Vegetation, diversity and rarity on the Cape Peninsula, South Africa.

Mark Trevor Simmons

Thesis presented for the degree of
MASTER OF SCIENCE
in the Department of Botany
Faculty of Science
University of Cape Town

August 1996

Acknowledgements

Amidst the periods of the frustration and grind, combined with moments of revelation and reward, surely one of the true pleasures of research is the interaction with colleagues for discussion, assistance and encouragement. I am grateful for a large number of people who have made contributions to this project.

My supervisor, Richard Cowling, who has not only provided initial motivation, guidance and expertise but also, just as significantly, enthusiasm and laudable patience.

Unpublished data was provided by James Jackelman, Hugh Taylor, the Botanical Society of South Africa and the National Botanical Institute. In addition, numerous undergraduates from the Botany Department have accumulated data over the last few years. I would like to thank Sean Privett, Chris Lotz and Cecilia Makua for their companionship in the field and dedication in the herbarium. The staff of the Bolus Herbarium were vital in the my journey up the learning-curve of fynbos identification. In particular, I thank Terry Trinder-Smith, Peter Linder, Pat Lorber and Anne Bean. Valuable methodological and interpretative discussions were held with, especially Dave McDonald and, additionally, with William Bond, Donovan Kirkwood, Debbie Mann, Michael Mann, Jeremy Midgely and Willie Stock. Finally, I wish to thank Eugene Moll who, so enthusiastically, was the first to show me, like he did for so many of my colleagues, the beauty and intrigue of looking for, and explaining, pattern in the landscape.

The study was funded by the Mazda Wildlife Fund, the Foundation for Research and Development and the Pew Charitable Trusts.

Abstract

The Cape Peninsula, (471 km^2) with over 2285 vascular plant species, is characterised by the combination of a diversity of habitats supporting a mosaic of vegetation types. This study attempts describe and explain some of the determinants of species pattern and distribution. The first part of the thesis compares a simple vegetation classification, derived from visual examination of dominant species and environmental characteristics, with the results of a multivariate classification derived from the analysis of an extensive database (835 plots, 833 species). This rapid system of classification of fynbos showed an 81% similarity with Two-Way Analysis (TWA) classification. Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were used to relate floristic variation to environmental factors. Theses analyses revealed that altitude, rainfall and soil fertility were the principle environmental factors explaining species distribution. The second part of the thesis examined patterns of local richness and turnover (beta and gamma diversity). Similar sized areas in other mediterranean-climate region biodiversity hot-spots support between 4.7 and 2.7 times fewer species than the Cape Peninsula. This high plant regional richness is due to the exceptionally high turnover between moderately species-rich sites in along steep environmental gradients (beta diversity) and between sites in similar habitats along geographical gradients (gamma diversity). Highest beta diversity, encompassing almost complete turnover, was recorded along soil fertility gradients. Although similar patterns for these independent components explain the richness of other regions in the Cape Floristic region, it is the very long and steep habitat gradients of the Cape Peninsula that makes this region exceptionally rich. Furthermore, the flora is characterized by a high degree of rarity, a phenomenon that undoubtedly influences the turnover. Thus, the third part of this thesis analyses the biological and habitat correlates of plant rarity. Given the lack of any general theory of causality, understanding rarity has become a considerable problem for reserve management. To date, there have been no studies which compare the attributes of rare and common plant species. There were no strong relationships between rarity status and biological attributes of species. However, rare species occupy wider resource niches as measured in multivariate space. Although some habitats contained a relatively larger proportion of rare plants, most were not restricted to particular vegetation types and exhibited a wide range of habitat infidelity. However, the distribution of many species, particularly those with high fidelity-indices could be successfully modelled regardless of rarity status abundance. Therefore, although rarity is difficult to predict at the phenomenon level, for management purposes, priority habitats can be identified and the distribution of rare species modelled individually. The results of theses studies are discussed in terms of management and conservation of the Cape Peninsula's uniquely high plant diversity.

Contents

CHAPTER 1

General introduction[1]

Introduction

The Cape Peninsula comprises a region of internationally renowned scenic beauty and exceptional biodiversity (e.g. Luckhoff, 1951; Moll and Campbell, 1976; UCT, 1994; Trinder-Smith, 1996a). It 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). With presently over two million people in the greater Cape Town area this is expected to increase to six million by 2020 (van Wilgen, 1996). The pressure of increasing development on the natural vegetation of the Cape Peninsula is already marked. Some 37% of the region has been transformed by agriculture and urbanization, and 44% of the remaining area of the natural ecosystems is invaded by alien plants (Richardson *et al.*, 1996). Fortunately, about 64% of the natural (i.e. non-transformed) area is included in the Cape Peninsula Protected Natural Environment (Fig. 1.1), which includes the present major reserves. Attempts are currently underway to apply for status as a National Park and World Heritage Site (van Wilgen, 1996). If the Cape Peninsula is to retain such status, both in terms of its international conservation ranking, as well its local economic potential, then adequate management plans have to be implemented. These will entail both the proclamation of reserves, in addition to those already existing (Trinder-Smith *et al.*, 1996b), and active management, to ensure maintenance of diversity (van Wilgen, 1996). This study attempted to extract information from which management strategies, applicable to these issues, can

---

[1] Aspects of this chapter have been published in *Biodiversity and Conservation* 6, 527-550

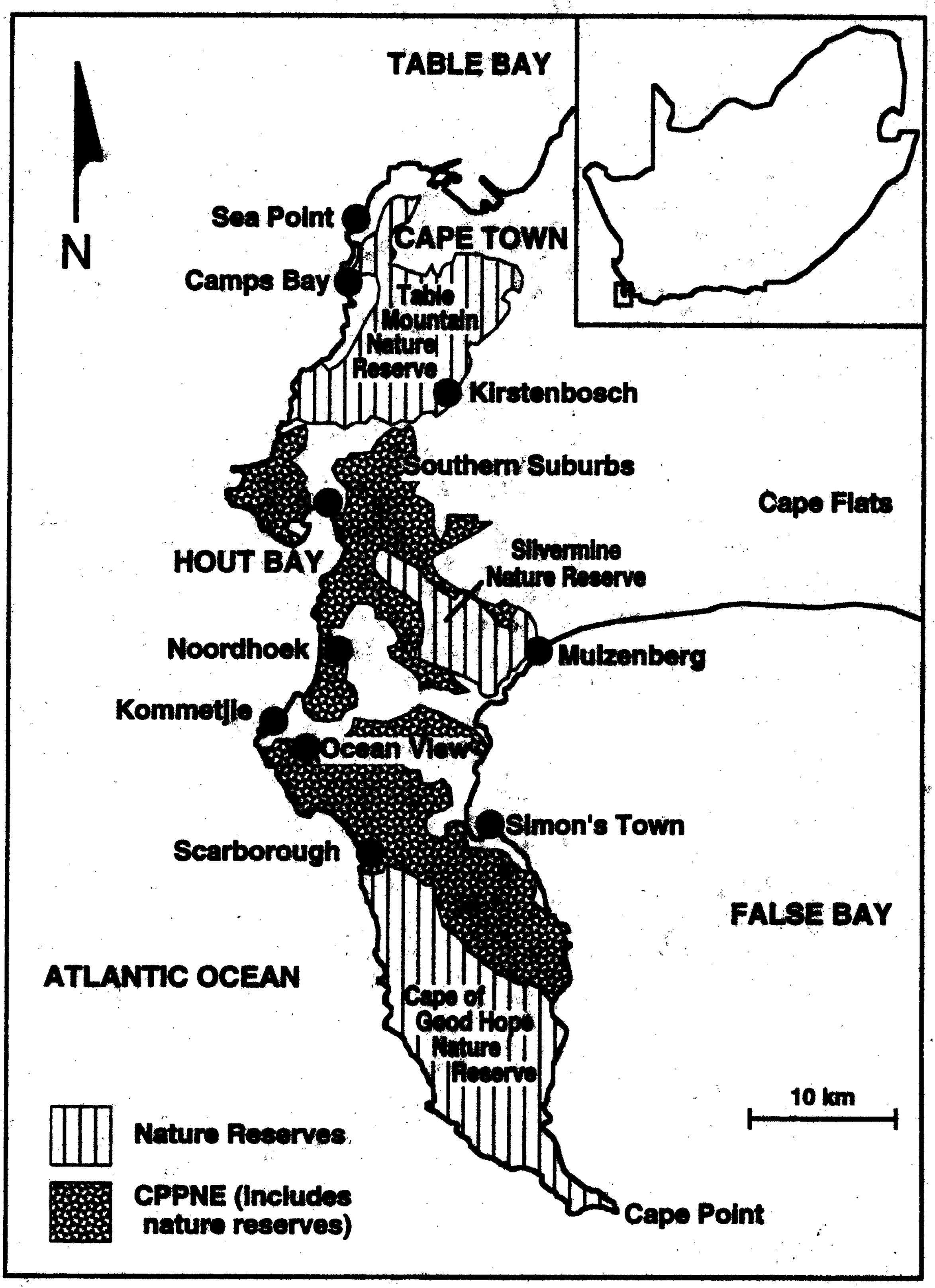


Figure 1.1 Location of the Cape Peninsula showing important place names, nature reserves and the location of the Cape Peninsula Protected Natural Environment (CPPNE).

be formulated. This was approached by examining the patterns of plant species distribution and their relationships with the environment, using an extensive phytosociological database of the area. The main objectives of this study were:

1. Classification of the vegetation units and correlation of these communities with environmental factors
2. Description and analysis of the patterns of diversity
3. Description and analysis of species abundance patterns.

Study Area

Geology, topography and soils

The Cape Peninsula, located at the southwestern corner of Africa, forms a mountain-chain, about 60 km long and 10 km wide, bordered on the east by False Bay and the west by the Atlantic Ocean. The topography is largely mountainous, but has several extensive level areas both at altitude (e.g. Table Mountain) and lower-lying areas in the Cape of Good Hope Nature Reserve, as well as valleys which bisect across or intrude into the mountains (Fig. 1.1). It forms part of the Cape-Folded Belt, an L-shaped band at the southwestern corner of the Africa, of erosion-resistant, quartzitic sandstone mountains underlain by softer shales, and mantled at the coastal margin with young siliceous and calcareous sediments (Deacon *et al.*, 1992). Underlying this formation on the Cape Peninsula, lie the Malmesbury Shales, which are predominantly deltaic marine shales (Theron, 1983), folded and sheared in the late Precambrian and subsequently intruded by granite (Cape Granite Suite) in the Cambrian (Du Toit, 1954; Deacon *et al.*, 1992). This basal group was consequently eroded to a relatively featureless peneplain (Theron *et al.*, 1992).

Subsidence of this basal surface formed localised estuarine deposition of a narrow (up to 65 m) bed of medium-grained sandstones, and mudstones (Graafwater Formation) followed by sedimentation of deep (up to 1200 m on the Cape Peninsula), almost pure quartzite sandstones of the Peninsula Formation from the Late Ordovician onwards (Deacon *et al.*, 1992; Theron *et al.*, 1992). These medium to coarse-grained sandstones formed in shallow marine environment of an extensive Cape basin, either in a marine deltaic environment or a riverine, braid plain system (Turner, 1987; Theron *et al.*, 1992).

Cape orogeny and uplift during the Permian and Triassic created mountain chains along the west and southern coast of South Africa. Geological stability during the Tertiary, and dominant erosional processes resulted in very slow denudation of these hard sandstones, principally along fault-lines and fractures. This resulted in remnant massifs of hard nutrient-poor sandstones (e.g. Table Mountain) surrounded by colluvial deposits on gentler slopes, overlying the softer, nutrient-rich, older formations exposed along lower mountain slopes (Deacon, 1983; Theron *et al.*, 1992). The Peninsula Formation sandstones are subsequently the most prominent unit in the mountain ranges of the Cape Peninsula.

Apart from recent, superficial Neocene deposits there is little evidence of major Tertiary sedimentation on the Cape Peninsula, suggesting largely erosional processes during this geologically stable period. The deep, coarse, quartz sands in the valleys on the southern Peninsula have lower bands of Miocene clays in the Noordhoek valley. The Quaternary is represented by deposits of mainly sand or clay alluvium along river courses or old marine sands (aeolian, fine-medium grained) around the coasts and more extensively across the Cape Flats to the east. The resulting landscape of the Cape Peninsula is a mountain chain of plateaus, ridges, peaks and valleys, exhibiting the highest topographical diversity of similar-sized ares in southern Africa (Cowling *et al.*, 1996) (Fig. 1.2).

Similar to other areas of the Cape Folded Belt, the soils are characterised by mostly nutrient-poor, shallow, grey, acidic, leached sands on mountain summits and upper slopes. These are normally well-drained, but winter-waterlogged soils occur on plateaus on Table Mountain and extensive low-lying flats on the southern Peninsula. The lower mountain slopes support marginally richer, sandstone-derived colluvium or, where the soil is underlain by granite or shale, heavier, more fertile soils. The Signal Hill-Lion's Head ridge, immediately north of Table Mountain, consists entirely of Malmesbury Shale and lacks a colluvial overburden. The soils are moderately fertile duplex form, characteristic of Renosterveld vegetation immediately to the north and east. 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.

Climate

The Cape Peninsula exhibits extreme climatic diversity (Fig. 1.3) owing to the influences of both east and west coasts and extreme topography. Winter rainfall from frontal depressions, originating from circumpolar westerlies, and the prevalence in summer of dry subtropical anticyclones dominate the mediterranean-type climate of the area (cool, wet winters, hot dry summers) (Tinley and Heydon, 1980; Preston-Whyte and Tyson, 1988). Thus, although most of the rain falls during the winter months, up to 25% of the Cape Peninsula's rain falls in summer, mainly associated with post-frontal conditions when the riding high pressure cells advect moist air from the south and south-east. Rainfall patterns are further modified by the orographic effects precipitation creating steep rainfall

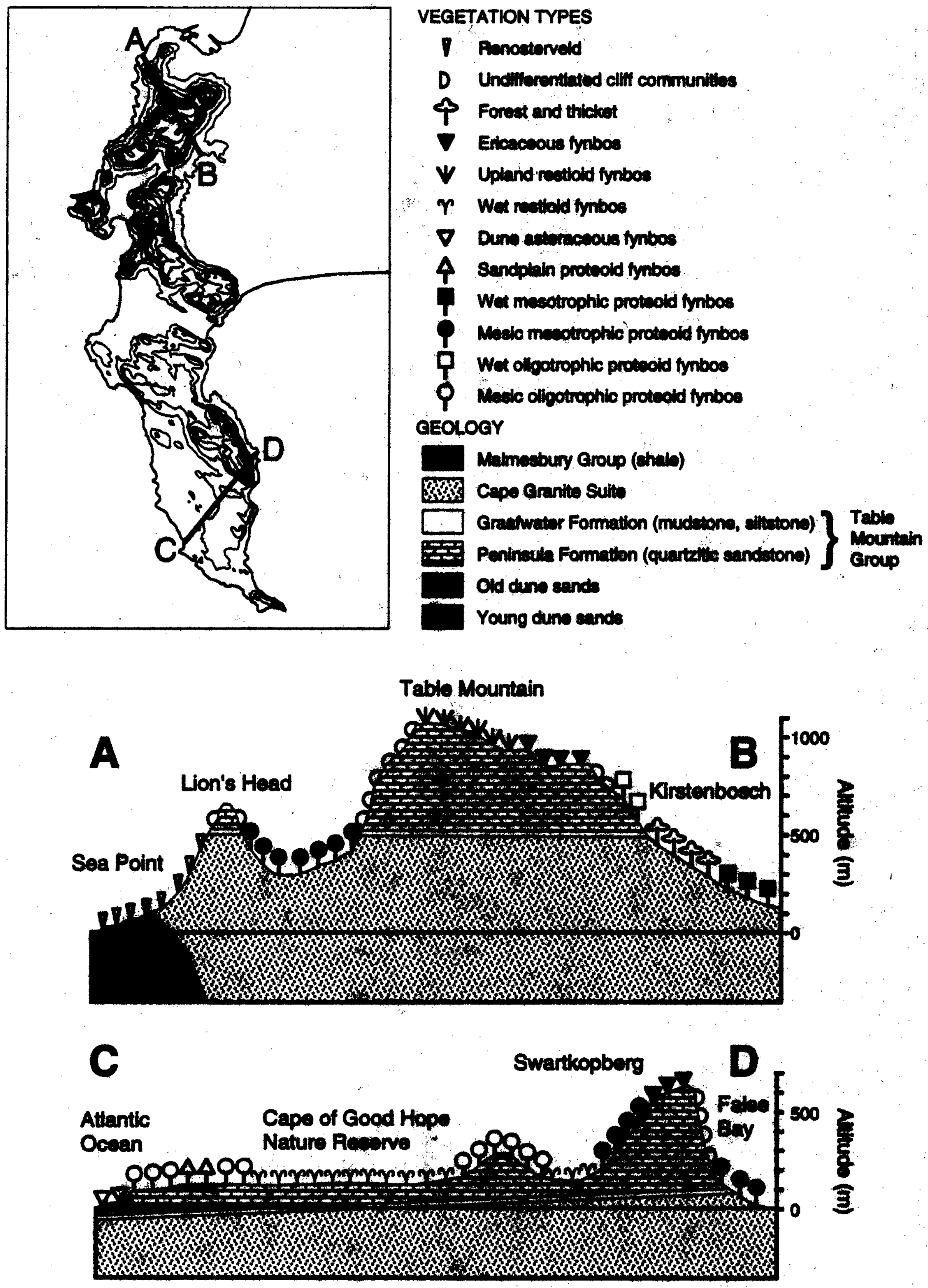


Figure 1.2 Transects across the Cape Peninsula showing the relationship between vegetation-type and geology, altitude and slope/aspect combinations.

