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# PLANT DIVERSITY OF THE CAPE REGION OF SOUTHERN AFRICA<sup>1</sup>

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## ABSTRACT

Comprising a land area of ca. 90,000 km<sup>2</sup>, less than one twentieth (5%) the land area of the southern African subcontinent, the Cape Floristic Region (CFR) is, for its size, one of the world's richest areas of plant species diversity. A new synoptic flora for the Region has made possible an accurate reassessment of the flora, which has an estimated 9030 vascular plant species (68.7% endemic), of which 8920 species are flowering plants (69.5% endemic). The number of species packed into so small an area is remarkable for the temperate zone and compares favorably with species richness for areas of similar size in the wet tropics. The Cape region consists of a mosaic of sandstone and shale substrata with local areas of limestone. It has a highly dissected, rugged topography, and a diversity of climates with rainfall mostly falling in the winter months and varying from 2000 mm locally to less than 100 mm. Ecological gradients are steep as a result of abrupt differences in soil, altitude, aspect, and precipitation. These factors combine to form an unusually large number of local habitats for plants. Sandstone-derived soils have characteristically low nutrient status, and many plants present on such soils have low seed dispersal capabilities, a factor promoting localized distributions. An unusual family composition includes Iridaceae, Aizoaceae, Ericaceae, Scrophulariaceae, Proteaceae, Restionaceae, Rutaceae, and Orchidaceae among the 10 largest families in the flora, following Asteraceae and Fabaceae, as the most speciose families. Disproportionate radiation has resulted in over 59.2% species falling in the 10 largest families and 77.4% in the largest 20 families. Twelve genera have more than 100 species and the 20 largest genera contribute some 31% of the total species. Species richness of the Cape flora is hypothesized to be the result of geographic and parapatric radiation in an area with a mosaic of different habitats due to local soil, climate, and altitudinal differences that combine to produce steep ecological gradients. Also contributing to the diversity has been a relatively stable geological history since the end of the Miocene that saw the establishment of a semi-arid and extreme seasonal climate at the southwestern part of southern Africa.

*Key words:* floristics, Mediterranean-type climate, phytogeography, plant diversity, southern Africa, speciation.

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Situated at the southwestern tip of the African continent between latitudes 31° and 34°30'S (Fig. 1), the area that has come to be called by biologists the Cape Region has a flora, and to a lesser extent a fauna (Stuckenberg, 1962), that is so sharply distinct from that of the land immediately adjacent to it that it has impressed naturalists from the time of its discovery by European explorers in the 16th century. Indeed, the floristic characteristics of the Cape Region are so unusual that it has sometimes been regarded as one of the world's six floral kingdoms (e.g., Good, 1974; Takhtajan, 1986). There are, however, no objective criteria for distinguishing such "floral kingdoms," and recognition of a Cape Floral Kingdom is not universal. We use the neutral term "floristic region" here simply for convenience.

Comprising a land area of ca. 90,000 km<sup>2</sup>, less than 5% of the total area of the southern African

subcontinent (Goldblatt, 1978, 1997), the Cape Floristic Region (CFR) is one of the world's most botanically diverse regions. An estimated 9030 species of vascular plants (ferns and other vascular cryptogams, gymnosperms, and flowering plants), the majority of which, some 8920 in total, are flowering plants, occur there, almost 69% of which are endemic (figures based on Goldblatt & Manning, 2000, but reflecting taxonomic changes made since the completion of that work). Thus, the flora of the Cape Region comprises 44% of the estimated 20,500 species that occur in all of southern Africa (Arnold & de Wet, 1993; de Wet, pers. comm.). The level of species richness is notable, particularly in Africa, the tropical flora of which is relatively depauperate, but is remarkable for the world's temperate zone, comparing favorably with species richness for areas of comparable size in the wet tropics rather than for areas of temperate climate.

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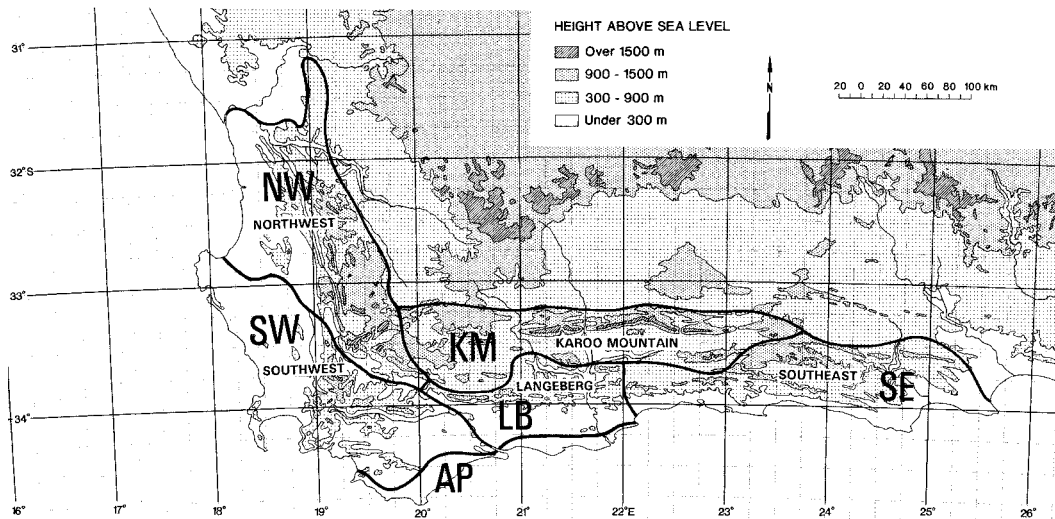


Figure 1. The Cape Floristic Region, showing relief, with the phytogeographic centers marked (from Goldblatt & Manning, 2000). Abbreviations: AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; NW, Northwestern; SW, Southwestern; SE, Southeastern.

Not only is the plant species richness of the Cape flora exceptional, but its familial and generic composition is remarkable (Bond & Goldblatt, 1984; Goldblatt, 1997; Goldblatt & Manning, 2000). Unexceptionally for a region of fairly dry climate, the largest families are the Asteraceae and Fabaceae, together comprising some 20% of the total species. The families next in size, however, are not matched in any other flora—nowhere else in the world do Iridaceae, Aizoaceae, Ericaceae, Proteaceae, and Restionaceae assume such numerical significance, except in some parts of Australia where Proteaceae and Restionaceae are also unusually well represented. Other peculiarities of the Cape flora are the dominance of fine-leaved sclerophyllous shrubs, the paucity of trees, and a remarkably large number of geophytes, here defined as seasonal herbaceous perennials with bulbs, corms, tubers, or prominent rhizomes (thus excluding shrubs and subshrubs that resprout from a woody caudex, usually after fire). Such geophytes, especially numerous among the monocots (notably, in order of importance, Iridaceae, Orchidaceae, Hyacinthaceae, and Amaryllidaceae), also include many species of *Oxalis* (Oxalidaceae) and *Pelargonium* (Geraniaceae) as well as other eudicots. Geophytes as so defined comprise slightly more than 17% of the species in the CFR. Conversely, the Cape flora has a surprisingly low proportion of annuals for an area of largely semi-arid climate. Approximately 6.8% of the species are annuals, which is a striking contrast to California

(30% annuals) or Chile (nearly 16% annuals) (Kalin Arroyo et al., 1994), areas of comparable latitude and climate. Both geophytes and annuals are primarily adapted to seasonally dry climates and escape the time of year unfavorable for growth by retreating to underground storage organs or by ensuring continued survival only by the production of seeds.

The compilation of a synoptic flora of the Cape Region (Goldblatt & Manning, 2000) replaces earlier vegetational analyses based on the work of Bond and Goldblatt (1984), now very much out of date. Statistics presented here are taken from Goldblatt and Manning (2000), with minor modifications reflecting taxonomic changes in press or published since its completion. Familial and ordinal taxonomy is that recommended by the Angiosperm Phylogeny Group (APG, 1998). Changes in the CFR made since this synoptic classification was published are recognition of Veronicaceae (now including Plantaginaceae and several genera previously of Scrophulariaceae), enlargement of Stilbaceae to include non-Cape genera, the reduction of Achariaceae in Flacourtiaceae, and Prioniaceae in Thurniaceae, and the transfer of *Hyaenanche* from Euphorbiaceae to Picrodendraceae (= Pseudanthaceae) (Olmstead et al., 2001, and pers. comm.; Chase et al., 2000; Savolainen et al., 2000). Tamaricaceae, represented by one species of *Tamarix*, was omitted in error from the account of the flora. These changes are represented in the revised familial statistics.

## PHYSICAL CHARACTERISTICS

### LANDSCAPE AND CLIMATE

Mountain belts of the Cape Region are not particularly high, generally 1000–2000 m in elevation, and although the peaks are well below a truly alpine zone at the latitude of the Cape region, they are high enough for winter freezing to be a factor affecting the vegetation. The mountains are rugged, and cliffs and exposed rock are evident everywhere. The rugged topography and vertical landscape amplify the effects of local climatic variation with the result that the mountains offer a greater diversity of habitats than are present in the lowlands.

The climate is largely mediterranean, and strictly so in the west, although the eastern half of the CFR receives substantially more summer precipitation. Rain thus falls mainly in the winter months and while summers are hot and dry, they are relatively less so in the east. In areas of low total rainfall, the average monthly precipitation distributed in the summer months may be higher, notably in the Little Karoo, but due to more favorable precipitation/evaporation (P/E) ratios effective rainfall is still mainly in the winter. South-facing mountain slopes benefit from summer moisture in the form of rain or fog from the southeast trade winds. The narrow coastal plain in the Knysna area, which has a comparatively equable climate and high rainfall, supports an evergreen, broad-leaved forest. Likewise, sheltered valleys and locally wet sites throughout the region, affording higher P/E ratios, support forest vegetation.

Local variation in rainfall is particularly pronounced in mountainous areas, and this is important when precipitation is orographic. Mountain slopes facing prevailing winds receive considerably more precipitation than those in the lee. Rainfall patterns in the Cape Region show dramatic variation in quantity, dropping from 2000 mm per year on the high mountains of the ranges immediately facing the coast, to less than 200 mm on the leeward slopes of the interior ranges. Mosaic effects of soils across the entire region are thus complicated by variation in precipitation from the coast to the interior, as well as changes in seasonality from the west to the east. In addition, elevation and aspect affect precipitation depending on the direction of moisture-bearing winds. The eastern and western parts of the CFR are considered to be under fundamentally differing climatic controls, probably a long enduring pattern that has affected the evolutionary histories of the areas and, hence, resulting in their distinctive floras and faunas (Cowling et al., 1999).

The number of ecological niches available to plant life is multiplied by soil differences, and this is particularly pronounced as precipitation levels drop. With ample rain the effect of soil on vegetational composition is less prominent. Rainfall is limiting almost throughout the region, however, and vegetation varies conspicuously with soil and available moisture. Climatic gradients are steep, although perhaps not more so than in most other areas of mediterranean climate, but the effect may be compounded in the Cape Region by soil diversity. Different soil types in the Cape Region support characteristic vegetation types depending on associated levels of precipitation. Forest vegetation is typical of deeper soils and sites where precipitation is high and fairly evenly spread throughout the year. As soil qualities change and precipitation becomes lower or more seasonal, forest gives way to shrubby or herbaceous vegetation types. On sandy soils, forest yields to a sclerophyllous vegetation (fynbos) in which species diversity decreases and composition changes until rainfall minimums reach about 300–250 mm p.a. when a succulent shrubland becomes dominant. On clay soils forest gives way to fynbos and then to the characteristic renosterveld, a shrubland dominated by shrubby, microphyllous Asteraceae. At precipitation levels below 100 mm p.a. renosterveld is increasingly dominated by succulent perennials. The dissected landscape ensures that broad sweeps of one vegetation type are isolated from others by habitats that will not support their growth. The mosaic of different soil types alone contributes to increasing diversity, but the peculiar nature of nutrient-poor soils may result in more pronounced effects on plant diversity, plant dispersal, and hence gene flow.

### GEOLOGY AND SOILS

Over most of its surface the Cape Region is covered by soils derived from rocks of pre-Carboniferous age (King, 1962), thus more than 400 mya (Fig. 2). Most of these rocks comprise part of the Cape System, an ancient Devonian–Ordovician series of sediments consisting of alternating layers of largely quartzitic sandstones (the Table Mountain and Witteberg Groups) or fine-grained shales (the Bokkeveld Group). During the Jurassic the land surface was folded and warped as Antarctica separated from the south coast of southern Africa and South America rifted away from the west coast. The folds consistently run parallel to the coasts, resulting in a series of east-west trending mountain ranges in the southern half of the Cape Region and north-south trending ranges in the west.

