Patterns of plant diversity and endemism in southern Africa: an overview

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Patterns of plant diversity and endemism in southern Africa: an overview

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ABSTRACT

Southern Africa has an extremely diverse flora with very high levels of endemism. The density of vascular plant species is on a par with many of the rich floras of tropical countries. The level of endemism is also very high, being more akin to those of oceanic islands than a portion of a continent. This endemic flora comprises a distinct phylogenetic assemblage, with 13 families being endemic to the region. This diversity is not uniformly distributed over southern Africa, but is concentrated in eight localized hot-spots. The diversity and levels of endemism within two of these, the Cape and the Succulent Karoo, are notable in comparison with similar areas elsewhere. The Cape flora in particular, is the richest of the world's hot-spots of plant diversity. The flora endemic to the southern African hot-spots is also not a random assemblage with regard to taxonomic composition, growth forms and other biological attributes. Of all the southern African hot-spots, the Cape and Succulent Karoo are most in need of conservation attention. Although the protected area network needs to be re-evaluated, considerable attention will have to be given to the sustainable use of biodiversity outside conservation areas. This is of particular importance in the light of the changing sociopolitical situation within South Africa.

INTRODUCTION

Internationally, most biodiversity analyses have focused on the extremely rich tropical regions of the earth (e.g. McNeely *et al.* 1990; Mittermeier 1988; Mittermeier & Werner 1990; Myers 1988). This focus on tropical countries has led to the neglect of biodiversity in temperate regions (Given 1990; McNeely *et al.* 1990; Platnick 1991), particularly the five warm temperate Mediterranean-climate regions of the earth which contain about 20% of the world's plant species, many of which are endemic to those regions.

Myers (1988) coined the term 'hot-spot' to describe areas that are characterized by high species richness, high concentrations of endemic species and which are experiencing high rates of habitat modification or loss. (The term hot-spot as defined by Myers (1988, 1990) is used throughout this paper.) Initially, Myers (1988) identified 10 hot-spots, all in the tropical rainforests. He then extended his hot-spot analysis (Myers 1990) to include additional tropical rainforest regions and four of the Mediterranean-climate regions, including the Cape Floristic Region of South Africa. The total endemic flora of the 18 hot-spots identified by Myers (1988, 1990) comprises about 50 000 species or 20% of the world's total flora on only 0.5% of the earth's surface. The Cape Floristic Region, with over 6 000 endemic species, emerged as the 'hottest' of the world's hot-spots (Myers 1990).

The *Flora of southern Africa* (FSA) region (the area south of the Kunene, Okavango and Limpopo Rivers, see Figure 1, but excluding Angola, Mozambique and Zimbabwe) has long been recognized as an area of remarkable plant diversity with high levels of endemism (Adamson 1938; Cowling *et al.* 1989; Gibbs Russell 1985; Goldblatt 1978; Good 1974; Levyns 1964). At the latest count, the region's flora comprised 21 137 species of vascular plants (Arnold & De Wet 1993) of which at least 80% are endemic (Gibbs Russell 1985; Goldblatt 1978). These high levels of plant diversity and endemism are, however, not evenly distributed across southern Africa (Cowling *et al.* 1989; Davis & Heywood 1994; Gibbs Russell 1987; Weimarck 1941). Although patterns of plant species richness at the regional level have been analysed for southern Africa (Cowling *et al.* 1989; Gibbs Russell 1987) and Centres of Plant Diversity (Davis & Heywood 1994) have recently been described (Hilton-Taylor 1994a, 1994b; Killick 1994; Rebelo 1994a; Van Wyk 1994), there has been no subcontinental-level study of patterns of plant endemism. The aims of this paper are therefore (1) to compare the species richness (for the purposes of this paper we have referred to species richness as diversity) and levels of endemism of the southern African (the FSA region as defined above) flora with other areas of the world; (2) to identify the hot-spots of plant diversity and endemism within southern Africa; (3) to determine whether the hot-spot endemics have any special characteristics; (4) to describe the major threats to the flora, particularly in the hot-spots; and (5) to propose methods of ensuring the conservation of plant resources.

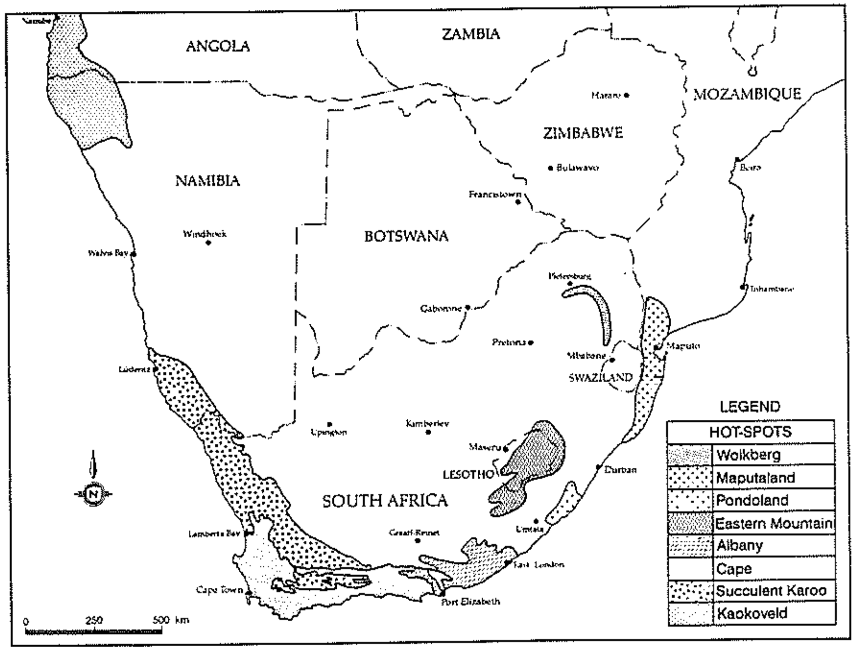

Figure 1.—Map of southern Africa (Botswana, Lesotho, Namibia, South Africa and Swaziland) with shaded areas indicating location of hot-spots mentioned in the text.

Our analysis includes data only for the vascular plants (gymnosperms and angiosperms) and the nomenclature used follows that in Arnold & De Wet (1993). We have also assumed that all species are of equal rank when used as measures of biotic diversity, despite the fact that it is unreasonable to give equal biotic or conservation value to each one of the 526 species of *Erica* endemic to the Cape Floristic Region, and to the phylogenetically and ecologically unique Namib Desert endemic, *Welwitschia mirabilis* (see Bond 1989). Although there are methods for ranking species on the basis of their genetic diversity (e.g. Crozier 1992; Vane-Wright *et al.* 1991; Williams *et al.* 1991), such an approach was deemed impractical for the purposes of this study. This type of approach is also premature if one considers the number of large and important families in the flora for which there is no recent and/or adequate taxonomic treatment.

