegetation surveys) were not usable, as geophytes can only be observed for a limited period of time each year, when they are either flowering or leafing, and in many cases it is only possible to identify flowering specimens. Given temporal niche separation in pollinator use (Goldblatt & Manning, 2000b) and phylogenetic constraints (Johnson, 1992), geophytes co-occurring at one site will have staggered flowering periods, thereby making it difficult to collect comprehensive data during one visit.

THE NUMBERS

Some 2098 species of geophytes were recorded in the study area, 84% of these being endemic (Table 1). The species belonged to 11 orders, 20 families and 107 genera. The great majority (83% of the species) were monocots, and most of these (79%) were concentrated in the largest monocot order, Asparagales. The largest six families were the Iridaceae (767 species), Hyacinthaceae (285), Orchidaceae (230), Oxalidaceae (181), Amaryllidaceae (147), and Asphodelaceae (105); all other families included less than 100 geophytic species. The largest genus was *Oxalis* (181 species), followed by *Moraea* (147), *Lachenalia* (121), *Gladiolus* (117), and *Ornithogalum* (102).

Shifting the borders of the study area north into Namibia or arid central South Africa, even by 500 km, does not result in a major increase in species numbers;

Table 1. Main groups of Cape geophytes. The number of species given in parentheses after each genus represents the total (geophytic and non-geophytic) number of species worldwide; followed by the number of geophytic species occurring in the Cape (endemics in parentheses). Due to the frequent changes in taxonomic status, all numbers must be regarded as tentative

Asparagales		
Orchidaceae		
Bartholina (2)	2 (0)	
Bonatea (20)	2 (0)	
Brachycorythis (33)	1 (1)	
Brownleea (7)	3 (0)	
Ceratandra (6)	6 (6)	
Corycium (14)	11 (9)	
Disa (162)	95 (83)	
Disperis (84)	15 (8)	
Eulophia (250)	16 (1)	
Evotella (1)	1 (1)	
Gastrodia (17)	1 (1)	
Habenaria (800)	7 (0)	
Holothrix (55)	16 (7)	
Liparis (250)	1 (0)	
Pachites (2)	2 (2)	
Pterygodium (18)	13 (13)	
Satyrium (88)	31 (23)	
Schizodium (6)	6 (4)	
Stenoglottis (4)	1 (0)	
Hypoxidaceae		
Empodium (9)	5 (4)	
Hypoxis (80)	7 (1)	
Pauridia (2)	2 (2)	
Spiloxene (25)	21 (20)	
Tecophilaeaceae		
Cyanella (8)	8 (6)	
Walleria (3)	1 (1)	
Iridaceae		
Babiana (80)	78 (76)	
Chasmanthe (3)	3 (2)	
Crocosmia (8)	1 (1)	
Devia (1)	1 (1)	
Dierama (44)	1 (0)	
Ferraria (11)	10 (9)	
Freesia (14)	11 (10)	
Geissorhiza (84)	84 (84)	
Gladiolus (260)	117 (101)	
Hesperantha (79)	41 (36)	
Ixia (50)	50 (50)	
Lapeirousia (40)	34 (26)	
Melasphaerula (1)	1 (1)	
Micranthus (3)	3 (3)	
Moraea (195)	147 (135)	
Pillansia (1)	1 (1)	
Romulea (95)	70 (61)	
Sparaxis (15)	15 (15)	
Syringodea (8)	5 (4)	
Thereianthus (8)	8 (8)	
Tritonia (28)	26 (23)	
Tritoniopsis (24)	24 (23)	
Watsonia (52)	34 (31)	
Xenoscapa (2)	2 (2)	
Asphodelaceae		
Bulbine (75)	51 (42)	
Bulbinella (23)	17 (17)	
Trachyandra (52)	37 (32)	
Alliaceae		
Allium (550)	1 (0)	
Tulbaghia (20)	8 (5)	
Agapanthaceae		
Agapanthus (3)	3 (2)	
Amaryllidaceae		
Amaryllis (2)	2 (2)	
Ammocharis (5)	1 (0)	
Apodolirion (6)	3 (3)	
Boophone (2)	2 (1)	
Brunsvigia (20)	12 (10)	
Clivia (5)	1 (1)	
Crinum (65)	2 (1)	
Crossyne (2)	2 (2)	
Cybistetes (1)	1 (1)	
Cyrtanthus (57)	27 (20)	
Gethyllis (32)	32 (31)	
Haemanthus (22)	17 (11)	
Hessea (14)	14 (10)	
Nerine (23)	4 (4)	
Scadoxus (9)	2 (0)	
Strumaria (24)	25 (23)	
Ruscaceae		
Eriospermum (102)	76 (49)	
Hyacinthaceae		
Bowiea (1)	1 (0)	
Daubenya (8)	8 (7)	
Drimia (131)	33 (27)	
Eucomis (10)	3 (1)	
Lachenalia (121)	121 (116)	
Ledebouria (46)	5 (2)	
Massonia (7)	7 (6)	
Merwilla (5)	1 (1)	
Ornithogalum (234)	102 (80)	
Pseudoprospero (1)	1 (1)	
Spetaea (1)	1 (1)	
Veltheimia (2)	2 (1)	
Dioscoreales		
Dioscoreaceae		
Dioscorea (400)	6 (2)	
Liliales		
Colchicaceae		
Androcymbium (40)	26 (25)	
Baeometra (1)	1 (1)	
Neodregea (1)	1 (1)	
Onixotis (2)	2 (2)	
Ornithoglossum (8)	6 (5)	
Wurmbea (37)	15 (14)	
Commelinales		
Haemodoraceae		
Dilatris (4)	4 (4)	
Wachendorfia (4)	4 (4)	
Caryophyllales		
Aizoaceae		
Phyllobolus (31)	11 (10)	
Saxifragales		
Crassulaceae		
Tylecodon (41)	5 (4)	
Geraniales		
Geraniaceae		
Pelargonium (300)	98 (87)	
Malpighiales		
Euphorbiaceae		
Euphorbia (1500)	1 (1)	
Oxalidales		
Oxalidaceae		
Oxalis (500)	181 (166)	
Gentianales		
Apocynaceae		
Brachystelma (110)	9 (3)	
Ceropegia (160)	14 (3)	
Eustegia (1)	1 (1)	
Fockea (6)	5 (4)	
Orbea (20)	4 (0)	
Pachycarpus (30)	2 (0)	
Woodia (3)	1 (0)	
Xysmalobium (40)	3 (0)	
Asterales		
Asteraceae		
Othonna (120)	30 (27)	
Total	2096 (1756)	

however, advancing the same distance into the grasslands of the Drakensberg Plateau and along the east coast could add a few hundred species, mainly orchids and irids from a variety of genera already well represented in the Cape. On the other hand the Hyacinthaceae flora of these areas is somewhat more distinct. By including all the borderline geophytes mentioned in the previous section, the numbers could increase by up to 100 species, although most of these are not endemics. Future changes to the data presented in Table 1 will be due largely to taxonomic reassessment of the species status in species-rich genera, and to the discovery of new species.