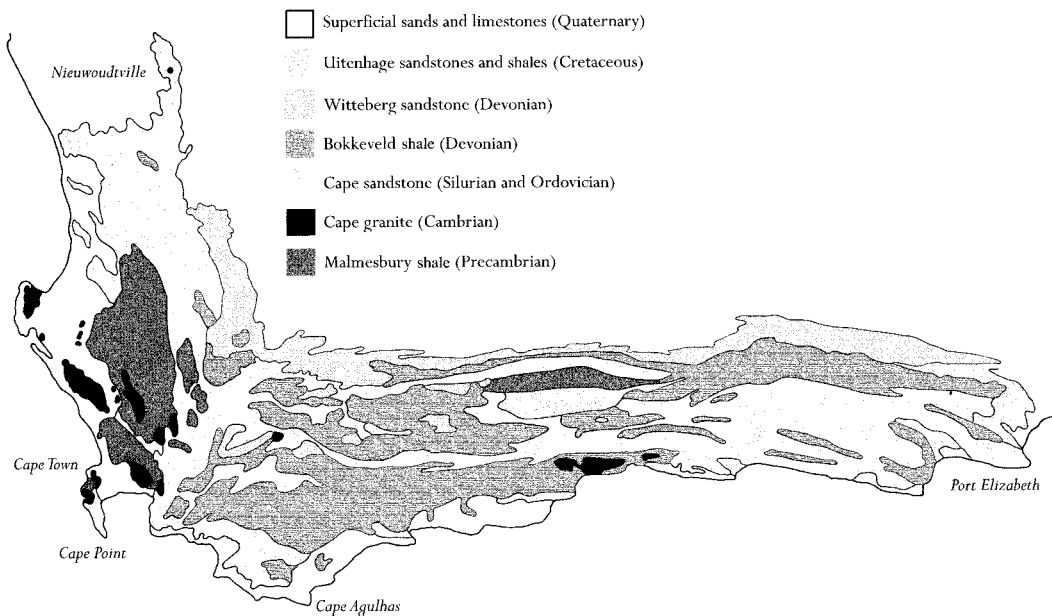


Figure 2. Geology of the Cape Floristic Region (adapted from Cowling, 1992).

Differential weathering of the components of the Cape System has yielded two fundamentally different soil types, coarse-grained sandy soils, poor in essential plant nutrients, and richer, clay soils of nutrient-intermediate status (Groves et al., 1983). At the low precipitation levels that are usual in the Cape Region, these factors become so limiting that these soils support markedly contrasting vegetation. Apart from variation in nutrient status, the soils depart significantly in their structure and water-retention properties. Erosional patterns differ on the two rock types, and the result is that the mountains consist primarily of sandstone rocks and the valleys of shale. Where folding or faulting have been severe, more ancient rocks of the Precambrian Malmesbury Group are exposed. These are largely shales that give rise to clay soils of the same type as do the shales of the Cape System. Granitic schists are locally exposed in deep valleys and along the west coast, and limestones, mainly of Tertiary age, are exposed near the coast where they are extensive only along the southern coast from the Agulhas Peninsula east to Mossel Bay. The coastal plain includes areas with aeolian sandy soils derived from reworking of Cape Sandstones. Since these major episodes of folding and rifting in the Mesozoic, only erosional forces have had a major impact on the Cape landscape, modified only slightly by minor uplift, associated with coastal downwarping in the mid to late Tertiary (King, 1962). Moving from the coastal plain to the interior,

the resultant landscape is a mosaic of coastal limestones and deep sands, or valleys with clay soils alternating with mountain ranges of nutrient-poor sands. Local faulting has added a secondary component of islands of one rock type embedded in another. Both the nutrient-poor and nutrient-intermediate soils favor the development of a fairly uniform, sclerophyllous, shrubby vegetation that is fire-adapted (see discussion under Diversity).

#### WINTER-RAINFALL AND CLIMATIC STABILITY

How important to the flora is the current mediterranean climate that prevails over most of the Region? The vegetation of the Cape Region prior to the establishment of a winter-rainfall climate was very different from that now found there. Evergreen forest has been decreasing since the middle of the Tertiary, and its diversity has dropped dramatically since the mid Miocene, some 16–14 mya, as well (Coetzee, 1993). Families such as *Arecaceae*, *Casuarinaceae*, *Chloranthaceae*, *Sarcolaenaceae*, and *Winteraceae*, no longer found on the African mainland but still extant in Madagascar, were present in the Cape Region at least until the mid Miocene (Coetzee & Praglowski, 1984; Coetzee & Muller, 1985). In addition, early to mid Miocene deposits on the Cape west coast indicate a fauna adapted to forest and woodland (Hendey, 1982).

The establishment of the cold Benguella Current along the west coast of southern Africa in the Mio-

cene, with its cooling and drying effects, was probably the single most important influence affecting vegetation change in the subcontinent. Summer drought became increasingly severe in the west as this current strengthened as a result of the spread of the Antarctic ice sheet at the end of the Miocene, ca. 5.5 mya. Even in the later mid Miocene, however, there was a fairly rich subtropical flora replete with palms (Coetzee & Rogers, 1982) near Saldanha Bay, on the west coast of the Cape Region in an area that today supports a largely treeless, succulent or sclerophyllous shrubland. No palm species occur today in the CFR. Faunal remains suggest that by the late Miocene the once widespread forest and woodland were being replaced by more open savanna (Hendey, 1982). It was probably not until after the beginning of the Pliocene, i.e., less than 6 mya, that the present Cape flora could be distinguished, although elements of that flora are recognized in Oligocene pollen cores taken within the Cape Region and nearby (Scholz, 1985). It seems clear that climatic change, including increased summer drought and lower overall rainfall, was the driving force for vegetational change in southern Africa into the Pliocene.

Although post-Pliocene changes in climate of the Cape Region are poorly documented, the climate appears to have been relatively stable. In comparison with southern Europe, North America, and southern South America, all of which experienced cycles of extreme climatic fluctuations with periods of mild climate alternating with extreme cold and dryness (Villagrán, 1994), the climate of the Cape Region appears to have been relatively stable throughout the Quaternary. Whereas in central Chile, southern Europe, and North America mountain glaciers developed and winter temperatures must have fallen to levels that large portions of their floras could not tolerate, the Cape appears to have merely undergone cycles of drier and cooler alternating with wetter and warmer conditions. The ameliorating affects of large oceans to the south and west would have prevented the extreme conditions that result in major extinction events. Although no glaciers developed, there is evidence of colder climates in the past (Deacon, 1979) consistent with a temperature depression of the order of 5°C at the latitude of the Cape Region.

The data of Meadows and Sugden (1991) are among few documenting the history of the Cape flora over the past 20,000 years. Their pollen profiles from the Cedarberg Mountains in the northwestern part of the CFR show no vegetational changes comparable to those known for Chile (Villagrán, 1994) or California (Raven & Axelrod, 1978). Instead,

there seems to have been a series of subtle shifts in conditions that favored one community type over another in the 14,600 years covered in their sampling. The Cedarberg data are especially notable because that range lies at the northern, more arid end of the Cape Region, an area that is therefore particularly sensitive to climatic change. In contrast, the somewhat older fossil wood assemblages from Elands Bay Cave on the west coast of the CFR (Cowling et al., 1999) document a shift from xeric to mesic thicket and fynbos and then to afro-montane forest at 18,000 BP, indicating higher moisture conditions in the west during the Last Glacial.

In the southern Cape the lowering of sea levels as much as 120 m below present levels at times during the Pleistocene resulted in the extension of the coastal plain off the southern coast of Africa. The vegetation along the coast at this time was probably grass-dominated, and it supported the dominant alcephaline and equid fauna (Klein, 1977). Even today, the vegetation on clay soils of this area has a large grass component.

#### FLORISTIC COMPOSITION

##### MAJOR FAMILIES AND GENERA

The Asteraceae, usually the largest family in floras of arid to semi-arid regions, are also the most speciose family in the Cape flora, with 1036 species (Table 1). Additions to several genera of Fabaceae since the flora was last documented (Bond & Goldblatt, 1984) now make this family the second largest in the flora (previously believed to be fourth largest), which is also unexceptional, as Fabaceae are well developed in most parts of the world. However, the huge contribution made by Iridaceae, Aizoaceae, and Ericaceae, next in numbers of species (Table 1), is a unique aspect of the flora (and consequently of the southern African flora as a whole). Scrophulariaceae, Proteaceae, and Restionaceae follow in importance, showing a pattern, described in more detail by Goldblatt and Manning (2000). Aizoaceae, with its huge southern African representation of Mesembryanthemoideae, are probably the second largest family in the southern African flora (Goldblatt, 1978) and appear to be the largest family in the Namaqualand–southwestern Namibia region (R. Cowling, pers. comm.) that lies to the north of the CFR and also has a winter-rainfall and summer-dry climate. This arid zone has such strong floral affinities to the Cape flora that the inclusion of Namaqualand–southwest Namibia in the CFR to comprise a Greater Cape flora has been given serious consideration (Bayer, 1984; Jürgens, 1991, 1997). The relationships of the extended Namaqua-

Table 1. Ranking of the 20 largest families in the Cape Flora Region as indicated by species number. Family circumscriptions reflect the recommendations of the Angiosperm Phylogeny Group (1998). These families contribute 6989 species to the flora, or 77.4% of the total.

Family	Total species	Number endemic (% of total species)	Total genera (number endemic)	Species/genus
1. Asteraceae	1036	655 (63.2)	121 (33)	8.6
2. Fabaceae	761	629 (82.7)	37 (6)	20.6
3. Iridaceae	677	540 (79.8)	28 (6)	24.2
4. Aizoaceae	659	524 (79.5)	76 (18)	7.5
5. Ericaceae	657	637 (96.9)	1 (0)	657
6. Scrophulariaceae	414	297 (71.7)	33 (7)	12.5
7. Proteaceae	329	319 (97.0)	14 (9)	23.5
8. Restionaceae	318	294 (92.5)	19 (10)	16.7
9. Rutaceae	273	257 (94.1)	15 (6)	18.2
10. Orchidaceae	227	138 (60.8)	25 (2)	9.1
11. Poaceae	207	80 (38.6)	61 (3)	3.4
12. Cyperaceae	206	101 (49.0)	29 (4)	7.1
13. Hyacinthaceae	191	83 (43.5)	14 (0)	13.6
14. Campanulaceae	183	140 (76.5)	13 (6)	14.1
15. Asphodelaceae	157	81 (51.6)	8 (0)	19.6
16. Geraniaceae	157	91 (58.0)	3 (0)	52.3
17. Polygalaceae	141	122 (86.5)	3 (0)	47.0
18. Rhamnaceae	137	127 (92.7)	5 (1)	27.4
19. Crassulaceae	134	35 (26.1)	5 (0)	26.8
20. Thymelaeaceae	125	94 (75.2)	4 (1)	31.3
	$\Sigma = 6989$	5244 (77.0)	514 (112)	

land flora (or Succulent Karoo Region) seem unquestionably closer to the Cape flora in its traditional sense than to the flora of the summer-rainfall karoo (Nama-Karoo Region) although their common boundary is not clearly fixed and there is evidence for its east–west shift in the past (Jürgens, 1991).

The large numbers of species of Proteaceae and Restionaceae, seventh and eighth largest families, respectively, are another striking feature of the flora. The importance of Ericaceae, Proteaceae, and Restionaceae both in terms of biomass and species diversity is widely appreciated, but the huge number of species of Iridaceae, predominantly a family of herbaceous, seasonal geophytes, is especially notable. Nowhere else in the world does this family comprise such a significant floristic component. Indeed, the adaptive radiation of Ericaceae and Iridaceae in the Cape flora is one of its most striking features. The diversification of Ericaceae, Proteaceae, Restionaceae, and even Cyperaceae, is closely associated with the impoverished sandstone soils of the Cape mountain ranges, and these families are poorly represented on other soils. The massive radiation of Fabaceae and Iridaceae shows no such correlation. Although the wealth of Scrophulariaceae, sixth largest family in the Cape flora, seems remarkable in a world context, the family is also

well represented across Africa, especially in the floras of drier areas (Maggs et al., 1998). In the Cape flora Scrophulariaceae contribute 166 species to the annual flora, far more than does the next most important family, Asteraceae, with 138 annual species. As circumscribed for the Cape flora (Goldblatt & Manning, 2000) Scrophulariaceae do not include the parasitic and hemiparasitic genera now referred to Orobanchaceae (APG, 1998) but, nevertheless, it remains a major family in the flora. Rutaceae, ninth largest family, are also a surprising aspect of the Cape's floristic composition. Over 95% of the 273 species of Rutaceae there are small shrublets belonging to the tribe Diosmeae, most members of which are restricted to the Cape flora, and reflect the large numbers of shrub species in the flora. The wealth of Polygalaceae, Rhamnaceae, and Thymelaeaceae, 17th, 18th, and 20th in size, respectively (Table 1), likewise exemplify the importance of the shrubby habit in the Cape flora.