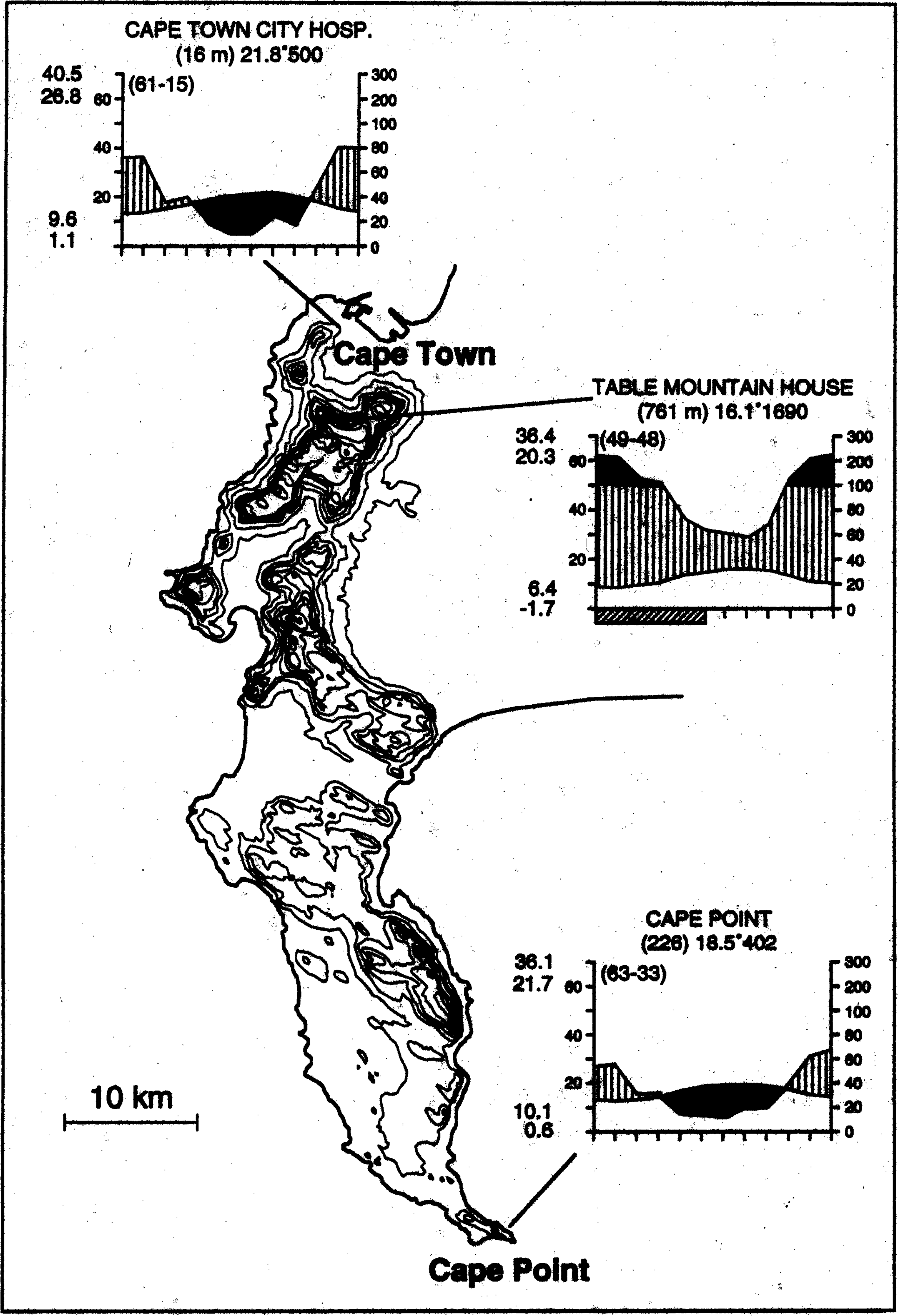


Figure 1.3 Topography and climate of the Cape Peninsula. Contours are at 100 m intervals.

gradients across the Cape Peninsula. For example, the top of Table Mountain receives 2270 mm y^{-1} whereas the annual rainfall at Cape Point is only 402 mm. The steep west-east rainfall gradient, especially across Table Mountain is demonstrated by Camps Bay receiving 618 mm y^{-1} and Kirstenbosch 1413 mm y^{-1}. These gradients may be even steeper than the rainfall data suggest, owing to the further contribution of cloud and mist, particularly at altitudes above 600 m (Marloth, 1905), both in winter, as a result of frontal systems, and in summer due to the predominant persistent south-easterly winds. Under such conditions, mist trapping by some fynbos species substantially elevates the effective total precipitation by to up to 10% (Marloth, 1903, 1905; Moll and Romoff, 1983; Snow, 1985).

Spatial and temporal variations of temperature are not pronounced on the Cape Peninsula, owing to the ameliorating influence of the ocean. 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 maximum temperatures vary between 18°C and 20°C with maximum and minimum temperature range only varying between 6°C at Cape Point and 10°C on Table Mountain.

A more distinctive feature of the Cape Peninsula's climate is the wind (Table 1.1). In winter, the cyclonic conditions produce a predominance of north-westerlies, associated with cold fronts, tending toward gale force with means over 30 km h^{-1} (Cape Point). During summer, the pattern is reversed with southerly and south-easterly winds as a result of high pressure ridging off the southern South African coast, with means ranging from 20 km h^{-1} (Cape Flats) to 40 km hr^{-1} (Cape Point) (Preston-Whyte and Tyson, 1988). These generalised patterns are further complicated by the effects of topography, and sea

Table 1.1 Frequency and mean speed of predominant winds for two stations on the Cape Peninsula for the year 1991 (Anon., 1992).

	SE		S		NW	
	freq.	mean speed km.h^{-1}	freq.	mean speed km.h^{-1}	freq.	mean speed km.h^{-1}
International Airport[1]	2%	10.8	34%	21.6	10%	18.0
Cape Point	19%	43.2	24%	21.6	18%	28.8

1 Airport is located on the Cape Flats approximately 12 km east of Kirstenbosch (Fig. 1.1).

and land temperature differences which result in wide variations in both wind speed and direction throughout the area.

Flora

The Cape Floristic Region is one of the world's "hotspots" of diversity and endemism (Goldblatt 1978; Takhtajan, 1986; Myers, 1990; Cowling *et al.*, 1992). The Cape Peninsula ranks as the foremost concentration of plant species in this region: 2285 species in 471 km^2 (Trinder-Smith, 1996a). The vegetation of some parts of the Cape Peninsula has previously been described: Cape of Good Hope Nature Reserve (Taylor, 1969,); Table Mountain; (Adamson, 1927; Glyphis *et al.*, 1978; Laider *et al.*, 1978); Orange Kloof (McKenzie *et al.*, 1977), Table Mountain forests (Campbell and Moll, 1977). However, only the Cape of Good Hope Nature Reserve (Taylor, 1969) and Table Mountain (Moll and Campbell, 1976), had been mapped prior to the production of a comprehensive map of the area produced by Cowling *et al.* (1996) (Fig. 1.4). In this study the vegetation was categorised into 14 units, based on Campbell's (1986a) system of vegetation classification for the mountains of the fynbos biome.

The Cape Peninsula falls within the Cape Floristic Region (Bond and Goldblatt, 1984) where summer droughts infertile soils and periodic fire are the predominant ecological

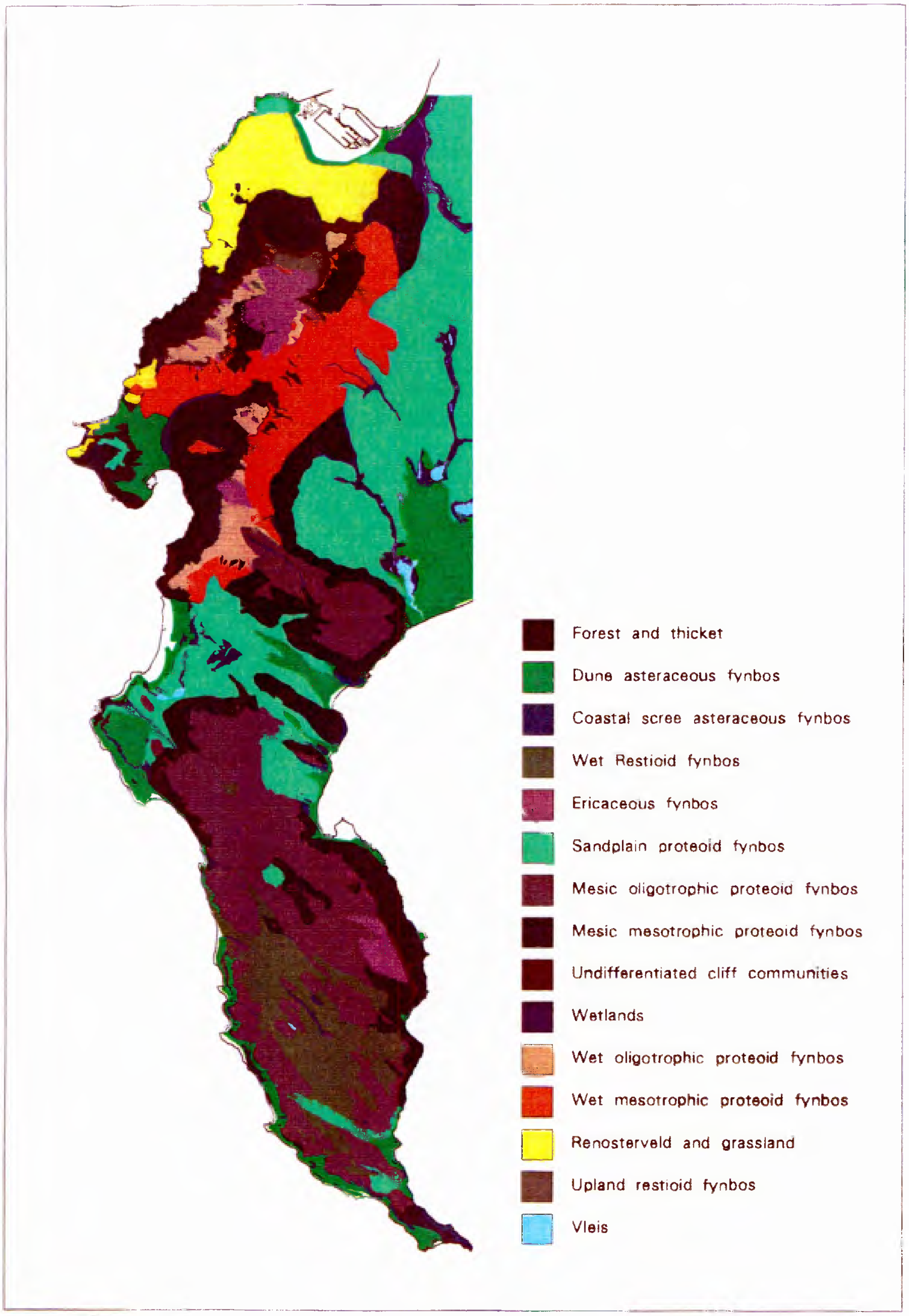


Figure 1.4 Major plant communities of the Cape Peninsula showing their areal extent prior to transformation (after Cowling *et al.*, 1996).

forces (Kruger, 1979; Cowling *et al.*, 1996). It is predominated by Fynbos Shrublands (Campbell, 1986a) (92% of the area), characterized by proteoid (large leaved, overstorey shrubs in the Proteaceae), ericoid (small leaves with rolled margins) and restioid (aphyllous gramnoids made up of Restionaceae and Cyperaceae) components. Renosterveld and associated grasslands, a fire-prone shrubland dominated by ericoid shrubs in the Asteraceae and grasses (Poaceae), covers 5% of the Cape Peninsula, and Forest and Thicket (3%), consisting of broad-leaved, evergreen shrubs and trees with strong Afromontane and subtropical thicket elements, make up the remainder of the area (Cowling and Holmes, 1992a).

Table 1.2. describes the most common species, structural characteristics and a summary of the environmental correlates for each vegetation type. The distribution of each vegetation type on the Cape Peninsula (Fig. 1.4), largely reflects variation in environmental factors (e.g. soil fertility and drainage, geology, altitude and the slope-aspect combination (or energy regime)) (Table 1.2). There now follows a brief overview of the major vegetation patterns on the Cape Peninsula.

The Cape Peninsula is dominated in the north by Table Mountain, a 1000 m plateau steep sided on the north, east and west slopes, but sloping more gently to the south. This massif provides a spectrum of habitats, ranging from the hot, dry slopes mixed proteoid communities of the Front Table and Camps Bay, to seasonally wet, ericaceous (i.e. taxa within the Ericaceae) and restioid vegetation on the summit, to the wetter, cooler forested slopes of Orange Kloof and Kirstenbosch. Further south, the more rounded mountains from Constantiaberg to Swartkopsberg, plunging steeply into the Atlantic Ocean and False Bay respectively, support a variety of proteoid fynbos types, directly reflecting the

Table 1.2 Characterization of the major vegetation types of the Cape Peninsula. Modified from R.M. Cowling *et al.* (1996).

Vegetation type	Structural characteristics[1]	Common species	Environment
Fynbos types			
Dune asteraceous fynbos	Low ericoid shrubland	*Metalasia muricata, Euclea racemosa, Rhus laevigata, Rhus glauca, Olea exasperata, Passerina vulgaris, Ischyrolepis eleocharis, Phylica ericoides, Passerina paleacea, Kedrostis nana.*	Recent, calcareous, coastal dune sands; MAR = 678 mm; mean slope = 17.0°; mean aspect = S
Wet restioid fynbos	Low restioid herbland	*Ischyrolepis cincinnata, Elegia stipularis, Ischyrolepis capensis, Tetraria cuspidata, Struthiola ciliata, Erica imbricata, Thamnocortus lucens, Pentaschistis colorata, Leucadendron laureolum, Tetraria microstachys.*	Shallow, seasonally waterlogged sands on sandstone at low altitudes; MAR = 634 mm; mean slope = 13°; mean aspect = WSW
Upland restioid fynbos	Low restioid herbland	*Chondropetalum ebracteatum, Restio bifidus, Thamnochortus nutans, Penaea mucronata, Erica hispidula, Cliffortia ruscifolia, Ursinia nudicaulis, Chondropetalum mucronatum, Anthospermum aethiopicum.*	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	*Thamnochortus erectus, Rhus glauca, Rhus laevigata, Leucadendron coniferum, Euclea racemosa, Eriocephalus africanus, Cineraria geifolia, Carpobrotus edulis, Ischyrolepis eleocharis, Metalasia muricata.*	Old marine (deep and well-drained) sands, occasionally on calcrete; MAR = 804 mm; mean slope = 16°; mean aspect = S
Mesic oligotrophic proteoid fynbos	Medium-height proteoid shrubland with a low ericoid and restioid understorey	*Leucadendron laureolum, Ischyrolepis cincinnata, Tarchonanthus camphoratus, Elegia stipularis, Saltera sarcocolla, Corymbium africana, Erica corifolia, Thamnochortus nutans, Elytropappus scaber, Cryptadenia grandiflora.*	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, Elytropappus scaber, Protea lepidocarpodendron, Leucadendron salignum, Leucadendron xanthoconus, Cliffortia falcata, Cliffortia stricta, Phylica stipularis, Phylica imberbis.*	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	*Elegia racemosa, Penaea mucronata, Leucadendron xanthoconus, Anthospermum galioides, Erica hispidula, Aristea macrocarpa, Helichrysum cymosum, Bobartia gladiata, Protea cynaroides, Erica plukenetii.*	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, Pteridium aquilinum, Rhus lucida, Widdringtonia nodiflora, Stoebe cinerea, Aristea macrocarpa, Anthospermum aethiopicum, Ficinia filiformis, Maytenus oleoides.*	Mainly deep, sandy loams associated with colluvium or granites on lower mountain slopes; MAR = 1136 mm; mean slope = 30°; mean aspect = SSE
Ericaceous fynbos$^{\text{Silvermine}}$	Low ericaceous and restioid shrubland	*Thamnochortus lucens, Hypodiscus aristatus, Selago dregei, Sympieza labialis, Erica corifolia, Stylapteris fruticulosus, Elytropappus scaber, Watsonia tabularis, Erica phylicifolia, Staberoha distachyos.*	Shallow, leached, organic-rich sands at high altitude subject to intermittent condensation from orographic cloud in summer; MAR^2 = 1910 mm; mean slope^2 = 19°; mean aspect^2 = NNW
Ericaceous fynbos$^{\text{Swartkopsberg}}$	Low ericaceous and restioid shrubland	*Leucadendron xanthoconus, Thamnochortus obtusus, Blaeria ericoides, Phylica imberbis, Thamnochortus fruticosus, Erica mammosa, Stoebe fusca, Restio perplexus, Protea lepidocarpodendron, Erica corifolia.*	Shallow, leached, organic-rich sands at high altitude subject to intermittent condensation from orographic cloud in summer; MAR^2 = 9820 mm; mean slope^2 = 19°; mean aspect^2 = SW
Ericaceous fynbos$^{\text{Table Mountain}}$	Low ericaceous and restioid shrubland	*Otholobium hirtum, Elegia vaginulata, Hypodiscus aristatus, Tetraria involucrata, Bobartia gladiata, Clutia polygonoides, Tetraria flexuosa, Ehrharta villosa, Pseudopentameris macrantha, Leucadendron xanthoconus.*	Shallow, leached, organic-rich sands at high altitude subject to intermittent condensation from orographic cloud in summer; MAR^2 = 1400 mm; mean slope^2 = 36°; mean aspect^2 = S
Undifferentiated cliff communities	Variable, mainly low and sparse ericoid shrubland	*Lampranthus falciformis, Felicia fruticosa subsp. fruticosa, Helichrysum cymosum, Cliffortia ruscifolia, Ficinia filiformis, Stoebe cinerea, Pelargonium cucullatum, Ischyrolepis guadichaudiana, Helichrysum panurifoli, Cullumia ciliaris.*	Steep to vertical sandstone cliffs; MAR = 1168; mean slope = 47°; mean aspect = SSW

