The Cape Peninsula, South Africa: Physiographical, biological and historical background to an extraordinary hot-spot of biodiversity

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The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity

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The Cape Peninsula, a 470 km^2 area of rugged scenery and varied climate, is located at the southwestern tip of the Cape Floristic Region, South Africa. The Peninsula is home to 2285 plant species and is a globally important hot-spot of biodiversity for higher plants and invertebrates. This paper provides a broad overview of the physiography, biological attributes and history of human occupation of the Peninsula. The Peninsula is characterized physiographically by extremely high topographical heterogeneity, very long and steep gradients in annual rainfall, and a great diversity of nutrient-poor soils. Thus, the Peninsula supports a high number of habitats and ecological communities. The predominant vegetation is fynbos, a fire-prone shrubland, and 12 broadly characterized fynbos types have been described on the Peninsula. Animal community structure, especially with regard to invertebrates, is poorly known. Vertebrate community structure is probably strongly influenced by nutrient poverty and recurrent fire. Generally, most vertebrates are small and typically occur in low numbers. Some invertebrates play keystone roles in facilitating ecological processes. Human occupation of the Peninsula was limited, until relatively recently, by nutrient poverty. After Dutch colonization in 1652, direct and indirect impacts on the natural ecosystems of the Peninsula escalated dramatically, and by 1994, some 65% of original natural habitat was either transformed by urbanization and agriculture, or invaded by alien plants. Nonetheless, there is still excellent potential to conserve the Cape Peninsula's remaining biodiversity.

Keywords: biodiversity; Cape Floristic Region; fynbos; human impacts.

Introduction

The Cape Peninsula, located at the southwestern extremity of Africa (Fig. 1), comprises a region of internationally renowned scenic beauty and exceptional biodiversity (e.g. Luckhoff, 1951; Moll and Campbell, 1976; UCT, 1994). The Peninsula is also girdled by one of South Africa's fastest growing metropolises, the greater Cape Town area, resulting in an exponential increase in the threats to biodiversity and scenic quality (Richardson *et al.*, 1996). The many attempts over the past 65 years to improve the conservation status of the Peninsula have met with only limited success (van Wilgen, 1996). This special issue of *Biodiversity and Conservation* collates and synthesizes data dealing with many aspects of the patterns, conservation and management of the Peninsula's extraordinary biodiversity.

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The major objective of this exercise is to provide policy makers, from international to local levels, with information that might aid them in formulating appropriate interventions to conserve the biota of what amounts to one of the world's most threatened nodes of high species diversity and endemism. Furthermore, the Peninsula's predicament is not unique (e.g. Myers, 1990) and this volume is likely to include information of relevance for the conservation and management of biodiversity elsewhere.

The other papers in this volume deal with patterns of plant species richness (Simmons and Cowling, 1996), endemic and threatened plant species (Trinder-Smith *et al.*, 1996a), faunal diversity and endemism (Picker and Samways, 1996), current and future threats to plant biodiversity (Richardson *et al.*, 1996), optimal reserve design (Trinder-Smith *et al.*, 1996b), and natural ecosystem management (van Wilgen, 1996).

The aims of this introductory paper are: (i) to place the Peninsula's biota in an international and regional context; and (ii) to provide details on the physiographical and biological characteristics of the Peninsula, as well as its history of human occupation, as a background to the other papers in this issue. We concentrate entirely, as do the other contributions, on the terrestrial biota and ecosystems of the Peninsula. Although the marine flora and fauna are very rich in species, this is largely the result of an overlap between two marine provinces (Emanuel *et al.*, 1992; Bolton and Anderson, 1996) rather than pronounced local endemism.

The Cape Peninsula in context

Undoubtedly, the outstanding feature of the Cape Peninsula's biota, both regionally and globally, is its rich flora (Adamson and Salter, 1950; Goldblatt, 1978; Kruger and Taylor, 1979; Cowling *et al.*, 1996; Simmons and Cowling, 1996). The Peninsula forms part of the Cape Floristic Region, an area of exceptionally high diversity and endemism at all taxonomic levels and recognized as one of the world's six floral kingdoms (Goldblatt, 1978). However, with 2285 plant species in an area of only 470 km^2, the Peninsula's regional species density is unparalleled elsewhere in the Cape Floristic Region, as well as in other temperate and tropical plant biodiversity hot-spots (Cowling *et al.*, 1992, 1996; Simmons and Cowling, 1996).

The Cape Floristic Region has the highest known incidence of local plant endemism in the world (Gentry, 1986; Cowling *et al.*, 1992). With 90 plant species endemic to the Peninsula, the highest level of local endemism thus far recorded in the Cape Floristic Region (Trinder-Smith *et al.*, 1996a), the area has the distinction of being home to the world's greatest density, for similar-sized areas, of narrow endemics.

While many of the Peninsula's animals are not as conspicuous as the flora, and many groups are poorly studied, the fauna nonetheless represents an impressive repository of biodiversity at a global scale (Picker and Samways, 1996). For example, of the 14 taxonomic groups of invertebrates on the Peninsula for which full species lists occur, endemism levels range from 5.3 to 67% (median of 33%): the endemic fauna comprises 112 species, probably the richest concentration of endemics in this group for any small area anywhere in the world (Picker and Samways, 1996). Many of the vertebrates, especially large mammals (Skead, 1980), were extirpated from the Peninsula before accurate inventories had been compiled. However, owing to the highly infertile soils and poor quality forage of the area, it is unlikely that the Peninsula ever supported large numbers of medium to large mammalian herbivores (Skead, 1980). Nonetheless, the region is home to