Poaceae are comparatively poorly represented in the Cape flora. Although they are the third largest family in the flora in number of genera (Table 1), they are only 11th in size in total species, with fewer representatives than Restionaceae and barely more than Cyperaceae, the two other families generally that occupy similar habitats. This situation is

Table 2. Endemic families of the CFR. Note that the characteristic and nearly endemic family *Bruniaceae* has 11 genera and 61 endemic species of a total 64 in the family and is not included here, its range extending eastward to southern KwaZulu-Natal. In addition, Olmstead et al. (2001) have proposed enlarging *Stilbaceae* to include non Cape genera rendering it no longer endemic.

Family	Number of genera	Number of species
<i>Penaeaceae</i>	7	23
<i>Stilbaceae</i> s. str.	5	14
<i>Grubbiaceae</i>	1	3
<i>Roridulaceae</i>	1	2
<i>Geissolomataceae</i>	1	1
Totals	15	43

paralleled only in southwestern Australia but contrasts sharply with adjacent southern Africa where *Poaceae* are prominent and diverse. *Poaceae* are the largest family in the flora of Namibia (Maggs et al., 1998) and one of the five largest in southern Africa excluding the CFR (Goldblatt, 1978).

Although 150 families of seed plants and another 23 of ferns and other vascular cryptogams are represented in the flora, remarkably few account for the bulk of the species. While 23 families in the flora have over 100 species, only 12 have over 200 species. In contrast, 38 families have just one species each. The largest 10 families account for 5351 species, well over half the total 9030 in the flora, and the largest 20 families account for 6989 species, over 77% of the flora (Table 1).

#### ENDEMIC FAMILIES

The unique floristic composition of the Cape Region, with its high representation of *Ericaceae*, *Iridaceae*, *Proteaceae*, and *Restionaceae* (Table 1), is emphasized by the presence of several families that are endemic or nearly so. The endemic families are all eudicotyledons of diverse affinity and relatively low evolutionary specialization (Table 2). The largest is *Penaeaceae* (Myrtales), followed by *Grubbiaceae* (Cornales), *Roridulaceae* (Ericales), and *Geissolomataceae* (together with *Ixerbaceae* and *Strasburgeriaceae*, sister to *Crossosomatales*) (classification following APG, 1998). Based on a molecular clock calibrated using 135 mya for the divergence of the eudicot lineage (V. Savolainen et al., 2000, and unpublished data), *Penaeaceae* may have diverged 20 mya from its sister clade, the African *Oliniaceae* plus the Neotropical *Alzateaceae*, while *Roridulaceae* diverged from *Ericaceae*, its closest relative (Savolainen et al., 2000), ca. 48

mya. *Geissolomataceae* appear older, having diverged perhaps 55 mya from *Ixerbaceae* plus *Strasburgeriaceae*. *Grubbiaceae* may have diverged from *Cornaceae* plus *Hydrostachyaceae* in the earliest Tertiary, 63 mya. We have no comparable data for the monotypic, near endemic monocot family *Lanariaceae*. *Stilbaceae* (including *Retziaceae*) (Lamiales) are provisionally regarded as a Cape endemic family, but if the changes to its circumscription suggested by Olmstead et al. (2001, and pers. comm.) are accepted, the family occurs across sub-Saharan Africa, Arabia, the Mascarenes, and Madagascar (see below).

*Bruniaceae*, one of the distinctive families of the Cape flora, are almost endemic. Of an estimated 64 species in 11 genera, just 3 species in 2 genera extend outside the confines of the Cape Region, 2 locally, and 1 as far east as southern KwaZulu-Natal. *Bruniaceae* are now thought to be the sister group to the order *Dipsacales* (Savolainen et al., 2000), perhaps meriting recognition at ordinal rank. The discovery of pollen matching modern *Bruniaceae* in early Tertiary and late Cretaceous (?Senonian) deposits in northern Namaqualand (S. E. de Villiers, pers. comm.), well to the north of the CFR, attest to considerable age for the family in southern Africa. The pollen record also accords with Savolainen's preliminary early Tertiary dating of the divergence between *Bruniaceae* and *Dipsacales* at about 57 mya (V. Savolainen, unpublished data).

*Retziaceae* (1 genus:1 species) have often been considered an endemic Cape family (e.g., Bond & Goldblatt, 1984), although its affinities have long been in dispute (Goldblatt et al., 1979). DNA sequence analysis shows the genus nested in *Stilbaceae* (Bremer et al., 1994; Savolainen et al., 2000). Floral specialization for bird pollination appears to be the source of most of its distinctive features. The familial status of *Stilbaceae* is not in question, but Olmstead et al. (2001) included the Afro-Arabian *Nuxia* in tribe *Stilbeae* and added the Afro-Madagascan *Halleria* and the southern African tribe *Bowkerieae* to the family (previously *Scrophulariaceae*) rendering *Stilbaceae* no longer endemic to the CFR or even to southern Africa.

In contrast to the Cape Region, which alone has 5 (or more likely 4) endemic families, all of southern Africa perhaps has just 10 endemic families (9 according to the revised concept of *Stilbaceae*). In addition to those absolutely restricted to the Cape Region, the southern African endemic families are the eudicots *Bruniaceae* (ordinal position sister to *Dipsacales*, 11: ca. 64), *Greyiaceae* (*Geraniales*, 1: 3), and *Rhynchoalycaceae* (*Myrtales*, 1:1); the

Table 3. Ranking by numerical size of the 20 largest genera in the CFR (endemic species number). An estimated 9030 species occur in the flora, of which 6208 are endemic (68.7%).

<i>Erica</i>	657 (637)	<i>Muraltia</i>	106 (100)
<i>Aspalathus</i>	272 (258)	<i>Gladiolus</i>	106 (86)
<i>Pelargonium</i>	148 (89)	<i>Selago</i>	100 (77)
<i>Agathosma</i>	143 (138)	<i>Crassula</i>	95 (26)
<i>Phylica</i>	133 (126)	<i>Disa</i>	92 (78)
<i>Lampranthus</i>	124 (118)	<i>Ruschia</i>	88 (79)
<i>Oxalis</i>	119 (94)	<i>Restio</i>	85 (82)
<i>Moraea</i>	115 (79)	<i>Leucadendron</i>	82 (79)
<i>Cliffortia</i>	114 (104)	<i>Helichrysum</i>	81 (34)
<i>Senecio</i>	110 (57)	<i>Thesium</i>	81 (35)

Total in largest 10 genera = 1935 spp. (21.4% of flora)  
 Combined total in largest 20 genera = 2851 spp. (31.6% of flora)

monotypic monocot genus *Lanaria* is also currently regarded as comprising its own family, Lanariaceae (Asparagales) (APG, 1998; Chase et al., 2000); and the cycad family Stangeriaceae (1:1). *Lanaria* is widespread in the Cape Region and extends outside its confines a short distance to the east. Aitonaceae, Curtisiaceae, and Ophiaceae have at times been accorded recognition but they are no longer considered to be separate families. They are readily referable to Meliaceae (Pennington & Styles, 1975), Cornaceae (Xiang et al., 1993), and Scrophulariaceae (Goldblatt, 1979), respectively. Prioniaceae (Poales), treated as a family by Munro and Linder (1998) for the monotypic and largely Cape *Pronium*, and recognized by Goldblatt and Manning (2000) for the Cape flora, are now regarded as belonging to Thurniaceae (Chase et al., 2000). Behniaceae, described for the monotypic southern African *Behnia*, is an endemic southern African family according to Conran et al. (1997), although it is reported to occur in Zimbabwe. However, the status of Behniaceae is in question and it is likely to be subsumed in a more widely circumscribed Agavaceae (M. W. Chase, pers. comm.). Likewise, Achariaceae (Malpighiales, current name for Flacourtiaceae, 3:3) (Savolainen et al., 2000), two species of which also occur in the Cape Region, are often regarded as a southern African endemic family. The genera are, however, nested in Kiggelariaceae (Savolainen et al., 2000) and are regarded here as members of that family.

#### GENERA

Some 944 genera of seed plants (or 990 genera of vascular plants), about half of those occurring in southern Africa, are represented in the Cape flora, of which some 160 or 16.3% are endemic (Goldblatt & Manning, 2000). The level of generic endemism is modest and reflects little of the unusual

nature of the flora. The number of near-endemic genera (those of moderate size with just one or two species extending locally outside the Cape Region) is, however, dramatically high. The largest genus in the flora by far is *Erica*, with some 657 species (Table 3). Changes in the circumscription of *Erica* (Oliver, 2000) have now resulted in the inclusion of all the minor genera of southern African Ericaceae: Ericoideae, leaving *Erica* with over 7% of the species in the entire flora. It is unclear whether this remarkable pattern of speciation without generic diversification is associated with the relatively recent arrival of ancestral ericaceous stock in the CFR, or with adaptive radiation following the establishment of a semi-arid climate there. By comparison, the smaller families Proteaceae and Restionaceae appear to belong to old African (or even Gondwanan) groups, now poorly represented elsewhere in Africa, and they show the highest levels of endemism at the generic level. These two families plus Bruniaceae are the only non-endemic families that show greater than 50% generic endemism.

*Aspalathus* (Fabaceae) is the second largest genus, with 272 species, followed by *Pelargonium* (Geraniaceae), *Agathosma* (Rutaceae), *Phylica* (Rhamnaceae), *Lampranthus* (Aizoaceae), and *Oxalis* (Oxalidaceae), each with between 118 and 148 species (Table 3). Thirty-six genera have over 50 species and 13 genera have over 100 species. The 10 largest genera contribute over 21%, or 1935 species, to the flora. The next 10 largest genera contribute an additional 922 species. The 20 largest genera in the Cape flora thus contain over 31% of the total species.

There is no one unifying ecological pattern evident in the species-rich genera. *Agathosma*, *Aspalathus*, *Cliffortia*, *Erica*, *Phylica*, and the two largest genera of Proteaceae, *Leucadendron* and *Protea*, are best developed on sandy soils and are most



Table 4. Selected statistics for the CFR and various comparable regions (emended from Bond & Goldblatt, 1984). The figures represent the percentage of the total flora. The ten largest genera were determined by species number.

Region	Mean sp. number per genus	10 largest genera	Percentage of total flora		Annual species
			Monocots	Asteraceae	
Cape flora	9.1	21.4	24.5	11.5	6.7
Southern Africa (incl. Cape flora)	9.6	15.1	23.0	11.0	7.0
Cape Peninsula	4.2	17.5	34.6	11.5	9.6
Natal	3.9	17.0	27.1	11.4	ca. 6.5
Eastern North America	5.2	21.8	28.2	12.7	8.7
Europe	7.8	14.0	18.0	12.0	?
California Flora	5.3	15.2	19.2	13.6	27.4
Sonoran Desert	3.3	12.8	12.1	15.0	21.4
Texas	3.9	10.2	24.4	13.4	20.4
Hawaii	4.4	81.0	11.8	15.9	0.04
New Zealand	5.1	26.3	27.3	12.5	6.0

diverse in montane habitats. In contrast, species of *Lampranthus*, *Moraea*, *Pelargonium*, *Oxalis*, *Gladiolus*, and *Crassula* appear to occur with equal frequency on nutrient-poor, nutrient-intermediate, or comparatively rich soils and favor lowland habitats. *Lampranthus* and *Crassula* are succulents, and *Disa*, *Oxalis*, *Gladiolus*, and *Moraea* are seasonal geophytes, as are some species of *Pelargonium*. The remaining genera among the largest 20 comprise mostly shrubs or small trees. A few species of *Pelargonium*, *Senecio*, *Crassula*, and *Helichrysum* are annual species. *Thesium* species are hemiparasitic shrubs.

The most obvious shared factors in diversified genera in the Cape flora seem to be either a shrubby habit or seasonal geophytism. Over 17% of the total species in the flora are geophytes with bulbs, corms, tubers, or rhizomes. The number of species with underground perennating buds would be even higher if plants with woody caudexes were regarded as geophytes.