THE SOUTHERN AFRICAN FLORA

Biodiversity

Southern Africa has a remarkably rich flora of vascular plants, with 23 404 taxa (species plus infraspecific taxa) being recorded from the region (Arnold & De Wet 1993), and it also has one of the highest species densities in the world (Table 1) (see also Cowling *et al.* 1989; Gibbs Russell 1985). Species richness for the subcontinent is higher than 8 of the 12 'megadiversity countries' identified by McNeely *et al.* (1990), namely Australia, Ecuador, India, Indonesia, Madagascar, Malaysia, Peru and Zaïre (Figure 2). In contrast to the above countries, southern Africa is a predominantly warm-temperate, semi-arid region with an overall mean annual rainfall of less than 400 mm (Schulze & McGee 1978). The amount and seasonality of rainfall do, however, vary considerably from north to south and from west to east across southern Africa, e.g. in the northwest, mean annual rainfall is less than 100 mm and occurs predominantly in the summer months; in the southwest it is 600 mm and occurs predominantly in the winter months; and in the eastern parts it may exceed 1 400 mm and occurs mainly in summer (Schulze & McGee 1978). Rainforests cover less than 1% of southern Africa (Rutherford &

TABLE 1.—Vascular plant species density in southern Africa and similar-sized regions

Region	Area (10^6 km^2)	Species density ($\times 10^3/10^6$ km^2)
Southern Africa	2.57	8.22
Zaïre	2.35	4.68
Argentina	2.77	3.25
Algeria	2.38	1.30
Sudan	2.51	1.27

Sources: World Conservation Monitoring Centre (1992, except for southern Africa (Arnold & De Wet 1993).

Westfall 1986), whereas most other species-rich regions include large areas of tropical rainforest (McNeely *et al.* 1990; Myers 1988, 1990).

A detailed assessment to determine why the southern African flora is so rich is beyond the scope of this paper, but much of the region's biodiversity can be attributed largely to contemporary ecological conditions. The subcontinent's transitional location relative to the subtropical summer rainfall and temperate winter

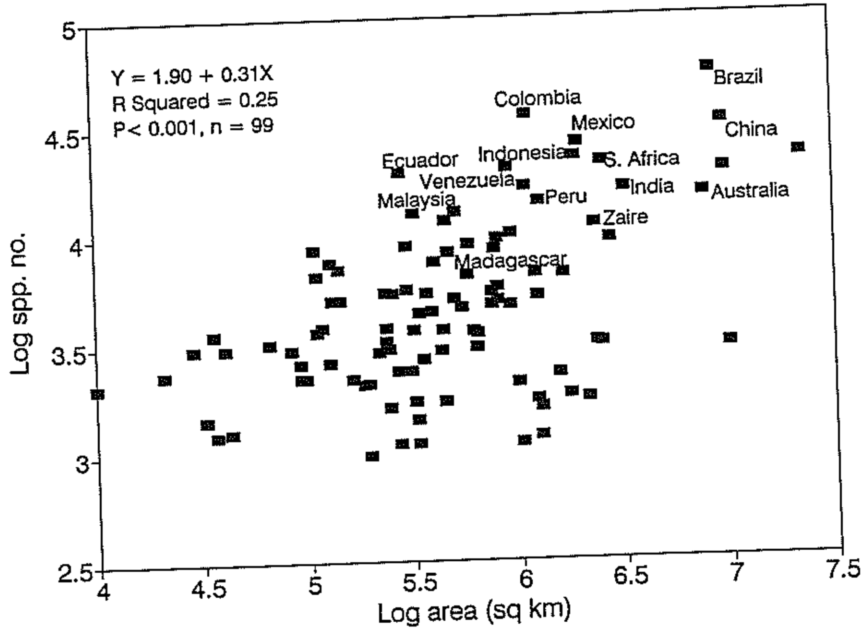

Figure 2.—Species-area relationships (vascular plants only) for 100 countries. Other than southern Africa and Venezuela, all the listed countries are the 'megadiversity countries' of McNeely *et al.* (1990). (Source: World Conservation Monitoring Centre 1992.)

rainfall climates, combined with a complex topography and heterogeneity of geology and soils (Rutherford & Westfall 1986; Werger 1978a), results in steep ecological gradients along which many species can occur (Cowling *et al.* 1989). The heterogeneity of the region is well illustrated by its classification into five phytochoria (Werger 1978b; White 1983), seven biomes (Rutherford & Westfall 1986) and, in South Africa alone, 70 major vegetation categories or Veld Types (Acocks 1953). Despite this heterogeneity, there are more species in southern Africa than in ecologically similar regions elsewhere in the world. This implies that unique historical processes have also contributed to the region's phenomenal biodiversity (Cowling *et al.* 1989, 1992).

Endemism

The number of vascular plant species endemic to southern Africa is exceptionally high, being more like what might be expected of an oceanic island than of a part of a continent (Goldblatt 1978; Table 2). This endemism is largely attributed to the diverse ecological conditions of southern Africa relative to the the rest of the continent. However, it is also the product of high speciation within some of the 560 genera endemic to the region, resulting in an island-like species : genus ratio of 9.6 (Gibbs Russell 1985; Goldblatt 1978). Most of these large genera are confined to the predominantly winter rainfall Fynbos and Succulent Karoo Biomes (Gibbs Russell 1987).

On a global scale, the flora endemic to southern Africa comprises a distinct phylogenetic assemblage. Examining the 26 largest families of flowering plants in the flora, which have levels of endemism significantly higher than or the same as the total flora, only eight rank among the 30 largest families in the world (Table 3). Southern Africa contains most of the world's species of Mesembryanthema [this is a monophyletic group within the family Aizoaceae without a taxonomic

TABLE 2.—Global patterns of vascular plant species endemism

Country	Endemism (%)	Country	Endemism (%)
New Zealand	82	Ecuador	21
Southern Africa	80	United States	21
Australia	80	Costa Rica	15
New Caledonia	80	Greece	15
Madagascar	68	Mexico	14
Indonesia	67	Panama	14
China	56	Algeria	8
Papua New Guinea	55	Mozambique	4
Chile	51	Nigeria	4
Zaïre	29	Zambia	4
Sri Lanka	28	Zimbabwe	2
Argentina	25	Germany	<1
Angola	24	Sweden	<1

Source: World Conservation Monitoring Centre (1992).