Non fynbos types			
Forest	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, Secamone alpini, Olinia ventosa, Scutia myrtina.*	Colluvium or granite-derived soils on wet slopes or fire protected kloofs (ravines) and coastal margins; MAR = 992 mm; mean slope = 30°; mean aspect = SSW
Dune thicket	Medium-height broadleaf shrubland with ericoid understorey	*Euclea racemosa, Rhus glauca, Olea exasperata, Ischyrolepis eleocharis, Rhus laevigata, Phylica ericoides, Passerina paleacea, Kedrostis nana, Cineraria geifolia.*	Recent, calcareous, coastal dune sands; MAR = 703 mm; mean slope = 9.4°; mean aspect = SW
Renosterveld and grassland	Low grassland/low-medium ericoid and broad-leaved shrubland	*Chrysocoma coma-aurea, Rhus rosmarinifolia, Helichrysum patulum, Anthospermum spathulatum, Helichrysum cymosum, Salvia africana-lutea, Hyparrhenia hirta, Mohria caffrorum, Cheilanthes hastata, Merxmuellera stricta.*	Sandy loams on clay subsoil, shale or granite-derived; MAR = 826 mm; mean slope = 24°; mean aspect = SW

1 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 Proteaceae);
Restioid = wiry, aphyllous and evergreen gramnoids belonging largely to the Restionaceae.

2 Data taken as mean values from interpolated plot values for MAR and actual values of slope and aspect.

nutrient status of the underlying soil (Adamson, 1927; Taylor, 1969). South of Table Mountain, only in fire-protected kloofs and on the western colluvial slopes of Constantiaberg do the forest species replace fynbos (Campbell and Moll, 1977). Forest elements also persist immediately adjacent to sea where the combination of more alkaline soils and reduced fire frequency, allow establishment of a narrow, broken belt of wind-pruned thickets. Where this coastal band widens at valley mouths (e.g. Fish Hoek-Noordhoek), or on more extensive level sites, particularly in the Cape of Good Hope Reserve, then the thickets form a mosaic with dune asteraceous fynbos species (Taylor, 1969). Where the landscape forms level plateau then seasonally fluctuating water table allows extensive restioid and ericoid elements to dominate either at altitude (Table Mountain, Vlaakenberg) (Glyphis *et al.*, 1978), or low lying areas in the reserve at Cape Point (Taylor, 1969). Seepage sites and the boundaries of more permanent wetlands harbour their own selection of restionaceae, sedges and a few structurally-prominent tall fynbos shrubs (Campbell, 1986a; Taylor, 1969).

Database

Data for all the analyses in this thesis were compiled from 835 phytosociological plots sampled throughout the Cape Peninsula (Fig. 1.5). Sources included published studies (Campbell and Moll, 1977; McKenzie *et al.*, 1977; Glyphis *et al.*, 1978; Laider *et al.*, 1978; Joubert and Moll, 1992) as well as unpublished phytosociological data of H.C. Taylor, D.J. Jeffery and N. Wilson, and R.M. Cowling and M.T. Simmons. With the exception of the Cape of Good Hope Nature Reserve, where plot location was based on a uniform grid, plots were neither uniformly nor randomly sampled. Instead, sample areas were located somewhat haphazardly, as determined by previous studies, across the Cape Peninsula. Within each sample area efforts were made to sample the full range of habitats and communities (e.g. McKenzie *et al.*, 1977; Glyphis *et al.*, 1978). The strategy for additional sampling of a further 328 plots, was designed to fill in gaps in the coverage. Nonetheless, the distribution of the sites was markedly clumped (Fig. 1.5).

The size of the plots varied from 25 m^2 to 100 m^2 which largely reflected the structural criteria (e.g. height and density of vegetation). In order to include all plot data in analyses, it was assumed that the scale of plot size employed in each case was representative of both community structure and local richness. This approach was justified by considering a vegetation community to be a group of interacting species (Magurran, 1988). Consequently, an increased plot size was necessary to accommodate the larger structural nature of each community. Thus, 177 of the forest and thicket (FOR) plots were 100 m^2; the remainder were 50 m^2. 518 of the fynbos plots were 50 m^2, and 86 plots, which were 25 m^2, consisted entirely of low-stature ericaceous fynbos and upland restioid fynbos. Most of the renonsterveld plots were 100 m^2 ($n = 54$) and this artificially inflated species diversity of this vegetation type (see Chapter 3).

To avoid sampling errors due to deciduous habit of many plant species, only perennially identifiable species were recorded. Thus, many seasonally active geophytes and all annuals were excluded. However, annuals form a small component of Cape Peninsula's flora (Bond and Goldblatt, 1984). The resulting data base included 833 species which represents 36.5% of the Cape Peninsula's flora.

Following standard techniques, species abundance data were for the most part, were recorded following the Braun-Blanquet scale (Mueller-Dombois and Ellenberg, 1974; Werger, 1974). For the analyses in this study, a single representative numerical value (the

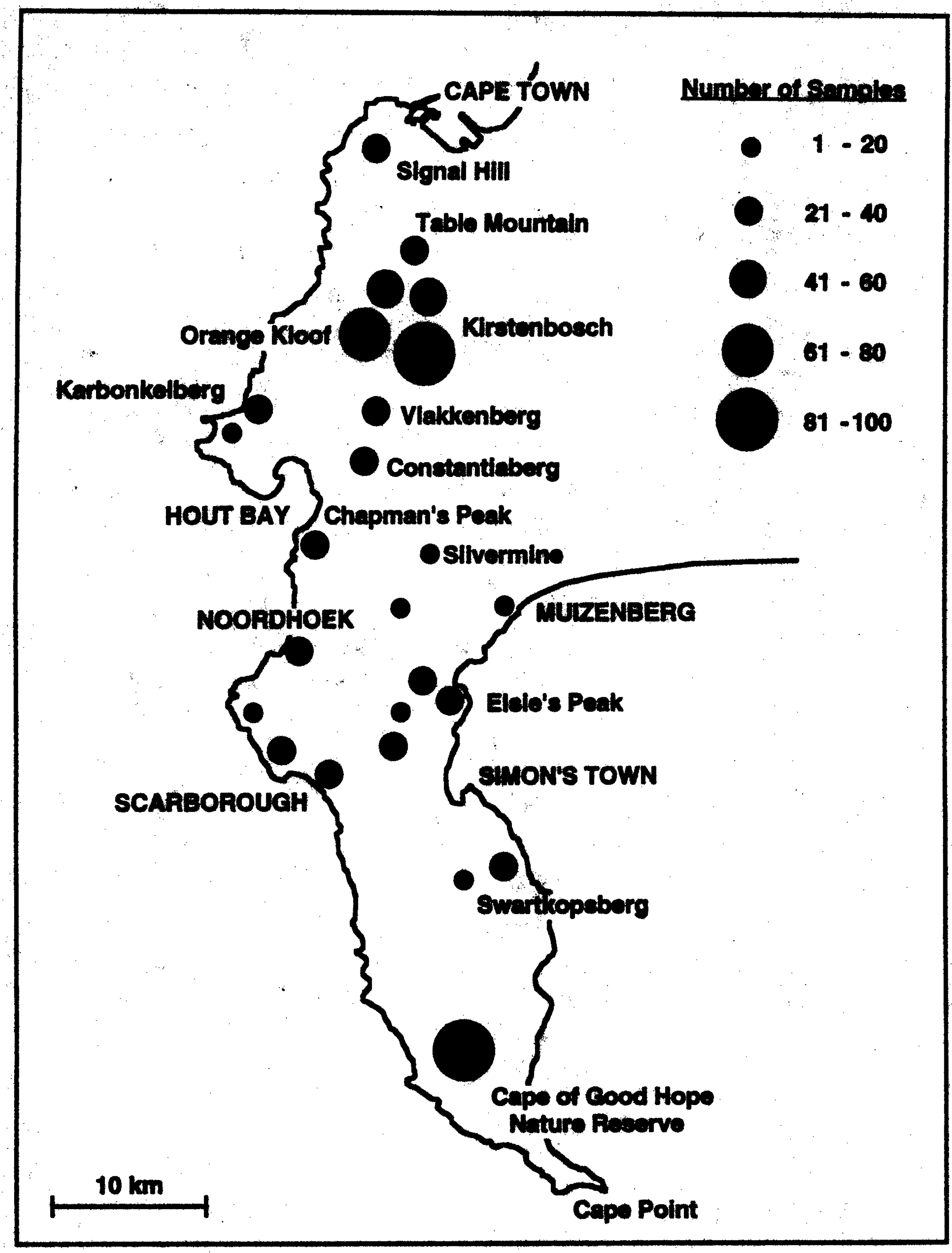


Figure 1.5 Distribution of 835 sample plots on the Cape Peninsula used in this study.

mid point of the class range) for each cover-abundance class was calculated as follows: 5 = 88%; 4 = 63%; 3 = 38%; 2 = 15%; 1 = 3%; + = 0.1%. Explanatory variables used in this analysis include measures of site favourableness and productivity such as elevation (a surrogate for mean annual temperature), annual rainfall, solar radiation, soil fertility and soil drainage. The measures used and data sources are shown in Table 1.3.

Table 1.3 Explanatory variables used in analyses.

Variable	Measure and source
Elevation (ALT)	Meters above sea level read from 1:50 000 topographical map (3318CD, 3418AB and 3418AD).
Average annual rainfall (RAI)	Millimetres. Interpolated from isohyets from 1:250 000 average annual rainfall map (3318).
Solar load (RAD)	Joules cm^{-1} day^{-1}. Annual solar energy reaching the ground corrected for latitude, slope and aspect of sample site. Calculated using algorithm derived by Swift (1976).
Soil fertility index (FER)	A crude index of decreasing fertility from 1 to 4 where 1 = granitic colluvium or shale derived soils; 2 = Plio-Pleistocene coastal sands; 3 = recent dune sands or sandstone derived colluvium soils; 4 = leached sands derived from sandstone.
Rock Cover (ROC)	Proportional cover of rock in each plot, expressed as a percentage.
Soil moisture index (DRA)	1 = poorly drained; 2 = moderately drained; 3 = well drained.

Thesis layout

This study set out to discuss patterns of plant species distribution, in such a way that would aid management and conservation of the Cape Peninsula. Therefore, this thesis is divided into three parts. For each chapter, a detailed rationale is given in the introduction, and specific implications for management are reviewed in the discussion.

Chapter 2 describes the patterns of vegetation units on the Cape Peninsula and their environmental correlates using multivariate analysis derived from the analysis of the database. A comparison is made between the classification produced by Two-Way Analysis (TWA) and a much faster, simpler, descriptive system produced by mapping vegetation boundaries from orthophotos, and describing basic structural features and dominant species from field examination.

Why are there so many plant species on the Cape Peninsula? Chapter 3 examines this question by examining the patterns and determinants of species diversity. This is addressed by analyzing correlates of the separating diversity components: alpha diversity (number of species in a defined area or point); beta diversity (turnover of species across an environment gradient); gamma diversity (turnover of species in similar environmental conditions but different geographic locations). The patterns and environmental relationships of the exceptionally high plant biodiversity are discussed in terms of implications for management.

Most species are not common, it is the rarer species that contribute most to the diversity on the Cape Peninsula. However, rarity is a phenomenon poorly understood, and if the biodiversity of the region is to be preserved, then examination of patterns of distribution of rarer plants is essential. Consequently, the biological and habitat correlates of rare species are analyzed in Chapter 4. To investigate whether management strategies need to be adjusted specifically to incorporate rare species, comparisons are made between attributes and environmental determinants of rare and common plants.

Finally, an overview of the major findings of the thesis, as well criticisms of the methods used are provided in Chapter 5.

CHAPTER 2

Plant community classification and plant-environment relationships on the Cape Peninsula.

Introduction

An important implication of the high species richness of the Cape Floristic Region (Goldblatt, 1978; Cowling *et al.*, 1992) is the difficulty in resolving plant associations into meaningful, readily identifiable floristic groups (Campbell, 1986b). This is especially problematic in species-rich areas like the Cape Peninsula. Given the need for a user-friendly, classification of the regions vegetation for management purposes (Taylor, 1978; Kruger and Taylor, 1979; van Wilgen *et al.*, 1992), this study attempted to test and describe a simple method of categorization of the vegetation on the Cape Peninsula into simple, readily identifiable units based on both floristic composition and environmental variables. Ideally, the most useful classification system would be based on indicator species which only occur in that plant community, However, while this approach may work for the non-fynbos groups (i.e. forest and thicket and renosterveld), the high number of generalist and rare species in fynbos made this problematic.The floristic complexity of fynbos renders a system based on species composition alone, somewhat impractical due to a high degree of species 'noise', that is, a large proportion of rare species which obscures phytosociological boundaries (Bond, 1981; Campbell, 1986a, 1986b and elsewhere). Previously, Cape fynbos has been successfully classified using dominant species characteristics, ignoring the distribution of rare species, thereby avoiding problems posed by the phytosociological approach (Campbell, 1986b; Cowling *et al.*, 1988; Cowling and Holmes, 1992a). However, floristic classification of fynbos on a similar scale to this study were successfully carried by McDonald (1993a, b, c, 1995), and Taylor (1996), and on a smaller scale by Richards *et al.* (1995). McDonald *et al.* (1996) compared the two techniques and concluded that the structural approach, applicable for landscape management, works successfully at a broader scale of sampling, whereas smaller-scale floristic sampling, which obscures structural evaluation due to the high number of rare species, provides data for diversity analysis and studies of endemism. Taylor (1996) argues that although floristic and structural survey results coincide at the highest hierarchical level, it can be just as time consuming when lower (i.e. more detailed) orders of species data are collected. Nonetheless, Taylor (1996) views the two methods as complimentary, and suggests a simpler structural method may be easier to implement and interpret. Furthermore, detailed floristic description within fynbos can take several years (e.g. Taylor 1996; MacDonald 1993a,b,c) and although this method delivers important data which can be further analyzed, for example, as used in this thesis, it does not necessarily produce a simple, field vegetation classification or vegetation map. Therefore, in this study, classification and initial simple, rapid qualitative biodiversity assessment of plant communities based on both dominant species composition and habitat (Cowling *et al.*, 1996) was tested against conventional phytosociological analyses.

Although there have been several phytosociological surveys of a variety of areas scattered throughout the Cape Peninsula (Campbell and Moll, 1977; McKensie *et al.*, 1977; Glyphis *et al.*, 1978; Laider *et al.*, 1978; Joubert and Moll, 1992), there has been no previous attempt at an analysis of the region as a whole. The nature of fynbos has been a complex subject for traditional phytosociological analyses, not only due to floristic complexity, but also species physiognomy. Both may be a result of fire history rather than underlying environmental patterns (Bond, 1981; Cowling, 1987; Cowling *et al.*, 1988), although there have been studies within fynbos which have shown that certain edaphic factors can be directly related to plant community structure (Cowling and Holmes, 1992a) and species composition (Campbell, 1986a; McDonald, 1987; McDonald *et al.*, 1996; Richards, 1993; Richards *et al.*, 1995). However, while suites of plant species may appear to fall into certain groups, it has been previously difficult to floristically assemble these into predictable units which are aligned with environmental factors over large areas. This chapter attempted to answer the following questions:

1. What are the major floristically characterized vegetation units on the Cape Peninsula?
2. What is the relationship between this classification and that derived from a classification based on dominant species and broad environmental features (i.e. a rapid biodiversity assessment)?
3. What are the major environment gradients which determine the distribution of plant communities on the Cape Peninsula?