It is clear that the Cape has the most diverse geophyte flora worldwide (Fig. 1). But at what spatial scale do species numbers become unusually high? It is unfortunately difficult to answer this question, given the scarcity of relevé data that include reliable lists of geophytes. Unpublished data of R. M. Cowling & R. H. Whittaker from fynbos and renosterveld sites across the Cape, which are at best under-estimates of actual numbers, show that most often (with 95% confidence) between one and four species of geophytes occur in a 1-m^2 plot, between two and ten in a 10-m^2 plot, between five and 13 in a 100-m^2 plot, and between seven and 16 in a 1000-m^2 plot (Table 2). In our comparisons, renosterveld plots had significantly (or near-significant) higher values compared to fynbos plots at all four scales considered, although one fynbos site (a *Protea repens*-dominated site in Elim fynbos underlain by ferricrete on the Agulhas Plain at Rietfontein) showed values typical of renosterveld, rather than fynbos. Additionally, the percentage of geophytes was higher in renosterveld than in fynbos. Western sites were

Table 2. Number of geophyte species for 1, 10, 100 and 1000 m^2 plots in fynbos and renosterveld vegetation in the Cape. The numbers for the 100 and 1000 m^2 scales are counts for single plots, at the 1 m^2 scale, $N = 10$, while at the 10 m^2, $N = 2$ (R. M Cowling & R. H. Whittaker, unpubl. data). Differences represent P-values for unpaired t-tests (in the case of percentages, arcsine-transformed data were used), with asterisks marking Bonferroni-corrected significance

	1 m^2	10 m^2	100 m^2	1000 m^2	Plants total	Percent geophytes
WESTERN FYNBOS						
Rietfontein	5.1 ± 0.5	13.5 ± 0.5	23	27	112	24.1
Brandewynkop	2.4 ± 0.4	5.0 ± 1.0	7	9	74	12.2
Jakkalsrivier	2.3 ± 0.3	4.0 ± 0.0	6	6	56	10.7
Groot Hagelkraal	1.0 ± 0.2	1.5 ± 0.5	2	5	57	8.8
Soetanysberg	0.2 ± 0.1	2.0 ± 1.0	4	4	47	8.5
EASTERN FYNBOS						
van Stadens Mountains	1.2 ± 0.2	2.0 ± 0.0	2	6	42	14.3
Hankey 1	1.3 ± 0.2	3.0 ± 1.0	7	10	83	12.0
Hankey 2	1.3 ± 0.2	2.5 ± 1.5	4	6	84	7.1
Humansdorp 1	0.5 ± 0.3	1.5 ± 1.5	3	4	45	8.9
Humansdorp 2	0.0 ± 0.0	0.0 ± 0.0	1	5	60	8.3
Humansdorp 3	1.4 ± 0.2	3.5 ± 0.5	4	6	88	6.8
WESTERN RENOSTERVELD						
Tygerberg, Cape Town	6.4 ± 0.6	17.0 ± 0.0	27	38	105	36.2
Signal Hill, Cape Town	3.1 ± 0.3	7.5 ± 1.5	11	18	99	18.2
Bontebok NP	5.0 ± 0.5	10.5 ± 0.5	16	18	51	35.3
EASTERN RENOSTERVELD						
Humansdorp 4	4.8 ± 0.4	12.0 ± 0.0	15	17	74	23.0
Humansdorp 5	3.9 ± 0.4	7.0 ± 0.0	9	11	59	18.6
Humansdorp 6	2.0 ± 0.4	6.0 ± 0.0	9	12	87	13.8
Humansdorp 7	2.1 ± 0.1	5.5 ± 1.5	11	11	85	12.9
Humansdorp 8	3.1 ± 0.3	6.0 ± 0.0	8	10	95	10.5
Grahamstown	2.5 ± 0.3	8.0 ± 1.0	13	15	95	15.8
DIFFERENCES						
fynbos/renosterveld	<0.0001*	<0.0001*	0.0120*	0.0198	–	0.0101*
western/eastern fynbos	<0.0001*	0.0387	0.1964	0.3366	–	0.2940
western/eastern renost.	0.0001*	0.3448	0.5354	0.3986	–	0.2639
west/east	<0.0001*	0.0329	0.1834	0.1645	–	0.1168

generally richer than eastern sites, although at some scales (10–1000 m^2) the differences were not significant (and less so in renosterveld than in fynbos) (Table 2). Similar local-scale numbers for western renosterveld have been observed independently (J. S. Donaldson, pers. comm.), while also showing a geology effect (dolerites being significantly richer than tillite sites) and geophyte cover values averaging 8–19%. Amazing density values in certain small-scale habitats (up to 20 000 corms/m^2 for *Syringodea longituba*) are reported from the same sites (J. S. Donaldson, pers. comm.). Comparative local diversity and abundance data for succulent karoo are needed.

The west is also richer in geophytes than the east at larger scales (16th degree, quarter degree, one degree), as shown in several surveyed genera (e.g. *Pelargonium*: van der Walt & Vorster 1983; *Oxalis*: Oberlander, Dreyer & Esler, 2002). A study documenting geophyte diversity in the winter rainfall region of southern Africa at the quarter degree scale (Proches *et al.*, 2005), indicates that this pattern is almost universal among Cape geophytes (see Fig. 3). As shown at this scale, the south-western Cape (including the

Figure 3. Geographic patterns of diversity in the Cape (at the quarter-degree scale), in two major geophyte families: A, Iridaceae; B, Orchidaceae (data from Proches *et al.*, 2005).

north-western Cape Floristic Region, as delimited in Goldblatt & Manning, 2000a) is definitely the world's geophyte capital, with more than 500 species potentially coexisting in one quarter-degree square (Proches *et al.,* 2005). In several localities in this area (e.g. Nieuwoodtville, Saldanha), geophytes are the dominant growth form, representing *c.* 40% of the total number of plant species (Snijman & Perry, 1987; Hopper & Manning, 2004).