TABLE 3.—Species endemism in the 30 largest families of flowering plants in the flora of southern Africa

Family	Rank in sthn Afr.	Rank in world	Number of species (%) Endemic	Number of species (%) Nonendemic	χ^2
Total flora	—	—	16 298 (80)	4 074 (20)	—
Endemism significantly higher than total flora					
Mesembryanthema†	1	—	2 360 (98)	48 (2)	552.0***
Asteraceae	2	1	1 820 (86)	296 (14)	52.9***
Liliaceae *s.l.*	4	11	943 (89)	123 (11)	49.8***
Iridaceae	5	—	828 (97)	30 (3)	151.4***
Ericaceae	6	21	802 (99)	2 (1)	202.8***
Asclepiadaceae	8	13	668 (87)	101 (13)	23.1***
Scrophulariaceae	9	8	471 (87)	72 (13)	16.5***
Proteaceae	13	—	355 (97)	11 (3)	66.2***
Rutaceae	15	—	274 (94)	17 (6)	36.1***
Restionaceae	16	—	265 (94)	17 (6)	34.0***
Geraniaceae	17	—	257 (96)	10 (4)	43.6***
Campanulaceae	18	—	236 (92)	20 (8)	23.3***
Crassulaceae	20	—	190 (89)	25 (11)	9.0**
Selaginaceae	21	—	208 (97)	10 (3)	31.7***
Polygalaceae	23	—	179 (88)	26 (12)	6.5*
Oxalidaceae	25	—	191 (98)	4 (2)	38.5***
Thymelaeaceae	26	—	180 (95)	9 (5)	26.7***
Aizoaceae *s.s.*	27	—	180 (98)	4 (2)	35.8***
Apiaceae	28	17	162 (90)	14 (10)	9.0**
Santalaceae	29	—	166 (94)	10 (6)	21.8***
Endemism same as total flora					
Euphorbiaceae	11	6	367 (80)	94 (20)	0.0NS
Orchidaceae	12	2	353 (81)	86 (19)	0.0NS
Amaryllidaceae	24	—	162 (82)	36 (18)	0.3NS
Sterculiaceae	30	—	148 (85)	27 (15)	2.0NS
Endemism significantly lower than total flora					
Fabaceae	3	3	1 147 (75)	393 (25)	31.4***
Poaceae	7	4	348 (44)	435 (56)	641.2***
Cyperaceae	10	9	240 (52)	224 (48)	235.5***
Acanthaceae	14	15	233 (66)	118 (34)	40.5***
Lamiaceae	19	7	142 (63)	83 (37)	39.5***
Rubiaceae	22	5	108 (52)	99 (48)	99.5***

World rank is among the 30 largest families.
*** = $P<0.001$; ** = $P<0.01$; * = $P<0.05$; NS = not significant.
Source: Gibbs Russell (1985).
† Mesembryanthemaceae sensu Dyer (1975).

rank, which comprises the two subfamilies Mesembryanthemoideae and Ruschioideae (Hartmann 1991)], Ericoideae (Ericaceae), Aizoaceae, Amaryllidaceae, Iridaceae and Restionaceae, as well as high proportions of Geraniaceae, Proteaceae and Rutaceae (Gibbs Russell 1985; Goldblatt 1978). In addition,

southern Africa has 13 endemic or near-endemic families, namely Achariaceae, Geissolomataceae, Bruniaceae, Grubbiaceae, Greyiaceae, Heteropyxidaceae, Penaeaceae, Rhynchocalycaceae, Aitoniaceae, Roridulaceae, Retziaceae, Stilbaceae and Lanariaceae (Dahlgren & Van Wyk 1988). Most of these familes are monogeneric with one, two or three species, the largest being the Bruniaceae with 76 species in 13 genera (Arnold & De Wet 1993; Goldblatt 1978). Nearly all of the above-mentioned families are concentrated in the winter rainfall region in the southwestern subcontinent. Families with levels of endemism significantly lower than the total flora (e.g. Fabaceae, Poaceae and Rutaceae) are widespread in other parts of the world.

SOUTHERN AFRICAN HOT-SPOTS

As mentioned previously, biodiversity is not uniformly distributed over southern Africa and some areas are clearly more species-rich than others. For example, Namibia which comprises 32% of the region's area has only 15% of southern African plant species, whereas the Cape Floristic Region, covering 3.5% of the region, has 41% of the species.

Under the auspices of the IUCN's Centres of Plant Diversity Project, seven centres of plant diversity have been identified in southern Africa (Davis & Heywood 1994). The criteria used for the inclusion of sites as Centres are that they must be both species-rich and have high levels of endemism. Most areas of southern Africa, but especially the region's centres of plant diversity (Davis & Heywood 1994), have been subject to, or are under threat from large-scale habitat modification and transformation (Macdonald 1989); hence we have used the term hot-spots (*sensu* Myers 1988) to describe these centres. We recognize eight hot-spots: seven Centres from Davis & Heywood (1994) and the Wolkberg Centre of Matthews *et al.* (1993). These hot-spots are distributed in an almost continuous arc below and including large portions of the Great Escarpment (Figure 1). They include the northeastern Transvaal Escarpment (Wolkberg), the Natal Drakensberg and associated uplands (Eastern Mountain), the coastal forelands of Maputaland, Pondoland and Albany, the entire Cape Floristic Region (Cape) and Succulent Karoo, and an outlier, the Kaokoveld, in northwestern Namibia and southwestern Angola. (It should be noted that although the study area for this paper is the FSA region, an area which is based on political boundaries, two of the hot-spots (Kaokoveld and Maputaland) extend northwards (Figure 1) outside the study area.) These hot-spots comprise diverse environments and vegetation types, ranging from humid summer rainfall areas with subtropical rainforests to arid winter rainfall climates with dwarf succulent shrublands (Table 4).

Biodiversity and endemism

When compared to other recognized hot-spots, southern African hot-spots are not particularly rich in plant species, with the exception of the Cape Floristic Region and Succulent Karoo (Figure 3). For its size, the Cape Floristic Region is

TABLE 4.—Characteristics of southern African hot-spots

Hot-spot	Area (km²)	Number of species	Endemics (%)	Rainfall (mm yr⁻¹)	Rainfall (season)	Vegetation
Wolkberg	5 980	2 700	4	500–2 000	Summer	**Temperate and subtropical grassland** and rainforest, savanna
Maputaland	26 734	1 100	15	600–1 200	Summer	**Savanna**, subtropical rainforest and grassland, wetland
Eastern Mountain	40 000	1 750	30	1 500–2 000	Summer	**Temperate grassland** and rainforest, sclerophyll shrubland
Pondoland	1 880	1 500	8	1 000–2 000	Summer	**Subtropical grassland** and rainforest
Albany	22 500	2 000	10	350–750	All year	**Subtropical thicket**
Succulent Karoo	111 212	4 750	35	20–300	Winter to all year	**Succulent shrubland**
Cape	90 000	8 600	68	250–3 000	Winter to all year	**Sclerophyll shrubland**, temperate rainforest
Kaokoveld	70 000	952	12	10–300	Summer	**Deciduous shrubland**, ephemeral herbland, savanna

Species number includes vascular plants only.
Dominant vegetation is in boldface.
Sources: Davis & Heywood (1994); Matthews *et al.* (1993).

the richest of the Mediterranean-climate region hot-spots and has more species than many tropical rainforest areas of similar size (Cowling *et al.* 1992). The richness of the Succulent Karoo flora is exceptional for a semi-arid region, both in terms of established hot-spots, but especially in comparison with regions of similar semi-arid environments (Figure 4; Cowling *et al.* 1989; Hilton-Taylor 1994a).

Endemism in southern African hot-spots ranges from 4% (Wolkberg) to 68% (Cape), with an average of 23% (Table 4). This is half the average value of 44% recorded for tropical rainforest areas and about a third of the average value of 58% recorded for Mediterranean-climate regions. However, with 6 000 endemic species, the Cape is the world's 'hottest' hot-spot (Myers 1990). The Succulent Karoo, with approximately 1 660 endemic plant species, ranks as the only semi-arid region to qualify as a hot-spot of global significance.