The ratio of species per genus, 9.1 (9.3% excluding ferns) in the Cape flora (Table 4), is particularly high compared to other floras and is one of the highest in the world (Fenner et al., 1997), although southern Africa as a whole, including the Cape Region, has a comparable ratio (9.6%, fide Goldblatt, 1997). A ratio of three dicots to one monocot species in the Flora is close to the average for floras across the world. Although the proportion of monocots does not seem unusual, the monocot families that are represented in the Cape flora are most distinctive. Some half of the species in the monocot families are geophytic and belong in the petaloid monocot families, notably Iridaceae, Orchidaceae, Hyacinthaceae, and Amaryllidaceae. The proportion of monocot to dicot species, match-

ing that elsewhere in the world, is thus no more than coincidence.

#### PALEOENDEMIC GENERA

The endemic and near-endemic families of the Cape Region are all small and contribute relatively few genera and species to the flora, and they are best regarded as paleoendemics. With the exception of the rhizomatous perennial *Lanaria*, members of these families are all evergreen, sclerophyllous shrubs. They are often summer-flowering, usually have small flowers, and typically grow on sandstone-derived soils. We speculate that these plants are relicts of an ancient temperate southern African flora adapted to nutrient-poor soils.

Among non-endemic families, these paleoendemic genera are often members of the geologically oldest communities, tropical thicket and evergreen forest. Especially notable are *Platylophus*, a monotypic genus of Cunoniaceae and one of two continental African members of this family. The other, *Cunonia capensis*, is common in the Cape Region but extends into eastern southern Africa. Other monotypic genera such as *Heeria* and *Laurophyllum* (Anacardiaceae), *Hartogiella* and *Maurocena* (Celastraceae), *Lachnostylis* (Euphorbiaceae), and *Smelophyllum* (Sapindaceae) also exemplify the paleoendemic component of the depauperate tree element of the flora and mostly have ranges restricted to the southern or eastern portion of the Cape Region (Goldblatt & Manning, 2000).

In non-forest habitats there are few paleoendemic genera or species apart from members of the endemic (and near-endemic) families of the Cape Region. These include the monotypic shrublets, *Empleuridium* (Celastraceae) and *Ixianthes* (Scro-

Table 5. Comparison of life forms in the California flora, central Chile, and the CFR. Figures are percentages of total species number; perennials below include geophytes and graminoids. Data for California and Chile are from Kalin Arroyo et al. (1994).

Region	Percentage of total flora			
	Trees	Shrubs	Perennials	Annuals
Cape Region	2.5	53.3	37.5	6.7
California	4.6	11.0	56.2	30.2
Central Chile	2.9	17.8	63.4	15.8

phulariaceae or Stilbaceae, Olmstead et al., 2001). The small tree, *Hyaenanche* (Euphorbiaceae or Picrodendraceae, Savolainen et al., 2000), also monotypic, and *Metrosideros angustifolia* (Myrtaceae), a member of an otherwise Australasian genus, show an odd pattern for the tree flora. Their ranges are restricted to the western half of the Cape Region where there are few tree species. *Metrosideros angustifolia*, the only African member of Myrtoideae: Metrosiderinae, seems as geographically isolated from its closest relatives as *Cunonia* and *Platylophus*. Like *Metrosideros*, *Bulbinella* is also a Cape–Australasian disjunct, but in this case the radiation within the genus has occurred largely in the Cape Region. The dwarf, tree-like monocot *Prionium* (Thurniaceae), of watercourses in nutrient-poor sandstone soils, is widespread in the Cape region but extends some distance to the east. The other member of the family is the Brazilian shield genus *Thurnia*, the pair thus exhibiting an unusual disjunction. The taxonomically isolated *Oldenburgia* (Asteraceae–Mutisieae), with three Cape species and one occurring a short distance beyond its eastern limits, is perhaps another example of that distribution pattern, for its closest allies occur in the Guyana Highlands. The small number of paleoendemic taxa emphasizes the huge contribution that recent speciation in a narrow range of families and genera has made to the total species diversity in the Cape Region.

#### LIFE FORMS

In contrast to other mediterranean floras, the Cape flora has relatively few trees, and this life form only accounts for some 220 species, about 2.5% of the flora. Trees in the California flora account for 4.6% of the species, but in Chile some 2.9% of the species are trees (Table 5). Most of the remaining elements of the Cape flora are shrubs and perennial herbs. The shrubby habit is the most common life form in the Cape Region, accounting

for an estimated 4797 species, 53.3% of the total flora. Shrubs are diverse in form, but typically include species with sclerophyllous, and mostly microphyllous leaves, the characteristic that has given rise to the word fynbos, an Afrikaans word describing fine-leaved vegetation. Shrubs also include large numbers of species with succulent leaves (especially Aizoaceae). Stem-succulents include species of Apocynaceae and Euphorbiaceae, some of which are so reduced in size that the term shrublet hardly seems appropriate. The Cape flora stands out when compared to that of both California and Chile in the overwhelming proportion of shrubs (Table 5), which is largely explained by the nutrient-poor soils that favor this life form.

The Cape flora shows some notable differences with other mediterranean floras. One of these is a surprisingly low proportion of annuals—only some 609 species, about 6.7% of the total flora, as compared to 30% and 15% respectively for California and central Chile (Table 5) (Kalin Arroyo et al., 1994; Cowling et al., 1996). No comparable figures are available for the Mediterranean Basin. Although the proportion of annual taxa in the CFR is low, the annual flora is quite species rich. The total number of annual species is actually almost twice as high as the 378 annuals recorded in central Chile, an area of comparable size, and although the Cape has less than half the 1279 annuals in California, its area is only about one fourth that of California. For its geographic area then, the Cape flora is not depauperate in annuals, but its wealth of other life forms makes the annual habit appear under-represented. A small annual flora is also characteristic of southwestern Australia, an area that has a recent geological history comparable to that of the Cape Region and a similar pattern of nutrient-poor sandstone soils and richer clay. The low proportion of annuals in the Cape flora has remained without a satisfactory explanation since it was first noted by Bond and Goldblatt (1984) but the answer may simply lie in the disproportionate numbers of other life forms, especially microphyllous shrubs that are particularly well adapted to the nutrient-poor soils.

Two families, Scrophulariaceae and Asteraceae, are especially important in their contribution to the annual flora. Scrophulariaceae, with 166 species, contribute the largest number of annuals, and not, as might be expected, Asteraceae, which have some 138 annual species (Table 6). The Aizoaceae, Brassicaceae, Campanulaceae, Crassulaceae, Cyperaceae, Fabaceae, and Poaceae, each contribute between 20 and 35 species to the annual flora. Campanulaceae, in particular, need taxonomic

Table 6. Families with more than 10 annual species in the CFR. Total: 609 species (6.7% of the flora).

Family	Species number
Scrophulariaceae	166
Asteraceae	138
Campanulaceae	35
Brassicaceae	33
Poaceae	31
Aizoaceae	25
Fabaceae	25
Crassulaceae	23
Cyperaceae	21
Gentianaceae	18
Molluginaceae	16

Table 7. Total species (percentage in parentheses) of the different life forms in the Cape flora.

Life form	Species number	Species % of total flora
*Perennials	1025	(11.4)
Trees	221	(2.4)
Shrubs	4805	(53.2)
Geophytes	1575	(17.4)
Graminoids	795	(8.8)
Total, all perennials	8421	(93.3)
Annuals	609	(6.7)
Total	9030	(100)

\* Perennials excluding trees, shrubs, geophytes, and graminoids.

study and our estimation of the number of species in the family, including its annual component, is subject to significant revision.

In contrast to the low proportion of annuals, the Cape Region has perhaps the highest proportion of geophytes of any part of the world, and is four to five times richer in this life form than is documented for other mediterranean floras (Esler, 1998; Esler et al., 1998; Goldblatt & Manning, 2000). At least 1550 species, over 17% of the total, have specialized underground organs including bulbs, corms, rhizomes, or tubers and are seasonally dormant (Table 7). The overwhelming number of geophytes are monocots, with over 1300 geophytic species, 662 of which belong to one family, Iridaceae. Most of these geophytes are seasonal and lie dormant underground in the dry season, but we have

included in the geophyte category the few more or less evergreen species (e.g., *Agapanthus*, *Kniphofia*) with similar underground organs. The other main category of the monocots are the graminoids, that is, the perennial species of Cyperaceae, Juncaceae, Poaceae, Restionaceae, and a few other families, which account for 795 species (8.8% of the flora).

#### VEGETATION

Far from having uniform vegetation, the Cape Region encompasses five biomes (Fig. 3) and several distinctive vegetation types, each with its own suites of species and physical characteristics (Rutherford & Westfall, 1994; Cowling & Holmes, 1992a). The most common and distinctive biome is heathland, locally called fynbos, an analogue of

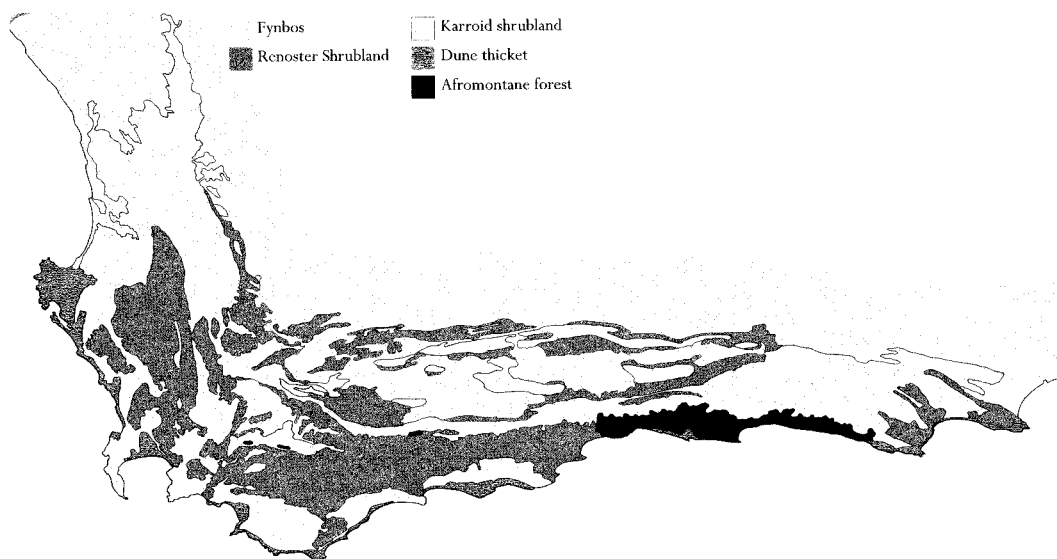


Figure 3. Major vegetation communities of the Cape Floristic Region (adapted from Louw & Rebelo, 1996).

Table 8. Comparison of species richness (indicated by species number per area), endemism, and the proportion of life forms in the floras of the six phytogeographic centers of the Cape flora (n/a = not available). For comparison, data are listed for the Cape Peninsula, a small area within the Southwest Center.

Floristic center (listed from west to east)	Physical area 10 <sup>3</sup> km <sup>2</sup>	Total species number	Species/ 10 <sup>3</sup> km <sup>2</sup>	% species endemic	Tree species	Annual species number (%)	Geophyte species number (%)
Northwest Center	22	4066	184.8	26.3%	69	415 (10.3)	855 (21.2)
Southwest Center	23	4661	202.7	32.0%	95	312 (6.8)	846 (18.2)
Agulhas Plain	3	1374	458.0	14.9%	24	92 (6.7)	202 (14.7)
Karoo Mountain	19	2151	113.2	15.5%	47	130 (6.1)	330 (15.5)
Langeberg Center	7	2363	337.6	11.7%	100	127 (5.4)	389 (16.4)
Southeast Center	18	2832	157.3	9.7%	163	156 (5.5)	427 (15.1)
Cape Peninsula	4.7	2250	478.7	7.5%	n/a	n/a	n/a
Cape Region	90	9030	100.3	68.7%	221	609 (6.7)	1575 (17.4)

Californian chaparral and Mediterranean maquis. Shrubs with ericoid or short, narrow, often needle-like leaves predominate, but most species of Proteaceae, a family common in this vegetation, have broad sclerophyllous leaves. Fynbos typically occurs on sandstone soils. A second distinctive vegetation type, renosterveld, is usually restricted to richer fine-grained soils. It shares few species with fynbos although they often grow adjacent to one another. Microphyllous Asteraceae are common in renosterveld, which consists of a dense shrubland with a rich herbaceous understory that becomes evident after fire or clearing but is often suppressed under a mature shrub cover. Dry sites with rainfall less than 200 mm p.a. support a vegetation of small succulent-leafed shrubs, including many Aizoaceae and Asteraceae, in a biome called succulent karoo. Thicket (a dense, semi-succulent and spinescent evergreen shrubland to low forest) and evergreen forest make up the remaining biomes.