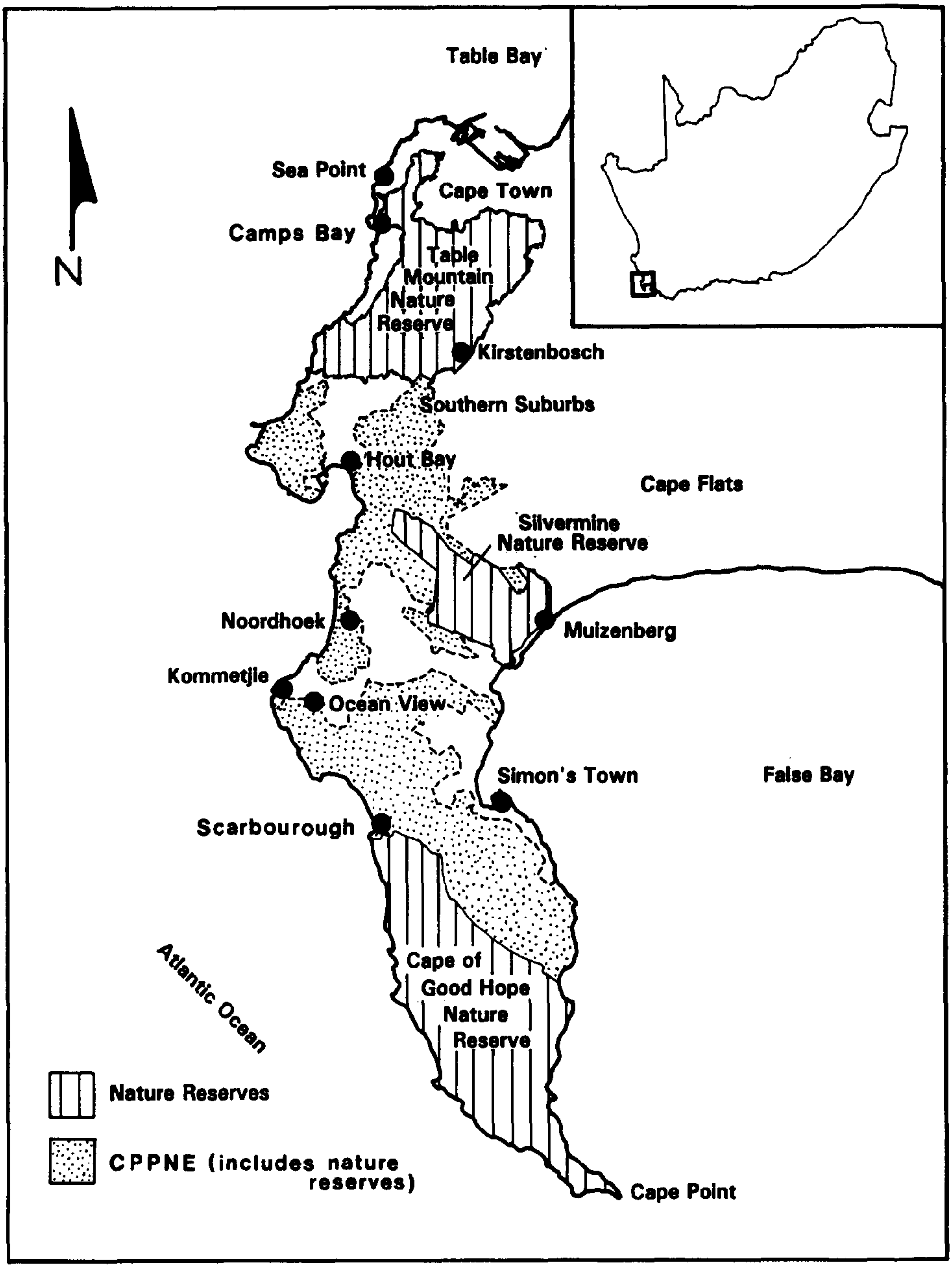
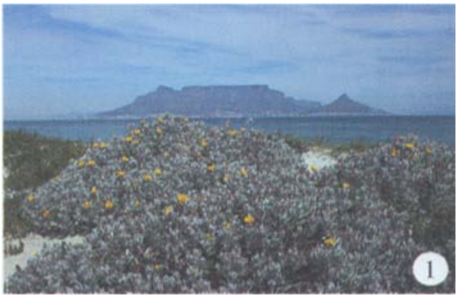


Figure 1. Location of the Cape Peninsula showing important place names and other features including nature reserves and the boundary of the Cape Peninsula Protected Natural Environment (CPPNE).



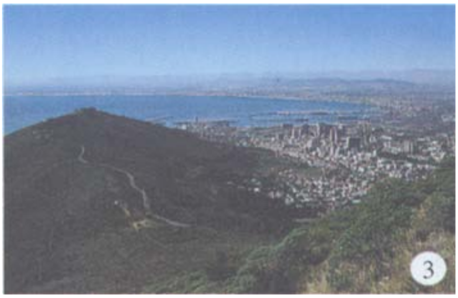


Plate 1. View of Table Mountain from the northern shores of Table Bay. *Didelta carnosa* (Asteraceae) in the foreground. Photo: Colin Paterson-Jones.

Plate 2. *Serruria hirsuta* (Proteaceae), a Cape Peninsula endemic, growing among Restionaceae near Simon's Town on the shores of False Bay. Photo: Colin Paterson-Jones.

Plate 3. The natural ecosystems of the Cape Peninsula are surrounded by a major metropolitan area. Species-rich renosterveld still persists on the clay-rich slopes of Lions Head and Signal Hill, immediately above the city centre of Cape Town. Photo: Colin Paterson-Jones.

Plate 4. Spring aspect of dune asteraceous fynbos on the shores of False Bay near Muizenberg. Photo: Colin Paterson-Jones.

Plate 5. Sandplain proteoid fynbos on Quaternary sands on the Karbonkelberg near Hout Bay. The conspicuous proteoid shrub is *Protea scolymocephala*. Photo: Colin Paterson-Jones.

Plate 6. Restioid fynbos, dominated by *Elegia filacea*, on seasonally waterlogged and highly infertile sands in the Cape of Good Hope Nature Reserve. Photo: Colin Paterson-Jones.

Plate 7. Restioid fynbos on the plateau of Table Mountain, near Maclear's Beacon. Photo: Colin Paterson-Jones.

Plate 8. Oligotrophic proteoid fynbos, with *Leucadendron xanthoconus* (foreground) and *L. laureolum*, on pale, leached sands in the Cape of Good Hope Nature Reserve. Photo: Colin Paterson-Jones.

Plate 9. Mesotrophic proteoid fynbos on the colluvial slopes of the Front Face of Table Mountain. *Erica plukenettii* in foreground and *Protea nitida* at the back. Photo: Colin Paterson-Jones.

Plate 10. Ericaceous fynbos on the top of Table Mountain. Photo: Colin Paterson-Jones.

an impressive number of vertebrate species. For example, the 7750 ha Cape of Good Hope Nature Reserve at the tip of the Cape Peninsula (Fig. 1) has 15 native amphibian species, 32 reptiles, 248 birds (including marine species and vagrants) and 35 terrestrial mammals (Fraser, 1996). These species-richness statistics are, in general, higher than those from similar sized-reserves in the Mediterranean-type climate regions of California and Chile (Macdonald *et al.*, 1988).

In conclusion, the exceptionally high levels of diversity and endemism for plants and selected invertebrate taxa on the Cape Peninsula serve to uphold its status as a biodiversity hot-spot of global significance, especially given the extreme threats to this biodiversity (Picker and Samways, 1996; Richardson *et al.*, 1996) and a history of generally inadequate stewardship of the region's natural ecosystems (van Wilgen, 1996).

Physiography

The principal features of the physiography of the Cape Peninsula are pronounced topographical heterogeneity and resultant spectacular scenery; great diversity of nutritionally-impoverished soils; and wide variation in local climatic conditions (Fig. 2).

GEOLOGY, TOPOGRAPHY AND SOILS

The Cape Peninsula forms part of the Cape Folded Belt, an L-shaped band at the southwestern corner of Africa of erosion-resistant, quartzitic sandstone mountains alternating with plains and valleys underlain by softer shales, and mantled at the coastal margin with young siliceous and calcareous sediments (Deacon *et al.*, 1992). The sandstones and shales of the Cape Supergroup, the predominant rocks of the Folded Belt, were deposited on earlier sediments and intruded granites at the margin of an inland sea, between 450 and 340 My. These earlier rocks (Malmesbury Shales and Cape Granite Suite) are exposed at many places along the lower slopes of the Peninsula mountains (Fig. 3). Cape Folded Belt landscapes are ancient, having changed little during the past 60 My, and having been spared extreme climatic conditions (including glaciation) during this period (Deacon *et al.*, 1983, 1992).

On the Peninsula, the Cape Supergroup is represented by the Graafwater and Peninsula Formations. The former comprise a narrow bed (up to 65 m deep) of medium-grained sandstones and mudstones, while the latter (and predominant rocks of the region) comprise a massive bed (up to 1200 m deep) of almost pure quartzitic sandstones (Deacon *et al.*, 1992; Theron *et al.*, 1992). These sediments were uplifted during a period of orogeny between 280 and 215 My and substantially eroded during the Mesozoic. Geological stability during the Tertiary has resulted in slow denudation of the hard sandstones, principally along fault lines and fractures, resulting in remnant massifs (e.g. Table Mountain) surrounded by extensive colluvial deposits on gentler slopes underlain by the older, softer rocks (Deacon, 1983; Theron *et al.*, 1992).

Tertiary deposits are poorly developed on the Peninsula: they comprise only some fossil-rich Miocene clays in the Noordhoek Valley (Theron *et al.*, 1992). The Quaternary is represented by occasional patches of alluvium and extensive areas of siliceous (older) and calcareous (younger) sands that mantle most of the Cape Flats and other coastal bottomlands.