There is a total of 8 830 endemic plant species in southern African hot-spots, comprising 52.2% of the region's endemic flora in 12.1% of its area (Table 5). These hot-spots include about 3.5% of the world's flora on 0.2% of the earth's surface, a ratio considerably higher than, for example, Mediterranean-climate and tropical rainforest regions (see Table 5). Therefore, although the levels of endemism and numbers of species are not always the highest, the exceptional species : area ratio shows that the hot-spots of southern Africa should be counted among the world's most important areas for conservation action.

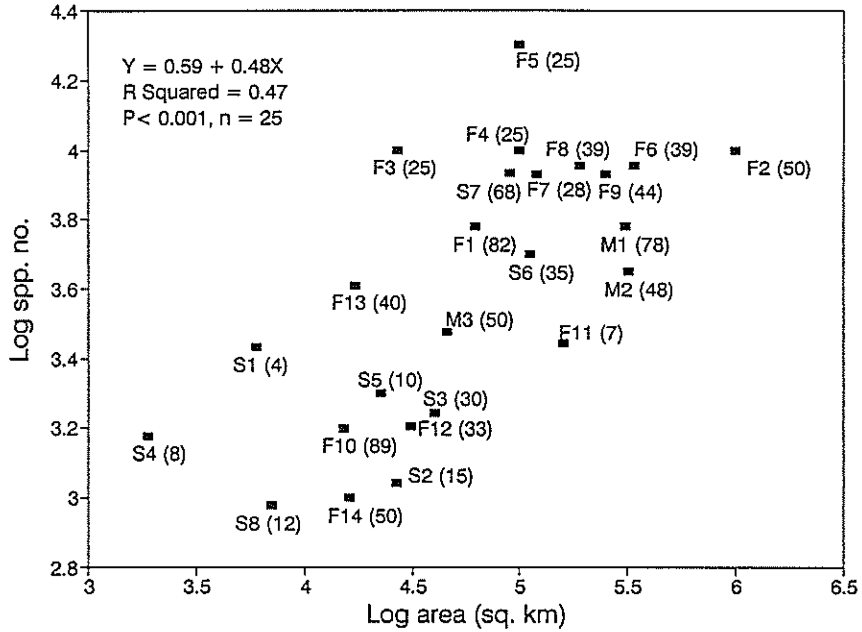

Figure 3.—Species-area relationships (vascular plants only) for southern African (S), Mediterranean-climate (M) and tropical rainforest (F) hot-spots. S1 = Wolkberg, S2 = Maputaland, S3 = Eastern Mountain, S4 = Pondoland, S5 = Albany, S6 = Succulent Karoo, S7 = Cape, S8 = Kaokoveld. M1 = South Western Australia, M2 = California Floristic Province, M3 = Central Chile. F1 = Madagascar, F2 = Atlantic coastal Brazil, F3 = Western Ecuador, F4 = Colombian Choco, F5 = Upland western Amazonia, F6 = Eastern Himalaya, F7 = Penisular Malaysia, F8 = Borneo (north), F9 = Philippines, F10 = New Caledonia, F11 = SW Ivory Coast, F12 = Eastern Arc Mts (Tanzania), F13 = Western Ghats (Tanzania), F14 = SW Sri Lanka. Figures in parentheses indicate the percentage of species endemic to the area. (Sources: Davis & Heywood 1994; Hopper 1992; Matthews *et al.* 1993; Myers 1988, 1990.)

TABLE 5.—Numbers of endemic species in southern African and other hot-spots

Hot-spot area	Area (km²)	% earth's area	Number of endemic species	Endemics as % of total plant species
Tropical rainforests	2 428 000	1.6	37 235	14.9
Mediterranean-climate	765 400	0.5	14 165	5.6
Southern Africa	305 306	0.2	8 830	3.5
Total	3 408 706	2.2	54 382	21.8

Area of hot-spots includes transformed land (cf. Myers 1988, 1990).
Cape is included in both Mediterranean-climate and southern African hot-spots but duplication has been avoided in the totals. Sources: Myers (1988, 1990); Table 4.

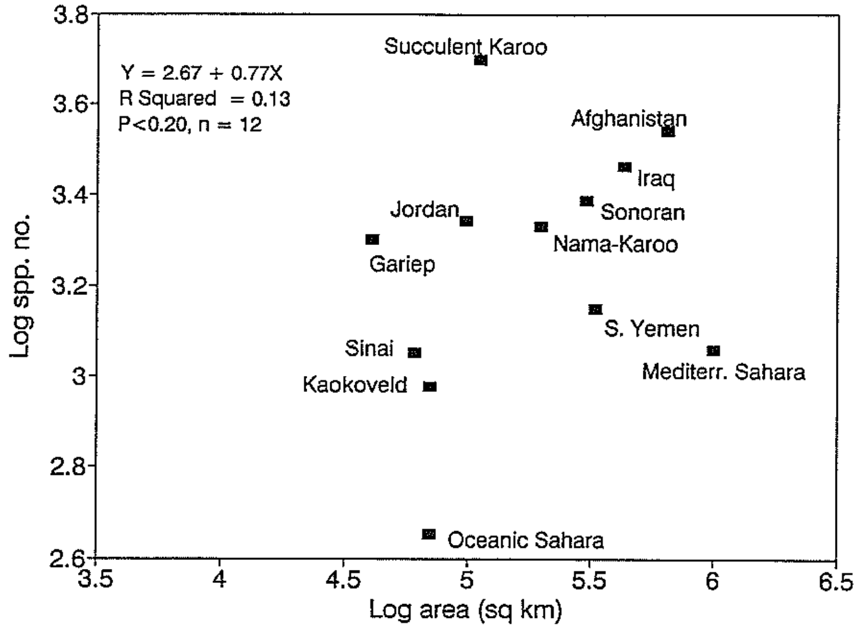

Figure 4.—Species-area relationships (vascular plants only) for arid and semi-arid regions of the world. (Sources: Cowling *et al.* 1989; Goldblatt 1978; Hilton-Taylor 1994b; Le Houérou 1992; World Conservation Monitoring Centre 1992; Hilton-Taylor unpublished data.)

Characterization of the endemic flora

In this section we investigate whether the endemic floras of the hot-spots are random assemblages with regard to their taxonomic affinities and biological traits.

Taxonomic aspects

An analysis of the floras from distinct portions of three hot-spots shows that taxonomically the endemics in southern African hot-spots are not a random assemblage (Table 6). The floras investigated were from the Agulhas Plain (Cape), southern Natal Drakensberg (Eastern Mountain) and the Gariep (mountainous area along the lower Orange River in the Succulent Karoo) (Figure 1).

In the southern Natal Drakensberg, families with higher than average levels of endemism include Asteraceae, Scrophulariaceae and Ericaceae. Most of the larger families have similar proportions of endemics as the total flora and endemics are significantly underrepresented in Poaceae and Orchidaceae.