Fire is an integral part of the ecology of the Cape Region and accounts for several aspects of the vegetation (Cowling, 1987). Growth form in mature fynbos and renosterveld is a relatively uniform, closed, low canopy of twiggy and microphyllous to sclerophyllous shrubs. These vegetation types are highly prone to periodic fire. Fire itself has a disruptive effect on the vegetation. It has obviously been a feature of the ecology for so long that there is a large flora of ephemerals, geophytes, other perennials, and short-lived shrubs that appear in the years following a fire, often flower profusely, and subsequently disappear, as they are succeeded by longer-lived shrubs. The long-term ecological consequence of fire on the flora is the existence of a niche for species that grow rapidly after fire to persist and bloom in the immediate post-fire years. This fire-adapted suite of species contributes substantially to the overall diversity in the flora. Ma-

ture vegetation is affected by fire in more subtle ways, but fire may cause local perturbations in species composition and the elimination of some taxa.

#### DIVERSITY

##### REGIONAL DIVERSITY

The patterns of endemism within the Cape Region are fairly consistent, and examination of these patterns in selected genera that have diversified largely on sandstone substrates has resulted in the recognition of several regional centers of endemism (Fig. 1, Table 8). Weimarck (1941) pioneered this field, which has now been refined by Cowling and his coworkers (e.g., Cowling & Holmes, 1992a; Cowling & McDonald, 1999). The presence of these centers suggests that exchange between them is limited because of effective geographic isolation or because different microclimates in each center favor local species at the expense of migrants.

One aspect of our account of the Cape flora (Goldblatt & Manning, 2000) has been the formal recognition of phytogeographic centers so that distributional data for species can be analyzed within the CFR. Thus, we have been able to estimate for the first time the floristic diversity for each center. To some extent the statistics are approximate because some centers are under-collected (or under-cited in taxonomic accounts). We suspect that the Karoo Mountain Center (KM) and the Agulhas Plain Center (AP) have more species (and thus lower levels of endemism) than our data suggest (Fig. 1).

At the geographic center of the Cape Region, the Southwestern Center (SW) has the largest number of species (4661) and the highest level of endemism (32%). The Northwestern Center (NW) follows in taxonomic size (4066 species) and endemism (26.3%). The Karoo Mountain and Southeastern

Centers have much smaller floras and substantially lower levels of endemism. Much smaller in extent, the Langeberg (LB) and Agulhas Plain (AP) Centers understandably have smaller floras. The Southeastern Center (SE), of almost the same physical size as the NW and SW Centers, has a markedly smaller flora (2832 species), and only 9.7% endemism. This may be explained by its more equable and apparently less diverse climate or simply by higher levels of extinction during colder and drier periods of the Pleistocene. Differences in levels of endemism across the Centers are striking. The SW and NW Centers each have about twice the proportion of endemic species as the others, which may be a reflection of their greater climatic diversity.

The different life forms are unevenly distributed across the Cape Region (see Table 8), and the numbers of species of the two most distinctive life forms, annual species and geophytes, drop dramatically moving from west to east. The summer-dry NW and SW Centers have the largest numbers of geophytes and the highest proportion of geophyte species in the Cape flora, 21.2% and 18.2%, respectively. These two centers each have over 50% of all the geophytes in the entire CFR. In comparison, the other centers have between 14.7% and 16.4% geophytes. Annual species are more common in the west, and the NW Center has 10.3% annual species, while the remaining Centers each have no more than 6.8% annuals. The NW Center alone has 65% of the total annual species in the Cape flora. The distribution of trees shows the converse, with relatively few tree species in the NW Center and the highest numbers by far in the SE Center, which may be explained by its less pronounced seasonality and more predictable rainfall. Cowling (pers. comm.) suggests that proximity to the source pool of species for recolonization during warmer (e.g., Holocene) periods is probably the most important factor in explaining tree distributions.

These patterns seem directly related to climate. Both geophytes and annual species seem best adapted to a seasonally extreme climate with a wet winter and dry summer. A climate with higher, seasonally more evenly distributed rainfall, characteristic of the LB and SE Centers, seems likely to favor a tree flora and fewer geophytes and annuals. Like annuals, geophytes are adapted for survival in semi-arid, seasonal habitats. This is reflected in the greater representation of annuals and geophytes in the western half of the Cape Region, where summer precipitation is lowest. The unexpectedly high numbers of trees in the SW Center reflect the dissected landscape with the presence of fire-sheltered

valleys and the regular occurrence of rainfall in the summer along its southern coast and interior.

#### COMPARISONS WITH OTHER FLORAS

An aspect of the Cape flora that is of particular interest is the high level of species diversity, both regional and local. For its size (ca. 90,000 km<sup>2</sup>), the number of species of vascular plants in the CFR, 9030 (8918 seed plants plus 112 pteridophytes), is comparable with areas of the wet Neotropics (Table 9). Thus Panama (75,000 km<sup>2</sup>) has 7300 seed plant species and Costa Rica (54,000 km<sup>2</sup>) may have over 9000 species (see Table 9). In fact, southern Africa as a whole has a particularly rich and diverse flora for a predominantly temperate region. The area customarily treated for floristic purposes as southern Africa (Botswana, Lesotho, Namibia, South Africa, and Swaziland) has about 20,500 native vascular plant species in an area of 2,674,000 km<sup>2</sup>, and South Africa alone may have some 18,500 species (ca. 18,275 seed plants plus 245 pteridophytes) in 1,221,000 km<sup>2</sup> (C. de Wet, pers. comm.). This is striking compared with an estimated 19,000 species in all of North America north of Mexico (19,341,000 km<sup>2</sup>), or the estimated 16,500 native vascular plant species (15,800 seed plants plus ca. 700 pteridophytes) recognized for Peru, an area of 1,285,000 km<sup>2</sup> (Brako & Zarucchi, 1993; Zarucchi, pers. comm.). To put this in a regional context, all of tropical Africa may have about 26,500 species (Lebrun & Stork, 1997), in an area nearly 10 times larger than that of southern Africa and about 250 times as large as the Cape Region. Southern Africa and North Africa have approximately 21,500 additional species (those not shared with adjacent tropical Africa), making a total of ca. 47,000 species for the entire African continent. The tiny Cape Region, less than 0.5% of the total area of Africa, then has about one fifth of all the species on the continent. Subtropical southern Africa, excluding the Cape Region, has only about 14,300 species, a figure comparable with that for Tropical East Africa (Polhill, unpublished data). For the African continent then, not only is the Cape Region remarkably rich in species, but southern Africa has a higher species diversity than would normally be predicted given the general trend that species diversity increases toward the equator.

The species richness in the Cape flora is, by any measure, remarkable. Moreover, some 6208 or about 68.7% of the species are endemic there (Table 9). The high degree of species endemism in the Cape flora compared to the California Floristic Province, for example, with some 4240 species,

Table 9. Comparison of endemism of native vascular plants in selected regions of the world. References: 1. C. de Wet (pers. comm.); 2. Brako & Zarucchi (1993); Zarucchi (pers. comm.); 3. Raven & Axelrod (1978); 4. Kalin Arroyo et al. (1994); 5. Kalin Arroyo & Cavieres (1997); 6. Beard (1970); 7. Hopper (1992); 8. Hammel & Grayum (pers. comm.); 9. D'Arcy (1987); 10. Wagner (1991), Wagner et al. (1990); 11. Schatz et al. (1996); 12. Médail & Quézel (1997).

	Physical area 10 <sup>3</sup> km <sup>2</sup>	Number of genera	Genera endemic %	Total species	Species endemic %	Reference	Species/ 10 <sup>3</sup> km <sup>2</sup>
<b>Continental areas</b>							
Southern Africa	2674	2130	20.0	20,367	80.3	1	7.6
Peru	1285	2210	2.1	16,500	31.2	2	12.8
<b>Areas of mediterranean climate</b>							
Cape Region, South Africa	90	990	16.4	9030	68.7		100.3
California floristic province	324	806	6.5	4240	47.7	3	13.1
Central Chile 1	104	591	—	2395	ca. 22.5	4	23.0
2	155	—	—	2537	ca. 23.4	5	16.4
Southwestern Australia	270	462	ca. 20	3650 or ca. 8000	68 ca. 75	6 7	13.5 29.6
<b>Moist to wet tropics</b>							
Costa Rica	54	1877	—	ca. 9000	—	8	166.7
Panama	75	1800	—	7300	ca. 15	9	97.3
<b>Tropical or temperate islands</b>							
Hawai'i	16.6	267	15	1138	86	10, 11	68.6
New Zealand	268	393	10	1996	81	3	7.4
Madagascar	594	ca. 1000	—	ca. 11,500	ca. 80	11	19.4
<b>Mediterranean islands</b>							
Crete	ca. 9	—	—	ca. 1706	ca. 10	12	189.6
Peloponnese	21	—	—	2400	ca. 12.5	12	114.3
Sardinia	24	—	—	2054	ca. 6	12	85.6
Sicily	26	—	—	ca. 2700	ca. 10	12	103.8

47.7% endemic (Raven & Axelrod, 1978), underscores the peculiarities of the Cape flora (Table 9). Such levels of endemism are usually associated with islands that have been isolated for long periods of geologic time, or with areas that have very sharp boundaries limiting direct plant migration. In a biological sense, the Cape Flora Region is virtually an island, not surrounded by ocean, but by a zone of dry climate or sharply different soils, or of seasonal rainfall distribution. The flora of southwestern Australia shares with the Cape Region an unusually high endemism for a local continental flora (Beard, 1970; Hopper, 1992), and so does that of southern Africa as a whole (Table 9). Why the latter region should have such a high level of endemism is not at all clear.

The high level of diversity and local endemism of the CFR is starkly emphasized by comparison of the phytogeographic centers of the region with other areas. The SW and NW Centers each have over 4000 species and over 31% or 26% endemism, respectively, compared with about 2400 species and an estimated 22–23% endemism (depending on the geographical definition of the region) for the entire mediterranean flora of Chile (Table 9), an area over five times greater than either of these phytogeographic centers of the Cape flora. Likewise, important centers of local endemism (hot spots) within the Mediterranean Basin, including the islands of Sicily, Sardinia, and Crete, or the Peloponnese Peninsula, all of more or less comparable size to the NW or SW Centers, have approximately half or less than half the number of species and between 6% and 12.5% endemism (Médail & Quézel, 1997).

#### ALPHA DIVERSITY

Aspects of plant species diversity have been addressed on several levels, and it has been shown that at the local level selected areas within the Cape Region are not unusual on a world scale (Cowling et al., 1992; Goldblatt, 1997) and are less species-rich than many areas sampled in the New and Old World lowland tropics (Gentry, 1988a, 1988b). Patterns of alpha diversity (the number of species in a homogeneous community, e.g., Cowling et al., 1992) in a range of vegetation types in the Cape Region, including fynbos, renosterveld, forest thicket, and evergreen forest, are surprising. Fynbos sites (with seasonal species not included in species counts) have a mean alpha diversity of 68 species per 1000 m<sup>2</sup>, with 121 the highest number of species recorded at any site (Cowling et al., 1992). Fynbos diversity is by no means uniform, and data indicate that diversity is higher in the west

than the south and in sites of intermediate productivity than in either more mesic or drier sites (Bond, 1983).

Non-fynbos sites have been less well studied. Figures in the literature for renosterveld include means of 66 (Tilman et al., 1983) and 84 (Cowling et al., 1992) species per 1000 m<sup>2</sup>. Forest thicket sites have a mean of 59 species per 1000 m<sup>2</sup>, forest sites have ranges of 44 to 52 species, and succulent karoo shrublands a mean of 43 species in the same area (Tilman et al., 1983).

Comparisons made by Cowling et al. (1992) indicate that California chaparral communities have alpha diversity levels around 34 species per 1000 m<sup>2</sup> but the more comparable southwestern Australian region has an average of 69 species per 1000 m<sup>2</sup> in heathland (kwongan), a vegetation type similar to fynbos. While these figures are consistent with higher total species richness in the CFR and southwestern Australia compared with the California Floristic Province, they do not explain the comparable regional diversity of the CFR and the lowland wet tropics. In the wet tropics mean alpha diversity of trees (including woody lianas) alone has been found to range from 129 species (Africa) to 140 species (Neotropics), to 193 species (Asia) per 1000 m<sup>2</sup> (Gentry, 1988b), about twice the alpha diversity found in mediterranean communities on nutrient-poor soils. Inclusion of epiphytes and other herbaceous plants raises alpha diversity in tropical sites. Gentry and Dodson (1987) have shown that a major component of the plant species diversity in tropical forests actually lies with the epiphytes. Similarly the inclusion of seasonal geophytes would increase the figures for the Cape flora, and until more comprehensive surveys are made any comparisons can only be tentative.