THE BROAD PHYLOGENETIC PICTURE

Cape geophytes belong to a large variety of unrelated groups, most of which have non-geophytic sister taxa. This suggests that, at least in large (family-level) taxa, geophytism must be regarded as a derived state. While looking for further taxonomic and phylogenetic patterns, three questions must be kept in mind. (1) How many times did the geophytic habit originate independently? (2) Were there cases where this was secondarily lost? (3) How many of these transitions are likely to have occurred in the Cape, or elsewhere in southern Africa?

The first distinction that needs to be made is between predominantly geophytic groups (most of the monocot families listed, and the Oxalidaceae); groups that have a significant geophytic component (Orchidaceae, *Pelargonium*); and predominantly non-geophytic groups with a few geophytic representatives (most of the dicots listed in Table 1 and some groups mentioned in the discussion over defining geophytism).

Significantly, many of the geophytes in the third category (genera of Apocynaceae, Aizoaceae, Asteraceae, etc.) are endemic to, or centred in, southern Africa, suggesting that their transition to geophytism happened in this region. This is also the case with *Pelargonium*, where all the geophytic taxa are endemic to southern Africa (Marais, 1994; Bakker *et al.*, 2004). In *Oxalis*, although geophytism is not restricted to the region, it is much more prevalent here than in South America, the other centre of diversity for this genus. This suggests that the Cape may have been globally important in the evolution of geophytism. In particular, the apparently multiple transitions in genera such as *Bulbine* (Asphodelaceae), *Tylecodon* (Crassulaceae), *Pelargonium* (Geraniaceae) or *Othonna* (Asteraceae), between no stored water, above-ground stored water (succulence) and below-ground stored water (geophytism) present a baffling show of morphological plasticity. The Cape is also a centre of diversity and diversification for succulents (Van Wyk & Smith, 2001; Klak, Reeves & Hedderson, 2004); the biogeographical and ecological connections between geophytism and succulence represent yet another interesting field requiring research.
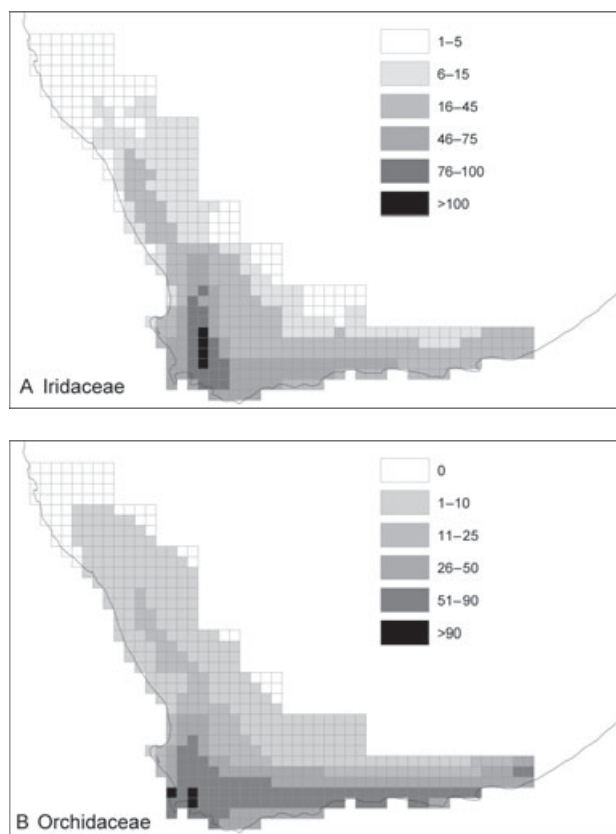
To ascertain the significance of southern Africa in the global context of geophytism, one needs to consider the two orders in which geophytism is best represented, namely Asparagales and Liliales. In the Asparagales, out of the 24 recognized families (APG II, 2003), 14 occur in southern Africa. Two of these, Lanariaceae and Agapanthaceae, are endemic to the region, and another seven have their worldwide centre of diversity here: Amaryllidaceae, Asparagaceae, Asphodelaceae, Hyacinthaceae, Hypoxidaceae, Iridaceae, and Ruscaceae (with the inclusion of *Eriospermum*) (see APG II, 2003). The Behnioideae in Agavaceae may also deserve family-level recognition (Conran, 1999).

While peak species diversity in southern Africa does not necessarily imply a southern African origin, this appears to be the case in at least five families, representing two multifamily clades (Fig. 4). The most suggestive southern African origin is indicated by the Agapanthaceae/Amaryllidaceae/Alliaceae clade. The monogeneric Agapanthaceae, endemic to southern Africa, are rhizomatous, and rhizomes are also found in the only southern African subfamily of Alliaceae, Tulbaghioideae (Fay & Chase, 1996). If rhizomes are plesiomorphic in the Amaryllidaceae (as implied by Nordal & Duncan, 1984 and Müller-Doblies & Müller-Doblies, 1996) then the bulbous habit may have evolved at least three times in the family: in Amaryllideae, in Haemantheae (both centred in the Cape),

and within the ancestral stock for the rest of the family (although alternative scenarios are plausible; see Meerow *et al*., 1999 for a familial phylogeny and discussion of character state evolution).

A second dichotomy, the one between Asparagaceae and Ruscaceae (Chase *et al*., 2000a; Fay *et al*., 2000; but not supported by Soltis *et al*., 2000), again points to southern Africa, the largely African genera *Dracaena* (including *Sansevieria*) and *Eriospermum* having a basal position in Ruscaceae, while the Asparagaceae are also most diverse in southern Africa. The origins of two other important geophytic families, Asphodelaceae and Hyacinthaceae, are less obvious. Evidence suggests a South American origin for Hyacinthaceae, followed by massive radiation in southern Africa (Manning *et al*., 2004), while the origins of Asphodelaceae were most likely Eurasian (Chase *et al*., 2000b).