Methods

The study area includes embodies the Cape Peninsula delimited on its eastern edge by the urban areas arranged north-south along the lower eastern slopes of the northern

half of the mountains (Fig. 1.1). The area lies entirely within the Cape Floristic Region (Goldblatt, 1978) and the vegetation is mainly mountain fynbos (Taylor, 1978; Campbell, 1986a), but also includes limited areas of renosterveld and isolated regions of afromontane forest and coastal thicket (Campbell, 1986a).

The allocation of sites of the database (Chapter 1) was unevenly and non-randomly distributed throughout the Cape Peninsula but covered a variety of habitats. For reasons of ease of manipulation of a database of such dimensions, and to reduce phytosociological 'noise' produced by rarer species, those species which occurred seven times or less were excluded from the analyses, reducing the number of species to 473. Environmental variables comprised elevation (a surrogate for mean annual temperature), annual rainfall, solar radiation, soil fertility and soil drainage, as described in Chapter 1. Initial vegetation classification was produced using Two-Way Indicator Analysis (TWA) using TWINSPAN (Hill, 1979). Due to the dimension limits of the data array imposed by this computer programme, the three communities, forest and thicket (FOR), renosterveld (REN) and dune asteraceous fynbos (DUN), samples were processed separately. These vegetation classes were assessed to be the most significantly floristically different from the main body of the data as indicated by discriminant analysis. Even with these data removed there were significant restrictions placed on possible choices made during the sorting by the programme on account of the size of the database. This reduced the number of cover classes to two (0-10%, 10-100%). To avoid the problems of interpretation due to axis 'compression effect' and 'arch effect' phenomena produced by correspondence analysis and reciprocal averaging (Hill and Gauch, 1980; Gauch, 1982), Detrended Correspondence Analysis (DCA) (Hill, 1979) and Canonical Correspondence Analysis (CCA) (ter Braak, 1991) were used to derive community floral and environmental relationships between sites.

Cowling *et al.* (1996), categorised the vegetation of the Cape Peninsula into 14 units, suitable as management units, based on Campbell's (1986a) system of vegetation classification for the mountains of the fynbos biome. Community descriptions were derived from basic structural features and dominant species (Table 2.1). The community boundaries were mapped in the field from 1:10 000 orthophotos and the vegetation boundary data were captured in a Geographical Information System (ARC/INFO version 6.1.1). Initial vegetation classification of the data points (plots) was taken directly from this GIS database.

While fynbos is the most widespread (92% of the area) vegetation type on the Cape Peninsula, renosterveld shrublands (5%) and forest/thicket patches (3%), both commonly encountered in the Cape Floristic Region (Cowling and Holmes, 1992a), are also represented in the area (Cowling *et al.*, 1996). Description of each vegetation unit within fynbos type (Table 2.1) reflected both the dominant species and soil characteristics as determined by rainfall, aspect, drainage and soil nutrient status. Thus wet (WOP) and mesic (MOP) oligotrophic proteoid fynbos found on the nutrient poor sandstone-derived soils, are largely differentiated by a increase in rainfall or the north-south rainfall gradient across the Cape Peninsula. Wet (WMP) and mesic (MMP) mesotrophic fynbos occur on the more nutrient-rich clay soils or colluvial soils on the lower slopes of mountains. Similarly, level sites with high annual rainfall combined with sandy, leached, poorly

Table 2.1 Characterization of the major vegetation types of the Cape Peninsula after Cowling et al. (1996).

Vegetation type	Structural characteristics[1]	Environment
Fynbos types		
Dune asteraceous fynbos (DUN)	Low ericoid shrubland	Recent, calcareous, coastal dune sands
Coastal scree asteraceous fynbos (CSA)	Low-medium ericoid and broad-leaved shrubland	Sandstone scree coastal slopes, subject to strong, salt-laden onshore winds
Wet restioid fynbos (WRF)	Low restioid and ericoid herbland	Shallow, seasonally waterlogged sands on sandstone at low altitudes
Upland restioid fynbos (URF)	Low restioid herbland	Shallow, seasonally waterlogged sands on sandstone
Sandplain proteoid fynbos (SND)	Medium-height proteoid shrubland with a low ericoid and restioid understorey	Old marine (deep and well-drained) sands, occasionally on calcrete
Mesic oligotrophic proteoid fynbos (MOP)	Medium-height proteoid shrubland with a low ericoid and restioid understorey	Shallow, leached sands on sandstone
Mesic mesotrophic proteoid fynbos (MMP)	Medium-height proteoid shrubland with an ericoid understorey	Mainly deep, sandy loams associated with colluvium or granites on lower mountain slopes
Wet oligotrophic proteoid fynbos (WOP)	Medium-height proteoid shrubland with an ericaceous and restioid understorey	Shallow, leached sands on sandstone
Wet mesotrophic proteoid fynbos (WMP)	Medium-height proteoid shrubland with ericoid understorey	Mainly deep, sandy loams associated with colluvium or granites on lower mountain slopes
Ericaceous fynbos (ERI)	Low ericaceous and restioid shrubland	Shallow, leached, organic-rich sands at high altitude subject to intermittent condensation from orographic cloud in summer
Undifferentiated cliff communities (CLF)	Variable, mainly low and sparse ericoid shrubland	Steep to vertical sandstone cliffs
Non-fynbos types		
Forest and thicket (FOR)	Low-medium (thicket), or medium to tall (forests) closed-canopy, broad-leaved formation with a sparse understorey	Colluvium or granite-derived soils on wet slopes or fire protected kloofs (ravines) and coastal margins

Renosterveld and grassland (REN)	Low grassland/low-medium ericoid and broad-leaved shrubland	Sandy loams on clay subsoil, shale or granite-derived
Wetlands (WET)	Medium-height ericoid shrubland with a ericoid and restioid understorey	Seasonal seepage sites with shallow-medium depth sandy soils with high organic matter over sandstone bedrock
Vleis (VLE)	No data	Freshwater lake and vleis (small, shallow water bodies)

[1] 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 Proteaceae);
Restioid = wiry, aphyllous and evergreen gramnoids belonging largely to the Restionaceae.

drained soils, especially during winter, are characterised by a large restioid component at both high and low altitude, i.e. upland restioid fynbos (URF), ericaceous fynbos and wet restioid fynbos (WRF). Vegetation immediately adjacent to the coast tends to be on slightly richer, calcareous soils on recent (dune asteraceous fynbos (DUN)) or sand plain proteoid fynbos (SND) on older, weakly acidic, better developed sands.

Results

Two-way indicator species analysis

TWA identified a total of twelve units which corresponded well to those described by Cowling *et al.* (1996). However, two vegetation types did not emerge from the classification, namely, scree asteraceous fynbos which was under-represented in the database (only one plot), and wetland (seepage) sites which were also under-represented (seven plots) and incorporated in adjacent communities. Conversely, the analysis justified the subdivision of two vegetation types into five further groups (Appendix I) (Table 2.2). Overall, the comparison indicated a 72% similarity between the two classification methods (Table 2.3). The main differences which accounted for this discrepancy were twofold. Firstly, nearly half (54 plots) of the TWA dune asteraceous fynbos plots were previously classified as forest and thicket (FOR) due to the presence of broad-leaved thicket species (e.g. *Euclea racemosa, Sideroxylon inerme, Pterocelastrus tricuspidatus*). Secondly, few of undifferentiated cliff communities (CLF) resolved into a separate group (12 plots), the remainder were incorporated as sub-communities of adjacent vegetation, especially in wet oligotrophic proteoid fynbos. With these two groups of plots removed, the total percentage convergence in classification for all groups rose from 72% to 81% (Table 2.3). Wet restioid fynbos (WRF) exhibited the largest error with 78% of the incorrectly labelled plots previously classified as mesic oligotrophic proteoid fynbos (MOP). This can be

Table 2.2 Floristic characterization of the major vegetation types of the Cape Peninsula. Botanical nomenclature here and elsewhere in the text follows Arnold and de Wet (1993).

Vegetation type	Very common[1] characteristic species	Common[2] characteristic species	Uncommon[2] characteristic species	Structurally dominant species
Fynbos types				
Dune asteraceous fynbos	*Metalasia muricata*	none	*Euclea racemosa, Rhus laevigata, Rhus glauca, Olea exasperata, Passerina vulgaris, Ischyrolepis eleocharis, Phylica ericoides, Passerina paleacea, Kedrostis nana.*	*Ischyrolepis eleocharis, Metalasia muricata, Passerina paleacea, Cliffortia obcordata, Helichrysum litorale, Phylica ericoides, Euclea racemosa, Rhus glauca, Ifloga repens, Chrysanthemoides incana.*
Wet restioid fynbos	*Ischyrolepis cincinnata, Struthiola ciliata.*	*Elegia stipularis, Ischyrolepis capensis, Tetraria cuspidata, Leucadendron laureolum. Thamnochortus lucens*	*Erica imbricata, Pentaschistis colorata, Tetraria microstachys.*	*Leucadendron laureolum, Elegia neesii, Erica imbricata, Cliffortia subsetacea, Ischyrolepis cincinnata, Salixis axillaris, Scyphogyne muscosa, Restio bifidus, Metalasia muricata, Roella ciliata.*
Upland restioid fynbos	*Penaea mucronata, Anthospermum aethiopicum.*	*Restio bifidus, Thamnochortus nutans, Cliffortia ruscifolia, Tetraria cuspidata.*	*Chondropetalum ebracteatum, Erica hispidula, Ursinia nudicaulis, Chondropetalum mucronatum.*	*Restio bifidus, Berzelia lanuginosa, Chondropetalum ebracteatum, Erica hispidula, Anthochortus crinalis, Platycaulos compressus, Chondropetalum mucronatum, Osmitopsis astericoides, Cliffortia ruscifolia, Penea mucronata.*
Sand plain proteoid fynbos	*Metalasia muricata.*	none	*Thamnochortus erectus, Rhus glauca, Rhus laevigata, Leucadendron coniferum, Euclea racemosa, Eriocephalus africanus, Cineraria geifolia, Carpobrotus edulis, Ischyrolepis eleocharis,*	*Leucadendron coniferum, Thamnochortus erectus, Metalasia muricata, Thamnocortus obtusus, Sideroxylon inerme, Euclea racemosa, Passerina vulgaris, Eriocephalus africanus, Coleonema album, Rhus laevigata.*
Mesic oligotrophic proteoid fynbos	*Ischyrolepis cincinnata.*	*Leucadendron laureolum, Erica corifolia, Thamnochortus nutans, Elytropappus scaber, Elegia stipularis.*	*Tarchonanthus camphoratus, Saltera sarcocolla, Corymbium africana, Cryptadenia grandiflora.*	*Tarchonanthus camphoratus, Leucadendron laureolum, Ischyrolepis cincinnata, Saltera sarcocolla, Elegia stipularis, Thamnochortus nutans, Cliffortia falcata, Leucadendron xanthoconus, Ficinia bulbosa, Thesium virgatum.*

Mesic mesotrophic proteoid fynbos	*Erica plukenetii, Penaea mucronata, Leucadendron xanthoconus, Phylica imberbis.*	*Elytropappus scaber, Protea lepidocarpodendron, Leucadendron salignum, Cliffortia stricta, Phylica stipularis.*	*Cliffortia falcata.*	*Protea lepidocarpodendron, Leucadendron xanthoconus, Leucospermum conocarpodendron, Leucadendron salignum, Cliffortia stricta, Erica plukenetii, Elytropappus scaber, Masterseilla digitata, Protea coronata, Metalasia muricata.*
Wet oligotrophic proteoid fynbos	*Penaea mucronata, Leucadendron xanthoconus.*	*Elegia racemosa, Anthospermum galioides, Bobartia gladiata, Erica plukenetii.*	*Erica hispidula, Alciope tabularis, Protea cynaroides, Aristea macrocarpa, Helichrysum cymosum.*	*Leucadendron xanthoconus, Cliffortia odorata, Elegia racemosa, Restio perplexus, Erica hispidula, Phylica buxifolia, Elegia thyrsifera, Protea lepidocarpodendron, Pentameris macrocalycinia, Anthospermum galioides.*
Wet mesotrophic proteoid fynbos	*Anthospermum aethiopicum.*	*Myrsine africana, Rhus lucida.*	*Rhus tomentosa, Pteridium aquilinum, Widdringtonia nodiflora, Stoebe cinerea, Aristea macrocarpa, Otholobium fruticans, Maytenus oleoides.*	*Pteridium aquilinum, Erica hirtiflora, Protea nitida, Aristea macrocarpa, Passerina vulgaris, Rhus tomentosa, Stoebe cinerea, Restio triticeus, Podalyria calyptrata, Protea coronata.*
Ericaceous fynbos^{SM}	*Hypodiscus aristatus.*	*Thamnochortus lucens, Erica corifolia, Elytropappus scaber, Watsonia tabularis.*	*Selago dregei, Sympieza labialis, Stylapteris fruticulosus, Erica phylicifolia, Staberoha distachyos.*	*Selago dregei, Sympieza labialis, Scutia myrtina, Thamnochortus lucens, Hypodiscus aristatus, Syncarpha speciosissimum, Staberoha distachyos, Elytropappus scaber, Cryptadenia grandiflora, Pseudopentameris macrantha.*
Ericaceous fynbos^{SK}	*Leucadendron xanthoconus, Phylica imberbis.*	*Erica corifolia, Protea lepidocarpodendron.*	*Thamnochortus obtusus, Blaeria ericoides, Thamnochortus fruticosus, Erica mammosa, Stoebe fusca, Restio perplexus.*	*Blaeria ericoides, Leucadendron xanthoconus, Thamnochortus obtusus, Diastella divaricata, Psoralea aphylla, Thamnochortus fruticosus, Erica mammosa, Syncarpha vestita, Staberoha vaginata, Stoebe fusca.*
Ericaceous fynbos^{TM}	*Hypodiscus aristatus, Leucadendron xanthoconus.*	*Bobartia gladiata, Clutia polygonoides, Pseudopentameris macrantha.*	*Otholobium hirtum, Elegia vaginulata, Tetraria involucrata, Tetraria flexuosa, Ehrharta villosa.*	*Elegia vaginulata, Tetraria flexuosa, Berzelia lanuginosa, Hypodiscus aristatus, Otholobium hirtum, Tetraria involucrata, Chondropetalum ebracteatum, Leucadendron xanthoconus, Anthocortus crinalis, Chondropetalum hookeria.*

Undifferentiated cliff communities	none	*Cliffortia ruscifolia, Ficinia filiformis.*	*Helichrysum cymosum, Lampranthus falciformis, Felecia fruticosa subsp. fruticosa, Cullumia ciliaris, Stoebe cinerea, Helichrysum panurifoli, Pelargonium cucullatum, Ischyrolepis guadichaudiana.*	*Ehrharta ramosa subsp. aphylla, Psoralea aphylla, Ficinia trichodes, Felicia fruticosa subsp. fruticosa, Helichrysum cymosum, Stoebe cinerea, Ficnia filiformis, Ischyrolepis gaudichaudiana, Cliffortia odorata, Ficinia acuminata, Ficinia nigrescens.* .
Non fynbos types				
Forest	none	none	*Rapanea melanophloeos, Diospyros whyteana, Cassine peragua, Knowltonia capensis, Myrsiphyllum scandens, Kiggelaria africana, Olea capensis, Secamone alpini, Olinia ventosa, Scutia myrtina.*	*Cassine peragua, Olinia ventosa, Rapanea melanophloeos, Cunonia capensis, Diospyros whyteana, Aspalathus argyrella, Olea capensis, Olea europaea subsp. africana, Chionanthus foveolatus, Kiggelaria africana.*
Dune thicket	none	none	*Euclea racemosa, Rhus glauca, Olea exasperata, Ischyrolepis eleocharis, Rhus laevigata, Phylica ericoides, Passerina paleacea, Kedrostis nana, Cineraria geifolia.*	*Euclea racemosa, Sideroxylon inerme, Olea exasperata, Ischyrolepis eleocharis, Passerina paleacea, Metalasia muricata, Clifforta obcordata, Rhus glauca, Rhus laevigata, Cassine maritima.*
Renosterveld and grassland	none	none	*Chrysocoma coma-aurea, Rhus rosmarinifolia, Helichrysum patulum, Anthospermum spathulatum, Helichrysum cymosum, Salvia africana-lutea, Hyparrhenia hirta, Mohria caffrorum, Cheilanthes hastata, Merxmuellera stricta.*	*Rhus rosmarinifolia, Hyparrhenia hirta, Helichrysum patulum, Rhus laevigata, Rhus glauca, Olea exasperata, Chrysocoma coma-aurea, Helichrysum cymosum, Mohria caffrorum, Cheilanthes capensis.*

1 Very common = of ten most frequently species occurring in that vegetation type which occurs in at least 20% of all fynbos plots
2 Common = of ten most frequently species occurring in that vegetation type which occurs in at least 10% of all fynbos plots
3 Uncommon = of ten most frequently species occurring in that vegetation type which occurs in less than 10% of all fynbos plots

SM Silvermine (central Peninsula)
SK Swartkopsberg (south Peninsula)
TM Table Mountain (north Peninsula)

Table 2.3 Comparison of TWA vegetation classification with Cowlings *et al.*'s (1996) original structural classification system.