#### BETA AND GAMMA DIVERSITY

Beta diversity (species turnover along a habitat or environmental gradient, Cowling et al., 1992) is relatively high in the Cape Region. Cowling (1990), for example, has reported nearly complete replacement in sites along the Agulhas plain that differed in soil features but were climatically and topographically similar. Differences in composition between communities on sandstone versus clay soils are so nearly complete that the plants on these two soils are treated as belonging to different vegetation types.

Gamma diversity (species turnover in equivalent habitats along geographic gradients, also called delta diversity, Cowling et al., 1992) is likewise extremely high in the Cape Region, and is reflected

in the high levels of regional endemism. Species replacement values of 46–70% have been reported by Kruger and Taylor (1979) for sites 25 km apart, and Linder (1985) has suggested that geographic replacement may account for 30% of the differences in species composition along geographic gradients in similar habitats. These figures are, however, lower than some estimates for lowland Neotropical sites (B. Boyle in Goldblatt, 1997).

#### REASONS FOR CAPE FLORISTIC DIVERSITY

Richer in species than any other temperate flora and most tropical ones occupying comparable physical area (Table 9), the Cape flora is also highly distinctive. One of five regions in the world with a mediterranean climate, the Cape has substantially more species than do either California or central Chile, which are substantially larger in land area. Although southwestern Australia has a flora that may have about the same number of species as the Cape Region (Table 9), it is at least three times larger in area. Only the Mediterranean Basin, approximately 25 times larger in area, has a flora that is larger than the Cape flora, with about 2.5 times as many species. A formal comparison of these patterns is provided by Cowling et al. (1996). The reasons for the substantially higher species diversity of the Cape Region compared with these floras are several, and include a range of factors, both physical and historic.

A diversity of soils, a rugged landscape, and extremely variable and complex rainfall patterns have combined in the Cape Region to produce a mosaic of sharply different habitats that lie in close proximity to one another in a pattern repeated across its entire area. This high physical heterogeneity, although striking, is not unique to the region, and may even be greater in other regions. For example, the California Floristic Province has a wide range of soils, including serpentine substrates not present in the Cape Region, diverse climates, a rugged topography with higher mountains than those in the Cape, plus a wider latitudinal extension. Likewise, the Mediterranean Basin, orders of magnitude larger than the CFR, has a wide diversity of soils and a rugged landscape, with the mountains also higher than those found in the CFR. Both areas are often cited as being species-rich compared to neighboring regions, yet both are substantially poorer in species than the Cape Region, California in absolute number, and the Mediterranean area in substantially less alpha diversity per unit area. Southwestern Australia, in contrast, which has a flora approaching that of the Cape in size, noticeably

lacks the rugged topography of other Mediterranean regions, although it exhibits some of the ecological features of the Cape Region. Physical heterogeneity alone cannot therefore account for the richness of the Cape flora, and edaphic factors as well as historical biogeography may be more significant.

Of the five mediterranean regions of the world only the Cape and southwestern Australia have soils that include large areas of nutrient-poor quartzitic sands, and at least part of the explanation for the higher species numbers here has been thought to relate directly to the particular effects of this substrate on plant life. High levels of local diversity have been considered characteristic of nutrient-poor soils (Tilman, 1982, 1983) and if this is correct, then the mere existence of large areas of such soils should account for the comparatively high alpha diversity of heathland vegetation in both South Africa and southwestern Australia compared with that in California or central Chile unless high levels of local and regional richness are not coupled. This hypothesis is, however, not supported either in the Cape or southwestern Australia, where alpha diversity levels on nutrient-poor and nutrient-intermediate soils appear to differ only minimally (Goldblatt, 1997). Although nutrient-poor soils may not support a flora significantly richer than that occurring on soils of other nutrient status in the Cape, they are able to maintain particularly high beta diversity in the associated fynbos vegetation, both on geographical gradients and on slightly different soils under the same climatic conditions. Comparable data for nutrient-intermediate and nutrient-rich sites are not yet available. Nutrient-poor soils in mediterranean climate zones have a higher proportion of reseeding versus resprouting shrubs (Wisheu et al., 2000), and these authors argue that this directly contributes to higher diversity because the high frequency of fires that destroy reseeders would lead to their shorter generation times and thus higher speciation rates. The high frequency of fire in areas of low-nutrient soils is thus another aspect that may contribute to diversity in the Cape Region. Fire is also significant in southwestern Australia and California but not in the mediterranean zone of Chile (Kalin Arroyo et al., 1994).

The combination of edaphic and topographic diversity, steep local climatic gradients, peculiar nutrient-poor soils, and frequent fires, although undoubtedly important in promoting species diversity in the Cape Region, is still inadequate to explain the presence of the unusually rich flora in the Cape Region, particularly when compared to southwestern Australia. A notable and perhaps crucial difference between the Cape and other areas of med-



iterranean climate, possibly excluding southwestern Australia, lies in their Pliocene–Pleistocene climatic history. Available data indicate a history for southern Africa very different from that experienced in the Northern Hemisphere and to a lesser extent Chile (Villagrán, 1994). Cycles of extreme cold and aridity alternating with warm wet phases made these areas largely uninhabitable by anything resembling their current floras, elements of which either became extinct or were locally restricted to sites of relatively mild climate. A similarly dynamic history for the Cape flora has been hypothesized in which Pleistocene glacial cycles caused a northward shift in the winter-rainfall zone, which in turn caused a northward expansion of the flora during the pluvial periods but local extinction and its restriction to refugia during dry periods (Axelrod & Raven, 1978). The limited evidence available for the Cape Region, however, indicates a more moderate climate without changes of such cataclysmic dimensions. Pollen cores reflect comparatively modest shifts in the flora (Meadows & Sugden, 1991), even in the semi-arid and ecologically sensitive Cedarberg mountains. Changes there might be expected to have been more severely influenced by the drier and colder climatic conditions that are postulated to have occurred during glacial periods, when belts of vegetation adapted to mediterranean climates contracted away from the dry zones that lay toward the equator. The absence of any evidence of major changes in the vegetation of the Cape Region during the Pleistocene suggests that the glacial cycles did not have the catastrophic effects on plant life in southern Africa that they did in the Northern Hemisphere or Chile. In the CFR relatively drier and wetter cycles may simply have induced changes in the local composition of vegetation, perhaps causing limited extinction, which in turn created opportunities for speciation.

The unusually high species richness of the Cape flora is thus, in all likelihood, a consequence of sustained climatic stability and reliability, enabling a more or less uninterrupted evolution and diversification of the flora to occur in a region of high physical complexity. The history of this evolution can be traced to some extent by considering the modes of speciation evident in the flora. Although there are few such studies for plant groups centered in the Cape flora, the available evidence suggests that parapatric speciation linked to substrate or microclimatic differences is an important mode of speciation in some families (Linder & Vlok, 1991; Cowling & Holmes, 1992b; Goldblatt & Manning, 1996). Vicariant species exhibit differences in ecology such as edaphic, microclimatic, seasonal, or

pollination characteristics. For example, vicariant species of *Rhodocoma* (Restionaceae), a genus restricted to nutrient-poor sandstone soils in montane habitats, favor different habitats and are not significantly isolated geographically (Linder & Vlok, 1991). Parapatric speciation also appears to have been more important than geographic isolation in Agulhas Plain shrubs (Cowling & Holmes, 1992b) and in the genus *Lapeirousia* (Iridaceae) in the CFR and adjacent parts of the southern African west coast (Goldblatt & Manning, 1996). High levels of both beta and gamma diversity likewise support the hypothesis that microgeographic speciation has played a major role in speciation in the Cape flora. Nearly adjacent habitats with the same climatic and topographical conditions, which differ only in their substrates (coarse sand or fine sand or limestone), can support plant communities that differ radically in their species composition while still being broadly similar in family and generic composition (Cowling & Holmes, 1992a).

Parapatric or microgeographic speciation may actually be the rule not the exception in plants (Levin, 1993), and is favored by reduced gene flow across strong selection differentials. The mosaic of contrasting substrates that characterizes the CFR appears to provide such a strong selective differential. Although the Cape flora may not differ from other floras in mean pollen dispersability (Linder, 1985), many of its most characteristic elements have low seed dispersal distances. The majority of species in the Cape Region show no evident adaptations for seed dispersal and are regarded as passively dispersed, with estimated seed dispersal distances under 5 m (and most likely much less than this) (Linder, 1985). Dispersal in most Aizoaceae is by rain drops falling on hydrochastic capsules, and this mechanism, although an active one, results in very small dispersal distances (Desmet & Cowling, 1999). Active seed dispersal by ants is disproportionately well represented in both the Cape Region (Bond & Slingsby, 1983) and Australia (Berg, 1975). Some 1000 Cape species, notably in the families Fabaceae, Proteaceae, Restionaceae, Rhamnaceae, and Rutaceae, produce seeds with lipid bodies (elaiosomes) that are attractive to ants, and an undetermined additional number are transported to underground nests by harvester ants. In vegetation types prone to frequent fires, such as fynbos, the burial of seeds is a valuable adaptation (Cowling & Holmes, 1992b). However, dispersal distances for ant-dispersed seeds are also short, up to 6 m (Linder, 1985). More effective dispersal strategies are relatively restricted in their occurrence. Wind-dispersal is characteristic of many As-

teraceae and Orchidaceae (which have comparatively low levels of endemism in the Cape flora), while long-distance dispersal involving flying vertebrates (birds and bats) is least common, and is especially rare in plants on nutrient-poor substrates. There is an assumption that plants on such soils cannot afford to allocate resources to protein-rich berry or drupaceous fruits (Bond & Slingsby, 1983). The low frequency of fruits with burs and spines, adapted for exochory, suggests that dispersal by non-flying vertebrates has long been unimportant in the flora, perhaps because the fauna has historically been a small one in terms of numbers of species and individuals. This may be due largely to the unpalatability, low nutrient status, and low productivity of the flora as a whole.

Indirect evidence of the importance of reduced gene flow distances in stimulating local species diversity comes from a comparison of the number of species and their level of endemism between taxa with widely dispersed seeds and those with reduced dispersal distances. Genera with fleshy diaspores or those that are well adapted for wind dispersal tend to have wide ranges, few species per genus, and low levels of local endemism. Compare the berry-fruited *Nylandtia* (Polygalaceae), which has two species, with its relative *Muraltia*, which has dry fruits and over 100 species, most with narrow ranges. Similarly, *Chasmanthe* (Iridaceae), which has fleshy or deceptive (brightly colored) seeds, has two widespread species and one localized one, whereas its close relative *Tritonia*, which has dry seeds, has 16 species in the flora, most of them with narrow ranges. Another striking example is *Chrysanthemoides* (Asteraceae), which has seeds enclosed in a fleshy pericarp. The two species of the genus extend throughout the Cape Region and one far beyond it into tropical Africa. The numerous species of the closely related genera *Osteospermum* and *Tripteris* have dry seeds and mostly have smaller geographic ranges. This comparison is also instructive at the family level. Low seed dispersability is typical of many of the larger and most characteristic families in the flora with high ratios of species to genus and high levels of local endemism. Ericaceae, Iridaceae, and Fabaceae, which largely lack highly developed mechanisms for long-distance seed dispersal, have ratios of above 20 species per genus and higher than 80% endemism at the species level. Levels of local and regional endemism for Asteraceae (63% endemic species) and Orchidaceae (60.8%), mostly with wind-dispersed seeds, and Poaceae (38.6%) and Anacardiaceae (32.1%), many with fruits adapted to wind and/or animal dis-

persal, show levels of local and regional endemism below the mean for the entire flora (68.7%).

The massive speciation in the Cape flora is, we suggest, most likely explained by a model of local speciation in the absence of catastrophic climatic or topographic perturbations. It appears that a relatively stable climate prevailed in the Cape during the Pleistocene and that local parapatric speciation across steep environmental gradients may account for a considerable proportion of the speciation events that occurred in the CFR. Because of this relative stability it seems reasonable to postulate that extinction rates in the main vegetation zones, fynbos, renosterveld, and succulent shrubland, were low and more than compensated for by local speciation events. The nutrient-poor soils scattered in a mosaic across the CFR must have stimulated local speciation rates because of the characteristic low vagility of the seeds in the great majority of the plants adapted to these soils. Likewise, the low vagility of many of the species in Succulent Karoo, although likely a result of different selective forces, has the same consequences, with high levels of local speciation, and thus high levels of diversity across geographic, environmental, and edaphic gradients (e.g., Cowling & Holmes, 1992b; Cowling et al., 1998; Desmet & Cowling, 1999).