TABLE 6.—Species endemism in largest families of flowering plants for selected areas within three southern African hot-spots

Family	Number of species (%) Endemic	Nonendemic	χ^2
EASTERN MOUNTAIN: SOUTHERN NATAL DRAKENSBERG (1 115 km²)			
Total flora	373 (29.3)	898 (70.7)	—
Endemism significantly higher than total flora			
Asteraceae	118 (41.5)	167 (58.5)	35.7***
Scrophulariaceae	36 (45.6)	43 (54.4)	9.9**
Ericaceae	15 (57.6)	11 (42.3)	8.9*
Endemism same as total flora			
Liliaceae *s.l.*	20 (23.8)	64 (76.2)	1.1NS
Fabaceae	14 (21.5)	51 (78.5)	1.6NS
Iridaceae	20 (30.8)	45 (69.2)	0.0NS
Cyperaceae	14 (23.7)	45 (76.3)	0.7NS
Asclepiadaceae	13 (29.5)	31 (70.5)	0.0NS
Campanulaceae	9 (36.0)	16 (64.0)	0.3NS
Apiaceae	7 (33.3)	14 (66.6)	0.0NS
Gentianaceae	6 (28.6)	15 (71.4)	0.0NS
Crassulaceae	6 (30.0)	14 (70.0)	0.0NS
Geraniaceae	5 (25.0)	15 (75.0)	0.0NS
Endemism significantly lower than total flora			
Poaceae	19 (17.6)	89 (82.4)	7.3**
Orchidaceae	15 (18.1)	68 (81.9)	4.9*
CAPE: AGULHAS PLAIN (1 609 km²)			
Total flora	513 (29.3)	1 238 (70.7)	—
Endemism significantly higher than total flora			
Ericaceae	80 (64.5)	44 (35.5)	78.1***
Restionaceae	35 (39.8)	53 (60.2)	4.4*
Mesembryanthema	26 (44.8)	32 (55.2)	6.2*
Proteaceae	39 (67.2)	19 (32.8)	39.8***
Rutaceae	34 (72.3)	13 (27.7)	41.1***
Polygalaceae	19 (54.3)	16 (45.7)	9.6**
Endemism same as total flora			
Asteraceae	52 (25.6)	151 (74.4)	1.3NS
Iridaceae	38 (25.5)	111 (74.5)	0.9NS
Fabaceae	49 (35.5)	89 (64.5)	2.5NS
Campanulaceae	14 (26.9)	38 (73.1)	0.1NS
Thymelaeaceae	15 (41.7)	21 (58.3)	2.1NS
Endemism significantly lower than total flora			
Poaceae	3 (4.6)	62 (95.4)	19.0***
Liliaceae *s.l.*	12 (16.0)	63 (84.0)	6.0*
Cyperaceae	7 (11.1)	56 (88.9)	9.5**
Scrophulariaceae	8 (14.3)	48 (85.7)	5.6*
Orchidaceae	2 (5.3)	36 (94.7)	9.7**
SUCCULENT KAROO: GARIEP (40 931 km²)			
Total flora	397 (19.8)	1 613 (81.2)	—
Endemism significantly higher than total flora			
Mesembryanthema	140 (54.7)	116 (45.3)	229.6***
Crassulaceae	40 (40.8)	58 (59.2)	27.5***
Asclepiadaceae	23 (42.6)	31 (57.4)	16.8***
Endemism same as total flora			
Liliaceae *s.l.*	37 (21.6)	134 (78.4)	2.6NS
Fabaceae	17 (18.3)	76 (81.7)	0.1NS
Iridaceae	18 (30.0)	42 (70.0)	3.5NS
Geraniaceae	15 (26.8)	41 (73.2)	1.4NS
Euphorbiaceae	11 (20.0)	44 (80.0)	0.0NS
Chenopodiaceae	6 (14.3)	36 (85.7)	0.5NS
Acanthaceae	3 (7.9)	35 (92.1)	2.7NS
Amaryllidaceae	11 (33.3)	22 (66.6)	3.1NS
Zygophyllaceae	2 (6.1)	31 (93.9)	3.1NS
Brassicaceae	5 (17.2)	24 (82.8)	0.0NS
Endemism significantly lower than total flora			
Asteraceae	29 (9.8)	266 (90.2)	20.7***
Poaceae	9 (7.4)	112 (92.6)	11.5***
Scrophulariaceae	3 (3.4)	86 (96.6)	14.7***
Aizoaceae *s.s.*	1 (1.2)	79 (98.8)	16.8***
Sterculiaceae	1 (3.5)	28 (96.5)	3.9*

Species numbers include vascular plants only. *** = $P<0.001$; ** = $P<0.01$; * = $P<0.05$; NS = not significant.
Sources: Southern Natal Drakensberg (Hilliard & Burtt 1987); Agulhas Plain (Cowling & Holmes 1992); Gariep (C. Hilton-Taylor unpublished data).

In the lowland Agulhas Plain flora, endemics were significantly over-represented in six families including typical Cape families such as the Ericaceae, Restionaceae and Proteaceae, but also the largely Karoo group, the Mesembryanthema (Table 6). In contrast to the Eastern Mountain flora, Asteraceae and Scrophulariaceae did not have proportionally high levels of endemism but in common with that flora, Poaceae and Orchidaceae were under-represented in terms of endemics.

Like the Eastern Mountain flora, a higher than average endemism in the Gariep portion of the Succulent Karoo flora was associated with only three families (Table 6). These are all succulent families with large concentrations of species in the winter rainfall arid and semi-arid areas of southern Africa (Gibbs-Russell 1985; Hilton-Taylor 1987, 1994a; Van Jaarsveld 1987). Interestingly, the Mesembryanthema have produced numerous endemics in both dry karroid and wetter, fire-prone fynbos habitats (Hartmann 1991). In common with the Cape Floristic Region flora, Poaceae and Scrophulariaceae in this Succulent Karoo flora are under-represented in terms of endemics.

We conclude from these results that the taxonomic apects of endemism show greater differences than similarities across these three hot-spots. The same families have different proportions of endemics in each region. This is to be expected, given the very different ecological conditions in each of the hot-spots (Table 4). Nonetheless, families such as Poaceae and Orchidaceae have consistently low proportions of endemic species.

Biological aspects

The endemics from southern African hot-spots are not a random assemblage with regard to growth form and other biological attributes. In the southern Natal Drakensberg, endemic forbs and shrubs are more frequent, and other growth forms less frequent, than nonendemics (Figure 5A). Despite relatively large areas of forest in the Eastern Mountain and Wolkberg hot-spots, there are no endemic trees in either region; most endemics are forbs and low shrubs associated with grasslands (Hilliard & Burtt 1987; Killick 1994; Matthews *et al.* 1993). This is not the case for the Maputaland and Pondoland hot-spots which harbour a number of endemic tree species, although most of the endemics are either forbs or low shrubs of grassland habitats (Van Wyk 1990, 1994).