	Number plots	TWA plots incorrectly labelled[1]	% correct	Adjusted incorrectly labelled[2]	Final % correct
Dune asteraceous fynbos	108	56	48	2	98
Wet restioid fynbos	60	38	37	38	37
Upland restioid fynbos	57	21	63	20	65
Sand plain proteoid fynbos	21	3	86	3	86
Mesic oligotrophic proteoid fynbos	30	4	87	1	87
Mesic mesotrophic proteoid fynbos	112	54	52	51	54
Wet oligotrophic proteoid fynbos	39	26	33	15	62
Wet mesotrophic proteoid fynbos	35	14	60	13	63
Ericaceous fynbos	90	14	84	14	84
Undifferentiated cliff communities	12	1	92	1	92
Forest and thicket	215	0	100	0	100
Renosterveld and grassland	53	0	100	0	100
Total	832	253	72	161	81

1 Plots classified by TWA which were classified in a different vegetation type by Cowling *et al.* (1996)'s method.

2 Adjusted number of incorrectly labelled plots does not include undifferentiated cliff communities (CLF) and dune asteraceous plots reclassified as dune thicket

expected as these two fynbos types, which dominate the southern Peninsula (Fig. 1.4; Chapter 1), form a mosaic, where MOP is replaced by WRF on flatter slopes where drainage is impeded. Wet and mesic mesotrophic proteoid fynbos (WMP, MMP) and wet oligotrophic proteoid fynbos (WOP) had the next largest errors, including a large number of sites from other upland proteoid groups (i.e. MOP, WOP, MMP, WMP). It appears that the community boundaries of these four proteoid groups are the most difficult to separate, given the large suite of species common to all four groups (Table 2.1; Appendix

I). Ericaceous fynbos (ERI) matched the mapped classification well (84%), but due to the high gamma turnover within this vegetation type (Chapter 3), the TWA split this group further into three separate divisions corresponding to the three geographic areas where those plots were sampled (i.e. Silvermine, Swartkopsberg and Table Mountain). Upland restioid fynbos (URF) resolved reasonably well (65%) and was more floristically aligned with proteoid communities than to the other predominantly restioid group (WRF), similar to sand plain proteoid fynbos (SND).

Because of the 'noise' produced by a large number of moderately rare species in such a large data set, TWA revealed few, if any, differential species at the level of the defined vegetation units. With the absence of true indicators for each vegetation type, therefore, the ten most frequently occurring species within each type were divided into three groups. These compared species frequency with that of other fynbos plots i.e. very common (occurring in at least 20% of all fynbos plots), common (at least 10% of all fynbos plots) and uncommon (less than 10% of the plots) (Table 2.2). The suite of species may be unique, but for practical purposes it is the dominants that provide best visual description of the plant community in conjunction with habitat description (Table 2.4). Therefore, the structural dominants, those with the greatest cover abundance values were included as characteristic species.

Table 2.4 Mean values and standard errors for environmental variables for each vegetation type. Groups with the same superscripts are not significantly different at the 0.05 level (Tukey multiple range test).

	n	Altitude (m)	Radiation load (Joules cm^{-1} day^{-1})	Fertility[1]	Mean annual rainfall (mm)	Drainage[1]	Rock cover (%)	Slope (°)
		F=135.01 P<0.0001	F=12.11 P<0.0001		F=89.16 P<0.0001	.	F=12.32 P<0.0001	F=39.83 P<0.0001
Dune asteraceous fynbos	22	92.5±13.0^{ab}	2852.2±53.6^{bcd}	3	660±100^{ab}	3	11.5±3.0^{abcde}	14.2±2.6^{acd}
Wet restioid fynbos	62	99.0±6.7^{ab}	3015.1±19.0^{d}	4	670±100^{abc}	3	13.5±2.7^{abcdef}	3.3 0.7^{ab}
Upland restioid fynbos	56	900.4±36.9^{i}	2821.4±4.8^{bcd}	4	1420±400^{h}	2	22.5±3.2^{abcdefg}	7.4±1.1^{abc}
Sandplain proteoid fynbos	10	6.0±0.7^{a}	3030.1±15.2^{bcd}	2	600±0^{a}	2	0.0±0.0^{a}	1.0±0.0^{a}
Mesic oligotrophic proteoid fynbos	29	288.1±9.8^{cd}	3015.9±35.8^{bcd}	4	810±100^{abcde}	3	17.6±4.5^{abcdefg}	6.5±0.8^{abc}
Mesic mesotrophic proteoid fynbos	124	318.0±13.7^{def}	2782.9±53.7^{bc}	4	960±200^{f}	3	12.5±1.5^{abcdef}	21.6±1.6^{de}
Wet oligotrophic proteoid fynbos	49	635.6±32.3^{gh}	2792.9±82.4^{bcd}	4	1220±100^{g}	3	31.8±3.5^{dg}	30.7±2.8^{f}
Wet mesotrophic proteoid fynbos	34	458.1±45.0^{ef}	2933.6±48.7^{bcd}	3	1250±500^{g}	3	25.4±4.1^{adefg}	22.6±3.3^{def}
Ericaceous fynbos^{SM}	14	300.0±0.0^{cde}	3053.2±2.3^{bcd}	4	900±0^{abdef}	2	11.1±1.0^{abcd}	1.4±1.1^{a}
Ericaceous fynbos^{SK}	27	556.3±21.6^{fg}	2973.8±88.7^{bcd}	4	990±200^{f}	3	5.1±1.6^{ab}	25.8±2.7^{def}
Ericaceous fynbos^{TM}	46	725.6±12.7^{h}	2884.7±11.8^{bcd}	4	1360±200^{gh}	2	14.8±3.06^{abcdef}	5.0±0.4^{g}
Undifferentiated cliff communities	5	303.0±41.3^{bcde}	935.4±349.1^{a}	4	1020±100^{bdefg}	3	99.0±0.0^{h}	90±1.4^{d}
Forest	216	322.3±10.4^{def}	2764.4±29.8^{b}	2	1320±200^{gh}	3	27.8±32.1^{deg}	19.9±0.8^{d}
Dune thicket	88	117.5±12.3^{ab}	3013.5±53.6^{d}	3	700±100^{abcd}	3	8.6±1.9^{abc}	9.4±1.1^{abc}
Renosterveld and grassland	53	222.8±6.0^{c}	2976.6±69.1^{cd}	1	900±0^{ef}	3	20.3±1.4^{abcdefg}	27.0±0.7^{ef}

1 Mode taken for fertility and drainage categories
SM = Silvermine (central Peninsula); SK = Swartkopsberg (south Peninsula); TM = Table Mountain (north Peninsula)

Ordination

DCA showed consistency high eigenvalues across the first three axes, with the first axes accounting for most of the variance (Table 2.5). Clustering across the first three axes conformed to those plant communities as classified by TWA, but with a considerable degree of overlap (Fig. 2.1). Axis 1 is essentially a gradient of both fertility and rainfall, from restioid (URF, WRF) through proteoid (MMP, MOP, WMP, WOP) to non-fynbos communities on relatively nutrient-rich soils (FOR, REN). Axis 2 reflects an altitude gradient from low lying and coastal communities (DUN, WRF), to mountain-slope (WOP) and high plateau communities (URF, ERI). This pattern is largely repeated in the DCA plot of fynbos plots alone (Fig. 2.2) but with clearer separation of proteoid from non-proteoid components. The forest, renosterveld and dune DCA (Fig. 2.3) clusters forest (FOR) and renosterveld (REN) independently, but the dune asteraceous fynbos (DUN) demonstrates its affinity to the forest and thicket communities, owing to the strong incidence of thicket species.

Table 2.5 Eigenvalues and percentage variance explained by the first three axes for DCA and CCA for the complete and divided data set.

		DCA			CCA		
		Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Complete data	Eigenvalue	0.95	0.82	0.79	0.72	0.59	0.32
	% variance	25	24	0	28	23	13
Fynbos (excluding dune fynbos)	Eigenvalue	0.81	0.77	0.70	0.68	0.53	0.37
	% variance	18	12	0	25	19	14
Forest/renosterveld /dune fynbos	Eigenvalue	0.95	0.83	0.76	0.67	0.35	0.26
	% variance	31	3	0	33	17	13

Canonical correspondence analysis

There were several strong correlations between floristic variation and the environmental

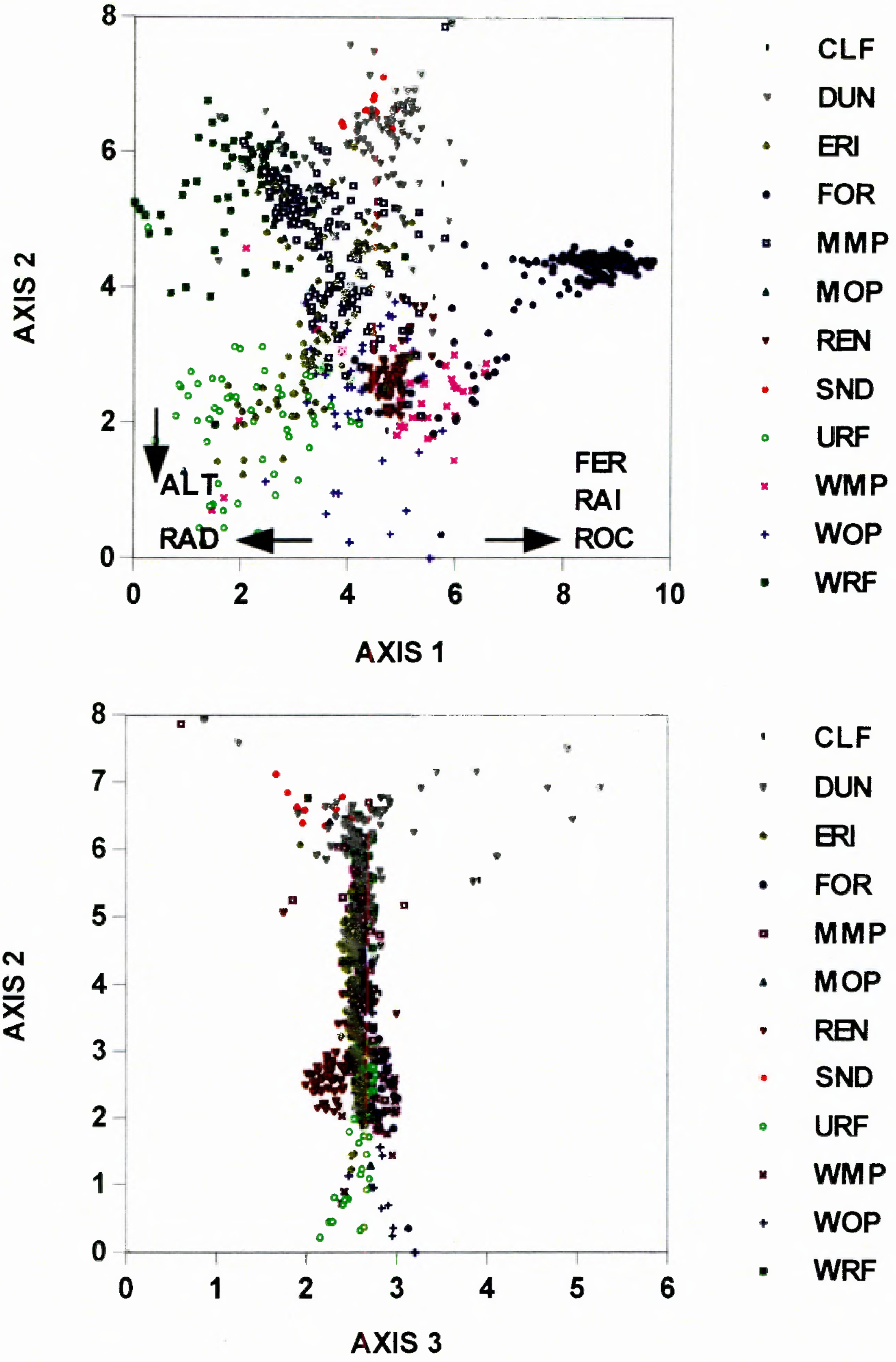
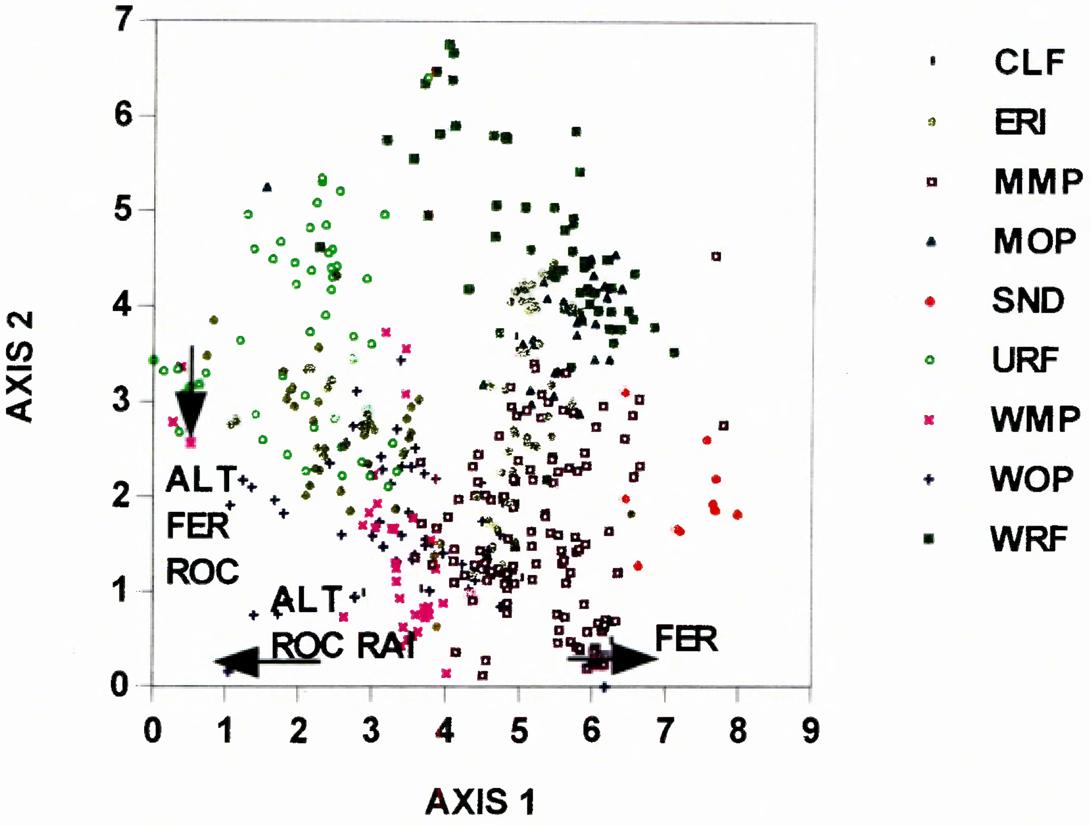


Figure 2.1 DCA ordination for the first three axes of the comlete data set. Arrows indicate direction of increasing magnitude of primary envronmental gradients. ALT = altitude; RAI = mean annual rainfall; RAD = solar load; FER = soil fertility; ROC = rock cover; DRA = soil drainage. For details see Table 1.3. Vegetation abbreviations Table 2.1.