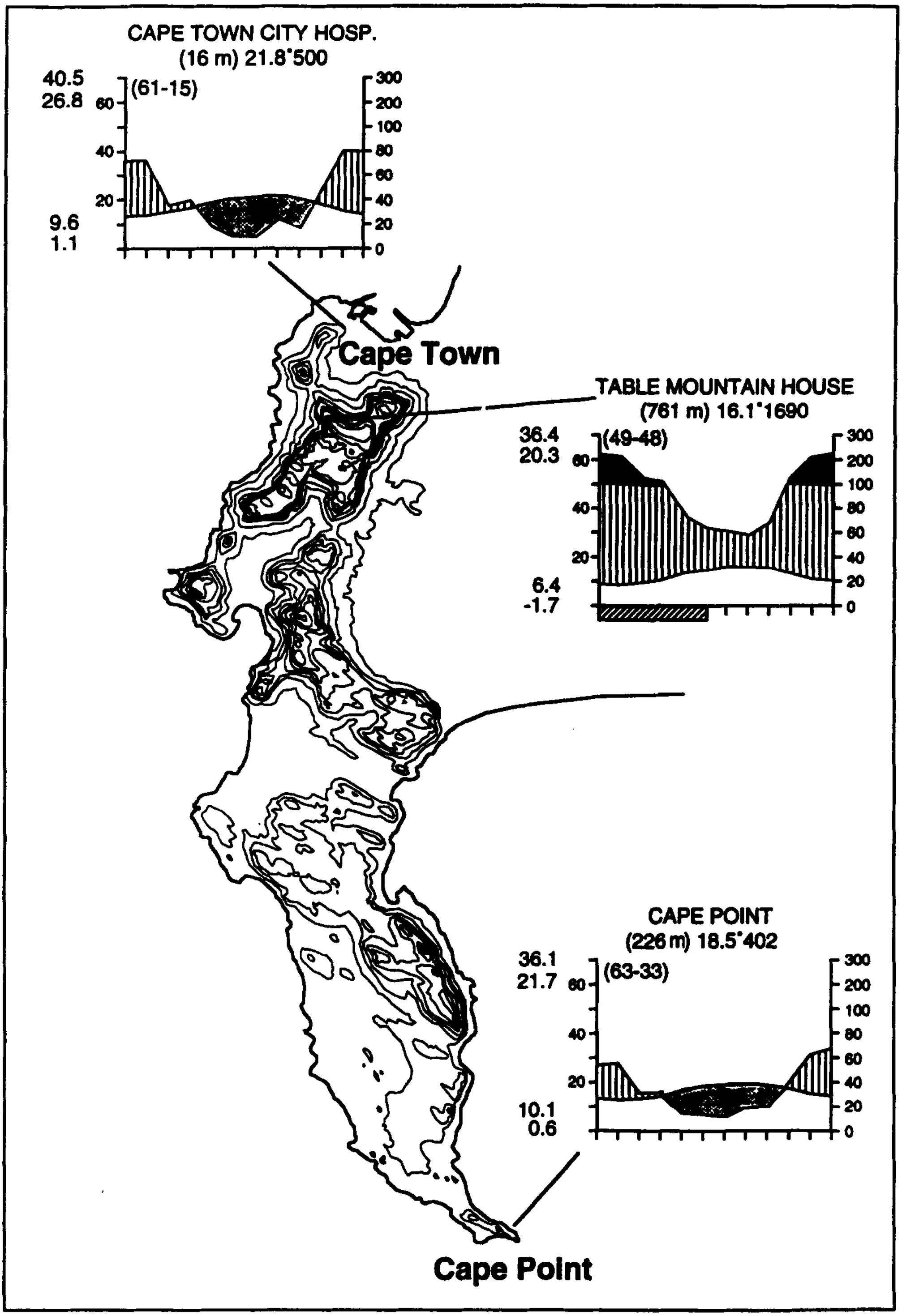


Figure 2. Topography and climate of the Cape Peninsula. Contours are at 100 m intervals.

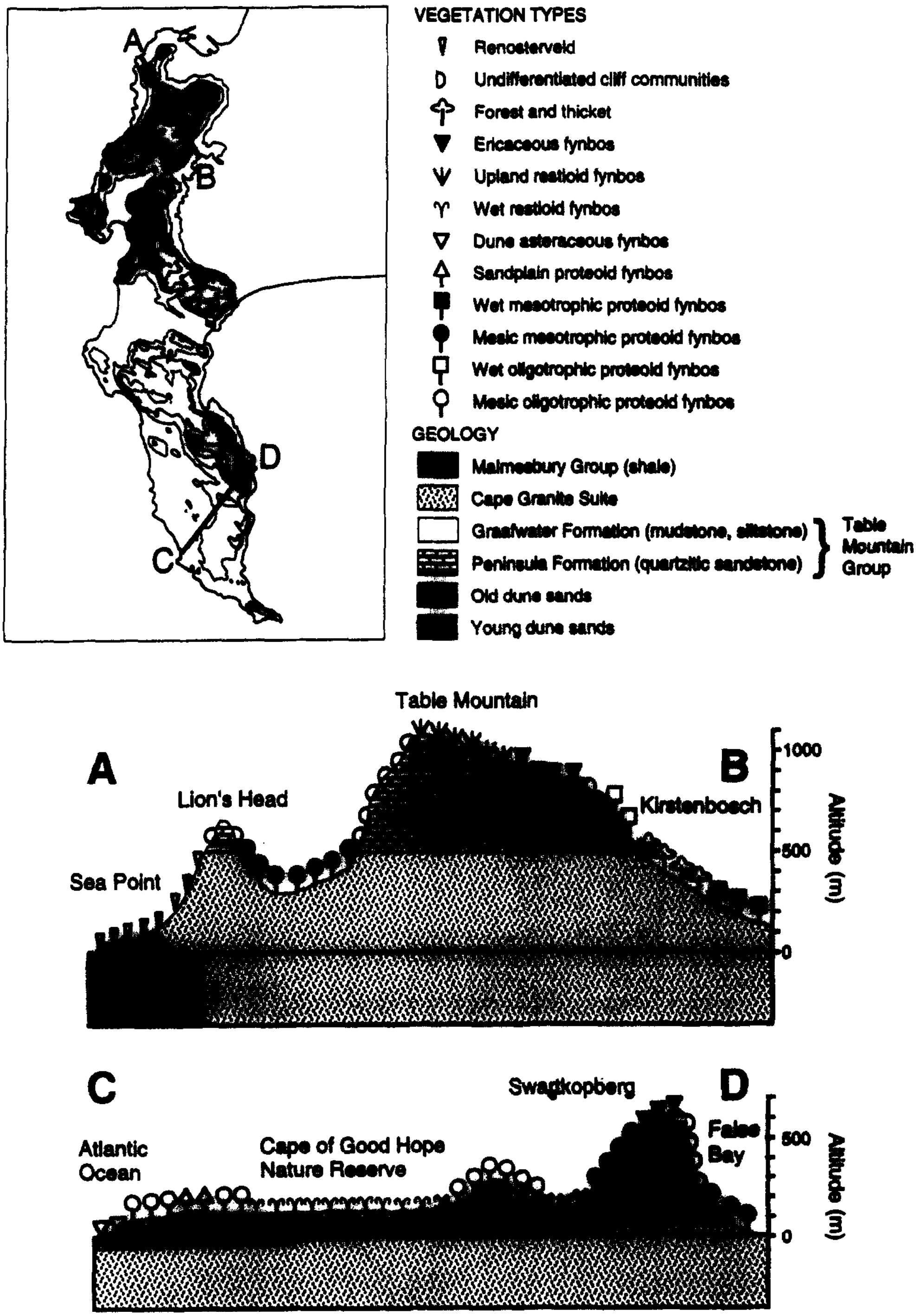


Figure 3. Transects across the Cape Peninsula showing the relationships between vegetation type and geology, altitude and slope/aspect combinations.