The biological aspects of endemism in the Cape Floristic Region have been well studied (Cowling *et al.* 1992; Cowling & Holmes 1992; McDonald & Cowling in press). From these studies it can generally be said that both the lowland and mountain floras exhibit a greater than average chance that an endemic will be a nonsprouting, low to dwarf shrub (Figure 5B) with soil-stored seed banks and short dispersal distances. In the Agulhas Plain flora both forbs and geophytes are underrepresented as endemics and tree endemics are absent (there are a few endemic trees elsewhere in the Cape Floristic Region). Levels of endemism among graminoids in the Cape hot-spot are the highest in comparison to those in

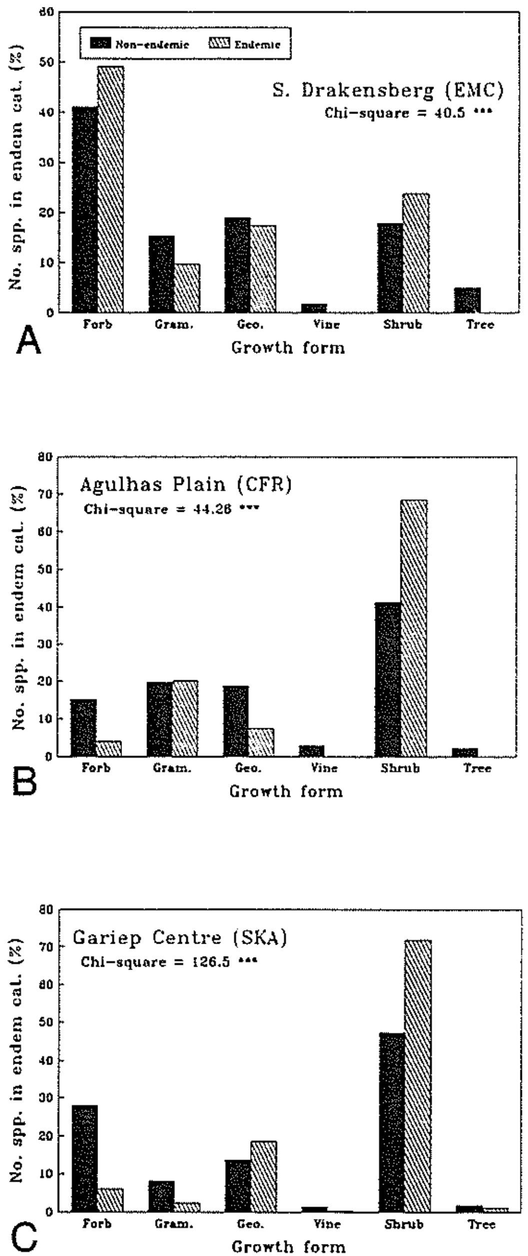

Figure 5.—Association between endemism and growth form in regional floras (vascular plants only) from portions of three southern African hot-spots. S. Drakensberg flora is from the Eastern Mountain hot-spot; Agulhas Plain from the Cape hot-spot; Gariep from the Succulent Karoo hot-spot. Gram. = graminoids; Geo. = geophytes. (Sources: Cowling *et al.* 1992; Hilliard & Burtt 1987; Hilton-Taylor unpublished data.)

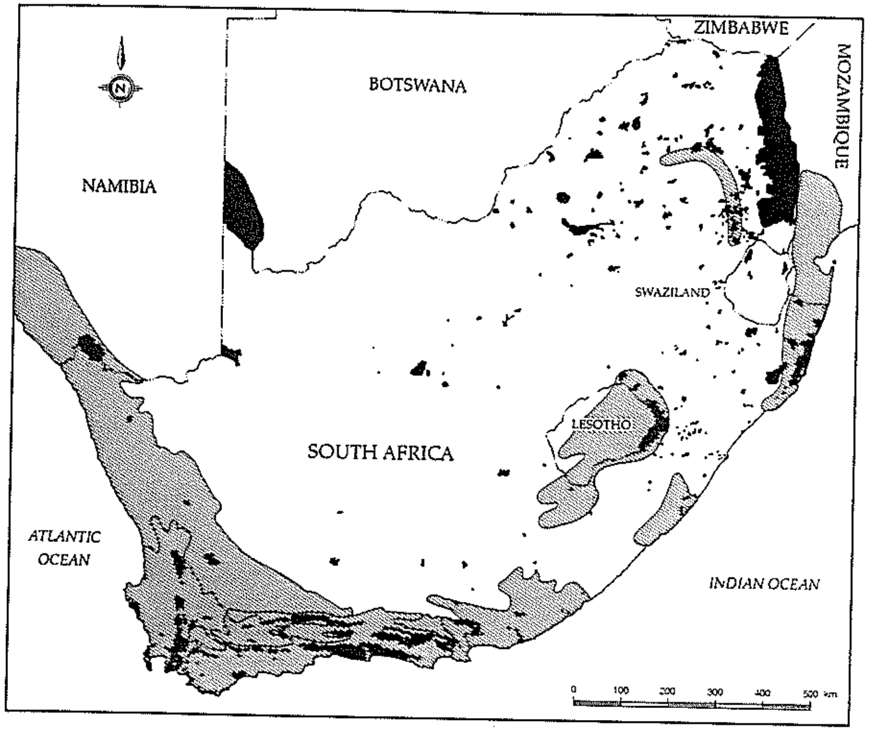

Figure 6.—Distribution of protected areas in South Africa (solid and dots) in relation to the hot-spots (hatched). (Source: adapted from an unpublished preliminary map of conservation areas produced by the Department of Environment Affairs in 1994.)

the other southern African hot-spots; this is due to the high number of endemics in the family Restionaceae.

The growth form profile of endemics in the Gariep flora (Succulent Karoo) is identical to an Albany flora profile (Cowling & Holmes 1991) and similar to that from the Cape except that the pattern for graminoids and geophytes is reversed (Figure 5C). An interesting pattern to emerge is that despite southern Africa having the richest petaloid geophyte flora in the world (Goldblatt 1978), endemic geophytes are more frequent than widespread species only in semi-arid winter rainfall areas. Succulents are enormously overrepresented as endemics in both the Succulent Karoo and Albany floras (Cowling & Holmes 1991; Hilton-Taylor unpublished). For example, in the Gariep flora 60% of endemics are succulents. Tree endemics in southern African arid areas are generally rare.

In conclusion, the biological aspects of endemism do show important differences across southern African hot-spots. Endemic forbs are common in moist,

summer rainfall eastern hot-spots; endemic shrubs are common in all hot-spots; endemic geophytes and succulents are common in the semi-arid southwest; and endemic trees are rare everywhere except for a relatively low occurrence in Maputaland and Pondoland.

Conservation

In this section we examine the conservation status of the hot-spots and the threats to the preservation of plant diversity in these regions. Wherever possible we draw on our analysis to make comments on conservation planning and management.