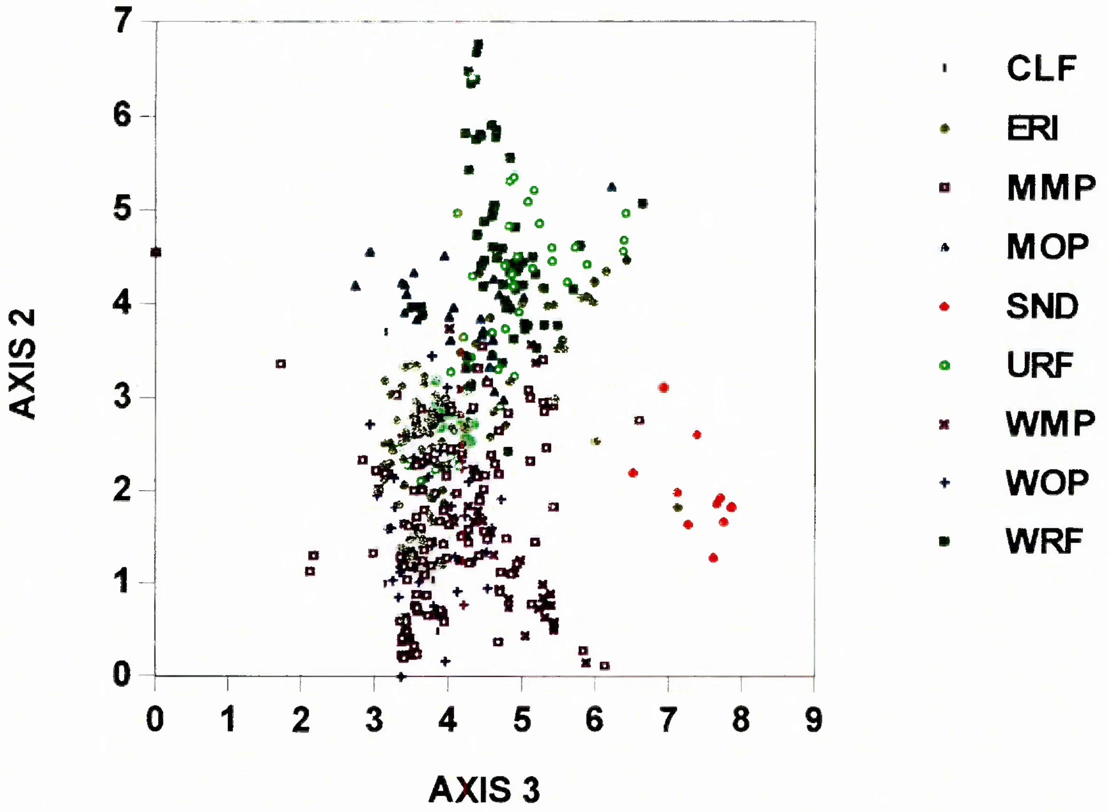
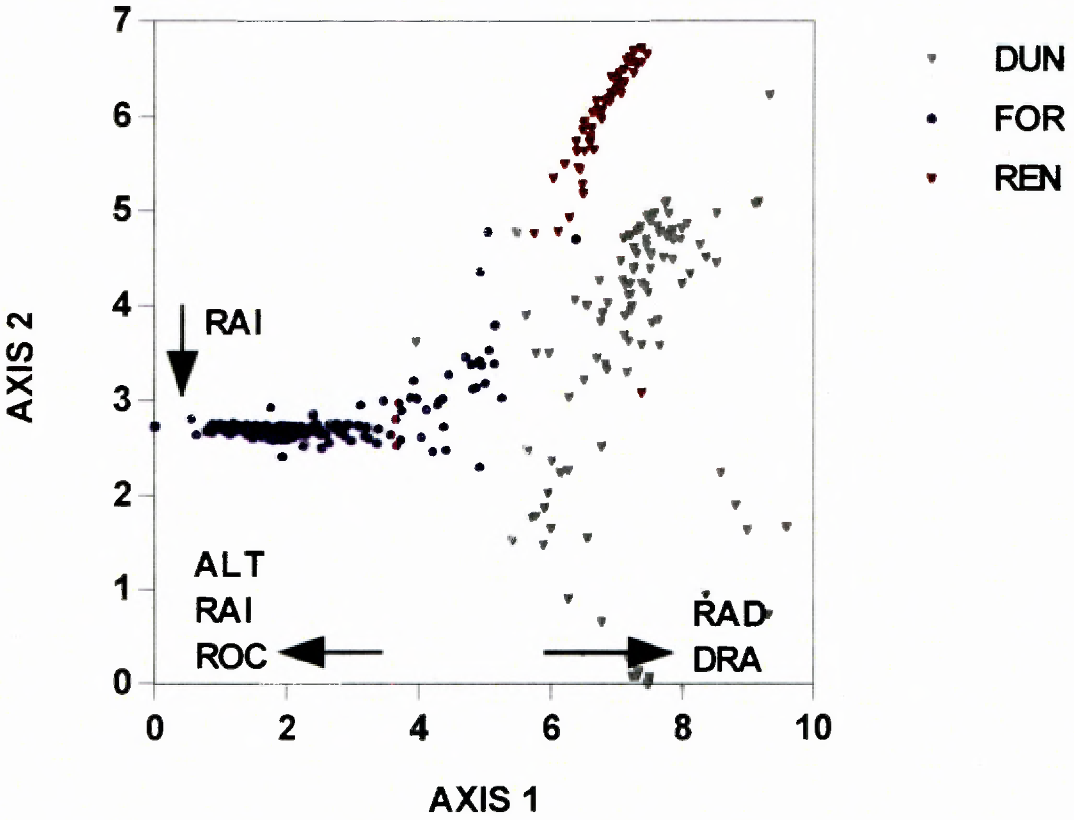


Figure 2.2 DCA ordination for the firest three axes of fynbos communities. Arrows indicate direction of increasing magnitude of primary environmental gradients. ALT = altitude; RAI = mean annual rainfall; RAD = solar load; FER = soil fertility; ROC = rock cover; DRA = soil drainage. For details see Table 1.3. Vegetation abbreviations Table 2.1.



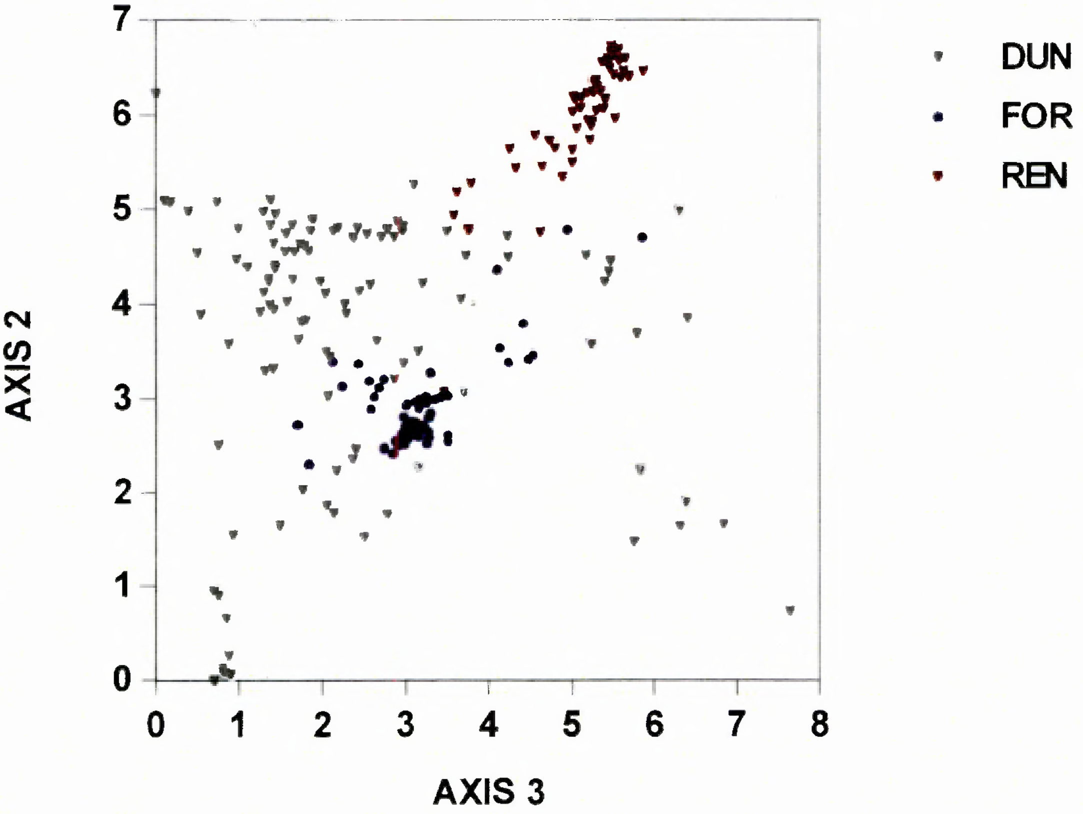


Figure 2.3 DCA ordination of the first three axes of forest/thicket, renosterveld and dune asteraceous communities. Arrows indicate direction of increasing magnitude of primary environmental gradients. ALT = altitude; RAI = mean annual rainfall; RAD = solar load; FER = soil fertility; ROC = rock cover; DRA = soil drainage. For details see Table 1.3. Vegetation abbreviations Table 2.1

variables for the first three axes of the CCA (Table 2.6). Axis 1 and axis 2 for the complete data set explained 28% and 23% of the variance respectively. The axis 1 eigenvalues (Table 2.5) and sum of all eigenvalues were significant ($p < 0.01$), calculated with Monte Carlo permutation tests for the CCAs of the complete data set, fynbos and non-fynbos sites. The highest canonical coefficients for the complete data set were exhibited by soil fertility (r=-0.72), rainfall (r=0.44) and rock cover (r=0.19) for axis 1, and altitude (r=0.93) and soil drainage (r=0.22) for axis two (Table 2.6) (Fig. 2.4). With the non-fynbos on soils with higher nutrient status and dune sites removed from the data set, altitude (r=0.66) and rainfall (r=0.37), both strongly correlated with each other, become the principle environmental components on axis 1 (Fig. 2.5). Despite the collinearity of these two variables, it is not the case that altitude is consistently a surrogate measure of mean annual rainfall. The steep rainfall gradient from north to south along the Cape Peninsula (Chapter 1) is somewhat independent of topography, especially in the southern region of the study area. These patterns largely concurred with those produced

Table 2.6 Eigenvalues and canonical coefficients of first three CCA axes for complete and divided data sets. (ASP = aspect; ALT = altitude; RAD = radiation load; FER = fertility index; RAI = mean annual rainfall; DRA = drainage index; ROC = % rock cover; SLO = slope).

	Complete data set			Fynbos (excluding dune fynbos)			Forest/renosterveld/dune fynbos		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
ASP	-0.09	0.00	-0.40	-0.03	-0.19	-0.32	-0.05	-0.31	0.52
ALT	-0.27	0.93	-0.73	0.66	-1.18	0.61	0.22	-0.77	0.27
RAD	-0.12	-0.03	-0.01	-0.01	-0.03	0.02	-0.20	-0.23	-0.38
FER	-0.72	-0.04	0.61	-0.04	-0.26	0.11	-0.45	0.42	0.63
RAI	0.44	0.07	0.99	0.37	1.14	-0.85	0.33	1.19	0.06
DRA	-0.07	-0.22	0.64	-0.11	0.31	0.56	-0.41	0.51	-0.17
ROC	0.19	-0.07	-0.05	0.03	0.26	0.46	0.10	-0.03	0.32
SLO	0.01	0.06	0.07	0.02	0.05	0.00	0.05	0.06	0.32

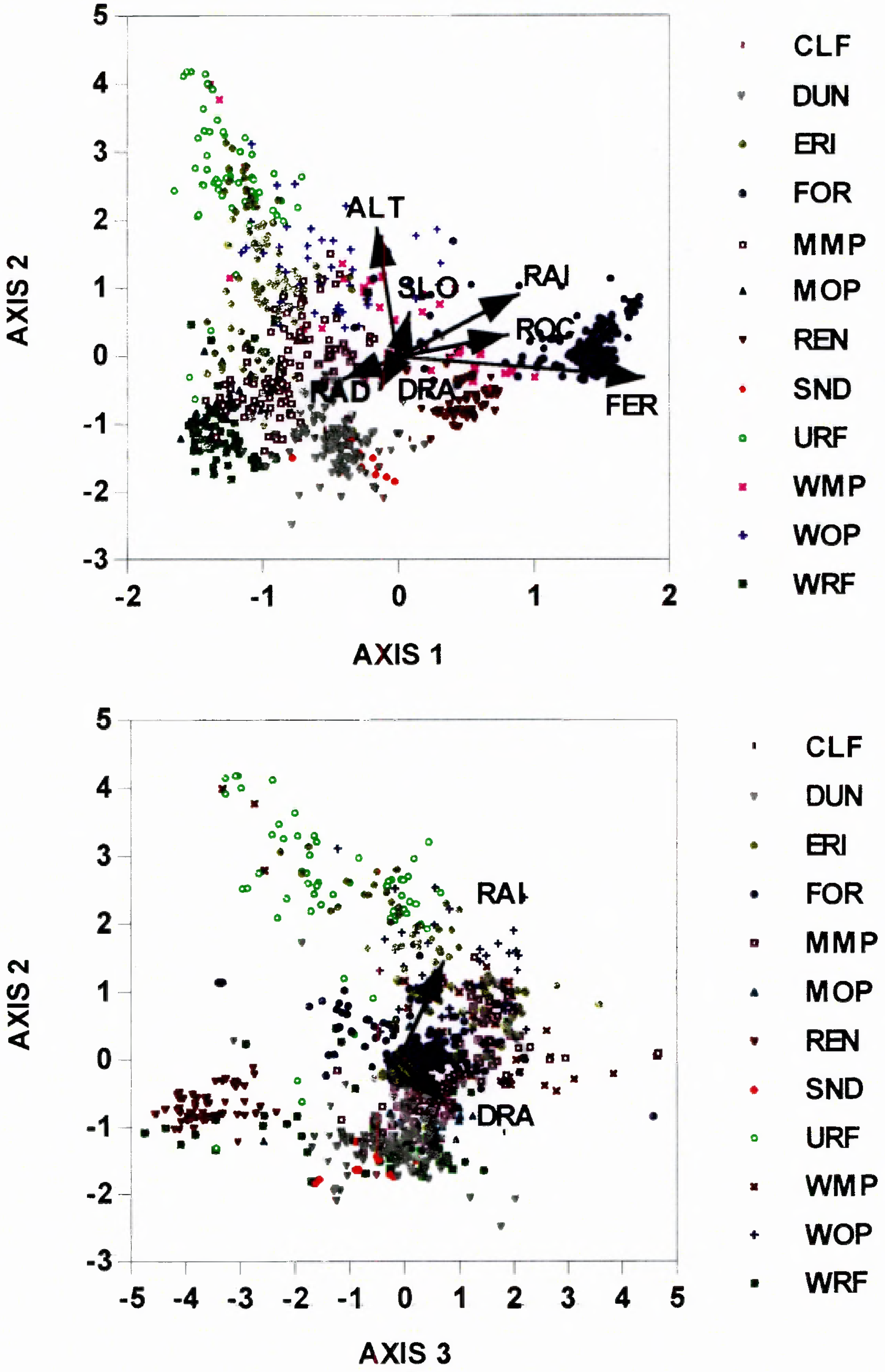
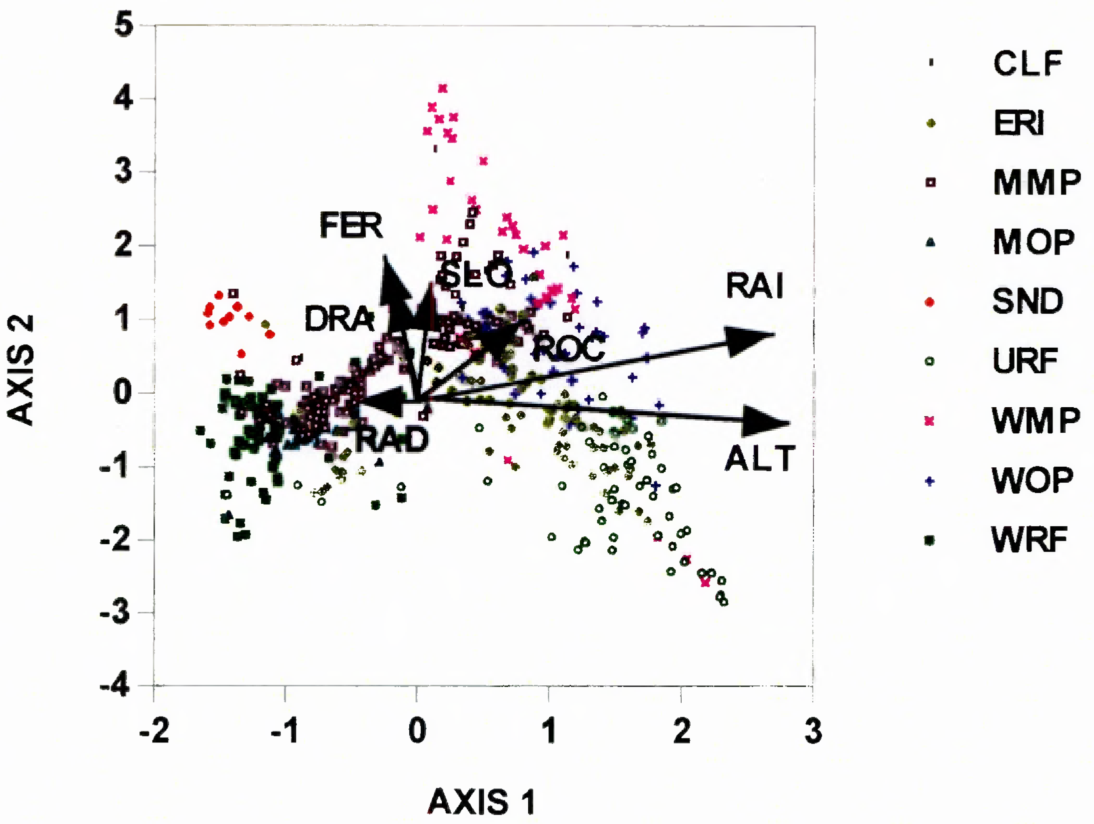