In Liliales, too, the most plesiomorphic groups (Alstroemeriaceae, Luzuriagaceae, Campynemataceae) have limited distributions in mainly non-mediterranean climates in the southern hemisphere, while the major radiations happened in mediterranean climates (the core Colchicaceae in the Cape, *Tulipa* and other Liliaceae in the Mediterranean Basin) (Vinnersten & Bremer, 2001).

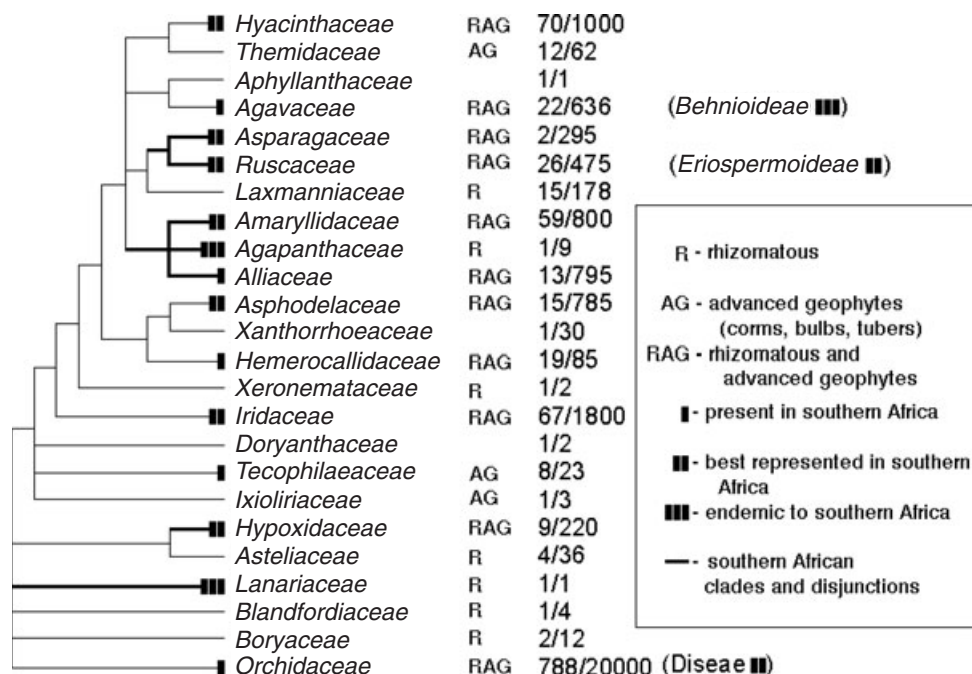Given the basal position of rhizomatous (geophytic or non-geophytic) herbs in most families of the Aspar-

Figure 4. Phylogenetic relationships in the Asparagales (based on Chase *et al*., 2000a; Fay *et al*., 2000; Soltis *et al*., 2000; APG II, 2003; Rudall, 2003; only recognizing clades with > 50% support), indicating geophytism (Stevens, 2001) and southern African taxa (see Leistner, 2000). Numbers of genera/species indicated for each family, based on Stevens (2001).

agales and Liliales (see Fay *et al.*, 2000; Stevens, 2001; Vinnersten & Bremer, 2001), it can be assumed that more efficient storage organs (tubers, corms, bulbs; see Lewis, 1954) evolved independently in almost each family, and more than once in some families (e.g. Iridaceae; see Reeves *et al.*, 2001). Family-level differentiation certainly occurred long before the onset of mediterranean climates in the mid Pliocene, and most of the isolated plesiomorphic lineages persist to the present day in non-mediterranean regions (in Australasia, South America and eastern South Africa). Later, within most families, more advanced storage organs evolved, and these transitions are likely to have been a key factor in diversification.

Such transitions almost certainly occurred in southern Africa in the cases of Iridaceae, Ruscaceae and Amaryllidaceae, probably triggered by the climate changes that started in the late Eocene, and became dramatic during the Oligocene and Miocene (see Axelrod & Raven, 1978; Goldblatt, 1983; Zachos *et al.*, 2001). Unfortunately, relatively few phylogenies are available for tracking this process. Speciation in *Androcymbium* (Colchicaceae) appears to have started in the late Eocene (when the genus was presumably already geophytic) and intensified during the Oligocene (Caujapé-Castells *et al.*, 2002), while the separation of *Moraea* and *Ferraria* happened during the Oligocene, followed by fairly constant speciation in *Moraea* during the Oligocene and Miocene (Goldblatt *et al.*, 2002; V. Savolainen & P. Goldblatt, unpubl. data). However, in the most species-rich Cape geophytic group, the Crocoideae (Iridaceae), the genera separated more recently, during the Miocene and Pliocene, and this radiation was followed by rapid speciation, probably triggered by the aridification and increased rainfall seasonality in the mid Pliocene (Reeves *et al.*, 2001; Goldblatt *et al.*, 2002, 2005). Rapid speciation during the Pliocene may also have occurred in many smaller groups, though more phylogenies are needed to confirm this hypothesis. In addition to climate change, another factor that may have contributed to this speciation process was the rejuvenation of the Cape landscapes following a massive uplift in the east during the Pliocene (Deacon, Jury & Ellis, 1992), which must have increased habitat diversity. Under the new climatic conditions geophytes were clearly favoured, as compared to their non-geophytic relatives, and speciated more extensively.

In several instances non-geophytic lineages are significantly poorer in species than their geophytic sister taxa. Thus there are ten (or less, depending on the species concept used) species of Agapanthaceae (all rhizomatous), compared with 230 species in the almost entirely bulbous sister taxon, the Amaryllidaceae (numbers for southern Africa only). This situation is repeated twice in Iridaceae: subfamily Nivenioideae (shrubby) has less than one hundred species, compared to almost a thousand species in the sister subfamily Crocoideae (cormous); in the Irideae, the rhizomatous *Dietes–Bobartia* grade has less than 20 species in all, while the embedded clade *Ferraria–Moraea*, made up entirely of cormous (and almost entirely African) species, totals over 200 species (Goldblatt, 1990; see Reeves *et al.*, 2001 for phylogeny, Lewis, 1954 for morphology). Almost every other geophytic family of Asparagales has a few rhizomatous genera with significantly lower diversity values than the geophytic sister clades (with corms, bulbs or tubers) (Fig. 4).