Conservation status

The protected area network in South Africa (we do not have information for the other countries in southern Africa) is not optimally located with regard to the region's hot-spots of plant diversity and endemism (Figure 6; Rebelo 1994b). Only in the case of the mountains of the Cape Floristic Region, and to a lesser extent the Wolkberg and Maputaland hot-spots, are reasonably large areas conserved (Table 7). Given the international significance of the Succulent Karoo as a semidesert hot-spot, the conservation status of the region is desperately poor (Hilton-Taylor & Le Roux 1989). The most alarming situation, however, is the highly inadequate conservation status of the lowlands of the Cape Floristic Region which harbour numerous endemic and threatened plant species (Rebelo 1992).

Both for its area and in an absolute sense, southern Africa has the highest concentration of *Red data book* plant taxa in the world (Figure 7). However, the

TABLE 7.—Conserved area and number of *Red data book* taxa in southern African hot-spots

Hot-spot	Area conserved (%)	*Red data book* taxa	
		Extinct	Other
Wolkberg	13.3	0	32
Maputaland	10.0	?	?
Eastern Mountain	5.5	0	27
Pondoland	7.0	0	33
Albany	6.5	1	51
Succulent Karoo	2.0	18	978
Cape: lowlands	3.0	29	1 406
mountains	50.0		
Kaokoveld	7.0	?	?

Conserved areas in Mozambique (Maputaland) and Angola (Kaokoveld) have been excluded. For the Cape hot-spot, the numbers of *Red data book* taxa given are for the whole region; separate figures for the lowlands and for the mountains are not available.
Sources: Davis & Heywood (1994); Everard (1988); Matthews *et al.* (1993); C. Hilton-Taylor (unpublished data).

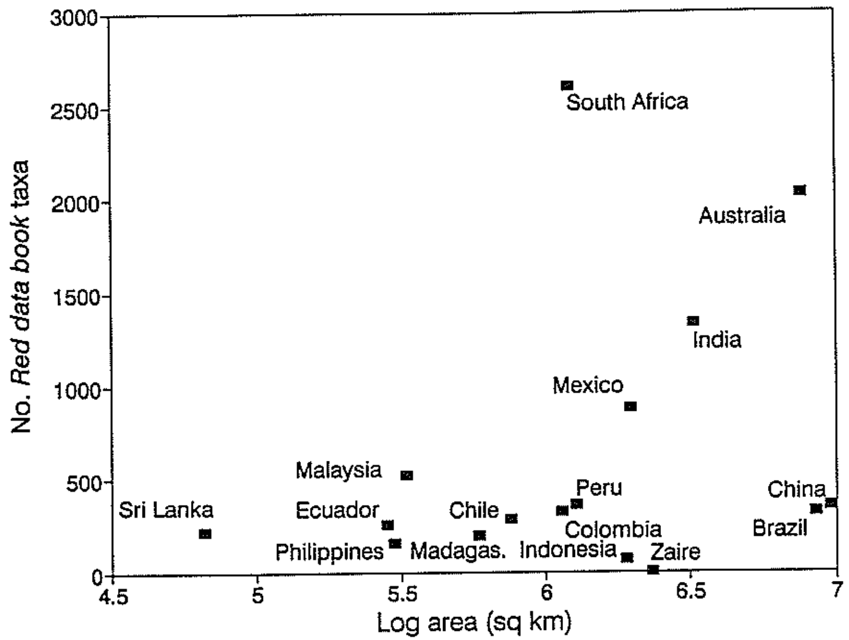

Figure 7.—Relationship between area and number of *Red data book* taxa in South Africa, the 'megadiversity countries' (McNeely *et al.* 1990) and other hot-spots (Myers 1988, 1990). All *Red data book* taxa are defined according to IUCN Red Data categories. Numbers include many taxa below species level. (Source: World Conservation Monitoring Centre 1992, except for South Africa: Hilton-Taylor unpublished data.)

TABLE 8.—Major threats to southern African hot-spots

Hot-spot	Threats
Wolkberg	Afforestation, invasive plants, overgrazing
Maputaland	Agriculture, afforestation, urbanization, overgrazing, plant harvesting, invasive plants, mining, tourism
Eastern Mountain	Overgrazing, agriculture, afforestation, plant harvesting, invasive plants
Pondoland	Overgrazing, veld burning, plant harvesting, agriculture, population growth
Albany	Overgrazing, agriculture, invasive plants, urbanization
Succulent Karoo	Overgrazing, mining, agriculture, plant harvesting
Cape	Invasive plants, agriculture (lowlands), urbanization, plant harvesting
Kaokoveld	Overgrazing, plant harvesting, tourism

Plant harvesting includes fuel wood, building materials, wild food and beverage crops, medicinal plants, wild flowers and succulents.
Source: Davis & Heywood (1994).

extent to which this is an artefact of inadequate data for other species- and endemic-rich areas is not known. There are at least 2 575 *Red data book* taxa (including both species and infraspecific taxa) recorded from southern African hot-spots (Table 7), representing about 98% of the total number recorded from the region (Hilton-Taylor unpublished data). Fifty-six per cent of these taxa occur in the Cape Floristic Region, where *Red data book* taxa show a very strong concentration in the lowland fynbos of the southwest, especially in the rapidly urbanizing areas of greater Cape Town (Rebelo 1992; Wood *et al.* 1994). Thirty-nine per cent of the *Red data book* taxa occur in the Succulent Karoo. The southwestern winter rainfall area is therefore extremely important as a repository of threatened and endemic plants.

Unfortunately the present IUCN threatened status categories used in classifying *Red data book* taxa do not provide an actual ranking of species from the most threatened to least threatened, and especially when dealing with large numbers of species as in the southern African case, are often too coarse to assist managers and conservationists in decision-making. However, the recent use of multivariate techniques by Given & Norton (1993) and Hall (1993) for assessing the threats faced by species and for determining priority groupings and rankings of threatened species, may provide a valuable tool for determining management and conservation priorities in southern Africa.

Threats

The major threats to the conservation of plant biodiversity in the southern African hot-spots are listed in Table 8. Specific details are given in the appropriate chapters in Davis & Heywood (1994), while Macdonald (1989) provides a general account of the impacts of land transformations and modifications on southern African biodiversity. The following major threats are briefly discussed here: (1) alien invasive plants; (2) afforestation; (3) land transformation for agriculture; (4) overgrazing; and (5) subsistence and commercial harvesting of indigenous plant products.

Invasive plants and afforestation are major threats to plant biodiversity in all hot-spots, with the exception of the Succulent Karoo and Kaokoveld (Table 8). In the Cape Floristic Region alien invasive plants have had an enormous impact on indigenous plant species and ecosystems (Richardson *et al.* 1992). The entire lowlands and most of the wetter mountain slopes have areas with moderate to dense infestations of alien species of *Acacia*, *Hakea* and *Pinus* (Richardson *et al.* 1992); these habitats also harbour a disproportionate number of endemic and threatened taxa (Cowling *et al.* 1992; McDonald & Cowling in press; Rebelo 1992). Even though alien thickets have negative economic costs due to their deleterious impact on water yields from mountain catchments, increased fire hazard and destruction of wildflower and ecotourism resources (Van Wilgen *et al.* 1992), it is unlikely that sufficient resources will be made available for the manual control of alien invasions in the future. The introduction of biological controls, some of which have been extremely successful (Dennill 1985; Hoffmann 1991; Hoffmann &

Moran 1988; Neser & Kluge 1986), is the only effective, long-term approach to this problem.