The Cape Peninsula has the highest topographical diversity of similar-sized areas in southern Africa (Cowling *et al.*, 1996; see also Simmons and Cowling, 1996) and has two landscape features of international renown, namely Table Mountain and Cape Point (Fig. 1). The impressive Peninsula Mountain Chain is separated from the north-south trending Folded Belt on its eastern margin by the relatively warm waters of False Bay and the narrow sandy isthmus of the Cape Flats; on its western margin it plunges, sometimes precipitously, into the cold waters of the Atlantic Ocean. The topography is dominated by the sandstone plateaux and ridges which reach a maximum altitude of 1113 m on Table Mountain (Figs 2 and 3). These drop steeply to the debris-covered and gentler slopes underlain by softer sediments. The Mountain Chain is interrupted by several gaps, most of which are covered by Quaternary deposits. The northeastern sector of the Peninsula comprises part of the featureless and sand-mantled Cape Flats. Toward the south, especially in the Cape of Good Hope Nature Reserve, the landscape comprises a low (ca 150 m) sandstone plateau, occasionally interrupted by narrow dunes of Quaternary sand (Taylor, 1969).

Like other landscapes of the Cape Folded Belt, the soils of the Cape Peninsula are mainly sandy and nutrient-poor (Deacon *et al.*, 1992). Surprisingly, there are few data on the ecologically relevant characteristics of Peninsula soils; nonetheless, it is possible to generalize for the region from data collected elsewhere in the southwestern part of the Folded Belt (see Deacon *et al.*, 1983 and 1992 for details).

The most impoverished soils – shallow, grey, acidic, leached sands deficient in all nutrients – are associated with the sandstone plateaux, summits and upper slopes. These are mostly well-drained but extensive areas of impeded drainage in the wet winter months occur on the more-or-less level plateaux on Table Mountain and in the southwest. High-lying ground (>600 m), subject to high winter rainfall and southeast cloud precipitation during summer, supports very acidic sands with high levels of organic matter. The deep soils of the colluvial slopes that are underlain by shale or granite, are heavier, orange to red in colour (especially where reworked ferricrete is present in the profile), less acid and richer in nutrients than the residual, sandstone-derived soils. Signal Hill, in the northwest, is comprised entirely of Malmesbury shale and lacks a colluvial overburden: soils are predominantly the moderately fertile duplex forms typical of the agriculturally transformed coastal plain (Swartland), north of Cape Town. Soils associated with the older Quaternary deposits are mainly deep, moderately acid sands that are marginally more fertile than those derived from sandstone. The younger sands along the coastal margin are poorly consolidated and highly alkaline. Large areas of mobile dunefield have been stabilized over the last century, principally with alien *Acacia* species.

CLIMATE

The Cape Peninsula experiences a Mediterranean-type climate, characterized typically by cool, wet winters and warm, dry summers (Fig. 2). Winter rain is associated with frontal depressions budded off from the circumpolar westerly belt; these occur with a frequency of at least one per week in the mid-winter months (June–August) (Heydorn and Tinley, 1980; Deacon *et al.*, 1992). In summer, the climate is influenced by the ridging cell of high pressure over the South Atlantic Ocean; the resultant southeasterly winds blow offshore along South Africa's southwest coast, and in the process lose whatever moisture they may have picked up over the warm Indian Ocean, as mist precipitation on the barrier peaks of the north-trending Folded Belt. However, up to 25% of the Peninsula's rain falls in the summer months (October to March) and much of this is associated with post-frontal conditions when the ridging high pressure cells advect moist air from the south and southeast.

The rainfall recorded in different parts of the Peninsula shows remarkable variation for so small an area (Adamson, 1927; Cowling *et al.*, 1996) (Fig. 2). For example, Maclear's Beacon on Table Mountain (the highest point on the Peninsula) receives 2270 mm y^{-1}, whereas the annual rainfall at Cape Point is only 402 mm. On average, areas on Table Mountain receive about 1000–2000 mm y^{-1}, Cape Town city: 600–800 mm y^{-1}, Southern Suburbs: 1000–1500 mm y^{-1}, Cape Flats: 500–600 mm y^{-1}, and southern Peninsula: 400–700 mm y^{-1}. Rainfall gradients are exceptionally steep and are influenced not only by altitude but also by aspect and other topographic features that serve to trap rain-bearing winds. These gradients may be even steeper than the rainfall data suggest, since precipitation from southeast cloud in the summer months is substantial at elevations greater than 600 m (Marloth, 1905; Snow, 1985).

Spatial and temporal variations in temperature are not pronounced on the Cape Peninsula (Fig. 2) owing to the ameliorating influence of the ocean on the narrow land mass as well as the relatively low maximum altitudes of the Mountain Chain. Mean annual temperature on the summit of Table Mountain is about 16°C, rising to 22°C at sea level in the warmer, north-facing city area. For all other sites, average temperatures vary between 18°C and 20°C. The difference between mean maximum and mean minimum temperatures for different stations are slight, ranging from 6°C at Cape Point to about 10°C on Table Mountain. Frost is unknown at sea level and even on Table Mountain the amount and severity of frost is not great. Snow is rare, falling only on Table Mountain and never persisting for more than a day or two.

A distinctive feature of the Cape Peninsula's climate is its strong wind regime. In winter, northwesterly winds frequently exceed gale force and have mean speeds ranging from 20 km h^{-1} (Cape Flats) to 30 km h^{-1} (Cape Point). Summer southerly and southeasterly winds may blow at gale force a week or more at a time; mean speeds range from 20 km h^{-1} (Cape Flats) to 40 km h^{-1} (Cape Point). However, there are many relatively windless areas, such as parts of the Southern Suburbs (Fig. 1), which escape the summer gales.

Biological characteristics

The biological characteristics of the Cape Peninsula are typical of the southwestern portion of the Cape Floristic Region where summer drought, infertile soils, strong winds and, especially, periodic fire (at 4–40 year intervals) are the driving variables for ecological patterns and processes (Taylor, 1978; Kruger, 1979; Cowling, 1992). In this section we provide a brief overview of the Peninsula's flora, fauna and ecological communities. The account is descriptive: details on some of the evolutionary and ecological processes that have shaped the biota, communities and ecosystems are given elsewhere in this issue (Picker and Samways, 1996; Richardson *et al.*, 1996; Simmons and Cowling, 1996; Trinder-Smith *et al.*, 1996a).

FLORA

The flora of the Cape Peninsula is typical of areas in the southwestern Cape Floristic Region (Cowling and Holmes, 1992). The five largest families are Asteraceae (286 spp.), Iridaceae (168 spp.), Fabaceae (162 spp.), Poaceae (141 spp.), and Ericaceae (112 spp.) (Trinder-Smith *et al.*, 1996a). These floras typically have a number of extremely speciose genera (Goldblatt, 1978); those in the Peninsula include *Erica* (103 spp.), *Aspalathus* (55), *Senecio* (47), *Oxalis* (28) and *Ficinia* (37) (Trinder-Smith, 1995). Biogeographically, the Peninsula flora is unusual in that it includes species typical of strictly winter-rainfall portions of the western Cape Floristic Region as well as species whose ranges extend eastwards, where more rain falls in summer (Taylor, 1984). This biogeographical mixing probably contributes to explaining the very high richness of the Peninsula's flora (Simmons and Cowling, 1996).