The Orchidaceae, with a basal position in Asparagales, do not appear to have had any association with southern Africa during their early history. Several orchid clades colonized the Cape area, but only one diversified extensively here. This is the largely African tribe Diseae, containing the spectacular and species-rich genera *Disa* and *Satyrium*. Unlike in higher Asparagales families, the geophytic condition appears to be primitive in orchids, and a great proportion of the orchid diversification happened secondarily in non-geophytic clades (mainly epiphytes). Among the lineages that diversified in the Cape, most are primarily geophytic; however, in some cases this habit was secondarily lost (e.g. there are evergreen species of *Disa*, *Satyrium*, and Coryciinae in which the storage organs are reduced or absent) (Linder & Kurzweil, 1999). Both in the core Asparagales and in Orchidaceae (and also in Hypoxidaceae), important radiations have also taken place in the summer rainfall region of southern Africa, in particular in the moister parts of the grassland biome.

Since geophytism has evolved numerous times, in different parts of the world, and flourished mainly in semiarid regions, it is interesting to examine whether there was any exchange of taxa between different mediterranean-climate areas. This is obvious in the northern hemisphere genus *Allium*, that has broad radiations in both the Mediterranean Basin and California, and which occurs in non-mediterranean climates in between the two regions, but southern hemisphere distributions are more ambiguous. Several highly disjunct generic distributions are known (e.g. *Wurmbea* and *Bulbine*: Africa and Australia; *Spiloxene*: Africa, Australia and New Zealand; *Bulbinella*: Africa and New Zealand; *Caesia*: Africa, Australasia and Madagascar; *Trachyandra*: Africa and Madagascar; *Dietes*: southern Africa and Lord Howe Island).

With the exception of *Bulbinella* and *Spiloxene*, none of these are true 'Cape' (or mediterranean-climate) genera and their species are distributed in both mediterranean and non-mediterranean climates. Comparable disjunct distributions are lacking within

the 'core' Cape geophytic clades (the Crocoideae and core Iridoideae of Iridaceae, Amaryllidaceae and Hyacinthaceae). The age of these clades is generally too young to represent Gondwanan relicts (Donato, Leach & Conran, 2000; Vinnersten & Bremer, 2001). At the same time, advanced geophytism is too old to have originally evolved in mediterranean climates (which are a Late Pliocene-Quaternary feature), and in some cases it may have coevolved with the pre-mediterranean sclerophyllous vegetation that was widespread in mediterranean-climate areas during the Tertiary (Axelrod, 1975; Herrera, 1992; Verdú *et al*., 2003). Despite this remarkable antiquity, several geophyte lineages are relatively range-restricted, suggesting limited dispersal abilities or habitat specialization (see Conran, 1995). At least in *Dietes* and *Wurmbea*, however, the disjunct distributions appear to be the result of single long-distance dispersal events, suggesting that, occasionally, such events do happen. Among the 'Cape' genera it is therefore very likely that the lack of suitable habitats across the southern Hemisphere was important in preventing the spread of taxa among the isolated mediterranean-climate regions.

In contrast, continuous distributions from the Cape to the Mediterranean Basin (*Androcymbium*, *Chlorophytum*, *Drimia*, *Gladiolus*, *Hesperantha*, *Moraea* sect. *Gynandriris*, *Ornithogalum* and *Romulea*) suggest that geophyte exchanges were more frequent between these two regions. More often, it is the Cape taxa that have invaded northwards, as suggested by biogeographical patterns and recent phylogenies for both geophytes and other plants (Quézel, 1978; Cowling, Procheş & Vlok, 2005b). For example, in *Androcymbium*, most of the species (the most plesiomorphic ones included) occur in southern Africa (Caujapé-Castells *et al*., 2002), while some derived species, as well as the embedded clade *Colchicum–Merendera–Bulbocodium* (Vinnersten & Reeves, 2003), are found in the Mediterranean Basin. A similar picture is starting to take shape in the Hyacinthaceae, with the Mediterranean species of *Drimia* and *Ornithogalum* embedded within southern African or sub-Saharan groups of species (Pfosser *et al*., 2003; Manning *et al*., 2004), and in *Ornithogalum* it appears that more than one invasion into the Mediterranean must have occurred. Overall, however, it is likely that the Cape has contributed significantly to the geophyte flora of the Mediterranean Basin, and possibly that of other regions.

MORPHOLOGICAL DIVERSITY AND SPECIATION

Cape geophytes have gained their reputation among horticulturists because of their spectacular flower displays, and this amazing floral diversity has been linked to pollinator specificity. Indeed, a variety of pollination systems have been described for each of several genera (e.g. *Lapeirousia*: Goldblatt, Manning & Bernhardt, 1995; *Satyrium*: Johnson, 1997; *Gladiolus*: Goldblatt, Manning & Bernhardt, 1998; *Sparaxis*: Goldblatt, Manning & Bernhardt, 2000). These studies show that long-tongued flies, bees, butterflies, moths, and birds have each driven the evolution of their own guild of plants containing, in each case, several unrelated taxa. It can hardly be contested that pollinator specificity accounts for a great proportion of the character diversity in Cape geophytes. However, it has not been conclusively demonstrated that pollinator specificity alone can trigger speciation. In most instances other factors are also involved, such as edaphic (e.g. in Iridaceae: Goldblatt, 1983; Goldblatt & Manning, 1996a, b), and climatic specialization (e.g. *Moraea* sect. *Galaxia*: Goldblatt, 1979, and *Disa* sect. *Herschelia*: Linder, 1995). Furthermore, the morphological diversity displayed by the vegetative parts (both above-ground and below-ground) has largely been neglected.