While alien invasions are also a problem in the wet, summer rainfall hot-spots, afforestation is a far greater threat to species conservation and ecosystem processes (Macdonald 1989). Of particular concern is afforestation of grassland habitats, areas which harbour a large proportion of the endemic and threatened species (Macdonald 1989; Matthews *et al.* 1993; Van Wyk 1994). For example, 30% of the *Red data book* plant taxa in the Transvaal occur in grassland habitats subject to afforestation, even though plantations presently cover only 2% of the province (Raal 1986).

Land transformation for agriculture is a major threat in the Cape Floristic Region, the wetter parts of the Succulent Karoo, and parts of Pondoland and Maputaland (Table 8). On the Cape lowlands, 79% of renoster shrubland and 49% of fynbos have been replaced by cereals, pastures and horticultural crops (Rebelo 1992, 1994a). The building of dams on mountain-fed perennial rivers in the southern Succulent Karoo has resulted in the transformation to irrigated lands of large areas of natural vegetation (Hilton-Taylor 1994a). More alarming is the extensive dry-land agriculture (2 269 km^2 in 1983) of southern Namaqualand (Macdonald 1989), an area too marginal for economically and ecologically sustainable agriculture (Hilton-Taylor 1994a).

With the exception of the Cape Floristic Region, overgrazing is a threat to biodiversity maintenance in all southern African hot-spots (Table 8). This threat is most severe in the communally owned land of Maputaland, Pondoland and the Succulent Karoo. However, extensive grazing-induced degradation, which reduces biodiversity and eliminates the endemic succulent and geophyte components, has also been recorded on privately owned farmlands in the Albany hot-spot (Hoffman 1989; Hoffman & Cowling 1990).

Subsistence and commercial harvesting of indigenous plant products is widespread in southern Africa (Cunningham 1989; Van Wilgen *et al.* 1992). In Maputaland, several rare and slow-growing species with medicinal value have been harvested almost to extinction (Cunningham 1989). Nonsustainable harvesting of fynbos for wild flowers (Van Wilgen *et al.* 1992) and the pillaging of succulents (Hilton-Taylor & Le Roux 1989) target precisely those taxa with high numbers of endemic species (Hilton-Taylor & Smith 1994).

CHALLENGES FOR THE FUTURE

Southern Africa is currently faced with uncertainty associated with the sociopolitical transformations occurring in South Africa. Although these changes may pose threats to plant conservation (Huntley *et al.* 1989), they also provide opportunities for new and appropriate interventions to prevent large-scale plant extinctions (Myers 1993) in southern African hot-spots.

Every effort must be made to establish southern Africa as a biodiversity hot-spot of international significance. Without this recognition, the subcontinent will continue to be overlooked by the international community when establishing priorities for funding and interventions. The appreciation by Myers (1990) of the status of the Cape Floristic Region as the world's 'hottest' hot-spot has contributed enormously to this end. Similarly, it is hoped that work on the Centres of Plant Diversity (Davis & Heywood 1994) will highlight the importance of the Succulent Karoo and other hot-spots in the region. The emergence of South Africa from a long period of political isolation may also result in an increasing awareness of the diversity of and threats to the region's biological resources.

The protected area network in the region must be re-evaluated in the light of the mismatch between reserve and hot-spot location (Figure 6; Rebelo 1994b). Priority areas for immediate action include the lowlands of the Cape Floristic Region (Rebelo 1992) and the Succulent Karoo (Hilton-Taylor 1994a; Hilton-Taylor & Le Roux 1989) (Table 7). However, despite the fact that a large percentage of the organisms making up our biodiversity is already preserved in the existing reserve network (Siegfried 1989), it is unlikely that extensions to the network will provide protection to representative examples of all ecosystems and sufficient numbers of populations of all species. Attention will rather have to be given to the sustainable use of biodiversity outside reserves.

With the current sociopolitical changes occurring in South Africa we also cannot afford to be complacent about the security of the existing protected areas. As pointed out by Grossman *et al.* (1992), all the protected areas are government subsidized and their persistence is subject to the taxpayers' goodwill and the health of the economy. With the increasing demands of other social priorities such as health, education and housing, why should state-financed, nonpaying ventures such as nature reserves be maintained?

A fast-growing literature in applied economics is showing that it is possible to estimate directly the value of environmental resources, including biodiversity (e.g. Tobias & Mendelsohn 1991; Western & Henry 1979). Southern Africa lags behind other developing regions in assessing the economic value of its natural ecosystems and indigenous biodiversity. The generation of income from the sustainable and imaginative use of the region's exceptional biodiversity will have to become the major economic engine for supporting conservation action, especially in the light of decreasing governmental funds for such purposes (Cowling 1993). Perhaps most importantly, in a subcontinent with a long history of dispossession, poverty and alienation from the natural environment (Ramphele & McDowell 1991), it is essential that the revenues generated from the utilization of our natural resources are used to provide tangible benefits to all those in the region who have been socially and politically marginalized.

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Botanical diversity and its conservation in Angola

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ABSTRACT

Angola is a large country (1.24 million km^2) with a rich but poorly documented botanical diversity. A wide range of ecosystems, from desert to rainforest, are represented in the six phytochoria (White 1983) found in the country. The Zambezian regional centre of endemism occupies over 80% of Angola, with the Karoo-Namib, Guineo-Congolian and Guinea-Congolia/Zambezia centres and transition zones making up most of the remaining area. Very small relic patches of Afromontane forest are found in the central western mountain zone, while a narrow tongue of the Kalahari-Highveld transition zone penetrates the southwestern escarpment foothills.

The present protected area network includes representative examples of 11 of the 32 major vegetation types recognized by Barbosa (1970). The expansion of this network to include examples of the Guineo-Congolian and Afromontane phytochoria and a better representation of vegetation types is proposed.

The impact of over 20 years of civil war on the conservation of botanical diversity is described and priorities for action are discussed.

INTRODUCTION

Angola is the second largest country in sub-Saharan Africa and includes an unusually wide diversity of habitats, from the vegetationless dunes of the Namib Desert to the tropical rainforests of Cabinda. Ironically, the rich biodiversity of Angola is poorly known. Before Independence was achieved in 1975, only two comprehensive studies of the country's vegetation had been published (Gossweiler & Mendonça 1939; Barbosa 1970), with a few further studies providing a little more detail of local areas (Teixeira *et al.* 1967; Teixeira 1968a; Matos & De Sousa 1970; Monteiro 1970; Menezes 1971). In contrast with the situation in most other African countries, an upswing in scientific and conservation action has not been witnessed in post-Independence Angola. The tragic consequences of the Angolan civil war which has continued unabated for 20 years have prevented any serious biological research and severely compromised the country's excellent network of national parks and reserves.

This paper will describe the major phytogeographic and vegetation characteristics of the country, and comment on the present situation and future prospects regarding biodiversity conservation.