VEGETATION

Because of its proximity to research institutions, the vegetation of the Cape Peninsula has received considerable attention, although no comprehensive account has been published. Adamson (1927) provided a descriptive account of the vegetation of Table Mountain. More recently, a number of phytosociological studies have been undertaken in various parts of the Peninsula: Cape of Good Hope Nature Reserve (Taylor, 1969, 1984); Table Mountain forests (Campbell and Moll, 1977); Table Mountain southern slopes (Orange Kloof) (McKenzie *et al.*, 1977); Table Mountain summit (Glyphis *et al.*, 1978; Laidler *et al.*, 1978); and Signal Hill (Joubert and Moll, 1992). Vegetation has been mapped in the Cape of Good Hope Nature Reserve (Taylor, 1969, 1984) and on Table Mountain (Moll and Campbell, 1976).

The vegetation map produced here (Fig. 4) is the first comprehensive treatment for the entire Cape Peninsula. Communities were characterized on the basis of crude structural features and dominant species, following the approach of Campbell (1986). Vegetation was mapped in the field on 1:10000 orthophotos and the data were captured in a Geographical Information System (ARC/INFO version 6.1.1). Where urbanization or alien plants have transformed natural ecosystems, environmental variables (mainly soil and rainfall data) were used to predict the pre-disturbance type. Thus, the map represents conditions prior to the colonial era (i.e. before 1652) at the Cape. The vegetation units are at a hierarchical scale that is appropriate for conservation planning (see Trinder-Smith *et al.*, 1996b). Given the richness of the flora, attempts to map phytosociologically-derived communities would have been impractical, if not impossible (see Taylor, 1969).

Plant communities

As is typical of other areas in the southwestern Cape Floristic Region (Cowling and Holmes, 1992), three major plant formations are represented on the Cape Peninsula: these are Cape Fynbos Shrublands, Renosterveld Shrublands and associated grasslands, and Forest and Thicket (Fig. 4; Table 1; see Campbell, 1986). Fynbos is the characteristic and most widespread vegetation formation of the Cape Floristic Region and is home to the vast majority of its species (Taylor, 1978; Kruger, 1979; Cowling and Holmes, 1992). This is also true of the Cape Peninsula where fynbos communities covered some 92% of its area, prior to transformation. Fynbos is a fire-prone, sclerophyllous shrubland uniquely characterized by a relatively high cover (>5%) of restioids (wiry aphyllous graminoids of the Restionaceae).

Renosterveld, which only occupies about 5% of the Peninsula, is also a fire-prone shrubland. However, restioids are replaced here by grasses (Poaceae) whereas proteoid shrubs (large-leaved, overstorey shrubs in the Proteaceae which are common in many

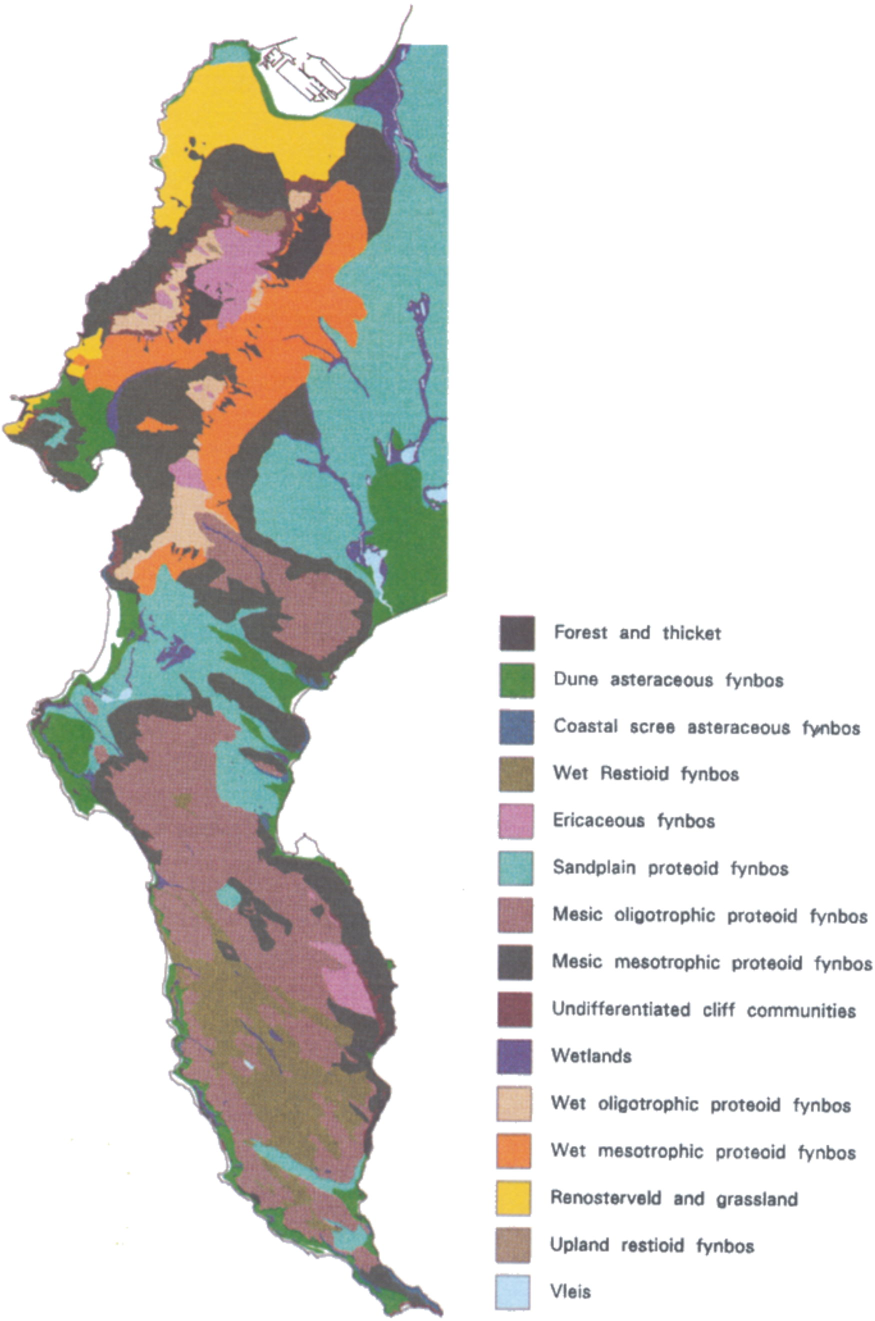


Figure 4. Major plant communities of the Cape Peninsula, showing their areal extent prior to transformation.

fynbos communities) are absent. Moreover, the shrub component is dominated by ericoid shrubs (which have small leaves with rolled margins) belonging to the Asteraceae and one of these, *Elytropappus rhinocerotis* (renosterbos or rhinoceros bush) is often dominant (Campbell, 1986; Cowling and Holmes, 1992). On the Peninsula, and elsewhere in the Cape Floristic Region, Renosterveld is confined to moderately dry sites with relatively fertile soils derived entirely from shale or granite (Table 1; Joubert and Moll, 1992). A distinctive feature of Renosterveld is its extremely rich geophyte flora (Cowling, 1990; Joubert and Moll, 1992). Since more than 90% of Renosterveld in the southwestern Cape has been replaced by agriculture (Moll and Bossi, 1984), the remnants on the Peninsula have high conservation importance.