The unusually high diversity of the Cape flora is matched by its extraordinary composition of families and genera. Instead of a balanced flora with relatively small numbers of species per genus there has been massive local radiation in a series of unrelated genera. This is so pronounced that almost 22% of the total species in the Cape Region fall in just 10 genera, while the 20 largest genera account for over 30% of the total species (Table 3). Typical examples of these genera are *Erica* (over 650 spp.), *Aspalathus* (272 spp.), *Agathosma* (143 spp.), *Phyllica* (133 spp.), and *Cliffortia* (114 spp.). Significantly, none of the genera that display a pattern of massive local radiation in the Cape Region are endemic there, but rather they extend northward into Namaqualand, eastward into southern KwaZulu-Natal, or even further to the northeast into tropical Africa. They are, however, primarily restricted to nutrient-poor soils wherever they occur.

In sharp contrast to these examples are the endemic families of the Cape flora, which are without exception depauperate in species, although they may contain several genera. These families are typically restricted to montane habitats in acidic sandstone soils, and many of their constituent species are highly local endemic plants of particular mountain chains or peaks. They display the characteristics of paleoendemism and probably represent el-

elements of a previously more widespread southern temperate flora adapted to nutrient-poor soils in a summer-rainfall regime. It is probably no coincidence that most of these species flower in summer, and are thus out of phase with the spring flowering peak of the flora. With the development of a winter-rainfall climate in the Pliocene (e.g., Coetzee, 1993), it is reasonable to infer that these pre-Cape flora elements were gradually restricted to mesic sites in which some moisture was present over the summer months. Concomitantly it appears that other elements of the flora were able to radiate into emerging niches, thereby establishing the huge neo-endemic element of the flora. The highly sclerophyllous or microphyllous habit developed by taxa adapted to nutrient-poor substrates can thus be regarded as an important pre-adaptation to the mediterranean climate. The highly seasonal nature of the mediterranean climate, as well as its regularity, would also have favored families and genera with a geophytic habit, for example, Amaryllidaceae, Hyacinthaceae, Iridaceae, and Oxalidaceae.

The rapid and extensive radiation of plant taxa in the CFR must have been favored by both the emergence of new habitats through climatic change and the exposure of the coastal plain as sea levels fell at times during the Pleistocene (Coetzee, 1993), as well as by the stability of the climate. At the same time the flora was increasingly isolated by the winter wet and summer dry climate regime from recruitment from the summer-rainfall-adapted flora of adjacent parts of southern Africa, which largely lack the low- or nutrient-intermediate soils so characteristic of the Region.

A final characteristic of the Cape flora is the great, and often extreme, diversity of flower form that is a feature of many of the genera. This is linked to a diversity of pollination strategies, many of which are poorly exploited outside the region. In particular, pollination by sunbirds, long-proboscid flies, hopliine beetles, rodents, and the butterfly *Aeropetes* are more extensively developed in the Cape flora than elsewhere in Africa (Manning & Goldblatt, 1996; Goldblatt et al., 1998; Goldblatt & Manning, 1999). All these strategies favor differently shaped, large, brightly colored flowers. Pollinator diversity is likely to be part of the explanation for the high species diversity in the CFR, particularly for certain families in the flora. Both Iridaceae and Ericaceae, for example, have adopted a range of pollination strategies not evident or only weakly expressed elsewhere across their range (Vogel, 1954; Goldblatt & Manning, 1996, 1998; Bernhardt & Goldblatt, 2000), and are often particularly striking when in bloom. In *Gladiolus*, a prime ex-

ample of a genus with diverse pollination systems and represented in the CFR by 106 species, the genus exhibits no less than 27 shifts in pollination system in southern Africa, most of these in the CFR (Goldblatt et al., 2001), and repeatedly evolved adaptations for long-proboscid fly, sunbird, moth, and butterfly pollination, which must have played a major role in its radiation. The short season favorable for both plant and insect growth is probably the overriding factor responsible for the diversification of pollination strategies and, more than anything else, has made the Cape flora so extremely appealing to human sensibilities.

#### CONSERVATION

Like other parts of the world with species-rich floras and an expanding human population, there are varied and serious threats to the Cape flora. Expanding agricultural activity for growing food or to supply other human needs has transformed lowland areas near population centers to the extent that little or no native plants remain locally (Rebello, 1992). Moreover, the peculiarly local distribution of many Cape plants (high beta diversity) means that a higher proportion is imminently threatened with extinction than would be the case with widespread species. The number of species known to be lost forever is relatively low, but the number of species represented by single, reduced, and diminishing populations is alarmingly high. Taylor (1978) estimated that some 500 endemic species in the CFR were threatened, while at least 60 species were known to be extinct (0.67%). Red Data Book numbers for southern Africa in 1985 include 1320 Cape plants (14.67% of the total) (Hall & Veldhuis, 1985). Criteria for classification of threatened species vary; Rebello (1992) estimated 218 threatened species (extinct, endangered, or vulnerable) in the CFR (ca. 4.8%), slightly less than half the figure provided by Taylor, but nevertheless, considerable.

In 2001 these figures are certain to be higher as a result of the expanding human population, despite ever more sophisticated conservation activity. A peculiar threat to the Cape flora is the spread of alien vegetation, largely woody species of Australian *Acacia* and *Hakea* and European *Pinus*. These species rapidly invade montane and lowland areas not currently suitable for agriculture, thus compounding the threats of agricultural activity and urban growth. The threat posed by this alien vegetation is being vigorously countered by biological control methods and manual removal, but the problem is immense and requires constant monitoring. Kruger (1977) estimated that 60% of fynbos had

been replaced by alien vegetation, agriculture, or urban development. Twenty-five years later, this figure is bound to have increased.

Concrete examples may better illustrate the situation. Rebelo (1992) estimated that of 306 endemic species of Proteaceae 65 were threatened (defined as extinct, endangered, or vulnerable) (ca. 21%), while 131 were treated as Red Data species. The pattern in other families is similar, although slightly less serious, with 10.5% of endemic Iridaceae, 9% of endemic Rutaceae, ca. 3% of endemic Ericaceae, ca. 2% each of endemic Asteraaceae and Fabaceae threatened (Rebelo, 1992). The number of species of each of these families included in the Red Data Book is substantially higher (Hall & Veldhuis, 1985).

A detailed analysis of reserves and other conservation areas in the CFR is presented by Rebelo (1992). Recent conservation efforts have secured substantial areas for preservation of diverse vegetation types in the CFR and a framework for a conservation plan to establish reserves to cover portions of all vegetation types has been developed (Cowling & Heijns, 2001; Cowling et al., 2001). Although such reserves cannot include populations of all endangered species because of their erratic distributions, future loss of distinctive vegetation types will be limited and preservation of substantial tracts of each will in the future be enhanced.

#### Literature Cited

- Angiosperm Phylogeny Group (APG). 1998. An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85: 531–553.
- Arnold, T. H. & B. C. de Wet (editors). 1993. *Plants of Southern Africa. Names and Distribution.* Mem. Bot. Surv. S. Africa 62. National Botanical Institute, Pretoria.
- Axelrod, D. I. & P. H. Raven. 1978. Late Cretaceous and Tertiary vegetation history of Africa. Pp. 77–130 in M. J. A. Werger (editor), *Biogeography and Ecology of Southern Africa.* W. Junk, The Hague.
- Bayer, M. B. 1984. The Cape flora and the karoo—A winter rainfall biome versus a fynbos biome. *Veld & Flora* 70(1): 17–19.
- Beard, J. S. 1970 (editor). *An Annotated Checklist of the Plants of Western Australia.* Kings Park Board, Perth.
- Berg, R. Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. *Austral. J. Bot.* 23: 475–508.
- Bernhardt, P. & P. Goldblatt. 2000. The diversity of pollination mechanisms in the Iridaceae of southern Africa. Pp. 301–308 in K. Wilson & P. Weston (editors), *Systematics and Biology of the Monocots.* Royal Botanic Gardens, Sydney, Australia.
- Bond, P. & P. Goldblatt. 1984. *Plants of the Cape Flora: A Descriptive Catalogue.* J. S. African Bot., Suppl. 13.
- Bond, W. J. 1983. On alpha diversity and the richness of the Cape flora: A study in southern Cape fynbos. Pp. 225–243 in F. J. Kruger, D. T. Mitchell & J. U. M. Jarvis (editors), *Mediterranean-Type Ecosystems. The Role of Nutrients.* Springer-Verlag, Berlin.
- & P. Slingsby. 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *S. African J. Sci.* 79: 231–233.
- Brako, L. & J. L. Zarucchi. 1993. *Catalogue of the Flowering Plants and Gymnosperms of Peru.* Monogr. Syst. Bot. Missouri Bot. Gard. 45.
- Bremer, B., R. G. Olmstead, L. Struwe & J. A. Sweere. 1994. *rbcL* sequences support the exclusion of *Retzia*, *Desfontainia*, and *Nicodenia* from the Gentianales. *Pl. Syst. Evol.* 190: 213–230.
- Chase, M. W., D. E. Soltis, P. S. Soltis, P. J. Rudall, M. F. Fay, W. H. Hahn, S. Sullivan, J. Joseph, M. Molvray, P. J. Kores, T. J. Givnish, K. J. Sytsma & J. C. Pires. 2000. Higher-level systematics of the monocotyledons: An assessment of current knowledge and a new classification. Pp. 3–16 in K. Wilson & P. Weston (editors), *Systematics and Biology of the Monocots.* Royal Botanic Gardens, Sydney.
- Coetzee, J. A. 1993. African flora since the terminal Jurassic. Pp. 37–61 in P. Goldblatt (editor), *Biological Relationships Between Africa and South America.* Yale Univ. Press, New Haven.
- & J. Rogers. 1982. Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa). *Palaeogeogr. Palaeoclim. Palaeoecol.* 39: 71–85.
- & J. Muller. 1985. The phytogeographic significance of some extinct Gondwana pollen types from the Tertiary of the southwestern Cape (South Africa). *Ann. Missouri Bot. Gard.* 71: 1088–1099.
- & L. Pragowski. 1984. Pollen evidence for the occurrence of Casuarinaceae and *Myrica* in the Tertiary of South Africa. *Grana* 23: 23–41.
- Conran, J. G., M. W. Chase & P. J. Rudall. 1997. Two new monocotyledon families: Anemarrhenaceae and Behniaceae (Liliana: Asparagales). *Kew Bull.* 52: 995–999.
- Cowling, R. M. 1987. Fire and its role in coexistence and speciation in Gondwanan shrublands. *S. African J. Sci.* 83: 106–112.
- . 1990. Diversity components in a species-rich area of the Cape Floristic Region. *J. Veg. Sci.* 1: 699–710.
- . 1992. *The Ecology of Fynbos.* Oxford Univ. Press, Cape Town.
- & C. E. Heijns. 2001. The identification of broad habitat units as biodiversity entities for systematic conservation planning in the Cape floristic region. *S. African J. Bot.* 67: 15–38.
- & P. M. Holmes. 1992a. Flora and vegetation. Pp. 23–61 in R. M. Cowling (editor), *The Ecology of Fynbos.* Oxford Univ. Press, Cape Town.
- & ———. 1992b. Endemism and speciation in a lowland flora from the Cape Floristic Region. *Biol. J. Linn. Soc.* 47: 367–383.
- & D. J. McDonald. 1999. Local endemism and plant conservation in the Cape Floristic Region. Pp. 171–188 in P. W. Rundel, G. Montenegro & F. Jaksic (editors), *Landscape Degradation in Mediterranean-Climatic Ecosystems.* Springer-Verlag, Berlin.
- & E. T. F. Witkowski. 1994. Convergence and non-convergence of plant traits in climatically and edaphically matched sites in Mediterranean Australia and South Africa. *Austral. J. Ecol.* 19: 220–232.
- , P. M. Holmes & A. G. Rebelo. 1992. Plant di-