Our analysis (Fig. 5) showed that while reproductive features do indeed account for the most obvious species-specific characteristics in the majority of Iridaceae (*Moraea*, *Gladiolus*, *Lapeirousia*), and even more so in Orchidaceae (*Disa*, *Satyrium*), the repro-
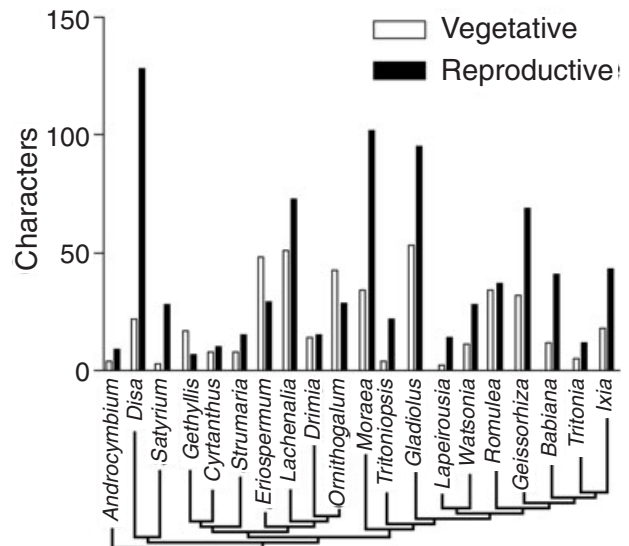

Figure 5. Diversity of reproductive and vegetative characters in some speciose geophytic genera in the Cape. Based on the characters cited in naural dichotomous keys from Linder & Kurzweil (1999) and Manning *et al*. (2002). Since generic-level keys were used, the ratio between vegetative and reproductive characters in each genus is likely to represent a good approximation of the reality; however, intergeneric comparisons may not be strictly valid. Phylogenetic relationships based on Meerow *et al*. (1999), Chase *et al*. (2000a), Reeves *et al*. (2001), and Goldblatt *et al*. (2005).

ductive component accounts for less than 50% of the character diversity in *Eriospermum* (Ruscaceae), and in some Hyacinthaceae (*Ornithogalum*) and Amaryllidaceae (*Gethyllis*). In other genera such as *Romulea* (Iridaceae), *Strumaria* (Amaryllidaceae) and *Lachenalia* (Hyacinthaceae), both vegetative and reproductive biology have contributed significantly to character diversity. While the proportions of characters recorded in this analysis cannot be automatically equated to the factors driving speciation, these results nevertheless suggest that reducing geophyte diversification in the Cape to its pollination component is simplistic. It must also be noted that not all the differences in the morphology of reproductive parts have to do with pollination (e.g. the shape of the inflorescence in many Amaryllideae enhances wind dispersal in the infructescence; Snijman & Linder, 1996), and not all those affecting pollination directly relate to pollinator specificity.

Most of the vegetative characters listed in geophyte keys referred to leaf shape, size and texture, indicating adaptations to local climatic conditions. Several characteristic leaf shapes recurring in unrelated groups of Cape geophytes represent a spectacular indication of geophyte morphological plasticity. The best known such case is the prostrate leaf syndrome, characterized by few (often two) flattened leaves, pressed to the ground, as observed in Amaryllidaceae (*Brunsvigia*, *Crossyne*, *Haemanthus*, *Strumaria*), Colchicaceae (*Androcymbium*), Hyacinthaceae (*Daubenya*, *Lachenalia*, *Massonia*, *Ornithogalum*), Ruscaceae (*Eriospermum*), Orchidaceae (*Bartholina*, *Holothrix*, *Satyrium*), and Iridaceae (*Freesia*, *Sparaxis*, *Xenoscapa*) (Esler *et al.*, 1999; Manning *et al.*, 2002). This strategy has been interpreted as representing an advantage in avoiding herbivory or competition from neighbours, in creating a CO_2-rich environment underneath the leaves, or in regulating evapotranspiration (Esler *et al.*, 1999). Coiled, wiry leaves are equally spectacular, and even less investigated, occurring in Amaryllidaceae (*Cyrtanthus*, *Gethyllis*) Colchicaceae (*Androcymbium*), Hyacinthaceae (*Ornithogalum*, *Drimia*), Iridaceae (*Moraea*, *Geissorhiza*) and Orchidaceae (*Disa*). Inspection of monographs and our own observations indicates that this trait is almost exclusively associated with sparse vegetation on rocky sites, especially gravel plains. Coiling may well be an adaptation to reduce wind damage to the relatively large photosynthetic organs required to maximize photosynthetic activity in the cool growing season.

Special mention must be made here of leaf-shape diversity in *Eriospermum*, whose current position is in Ruscaceae (APG II, 2003) but which has been considered to represent a family on its own (Eriospermaceae; see Perry, 1994). This remarkable genus contains over 100 species, most of which occur in succulent karoo, but with numerous fynbos, thicket, grassland, and savanna species. Although floral characters are used in its subgeneric classification, these are far less spectacular than the leaves. In this genus, the number of leaves has been reduced – generally to one – and this can take a variety of shapes, from linear or terete to heart-shaped. However, the most interesting evolutionary process in *Eriospermum* is one through which the reduction in photosynthetic surface area brought about by the reduced number of leaves is reversed by the development of unusual outgrowths ('enations') on the leaf surface. These take the form of solitary or numerous, often tree-shaped excrescences, with varying degrees of hairiness, representing a whole new class of photosynthetic organs (see Perry, 1994). This feature – associated with an enlargement of the photosynthetic organ – may have evolved in response to the development of winter-wet climates, characterized by low-energy growth conditions for shallow-rooted plants.

Herbivory has also been invoked as a selective force driving plant speciation (Westoby, 1989). However, leaf characteristics associated with antiherbivore specialization, such as hair cover, are uncommon in Cape geophytes, suggesting that above-ground herbivory was probably less important in species differentiation (but see Amaryllidaceae: *Brunsvigia*, *Crossyne*, *Gethyllis*, *Haemanthus*, *Strumaria*, and Hypoxidaceae: *Hypoxis*). More important appears to be below-ground herbivory. Underground organs, unlike leaves and flowers, are present throughout the year, offering greater opportunities for herbivore specialization. At least two species-rich groups of herbivores have diversified in the Cape, mainly in association with geophytes: the *Brachycerus* weevils (Coleoptera: Curculionoidea), of which there are more than a hundred species in the region, and the mole rats (Rodentia: Bathyergidae), with at least five species. Up to three species of mole rat can co-occur in the same habitat (Lovegrove & Jarvis, 1986). Numerous geophytes are restricted to rocky areas, where mole-rat activity is limited (cf. Thomson *et al.*, 1996), while other species survive in the protection offered by Restionaceae tussocks. Special adaptations, including storage and perennation organs situated at different depths in the soil, have developed in geophytes that occur in mole-rat populated habitats (Lovegrove & Jarvis, 1986), and these may be a significant force in speciation, having to do with both predation avoidance and dispersal (e.g. in *Micranthus*). Both below-ground and above-ground predation may also be avoided by the accumulation of highly toxic substances (especially in Amaryllidaceae, Colchicaceae and Hyacinthaceae). The potential role that this chemical evolution may have played in Cape geophyte diversification is not clear and requires further study.