Forest and thicket, which covers only about 3% of the Peninsula, differs from the two preceding formations in a number of ways (see Cowling and Holmes, 1992 for details). First, it is made up of broad-leaved, evergreen trees and shrubs with strong Afromontane and subtropical affinities – most component species are widespread outside the Cape Floristic Region. Second, it is relatively species-poor at both the local and regional scales. Third, it is not fire-prone and regeneration occurs largely from bird-dispersed propagules that establish in the intervals between fires. Forest and thicket grows in a wide range of habitats on the Peninsula but is best developed in moist, relatively fertile sites that are protected from fire such as scree slopes, stream banks and the coastal margin (Campbell and Moll, 1977; McKenzie *et al.*, 1977). It appears that fire-protection is the overriding determinant of this formation's distribution (M.T. Simmons and R.M. Cowling, unpubl. data), and in the prolonged (centuries-long) absence of fire, much of the Peninsula would be covered in this species-poor forest and thicket.

Table 1 provides a brief structural characterization for each of the communities mapped in Fig. 4 and lists the most frequent species and major environmental correlates. The relationships between community type and geology, altitude (largely a surrogate variable for rainfall) and slope-aspect combination (or energy regime) are depicted along two transects, one in the northern and the other in the southern Peninsula (Fig. 3). The major factors determining the boundaries between fynbos plant communities are soil moisture, drainage, depth and nutrient status. Vegetation of the nutrient-poor plateau and summit soils is distinct from that of the more fertile colluvial slopes and bottomlands (Adamson, 1927; Taylor, 1969; Simmons and Cowling, 1996). Well-drained sands in the drier southern Peninsula support mesic oligotrophic proteoid fynbos (Table 1) whereas a wet and floristically distinct form of this type is found in the higher rainfall regions of the northern Peninsula. In areas subject to prolonged exposure to summer cloud and mist, oligotrophic proteoid fynbos is replaced by ericaceous fynbos, a true heathland with a high cover and richness of Ericaceae (Adamson, 1927; Glyphis *et al.*, 1978; Laidler *et al.*, 1978). Where soil drainage is impeded during the winter months, the vegetation is dominated by restioids (restioid fynbos) (Campbell, 1986): two communities occur – one on the plateau on Table Mountain and the other on the lowland plateau in the south (Taylor, 1969; Glyphis *et al.*, 1978; Laidler *et al.*, 1978).

The more fertile and clay-rich soils of the colluvial slopes support mesotrophic proteoid fynbos: a mesic form in the drier south Peninsula and west-facing slopes of Table Mountain, and wet form on the south- and east-facing slopes of Table Mountain and the central Mountain Chain (Adamson, 1927; Taylor, 1969; McKenzie *et al.*, 1977) (Fig. 3; Table 1). Where scree and colluvial slopes plunge into the ocean, and especially on the west coast where the salt-laden aerosol, generated from heavy seas, is carried landwards by

Table 1. Characterization of the major vegetation types of the Cape Peninsula (unpublished data from M.T. Simmons and R.M. Cowling, and from Forestek:CSIR)

Vegetation type	Structural characteristics[a]	Common species	Environment
Fynbos types			
Dune asteraceous fynbos	Low ericoid shrubland	*Metalasia muricata, Ischyrolepis eleocharis, Rhus glauca, Phylica ericoides, Euclea racemosa, Passerina paleacea, Ficinia lateralis, Hellmuthia membranacea, Otholobium fruticans, Ehrharta villosa*	Recent calcareous coastal dune sands; MAR = 678 mm Mean slope = 17.0° Mean aspect = S
Coastal scree asteraceous fynbos	Low-medium ericoid and broad-leaved shrubland	*Coleonema album, Euclea racemosa, Tarchonanthus camphoratus, Maytenus oleoides, Eriocephalus africanus, Pentaschistis curvifolia, Felicia fruticosa, Colpoon compressum, Cassine peragua, Olea europaea* subsp. *africana*	Sandstone scree coastal slopes, subject to strong salt-laden onshore winds; MAR = 656 mm Mean slope = 30° Mean aspect = S
Wet restioid fynbos	Low restioid herbland	*Ischyrolepis cincinnata, Tetraria cuspidata, Elegia filacea, Thamnochortus lucens, Cliffortia subsetacea, Erica imbricata, Leucadendron laureolum, Pentaschistis curvifolia, Restio quinquefarius, Restio bifurcus*	Shallow seasonally waterlogged sands on sandstone at low altitudes; MAR = 634 mm Mean slope = 13° Mean aspect = WSW
Upland restioid fynbos	Low restioid herbland	*Thamnocortus nutans, Chrondropetalum ebracteatum, Ursinia nudicaulis, Restio bifidus, Ehrharta setacea, Watsonia borbonica* subsp. *borbonica, Penaea mucronata, Cliffortia ruscifolia, Erica hispidula, Chondropetalum mucronatum*	Shallow seasonally waterlogged sands on sandstone; MAR = 1404 mm Mean slope = 32° Mean aspect = SW

Sandplain proteoid fynbos	Medium-height proteoid shrubland with a low ericoid and restioid understorey	*Thamnocortus erectus, Metalasia muricata, Euclea racemosa, Carpobrotus edulis, Rhus laevigata, Leucadendron coniferum, Rhus glauca, Eriocephalus africanus, Agathosma imbricata, Diosma hirsuta*	Old marine (deep and well-drained) sands, occasionally on calcrete or limestone; MAR = 804 mm Mean slope = 16° Mean aspect = S
Mesic oligotrophic proteoid fynbos	Medium-height proteoid shrubland with a low ericoid and restioid understorey	*Thamnochortus lucens, Elegia stipularis, Metalasia muricata, Phylica imberbis, Elytropappus scaber, Salixis axillaris, Struthiola ciliata, Ischyrolepis cincinnata, Hypodiscus aristatus, Tetraria eximia*	Shallow, leached sands on sandstone; MAR = 765 mm Mean slope = 21° Mean aspect = SW
Mesic mesotrophic proteoid fynbos	Medium-height proteoid shrubland with an ericoid understorey	*Erica plukenetii, Penaea mucronata, Protea lepidocarpodendron, Cliffortia falcata, Elytropappus scaber, Rhus lucida, Phylica imberbis, Passerina vulgaris, Leucadendron salignum, Cliffortia stricta*	Mainly deep, sandy loams associated with colluvium or granites on lower mountain slopes; MAR = 947 mm Mean slope = 30° Mean aspect = SSW
Wet oligotrophic proteoid fynbos	Medium-height proteoid shrubland with an ericaceous and restioid understorey	*Anthospermum galioides, Leucadendron xanthoconus, Penaea mucronata, Elegia racemosa, Bobartia gladiata, Erica plukenetii, Leucadendron salignum, Rhus lucida, Otholobium fruticans, Myrsine africana*	Shallow, leached sands on sandstone; MAR = 1168 mm Mean slope = 30° Mean aspect = SSW
Wet mesotrophic proteoid fynbos	Medium-height proteoid shrubland with ericoid understorey	*Rhus tomentosa, Myrsine africana, Penaea mucronata, Widdringtonia nodiflora, Protea nitida, Rhus lucida, Leucadendron xanthoconus, Stoebe cinerea, Maytenus oleoides, Erica plukenetii*	Mainly deep, sandy loams associated with colluvium or granites on lower mountain slopes; MAR = 1136 mm Mean slope = 30° Mean aspect = SSE

Table 1. (*Continued*)