- versity and endemism. Pp. 62–112 in R. M. Cowling (editor), *The Ecology of Fynbos*. Oxford Univ. Press, Cape Town.
- , P. W. Rundell, B. B. Lamont, M. Kalin Arroyo & M. Arianoutsou. 1996. Plant diversity in mediterranean-climate regions. *Trends Ecol. Evol.* 11: 362–366.
- , P. W. Rundell, P. G. Desmet & K. J. Esler. 1998. Extraordinary high regional-scale plant diversity in southern African arid lands: Subcontinental and global comparisons. *Diversity & Distributions* 4: 27–36.
- , C. R. Cartwright, J. E. Parkington & J. C. Allsop. 1999. Fossil wood charcoal assemblages from Elands Bay Cave, South Africa: Implications for Late Quaternary vegetation and climates in the winter-rainfall fynbos biome. *J. Biogeogr.* 26: 367–378.
- , R. L. Pressey, A. T. Lombard, C. E. Hejnis, D. M. Richardson & N. Cole. 2001. Framework for a Conservation Plan for the Cape Floristic Region. Institute for Plant Conservation Report 9902 submitted to WWF: SA.
- D'Arcy, W. D. 1987. *Flora of Panama. Checklist and Index*. Missouri Botanical Garden, St. Louis.
- Deacon, H. J. 1979. Palaeoecology. Pp. 58–66 in J. Day, W. R. Siegfried, G. N. Louw & M. L. Jarman (editors), *Fynbos Ecology: A Preliminary Synthesis*. S. African Nat. Sci. Progr. Rep. 40. CSIR, Pretoria.
- Desmet, P. G. & R. M. Cowling. 1999. Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa. *Pl. Ecol.* 142: 23–33.
- Esler, K. J. 1998. Unusual geophytes of the succulent karoo. *Veld & Flora* 84: 6–9.
- , P. W. Rundell & P. Vorster. 1998. Biogeography of prostrate-leaved geophytes in semi-arid South Africa: Hypotheses on functionality. *Pl. Ecol.* 142: 105–120.
- Fenner, M., W. G. Lee & J. Barstow Williams. 1997. A comparative study of the distribution of genus size in twenty angiosperm floras. *Biol. J. Linn. Soc.* 62: 225–237.
- Gentry, A. H. 1988a. Tree species richness of upper Amazonian species. *Proc. Natl. Acad. Sci. U.S.A.* 85: 156–159.
- . 1988b. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.* 75: 1–34.
- & C. Dodson. 1987. Diversity and phytoecology of neotropical vascular epiphytes. *Ann. Missouri Bot. Gard.* 74: 205–233.
- Goldblatt, P. 1978. An analysis of the flora of southern Africa: Its characteristics, relationships, and origins. *Ann. Missouri Bot. Gard.* 65: 369–436.
- . 1979. Miscellaneous chromosome counts in angiosperms, II, including new family and generic records. *Ann. Missouri Bot. Gard.* 66: 865–861.
- . 1997. Floristic diversity in the Cape Flora of South Africa. *Biodiversity & Conservation* 6: 359–377.
- & J. C. Manning. 1996. Phylogeny and speciation in *Lapeirousia* subgenus *Lapeirousia* (Iridaceae subfamily Ixioidae). *Ann. Missouri Bot. Gard.* 83: 346–361.
- & ———. 1998. *Gladiolus* in Southern Africa. Fernwood Press, Cape Town.
- & ———. 1999. The long-proboscid fly pollination system in *Gladiolus* (Iridaceae). *Ann. Missouri Bot. Gard.* 86: 758–774.
- & ———. 2000. *Cape Plants*. National Botanical Institute, Cape Town.
- , R. Dahlgren, B. J. Nielsen & J. P. Rourke. 1979. Further notes of Retziaceae: Chemical contents and affinities. *Ann. Missouri Bot. Gard.* 66: 545–556.
- , P. Bernhardt & J. C. Manning. 1998. Pollination of petaloid geophytes by monkey beetles (Scarabaeidae: Rutelinae: Hopliini) in southern Africa. *Ann. Missouri Bot. Gard.* 85: 215–230.
- , J. C. Manning & P. Bernhardt. 2001. Radiation of pollination systems in *Gladiolus* (Iridaceae: Crocoideae) in southern Africa. *Ann. Missouri Bot. Gard.* 88: 713–734.
- Good, R. 1974. *The Geography of the Flowering Plants*, ed. 4. Longmans Green, London.
- Groves, R. H., J. S. Beard, H. J. Deacon, J. J. N. Lambrechts, A. Rabinovitch-Vin, R. L. Specht & W. D. Stock. 1983. Introduction: The origins and characteristics of mediterranean ecosystems. Pp. 1–17 in J. A. Day (editor), *Mineral Nutrients in Mediterranean Ecosystems*. S. African Nat. Sci. Progr. Rep. 71. CSIR, Pretoria.
- Hall, A. V. & H. A. Veldhuis. 1985. *South African Red Data Book: Plants—Fynbos and karoo biomes*. S. African Nat. Sci. Progr. Rep. 117. CSIR, Pretoria.
- Hendey, Q. B. 1982. *Langebaanweg. A Record of Past Life*. South African Museum, Cape Town.
- Hopper, S. D. 1992. Patterns of plant diversity at the population and species levels in south-west Australian mediterranean ecosystems. Pp. 27–46 in R. J. Hobbs (editor), *Biodiversity in Mediterranean Ecosystems in Australia*. Surrey Beatty & Sons, Chipping Norton.
- Jürgens, N. 1991. A new approach to the Namib region. Part 1. Phytogeographic subdivision. *Vegetatio* 97: 21–38.
- . 1997. Floristic biodiversity and history of African arid regions. *Biodiversity & Conservation* 6: 495–514.
- Kalin Arroyo, M. T. & L. Cavieres. 1997. The mediterranean type-climate flora of central Chile—What do we know and how can we assure its protection. *Notic. Biol.* 5: 48–56.
- , C. Marticorena & M. Munoz-Schick. 1994. Convergence in the Mediterranean floras in Central Chile and California: Insights from comparative biology. Pp. 43–88 in M. T. Kalin Arroyo, P. H. Zedler & M. D. Fox (editors), *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia*. *Ecol. Stud.* 108. Springer-Verlag, New York.
- King, L. 1962. *The Geology of the Earth*. Oliver & Boyd, Edinburgh.
- Klein, R. G. 1977. The ecology of early man in southern Africa. *Science* 197: 115–126.
- Kruger, F. J. 1977. Ecological reserves in the Cape fynbos: Toward a strategy for conservation. *S. African J. Sci.* 73: 81–85.
- & H. C. Taylor. 1979. Plant species diversity in Cape fynbos: Gamma and delta diversity. *Vegetatio* 41: 85–93.
- Lebrun, J.-P. & A. L. Stork. 1997. *Enumeration des Plantes à Fleurs d'Afrique Tropicale*. 5: Conservatoire et Jardin Botanique de la Ville de Genève, Geneva.
- Levin, D. A. 1993. Local speciation in plants: The rule not the exception. *Syst. Bot.* 18: 197–208.
- Linder, P. H. 1985. Gene flow, speciation and species diversity patterns in a species-rich area: The Cape flora. Pp. 53–57 in E. S. Vrba (editor), *Species and Speciation*. Transvaal Mus. Monogr. 4. Transvaal Museum, Pretoria.
- & J. H. J. Vlok. 1991. The morphology, taxonomy

- and evolution of *Rhodocoma* (Restionaceae). *Pl. Syst. Evol.* 175: 139–160.
- Louw, A. B. & A. G. Rebelo. 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.
- Maggs, G. L., P. Craven & H. Kolberg. 1998. Plant species richness, endemism and genetic resources in Namibia. *Biodiversity & Conservation* 7: 435–446.
- Manning, J. C. & P. Goldblatt. 1996. The *Prosoeca peringueyi* (Diptera: Nemestrinidae) pollination syndrome in southern Africa: Long-tongued flies and their tubular flowers. *Ann. Missouri Bot. Gard.* 83: 67–86.
- Meadows, M. E. & J. M. Sugden. 1991. A vegetation history of the last 14 000 years on the Cedarberg, south-western Cape Province. *S. African J. Sci.* 87: 34–43.
- Médail, F. & P. Quézel. 1997. Hot spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Ann. Missouri Bot. Gard.* 84: 112–127.
- Munro, S. L. & H. P. Linder. 1998. The phylogenetic position of *Prionium* (Juncaceae) within the order Juncales based on morphological and *rbcL* sequence data. *Syst. Bot.* 23: 43–55.
- Oliver, E. G. H. 2000. Systematics of Ericaceae (Ericaceae: Ericoideae), species with indehiscent and partially dehiscent fruits. *Contr. Bolus Herb.* 19: 1–483.
- Olmstead, R. G., C. W. dePamphilis, A. D. Wolfe, N. D. Nelson, W. J. Elisens & P. A. Reeves. 2001. Disintegration of the Scrophulariaceae. *Amer. J. Bot.* 88: 348–361.
- Pennington, T. D. & B. T. Styles. 1975. A generic monograph of the Meliaceae. *Blumea* 22: 419–540.
- Raven, P. H. & D. I. Axelrod. 1978. Origin and relationships of the California flora. *Univ. California Publ. Bot.* 72.
- Rebelo, A. G. 1992. Preservation of biotic diversity. Pp. 308–344 in R. M. Cowling (editor), *The Ecology of Fynbos*. Oxford Univ. Press, Cape Town.
- Rutherford, M. C. & R. H. Westfall. 1994. Biomes of southern Africa: An objective categorization. *Mem. Bot. Survey S. Africa* 63.
- Savolainen, V., M. F. Fay, D. C. Albach, A. Backlund, M. van der Bank, K. M. Cameron, S. A. Johnson, M. D. Lledo, J.-C. Pintaud, M. Powell, M. C. Sheahan, D. E. Soltis, P. S. Soltis, P. Weston, W. M. Whitten, K. J. Wurdack & M. W. Chase. 2000. Phylogeny of the eudicots: A nearly complete familial analysis based on *rbcL* gene sequences. *Kew Bull.* 55: 257–309.
- Schatz, G. E., P. P. Lowry, M. Lescot, A. E. Wolf, S. Andriambololona, V. Randrianasolo & J. Raharimampionona. 1996. Conspectus of the vascular plants of Madagascar: A taxonomic and conservation electronic data base. Pp. 10–17 in L. J. G. van der Maesen et al. (editors), *The Biodiversity of African Plants*. Proceedings of the XIV AETFAT Congress, Wageningen, The Netherlands. Kluwer Academic Publications, Dordrecht.
- Scholz, A. 1985. The palynology of the upper lacustrine sediments of the Arnot pipe, Banke, Namaqualand. *Ann. S. African Mus.* 95: 1–109.
- Stuckenberg, B. R. 1962. The distribution of the montane palaeogenic element in the South African invertebrate fauna. *Ann. Cape Prov. Mus.* 2: 190–205.
- Takhtajan, A. 1986. *Floristic Regions of the World*. Univ. California Press, Berkeley. [Translated by T. Crovello.]
- Taylor, H. C. 1978. Capensis. Pp. 171–229 in M. J. A. Werger (editor), *Biogeography and Ecology of Southern Africa*, Vol. 1. W. Junk, The Hague.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton Univ. Press, Princeton.
- . 1983. Some thoughts on resource competition and diversity in plant communities. Pp. 322–336 in F. J. Kruger, D. T. Mitchell & J. U. M. Jarvis (editors), *Mediterranean-Type Ecosystems. The Role of Nutrients*. Springer-Verlag, Berlin.
- , W. J. Bond, B. M. Campbell, F. J. Kruger, H. P. Linder, A. Scholz, H. C. Taylor & M. Witter. 1983. Origin and maintenance of plant species diversity. Pp. 125–135 in J. A. Day (editor), *Mineral Nutrients in Mediterranean Ecosystems*. S. African Nat. Sci. Progr. Rep. 71. CSIR, Pretoria.
- Villagrán, C. M. 1994. Quarternary history of the mediterranean vegetation of Chile. Pp. 3–20 in M. T. Kalin Arroyo, P. H. Zedler & M. D. Fox (editors), *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia*. *Ecol. Stud.* 108. Springer-Verlag, New York.
- Wisheu, I. C., M. L. Rosenzweig, L. Olsvig-Whittaker & A. Schmida. 2000. What makes nutrient-poor mediterranean heathlands so rich in plant diversity. *Evol. Ecol. Res.* 2: 935–955.
- Vogel, S. 1954. Blütenbiologische Typen als Elemente der Sipplgliederung. *Bot. Stud.* 1: 1–338.
- Wagner, W. L. 1991. Evolution of waif floras: A comparison of the Hawaiian and Marquesan Archipelagoes. Pp. 267–284 in E. C. Dudley (editor), *The Unity of Evolutionary Biology* Vol. 1. Dioscorides Press, Portland, Oregon.
- , D. R. Herbst & S. H. Sohmer. 1990. *Manual of the Flowering Plants of Hawai'i*. Univ. Hawai'i Press, Honolulu.
- Weimarck, H. 1941. Phytogeographical groups, centers and intervals within the Cape flora. *Acta Univ. Lund. new ser.* 37(5): 1–143.
- Xiang, Q.-Y., D. E. Soltis, D. R. Morgan & P. S. Soltis. 1993. Phylogenetic relationships of *Cornus* L. sensu lato and putative relatives inferred from *rbcL* sequence data. *Ann. Missouri Bot. Gard.* 80: 723–734.