Figure 2.4 CCA ordination of the first three axes of the complete data set. Arrows indicate direction and relative magnitude of primary environmental gradients. ALT = altitude; RAI = mean annual rainfall; RAD = solar load; FER = soil fertility; ROC = rock cover; DRA = soil drainage. For details see Table 1.3. Vegetation abbreviations Table 2.1



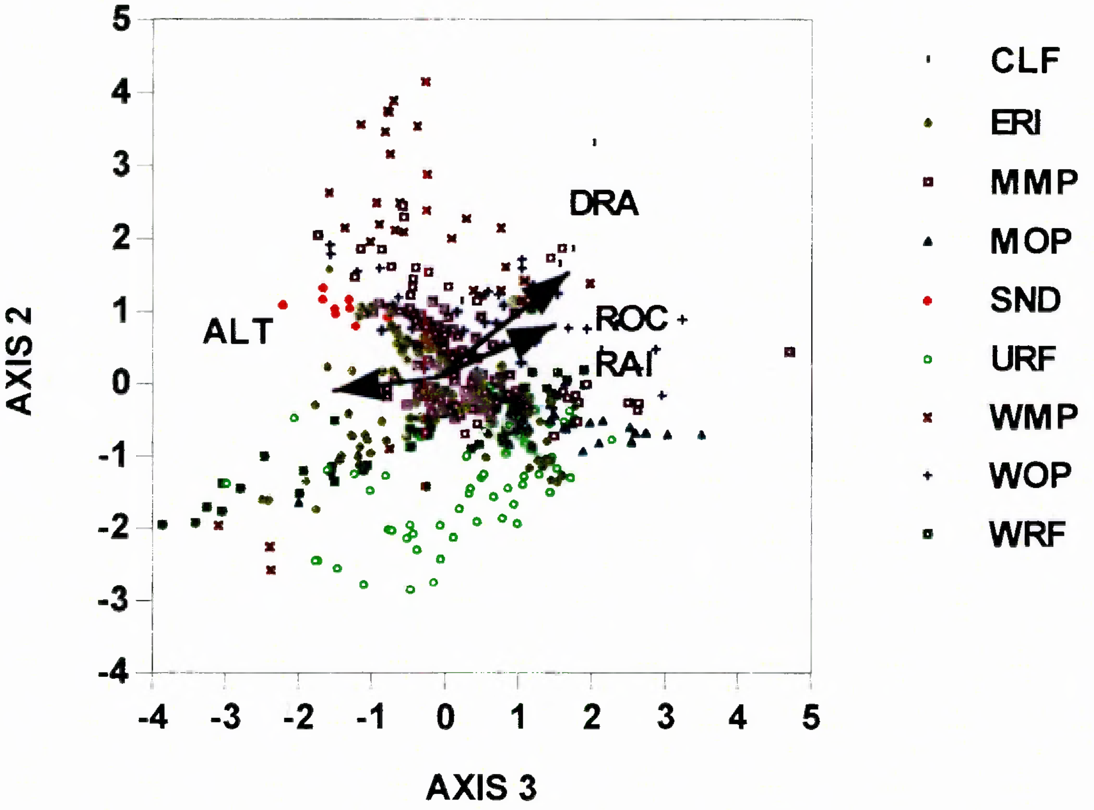


Figure 2.5 CCA ordination for the first three axes of fynbos communities. Arrows indicate direction and relative magnitude of primary environmental gradients. ALT = altitude; RAI = mean annual rainfall; RAD = solar load; FER = soil fertility; ROC = rock cover; DRA = soil drainage. For details see Table 1.3. Vegetation abbreviations Table 2.1.

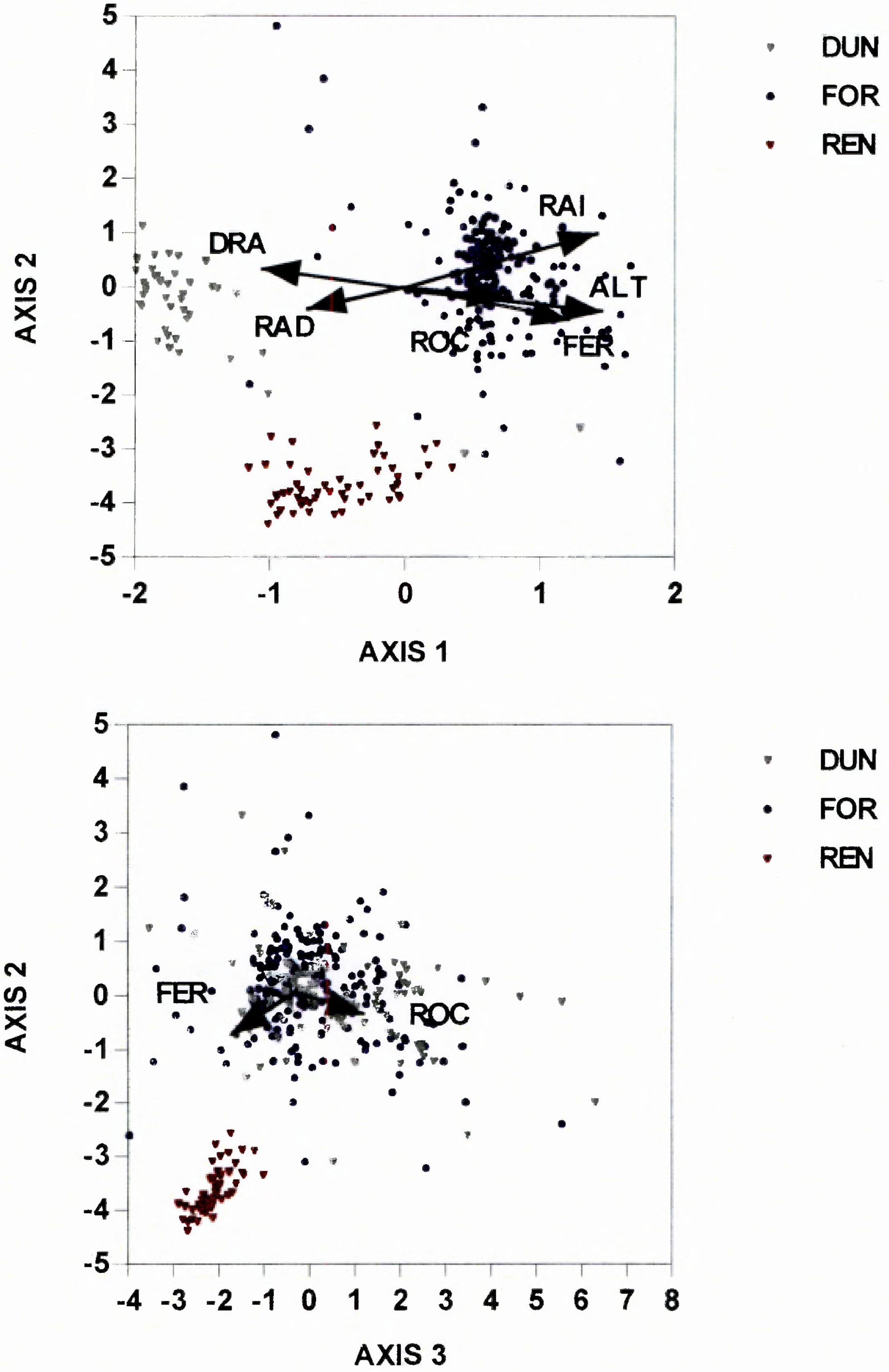


Figure 2.6 CCA ordination of the first three axes of forest/thicket, renosterveld and dune asteraceous communities. Arrows indicate direction and relative magnitude of environmental gradients. ALT = altitude; RAI = mean annual rainfall; RAD = solar load; FER = soil fertility; ROC = rock cover; DRA = soil drainage. For details see Table 1.3. Vegetation abbreviations Table 2.1.

Table 2.7 Correlation coefficients between all environmental variables.

	ALT	RAD	FER	RAI	DRA	ROC	SLO
SLO	0.28	-0.06	0.26	0.17	0.14	0.02	1.00
ROC	0.21	-0.10	0.05	0.22	0.08	1.00	
DRA[1]	-0.01	-0.08	0.02	-0.25	1.00		
RAI	0.62	-0.07	0.09	1.00			
FER[1]	-0.28	-0.01	1.00				
RAD	-0.16	1.00					
ALT	1.00						

1 Spearman rank coefficient

by the DCA. Across fynbos sites, the analysis produces a cluster of low altitude, low rainfall communities (WRF, SND) at one end of axis 1, with higher altitude communities (URF, ERI) at the other extreme. Other less significant environmental factors, such as rock cover (ROC) are indicated by lower canonical coefficients. However, the significance of these is difficult to discern due to the correlation with these and the other principle gradients (Table 2.7). For example, rock cover (ROC) and angle of slope (SLO) correlated positively with altitude.

Discussion

Vegetation classification

Mountain fynbos comprises a very complex mixture of species and habitats to the ecologist and description is inherently problematic (Campbell, 1986a). The traditional phytosociological approach to fynbos is both very time consuming and may not offer general explanation of pattern (Cowling *et al.*, 1988). Floristic classification produced from small (a few km^2) local studies on the Cape Peninsula (Campbell and Moll, 1977; McKensie *et al.*, 1977; Glyphis *et al.*, 1978; Laider *et al.*, 1978; Joubert and Moll, 1992) may have little predictive value for the rest of the area. This study has shown that description of one vegetation type may differ floristically from similar habitat within the same geographic area due to the high beta and gamma diversity (Chapter 3).

The classification method employed by Cowling *et al.* (1996), combining local knowledge of the relationships between flora and environment with vegetation unit boundaries as indicated from small-scaled (1:10000) aerial photographs, appears to be well-suited to describing the vegetation and has significant potential, both as a management tool and as a descriptive method. The classification conforms to Campbell's (1986b) system with a few refinements for this study area. Those species most common to each plot are by definition, not good phytosociological indicators. However, the suite of species combined with habitat description provides a reliable classification of fynbos (Table 1.2).

Vegetation environment relationships

This analysis demonstrated that despite the use of relatively simple measures of environmental variables, a considerable proportion of the variation in the communities can be explained. The distinction between fynbos and non-fynbos types has been explained by the contrast between the low soil nutrient status of sandy soils derived from quartzite sandstones (Cowling and Holmes, 1992a). As expected, both forest and renosterveld communities exhibited clear distinction from fynbos as indicated by both DCA and CCA, Apart from the significant floristic dissimilarity, this division is largely accounted by the underlying geological patterns with renosterveld on moderately nutrient-rich shale and granite soils, and forest on both granite soils and deeper, moister, fire protected sites in ravines (Manders, 1990; Cowling and Holmes, 1992a).

Coastal communities also exhibited large floristic differences from fynbos on higher altitude sites (Taylor, 1978). The thin coastal dune band is a mosaic of asteraceous and ericoid shrubs with dense, sometimes continuous patches of fire-resilient thicket. These thickets tend to establish due to the reduction of the probability of fire on the coastal margin.

Within fynbos, annual rainfall, altitude, and soil fertility emerged as the best predictors of community pattern. Higher altitude and annual rainfall separated upland ericaceous and restioid communities where the combination of higher winter precipitation and summer orographic mists contributes to high total moisture input. Although similar in structure (high-altitude, low ericaceous-restioid heathland), geographically disjunct ericaceous communities (ERI) differed both floristically and in relation to edaphic factors. Such high differences in species composition between similar, but geographically separate, communities is a distinctive feature of the Cape Peninsula and fynbos in general (Chapter 3).

The crudity of the nature of the soil fertility gradient used in this study may have limited explanatory value compared to detailed soil characteristics which have previously been invoked to explain patterns in fynbos (Richards *et al.*, 1995; McDonald *et al.*, 1996). However, the spread of floristically allied proteoid communities, between mesic (MMP, WMP, SND) on lower colluvial slopes and oligotrophic (MOP, WOP) on nutrient-leached soils, illustrates its strength as explanatory variable (Table 1.2).

The unexplained variance suggests that significant factors are absent from the model. Other environmental variables not recorded here may increase the predictive power of the analysis. Fire perhaps remains the other most significant variable influencing species distribution. Structurally dominant species in most habitats are good plant community 'indicators' at this scale, but the stochastic effects of fire (intensity, season of burn and post-fire age) can have a significant effect on species composition of fynbos (Cowling, 1987; Le Maitre, 1987; Cowling and Gxaba, 1990). Consequently, differential post-fire recruitment, while inevitably altering species composition during early successional stages (Bond *et al.*, 1984; Cowling and Gxaba, 1990) may only cause 'reshuffling' of dominant species (McDonald *et al.*, 1996), without eliminating them altogether from that community. Overall, this implies that the diversity of species relies not only on variations in post-fire recruitment, but also on the long environmental gradients on the Cape Peninsula which support the mosaic of vegetation types. This feature is examined in the next chapter.

Conclusions

A relatively simple, rapid method of classifying the flora of the Cape Peninsula has been shown to hold up to comparison with conventional floristic analysis. If a simple vegetation classification system and vegetation map is required (as they often are) by managers then this study demonstrates the accuracy of this time- and money-saving method. The vegetation units on the Cape Peninsula are best described using dominant species in conjunction with environmental variables. Although there are strong environmental components which go some way in explaining the patterns of distribution of species, other influences, such as fire characteristics may needed to be added to refine the model. Thus, to ensure conservation of the species diversity accommodated by these different vegetation types the full range of habitats on the Cape Peninsula must be managed under different fire regimes.

CHAPTER 3

Why is the Cape Peninsula so rich in plant species? An analysis of the independent diversity components[1]

Introduction

The Cape Floristic region is one of the world's foremost centres or "hotspots" of plant diversity and endemism (Takhtajan, 1986; Myers, 1990; Cowling *et al.*, 1992). Within this region, species are neither uniformly nor randomly distributed, but concentrated in smaller nodes (Levyns, 1964; Kruger and Taylor, 1979; Linder *et al.*, 1992; Cowling *et al.*, 1992; Cowling *et al.*, in press). For example, regions in the southwest (winter-rainfall) parts of the Cape Floristic Region have, on average, twice the number of plant species as physiographically similar areas of identical size in the non-seasonal rainfall zone of the south and southeast.

Within the southwest region, the Cape Peninsula, an area dominated by fire-prone fynbos shrublands with occasional patches of fire-proof afromontane forest and subtropical thicket (Cowling *et al.*, 1996), is extraordinarily rich with 2285 species of higher plants in 471 km^2 (Trinder-Smith *et al.*, 1996a). This raises the following questions: why is this region so species rich, and how are all these species packed into such a small area? The answer may lie in one or more of the following hypotheses:

(i) The Cape Peninsula has unusual patterns of resource quality and quantity, within habitats and landscapes, thereby promoting high local and regional richness (Wright *et al.*,

---

[1] Aspects of this chapter have been published in *Biodiversity and Conservation* 6, 551-574.

1993; Brown, 1988; Tilman and Pacala, 1993). This is shown by the extraordinarily steep and long ecological gradients along which species may be packed; i.e. high environmental heterogeneity promoting high beta diversity (Shmida and Wilson, 1985; Williamson, 1988; Rosenzweig, 1992).

(ii) Unusual historical and biological factors, over geological time, have resulted in a high rate of diversification of habitat specialists (increasing beta diversity) and ecological equivalent species (increasing gamma diversity) (Shmida and Wilson, 1985; Cody, 1986; Cowling *et al.*, 1992; Ricklefs and Schluter, 1993).

(iii) The transitional location of the Cape Peninsula with respect to the winter (western) and non-seasonal (eastern) rainfall zone floras of the Cape Floristic Region, has resulted in the macro-scale mass effects, whereby species from these distinct floras (Oliver *et al.*, 1983) establish or persist outside their normal range in relictual or transitory populations (Shmida and Wilson, 1985).

Very few studies have attempted to decompose regional richness in terms of the three independent diversity components, namely alpha, beta and gamma diversities (but see Whittaker, 1977; Cowling, 1990; Cody, 1993). In a topographically and climatically uniform region of the Cape Floristic Region, about 150 km southeast of the Cape Peninsula, Cowling (1990) was able to demonstrate that the high regional plant richness was a function of the extremely high turnover of species along habitat and geographic gradients, and moderately high local richness. In landscapes of similar environmental heterogeneity further east, the two-fold lower richness was mainly due to lower turnover rather than lower local richness (Cowling *et al.*, 1992). Cowling *et al.*, (1992) invoked differential rates of diversification as the reason for these different patterns of turnover and consequently, regional richness.