Very little is known of the possible effect of storage organs size on habitat specialization. It has been shown (Procheş *et al.,* 2005) that larger storage organs are more likely to occur where rainfall is less abundant or less predictable, although storage organ size may also have to do with microhabitats, possibly with the local drainage conditions. Within the seven genera analysed here (*Geissorhiza*, *Moraea*, *Watsonia*, *Gladiolus*, *Eriospermum*, *Haemanthus* and *Cyrtanthus*), a remarkable variation was observed in the size of the storage organs (Fig. 6). Some genera, such as *Haemanthus*, are characterized by relatively large bulbs; others, like *Geissorhiza* and *Gladiolus*, by relatively small corms. In most other genera, however, the size of the storage organs varies from species to species, even by a few orders of magnitude. Figure 6 does not reflect the complete range of sizes, the corms in minute geophytes like *Romulea* being smaller than in any of the included taxa, while the (arguably geophytic) tubers of *Dioscorea* and some Apocynaceae can reach 1 m in diameter. The possibility that underground organs may actually fulfil several basic functions could add new dimensions to habitat specialization. Thus, while the main function of geophytism is currently understood as that of water storage (Rees, 1989), it is clear that geophytism also presents an advantage in mineral ion storage (Ruiters & McKenzie, 1994). The different types and sizes of underground organs could, interpreted in this light, yield much more information relating to habitat (and especially edaphic) specialization.
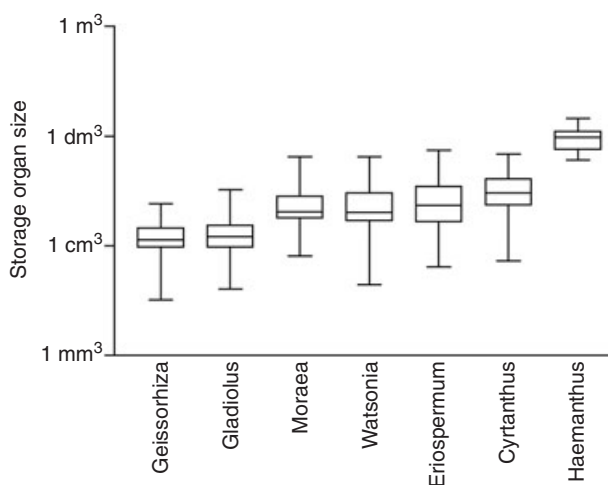

Figure 6. Storage organ size for seven large Cape geophyte genera. Median, central 50% of the values, and ranges are given (data from Reid & Dyer, 1984; Snijman, 1984; Goldblatt, 1985, 1986, 1989; Perry, 1994; Goldblatt & Manning, 1998). The storage organs are annually replaced in the first four genera, but not in the last three, in which they have continuous growth.

In addition, little is known of whether certain types of storage organ are more appropriate than others in specific habitats. According to Ruiters (2001), the four basic types of storage organ showed similar diversity patterns in the south-western Cape (41% of the species had corms, 32% tubers, 17% bulbs, and 10% rhizomes). Similar patterns were found by Hoffmann *et al.* (1998) for the geophyte flora of Chile. This is surprising, considering that most corms and tubers are replaced annually, thereby imposing a size limit on these types of organ, while bulbs, rhizomes and hypocotyledonary tubers are not. However, no clear size differences were observed between bulbous and cormous organs in the genera examined here (Fig. 6), although the largest storage organs were indeed found in the last three genera, where continuous growth occurs. While the corms of Colchicaceae, Hypoxidaceae or Iridaceae never approach the maximum dimensions achieved by the largest bulbs in certain genera of Amaryllidaceae (e.g. *Boophone*, *Brunsvigia* and *Crinum*), in several other genera of Amaryllidaceae (*Hessea*, *Nerine* and *Strumaria*) the bulbs of many species are no larger than most corms.

Another set of interspecific differences refer to phenology. Our review of patterns in seven genera shows Cape geophyte phenology to be very variable and characterized by a considerable percentage of evergreen species. Among the deciduous species, both synanthous and hysteranthous species are represented, the former leafing and flowering at the same time, while in the latter the flowers are produced in the dry season prior to or after the leaves (Dafni, Cohen & Noy-Meir, 1981; Ruiters & McKenzie, 1994). Among the seven genera analysed, 69% of the species were synanthous, 22% hysteranthous, and 9% evergreen. Including orchid genera in this analysis would undoubtedly increase the proportion of evergreen species. The percentage of evergreen species in the local geophyte floras increased from zero (in the dry areas of Namaqualand) to 20% in moister, less seasonal areas, such as Knysna, in the southern Cape. In typical deciduous species, the coupling between flower emergence and leaf emergence also varied geographically, with hysteranthous species being more numerous in Namaqualand (40%) and rare in the eastern part of the Cape (14% Knysna, 12% Humansdorp) (Fig. 7).

The differences between synanthous and hysteranthous geophytes have been attributed to resource allocation, as optimized for different environments (Dafni *et al.*, 1981; Gutterman & Boeken, 1988), and this seems to correspond to the results presented here, hysteranthous species occurring mainly in areas of scarce and more strictly seasonal rainfall. A different pattern characterizes *Gladiolus*, where hysteranthy is more common in the south-west (see Goldblatt & Manning, 1998). It has been shown that there is sometimes
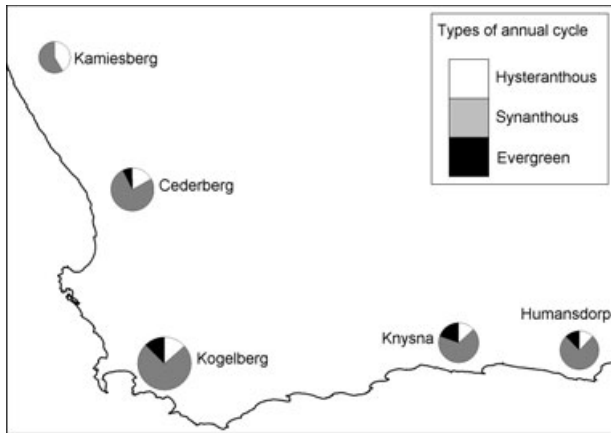
Figure 7. Representation of hysteranthous, synanthous, and evergreen geophytes at five localities in the Cape. Pie size is proportional to the total numbers of species (data from Reid & Dyer, 1984; Snijman, 1984; Goldblatt, 1985, 1986, 1989; Perry, 1994; Goldblatt & Manning, 1998).

also a phylogenetic component to phenology, with certain groups that originated in summer-rainfall areas (e.g. some Amaryllidaceae) adhering to their summer-flowering patterns even in the winter-rainfall region (Johnson, 1992; Snijman, 1999).