Vegetation type	Structural characteristics[a]	Common species	Environment
Ericaceous fynbos	Low ericaceous and restioid shrubland	*Penaea mucronata, Hypodiscus aristatus, Erica hispidula, Leucadendron xanthoconus, Pseudopentameris macrantha, Corymbium glabrum, Erica plukenetii, Clutia polygonoides, Thamnocortus nutans, Tetraria cuspidata*	Shallow, leached, organic-rich sands at high altitude subject to intermittent condensation from orographic cloud in summer; MAR = 1197 mm Mean slope = 30° Mean aspect = SSW
Undifferentiated cliff communities	Variable, mainly low and sparse ericoid shrubland	*Cliffortia ruscifolia, Helichrysum cymosum, Cullumia ciliaris, Lampranthus falciformis, Cliffortia odorata, Ehrharta ramosa* subsp. *aphylla, Peucedanum galbanum, Anthospermum galioides, Anthospermum aethiopicum, Pelargonium cucullatum*	Steep to vertical sandstone cliffs; MAR = 1168 mm Mean slope = 47° Mean aspect = SSW
Non-fynbos types			
Forest and thicket	Low-medium (thicket), or medium to tall (forests) closed-canopy, broad-leaved formation with a sparse understorey	*Rapanea melanophloeos, Diospyros whyteana, Cassine peragua, Knowltonia capensis, Myrsiphyllum scandens, Kiggelaria africana, Olea capensis, Olinia ventosa, Secomone alpini, Chionanthus foveolatus*	Colluvium or granite-derived soils on wet slopes or fire protected kloofs (ravines) and coastal margins; MAR = 992 mm Mean slope = 30.0° Mean aspect = SSW

Renosterveld and grassland	Low grassland/low-medium ericoid and broad-leaved shrubland	*Rhus lucida, Chrysocoma coma-aurea, Helichrysum patulum, Anthospermum spathulatum, Helichrysum cymosum, Salvia africana-caerulea, Hyparrhenia hirta, Mohria caffrorum, Rhus glauca, Merxmuellera stricta*	Sandy loams on clay subsoil, shale or granite-derived; MAR = 826 mm Mean slope = 24° Mean aspect = SW
Wetlands	Medium-height ericoid shrubland with an ericoid and restioid understorey	*Penaea mucronata, Berzelia abrotanoides, Platycaulos compressus, Leucadendron laureolum, Berzelia lanuginosa, Pentaschistis curvifolia, Osmitopsis astericoides, Watsonia tabularis, Psoralea pinnata, Restio quinquefarius*	Seepage sites with shallow-medium depth sandy soils with high organic matter over sandstone bedrock; MAR = 779 mm Mean slope = 12° Mean aspect = SSW
Vleis	No data	No data	Freshwater lake and vleis (small, shallow water bodies) MAR = 844 mm Mean slope = 5° Mean aspect = SE

[a]Low = <1 m, medium = 1.3 m, tall = >3 m.
Broad-leaved = nanophyllous and larger dorsiventral leaves, typical of subtropical taxa (*Olea, Cassine, Maytenus,* etc.) on the Cape Peninsula.
Ericoid = shrubs with leptophyllous smaller leaves with revolute margins.
Ericaceous = same as above except all members of the Ericaceae.
Proteoid = shrubs with large (nanophyllous or larger) isobilateral leaves (all members of the Proteceae).
Restioid = wiry, aphyllous and evergreen graminoids belonging largely to the Restionaceae.

winter northwesterly winds (Taylor, 1969), the vegetation is a form of asteraceous fynbos (dominated by ericoid shrubs) (Campbell, 1986). The distribution of vegetation on the lowland, Quaternary deposits is determined by the age of the sands: younger and well-drained calcareous sands support a form of asteraceous fynbos whereas older, weakly acidic and better developed sands support a distinctive form of proteoid fynbos (Taylor, 1969). The latter was once widespread on the Cape Flats but has now almost entirely succumbed to urbanization (Richardson *et al.*, 1996). Steep to vertical cliff faces support a floristically and structurally variable vegetation. Permanently wet but freely draining seepage sites support a tall, hygrophillous fynbos (cf. Campbell, 1986) or wetland.

This brief account cannot do justice to the enormous floristic complexity of the Cape Peninsula. Even within the communities we have described, there is great floristic variation from site to site (Adamson, 1927; Simmons and Cowling, 1996). Given the profound influence of stochastic fire regimes on community structure (Simmons and Cowling, 1996), the identification of meaningful patterns at a hierarchical level below those described here is likely to be difficult.

TERRESTRIAL FAUNA AND ANIMAL COMMUNITIES

As stated above, the Peninsula's fauna is less well known than the flora. The general pattern for vertebrate groups is moderate species richness and low endemism, while certain invertebrate groups are very speciose and have exceptionally high levels of endemism: at 112 species, there are more endemic animals than plants on the Peninsula (Picker and Samways, 1996). Interestingly, three of the six bird species endemic to the Cape Floristic Region have not been recorded in the area (Hockey *et al.*, 1989), possibly a consequence of higher Pleistocene sea levels when the Peninsula was an island.

The structure of animal communities in the Cape Floristic Region, including the Cape Peninsula, has been relatively poorly studied (Richardson *et al.*, 1995). However, a generalization that emerges for most guilds, and this is certainly true of the Peninsula, is the low abundance of individuals in the predominantly fynbos vegetation (Wright, 1988; Fraser, 1990; Johnson, 1992a). This pattern is probably a consequence of infertile soils (and, consequently, low forage quality), recurrent fire, and strong winds.

Although early records confirm that large mammalian herbivores (including elephant, black rhinoceros, hippopotamus and a variety of antelope) and carnivores such as lion and leopard once occurred on the Peninsula (Skead, 1980), herding species at least were almost certainly not permanent residents (Fraser and McMahon, 1994). Poor forage quality and trace element deficiencies associated with the fynbos (Zumpt and Heine, 1978) would have placed severe constraints on large, generalist herbivores. Resident herbivores today include small antelope such as klipspringer (*Oreotragus oreotragus*) (now locally extinct), grey rhebok (*Pelea capreolus*), grysbok (*Raphicerus melanotis*) and steenbok (*R. campestris*), as well as rock hyrax (*Procavia capensis*), which either browse and graze selectively on nutrient-rich plant parts or concentrate in relatively nutrient-rich habitats. An unusual group of small mammals is the molerats (Bathyergidae), fossorial herbivores that feed on roots, bulbs and corms and may be very common in deep, lowland sands (Lovegrove and Jarvis, 1986). Several species of rodent are important consumers of seeds and may influence post-fire population size of Proteaceae (Bond, 1984; van Hensbergen *et al.*, 1992).

Generally, avifaunal community structure and abundance in fynbos habitats on the

Peninsula are influenced more by floristics than by vegetation structure (Fraser, 1990). Thus, large numbers of nectarivores such as Cape Sugarbird (*Promerops cafer*) and sunbirds (Nectarinidae) congregate seasonally on ornithophilous nectar-producing plants, particularly Proteaceae (see also Rebelo, 1987). Otherwise, communities comprise low numbers of relatively few, small, insectivorous species (Siegfried, 1983; Fraser, 1990). Forest and thicket, owing to its greater resource availability, including a year-round supply of fleshy fruits (Knight, 1988), supports a much higher richness, density and biomass of birds than fynbos (Fraser, 1996).

Invertebrate community structure on the Peninsula has received almost no attention. Research, which has focused mainly on plant–insect interactions such as myrmecochory (Bond and Stock, 1990) and pollination (Johnson, 1992a, b; Johnson and Bond, 1994), has shown that important ecological processes and many morphological traits in fynbos are sustained and shaped by small and often inconspicuous invertebrates. Ants, such as *Anoplolepis custodiens*, play a keystone role in dispersing the seeds of many hundreds of species, including the majority of Peninsula endemics (Trinder-Smith *et al.*, 1996a), to below-ground sites where they are protected from predators (Bond *et al.*, 1991). Much of the floral variation in fynbos is the result of insect pollinator-induced adaptive radiation (Johnson, 1992a). Several red-flowered species on the Peninsula are exclusively pollinated by the mountain pride butterfly (*Aeropetes tulbaghia*) which, interestingly, occurs throughout South Africa (Johnson and Bond, 1994). A generalization for many insect-pollinated species, including some Peninsula endemics and near-endemics, is that seed set is limited by pollinator activity (Wright *et al.*, 1991; Johnson, 1992b), which itself is a consequence of low pollinator abundance in a nutrient-poor and windy environment (Johnson, 1992a).

Human settlement and impacts

Human settlement of the Cape Peninsula was initially constrained by the same factor that limited animal numbers, namely the widespread occurrence of nutritionally impoverished soils. It was only after the colonial era, when European crops that were well-suited to the winter growing season of the southwestern Cape, were introduced, that the human population and its impacts on the Peninsula's natural ecosystems began to grow significantly (Deacon, 1992). Nonetheless, the Peninsula has a very long history of human settlement and there is little doubt that the many ecosystems of the area were not 'pristine' when the Dutch established their outpost there in 1652.

Evidence for human occupation of the Peninsula dates back to at least 200 000 BP (Deacon, 1992). Hunter–gatherer San or 'Bushmen', who practiced 'firestick farming' to manage the veld for game and geophytes, inhabited the Peninsula at least 20 000 years ago. About 2000 years ago the San were displaced by the Khoikhoi, nomadic pastoralists who kept sheep and cattle. It is estimated that shortly after the arrival of Europeans at the Cape, there were between 4000 and 8000 Peninsular Khoikhoi encamped at various lowland and relatively fertile sites in the central and northern Peninsula (Elphick, 1985). Although some communities lacked stock and subsisted by foraging along the productive coastline (the so-called Strandlopers), stock numbers were relatively high. For example, 20 000 cattle as well as sheep were driven from the hinterland to the northern fringes of the Peninsula, eight months after Jan van Riebeek established a revictualling station at Table Bay for the Dutch East India Company in 1652 (Thom, 1952). However, Khoikhoi transhumance patterns meant that these stock remained on the Peninsula only for the dry summer months (December to March) and were moved to the hinterland beyond the Cape Flats for the rest of the year (Elphick, 1985). It is unlikely that significant numbers of stock were kept in the predominantly infertile and mountainous Peninsula south of the Noordhoek valley.

Dutch colonization resulted in immediate and significant transformation of the lower lying natural ecosystems of the northern Peninsula. Rapidly expanding agriculture, including viticulture, transformed much of the lower slopes and flats from Table Bay to Wynberg, and the forests that covered the lower eastern slopes of Table Mountain and the entire Hout Bay Valley were rapidly depleted (Thom, 1952). In response to this, oaks (*Quercus*) and pines (*Pinus*) (some of which were to become troublesome invasives) were introduced from Holland as early as 1655, and large-scale planting schemes of alien tree species were later initiated (Richardson *et al.*, 1992).

The expansion of the Dutch colony into the southern Peninsula was relatively slow. A large area of Simon's Bay was 'bought' from the Khoikhoi in 1672. This site eventually became a winter anchorage in 1743. Farms in the area were granted to 'free burghers' but were used mainly for hunting (leading to the local extinction of most of the larger mammals) and limited vegetable production on the restricted patches of more fertile soils (Thom, 1952). This expanding colonial frontier was disastrous for the Khoikhoi and, together with a smallpox epidemic, led to their total social and economic disintegration by 1713 (Elphick, 1985).

After the British occupied the Cape in 1806, they liberalized trade regulations and the economy and population of the Peninsula grew rapidly (Christopher, 1976). At this stage there were 22 000 settlers and 25 000 slaves in the greater Cape Town area, together with a few remaining Khoikhoi. A large contingent of British settlers arrived in 1820, swelling the European population of the area to 47 000. After the British made Simon's Town their official naval base, transport and other infrastructure expanded rapidly in the southern Peninsula. The economy of Simon's Town flourished during the Anglo-Boer War (1899–1902) and again during the two World Wars. However, agriculture was, as always, limited by the rugged terrain and lack of suitable soils (see Richardson *et al.*, 1996) and most of the farming produce to supply the visiting ships had to be brought from the hinterland.

The establishment of extensive plantations during the mid to late 19th century of fast-growing alien trees on the slopes of Table Mountain and the central Peninsula (mainly pines and eucalypts) and on the mobile sands of the Cape Flats (mainly Australian acacias), was ultimately to lead to the alien plant invasions which so seriously threaten the natural ecosystems of the Peninsula today (Richardson *et al.*, 1996). This period also witnessed the expansion of urban areas, initially along the eastern slopes of Table Mountain, but later along the Atlantic Seaboard, on the Cape Flats and in the southern Peninsula from Muizenberg to Simon's Town. The population of the greater Cape Town area grew rapidly during the 20th century and by the mid 1960s it totalled about half a million. The repeal in the late 1980s of discriminatory legislation, introduced during the apartheid era to prevent black people from settling in the Western Cape, saw an upsurge in the population and the establishment of numerous informal settlements in and around the Peninsula. By 1994, the population of the Peninsula was some 2.2 million and it is expected to reach 6 million by 2020 (van Wilgen, 1996). This rapid rate of growth will undoubtedly place enormous pressures on the Peninsula's remaining and already beseiged natural ecosystems. Already, some 37% of the region has been transformed by agriculture and urbanization and 44% of the remnant area of natural ecosystem is invaded by alien plants (Richardson *et al.*, 1996). Fortunately, about 64% of the Peninsula is included in the Cape Peninsula Protected Natural Environment (van Wilgen 1996; Fig. 1) which includes three major nature reserves (Fig. 1). Nonetheless, it remains a major challenge to ensure that the remaining biodiversity on the Peninsula is conserved for posterity (Trinder-Smith *et al.*, 1996b).

Concluding discussion

The Cape Peninsula's enormous plant and distinctive terrestrial invertebrate biodiversity is of global significance. The exceptional richness of its flora and resultant vegetational complexity can, in part, be explained by the Peninsula's high topographic, climatic and edaphic diversity (Adamson, 1927; Taylor, 1969; Cowling *et al.*, 1996; Simmons and Cowling, 1996). However, historical factors relating to the Peninsula's island-like geography and transitional location with regard to two major species-pools within the Cape flora, have also played a role (Picker and Samways, 1996; Simmons and Cowling, 1996).

The Cape Peninsula represents a microcosm of the forces threatening biodiversity in the developed (formal urbanization, pollution, industry, alien organisms) and developing (informal housing, domestic pollution, injudicious plant harvesting, snaring etc) worlds. We have the spectre of what is arguably the world's foremost hot-spot of terrestrial biodiversity inexorably falling victim to satisfy immediate human demands. Yet the Peninsula still has 'wilderness' landscapes and, perhaps somewhat miraculously, some 99% of its biodiversity is extant (Trinder-Smith *et al.*, 1996b). The opportunity exists to reverse the decline by using the impressive amount of data and knowledge collated in this special issue to manage and maintain the Peninsula's biodiversity. The direct and indirect economic rewards, in the form of increased ecotourism, recreational opportunities and generally improved quality of life within a major metropolis, and a natural landscape that attracts investment in environment-friendly industries, are likely to be substantial. Indeed, healthy ecosystems on the Peninsula should be seen as a barometer of economic vibrancy and sustainability in the Western Cape.

There can be no doubt that the Cape Peninsula is worthy of conservation status at the highest national (e.g. National Park) and international (e.g. World Heritage Site status) levels. The tools and expertise exist to manage the area competently (van Wilgen, 1996). What is urgently required is the political will to rationalize and fund management structures. Failure to do so will result in cascading losses of biodiversity over the next few decades (Richardson *et al.*, 1996).

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