FINAL LINES

What are the mechanisms making it possible for so many geophyte species to coexist at different spatial scales in the Cape? The importance of topographic heterogeneity in the maintenance of species diversity in the Cape has been shown for plants in general (Cowling *et al.*, 1997) and specifically for geophytes (Ruiters, 2001), at scales close to quarter-degree. At this scale, which encompasses entire landscapes and much heterogeneity, it is likely that non-reproductive adaptations are the main explanation for geophyte species diversity. The high species replacement rates within landscapes that characterize much of the fynbos biome (Cowling *et al.*, 1997) indicate that climatic or edaphic specialization may hold the key to coexistence.

At the local (community) scale, it appears that environmental heterogeneity alone cannot alone explain richness, since highest diversity is recorded in renosterveld, even in relatively homogeneous environments. Clearly, other factors such as pollination biology have an important role to play. Given the relatively small number of pollinator species (Johnson & Bond, 1997), additional specializations such as staggered flowering season (Gleeson, 1981), nototribic vs. sternotribic pollen deposition (e.g. Goldblatt & Manning, 2000b) or sterility barriers (e.g. Johnson *et al.*, 1998), are certainly of importance in enabling several

different plant species to coexist without competing for pollinators. Frost-free sites at low altitudes in the Cape can benefit from pollinator activity year-round, and indeed these have remarkable geophyte diversities, but comparisons with high altitudes are not possible, as comprehensive records of geophyte diversity are lacking in this latter environment. Additionally, phenological differences – some directed by phylogenetic constraints (Snijman, 1999) – may add extra niche space.

However, these different explanations for different scales need not always imply different speciation histories. In some instances, pollinator and edaphic specificity go together, and it has been suggested that the main factor leading to divergence may be the adaptation to a new substratum, while pollination serves to seal the speciation process (Goldblatt & Manning, 1996a). More two-species case studies, ideally involving plant translocation, would be needed to partition the contribution of pollinators, substratum, and possibly other factors to present-day diversity.

At the scale of the entire Cape region, the western vs. eastern contrasts are unlikely to be explained by differences in edaphic or topographic heterogeneity, since these do not vary significantly at the local and landscape scales along this gradient (Campbell, 1983; Deacon *et al.*, 1992; Cowling & Lombard, 2002). The more heterogeneous rainfall seasonality in the east should, if anything, produce higher diversity here, by enabling summer-active bulbs to invade and persist (e.g. Drakensberg species). While eastern landscapes do include many summer rainfall species, especially in the orchids but also other groups (e.g. *Ledebouria, Tritonia*), this does not seem to have had an effect on richness at all scales. For a given rock type, eastern soils are marginally more fertile than western ones (Campbell, 1983). However, our renosterveld–fynbos and west–east comparisons are not consistent with the hypothesis that lower soil fertility should result in higher richness via finer niche partitioning (Tilman, 1986). With regard to biological factors, pollinator diversity is probably greater in the east (Ş. Proches & R.M. Cowling, unpubl. data). Most likely, the greater diversity in the west has to do with long-term climatic stability, which reduced extinction rates and allowed diversification processes to continue uninterrupted throughout the Quaternary, whereas in the eastern fynbos, climate change appears to have caused large-scale vegetation disruption, thereby enhancing extinction rates (Cowling *et al.*, 1999a). On shorter time scales, the less predictable rainfall regime in the east (Cowling *et al.*, 2005a) may limit geophyte diversity by filtering out those species that require predictable rains in order to amass adequate resources for reproduction. Competition from grasses may also limit the spread of certain geophyte groups in the east, where

grass cover is greater, although this hypothesis, too, would need proper testing.

On a global scale, mediterranean-type ecosystems are likely to owe their geophyte richness to pronounced rainfall seasonality and to the occurrence of fire, which creates a second (multiyear) periodicity, and temporarily reduces competition (see e.g. Hoffman, Moll & Boucher, 1987; Schwilk, Keeley & Bond, 1997). In geophytes, fire does not create a reproductive barrier between generations, speeding up evolution, as has been suggested in the case of plants that are killed by fire (Cowling, 1987). However, the increased patchiness of fire-prone landscapes is likely to increase speciation in geophytes too (cf. Verboom, Linder & Stock, 2003, where the case of some bulbous grasses is discussed). Fire also creates special niches for geophytes. In the Cape, there are numerous species that only flower or germinate after burning (in Amaryllidaceae, Asphodelaceae, Geraniaceae, Haemodoraceae, Hyacinthaceae, and Iridaceae; Le Maitre & Brown, 1992; Brown, van Staden & Johnson, 2003). Fire and seasonality concur to temporarily eliminate competition from shrubs and grasses, and encourage the geophytic lifestyle. In comparison to other mediterranean-type ecosystems, the key to the Cape's unequalled geophyte richness may again have to do with climatic stability. During the Quaternary, southern Africa is likely to have been one of the world's most climatically stable land masses (Weaver *et al.*, 1998). In terms of short-term rainfall reliability, it comes second only to south-western Australia (Cowling *et al.*, 2005a), which, on the other hand, has much less to offer in terms of topographical diversity.

A stable climate with reliable seasonal rainfall over a relatively long period of geological time, in combination with topographically diverse landscapes, was perhaps the key factor determining the amazing diversity of geophytes in the Cape. While the examined landscapes enabled population isolation on different substrata and the associated diversification processes (augmented by pollinator specialization), climatic stability minimized extinction, thus leading to the uninterrupted accumulation of species over the last few millions of years. Within the huge array of resulting taxa, it was more likely here than anywhere else in the world that unusual pollination syndromes and leaf shape adaptations should recur in numerous unrelated taxa.

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