This study attempted to provide an explanation for the high plant species richness of the Cape Peninsula by addressing the following questions:

(i) Is the Cape Peninsula flora unusually rich when compared with other regions in southern Africa and the world?
(ii) What are the patterns and determinants of the different diversity components (i.e. alpha, beta and gamma diversities)?
(iii) Which of these components contribute most to explaining the region's high richness?
(iv) What is the relationship between the diversity components and rarity?
(v) What are the implications of these patterns and determinants of diversity for the conservation of plant biodiversity.

These issues are addressed by first examining the richness of the Cape Peninsula in a subcontinental and global context. Secondly, examining patterns and determinants of alpha, beta and gamma diversities using a database derived from 835 phytosociological plots located throughout the Cape Peninsula. Finally, the role of turnover and rarity in determining regional richness is assessed, and the implications of these diversity patterns for plant species conservation are discussed.

Regional richness

Regional plant species richness of the Cape Peninsula is exceptionally high in both a subcontinental and global context. High richness at the subcontinental level is clearly shown in an analysis of the correlates of regional richness (63 samples) throughout southern Africa (Cowling *et al.*, in press). In simple bivariate analyses, measures of environmental heterogeneity (topographical diversity, annual rainfall range, mean winter temperature range) emerged as the best predictors of richness at this scale (Fig. 3.1). Other explanatory variables used in this analysis, included measures of area, environmental favourability, available energy, seasonality and irregularity. Although the Cape Peninsula had the richest flora of all sites, it also had the highest values of two of the three measures of heterogeneity, namely, topographical diversity and annual rainfall range (Fig. 3.1a and 3.1b). Thus, the unusually high richness of the Cape Peninsula flora when compared to other southern Africa sites, may be largely a function of the region's extraordinarily high environmental heterogeneity (Cowling *et al.*, 1996). Although not a random sample, the 63 sites of Cowling *et al.* (in press) did include other areas of high environmental heterogeneity on the subcontinent such as elsewhere in the Cape Floristic Region (11 sites) and along the Great Escarpment (eight sites).

Global comparisons are best made by comparing patterns in other mediterranean-type ecosystems also recognized as major "hot-spots", namely, south-western Australia, central Chile and south-central cismontane California (Myers, 1990). Computation of species-area regression (double logarithmic form) data from these areas (Arroyo *et al.*, 1995; Cowling *et al.*, in press) demonstrates that for the equivalent area of the Cape Peninsula (471 km^2), Chile has 4.7 times fewer species than predicted by the species area curve; California 3.3 times and southwestern Australia 2.7 times fewer species. Cowling *et al.* (in press) discuss these differences in terms of contemporary ecological as well as historical factors.

Alpha diversity

Approach and methods

Data for the analysis of alpha diversity, measured as number of perennially identifiable species, and associated site environmental variables, were compiled from 835

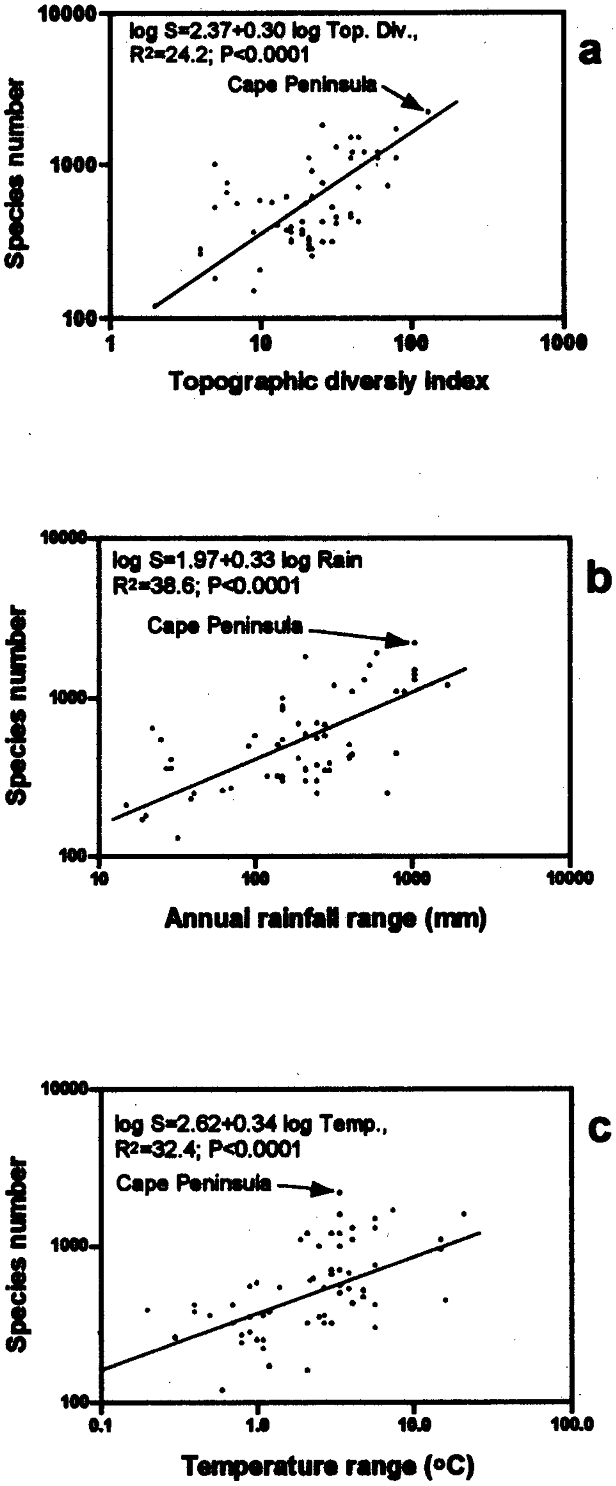


Figure 3.1 Relationship between plant species richness of 63 regions within Southern Africa and measures of environmental heterogeneity. (a) Topographical diversity index (the coefficient of variation of all grid altitude values). (b) Annual rainfall range (difference between highest and lowest gridded value of mean annual rainfall). (c) Temperature range (difference between the highest and lowest gridded values of July's (winter) mean daily minimum temperatures). From Cowling *et al.* (in press).

phytosociological plots sampled throughout the Cape Peninsula from published and unpublished sources (see Chapter 1 for details). For the purposes of this study it was assumed that the scale of plot size employed in each case was representative of local richness. This approach was justified by considering a vegetation community to be a group of interacting species (Magurran, 1988). Therefore, any measure of alpha diversity must allow for the physical scale of the community, such as the average height of the dominant species. Consequently, an increased plot size was necessary to accommodate the larger structural nature of each community. Thus, most of the forest plots were 100 m^2 whereas the majority of the fynbos plots were 50 m^2. However, nearly all of the renosterveld plots were 100 m^2, and due to the overall low stature of this vegetation type, the alpha diversity data were considered to be moderately inflated. This did not however, affect the beta and gamma indices, because the analyses employed were independent of alpha diversity (Wilson and Shmida, 1984)

Patterns and correlates

Alpha diversity on the Cape Peninsula (Table 3.1) is not significantly different from other fynbos sites in the Cape Floristic Region. The average species richness on the Cape Peninsula of 21.4 in 50 m^2 can be qualitatively compared with that in the southern Cape mountains with an average of 47.1 species in 100 m^2 (Bond, 1983) and the Agulhas Plain with 16.0 species in 1 m^2 (Cowling, 1990) (see also Cowling, 1983a; Cowling *et al.*, 1992). Lowest mean values were recorded in high-moisture types such as wetlands, upland restioid fynbos, ericaceous fynbos, and forest and thicket. High values were recorded in low elevation (wet restioid fynbos) and drier (mesic oligotrophic fynbos) communities, as well as renoster shrubland on relatively fertile, shale-derived soils. However, there was

Table 3.1. Mean alpha richness of the different vegetation types (Cowling *et al.*, 1996). Groups with the same superscripts are not significantly different at the 0.05 level (Tukey multiple range test). F=23.94 $p < 0.0001$.

Vegetation type	Mean	SD	Range	n
NON FYNBOS TYPES				
Forest and thicket (FOR)^{ad}	18.1	6.3	1-43	253
Renoster shrubland (REN)^{f}	28.1	7.0	17-46	56
FYNBOS TYPES				
Dune asteraceous fynbos (DUN)^{acd}	16.9	13.0	3-63	55
Sandplain proteoid fynbos (SND)^{abcd}	17.2	14.1	4-61	21
Mesic oligotrophic proteoid fynbos (MOP)^{f}	31.2	16.2	11-78	80
Wet oligotrophic proteoid fynbos (WOP)^{de}	19.7	8.9	4-39	38
Mesic mesotrophic proteoid fynbos (MMP)^{d}	19.1	9.0	5-51	91
Wet mesotrophic proteoid fynbos (WMP)^{e}	23.9	7.2	12-41	30
Wet restioid fynbos (WRF)^{f}	32.4	13.4	14-62	22
Upland restioid fynbos (URF)^{ab}	12.9	6.6	2-31	44
Ericaceous fynbos (ERI)^{ad}	16.9	6.5	4-32	103
AZONAL TYPES				
Undifferentiated cliff communities (CLF)^{abc}	13.2	6.4	3-27	34
Wetlands (WET)^{a}	12.7	6.4	5-23	9

considerable variation within all vegetation types. Some sites were extremely rich with up to 78 species in a single plot of mesic oligotrophic proteoid fynbos. The most species-poor plots were sampled in forest and thicket (e.g. one species).

Numerous models have been invoked to explain patterns of local richness in plant communities (see Tilman and Pacala (1993) for a review). Below we discuss models and explanations of local richness patterns on the Cape Peninsula.

Resource-based models

There is a greater chance that species-rich sites will be found in areas of lowest resource levels on the Cape Peninsula. The highest values for alpha diversity on the Cape Peninsula within fynbos, tended to be recorded at low altitude (Fig. 3.2a), high radiation (Fig. 3.2b), low rainfall (Fig. 3.2c) and low fertility (Fig. 3.2d) sites. These patterns may be consistent with unimodal curve relating species richness to measures of site productivity and "favourableness" (e.g. rainfall, solar load) (Tilman and Pacala, 1993; Roesenzweig and Abramsky, 1993), as suggested by the trend of the relationship between species numbers and radiation load (Fig. 3.2b). Both Bond (1983) and Kruger (1974) observed a unimodal relationship between local richness and surrogate variables for productivity (biomass) in fynbos in the south and south-west Cape mountains, respectively. This unimodal curve is evident across the radiation gradient only, but it could be that the Cape Peninsula does not include the extreme, low productive (e.g. very dry) sites to show this curvilinear relationship for other variables. Suppression of high species-richness values in more 'favourable' sites, could be accounted for by canopy suppression of understorey species under high resource conditions, for example, in forest and thicket and wet mesotrophic proteoid communities (Esler and Cowling, 1990; Cowling and Gxaba, 1990).

Fire-related stochastic models

The high variation in species number within low resource sites may be due to fire-related effects. Fire has a profound effect on species composition of fynbos (Cowling, 1987) in terms of quality and season of burn, and post-fire age (Le Maitre, 1987). Different fires may influence regeneration guilds differentially, thereby rearranging competitive hierarchies causing non-equilibrium composition over several fire cycles. Fire season influences the density of the overstorey proteoid shrubs (Bond *et al.*, 1984) which, in turn, influences the understorey diversity and composition (Cowling and Gxaba, 1990). In some cases the overstorey component may migrate across the landscape as wind-dispersed propagules are blown away from dense stands after summer fires, under the

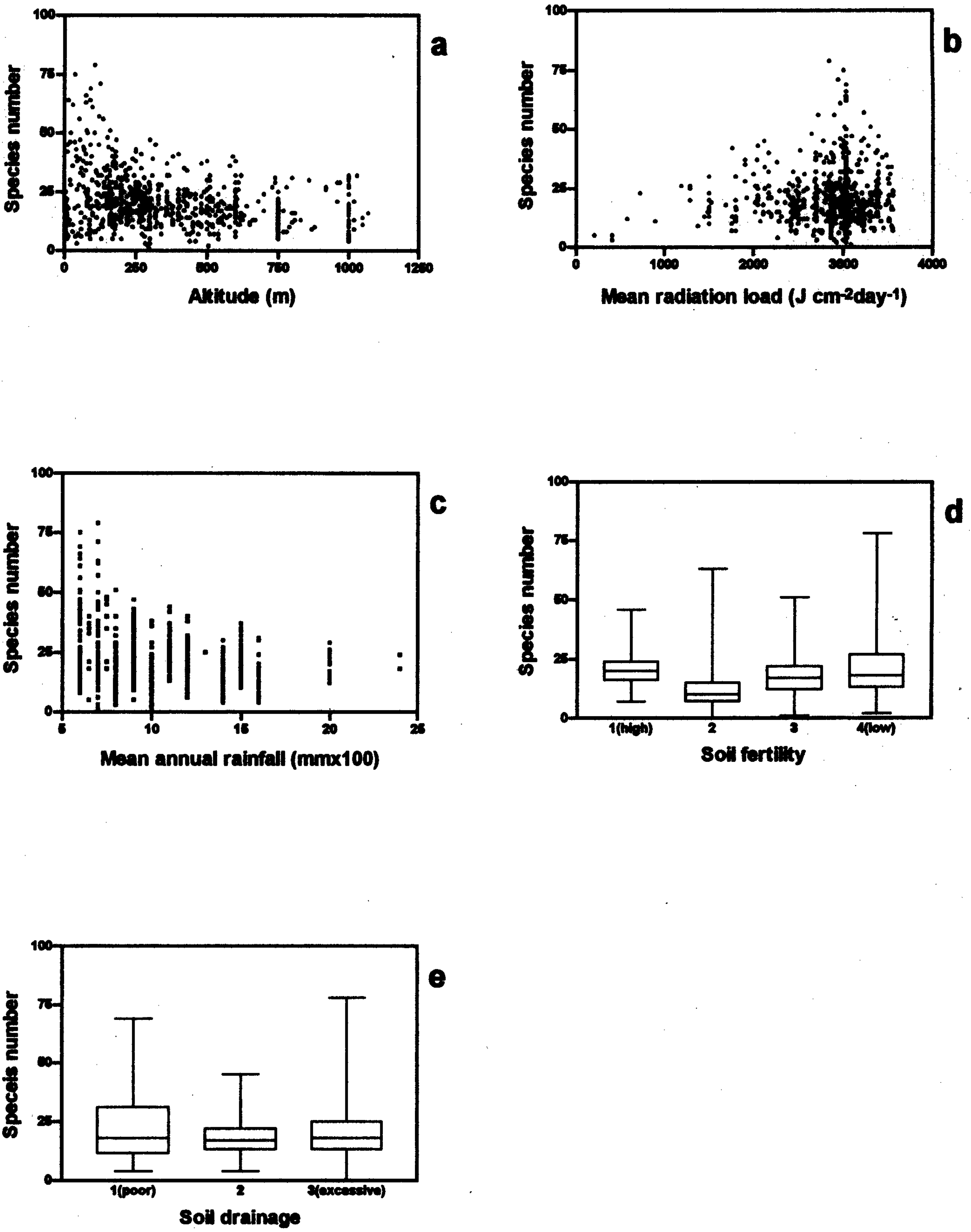


Figure 3.2 The relationship for the Cape Peninsula between species richness in plots (alpha diversity) and (a) altitude; (b) mean daily radiation load; (c) mean annual rainfall; (d) soil fertility; (e) soil drainage. Box and whisker symbols: quartile box with median; whiskers show the data range.

influence of strong wind regimes (Bond, 1988; Cowling and Gxaba, 1990). These "marauding" populations leave their mark on community composition for decades or longer. Similarly, variation in fire intensity results in the differential recruitment of species, largely as a function of seed size (Bond *et al.*, 1990; Bond and Van Wilgen, 1996). On certain sites very hot fires stimulate the regeneration *en masse* of *Aspalathus* species (Fabaceae), resulting in dense thickets that suppress other community components, especially non-sprouting shrubs (R.M. Cowling, unpublished data). Such a fire would therefore reduce the number of species expected at an otherwise species-rich site.

Regional phenomena

Local richness may be significantly influenced by regional phenomena (Ricklefs, 1987; Ricklefs and Schluter, 1993). For example, local richness may be influenced by the size of the regional species pool within a particular habitat. Thus, habitats which occupy a small area regionally and therefore support a lower number of species (Williamson, 1988; Diamond, 1988), may have lower local richness owing to the limited size of the regional pool available for colonization of local sites. This is certainly the case for the Cape Peninsula, where the low resource habitats (and communities) occupy the largest area and have the highest mean local richness, whereas communities occupying a smaller area were consistently species-poor (Fig. 3.3).

Beta diversity

Approach and methods

The usual approach for analyzing beta diversity is to sample along a predetermined environmental gradient (usually the dominant one in the landscape) and then compute beta diversity using one or more of the several indices available (Whittaker, 1972; Shmida and

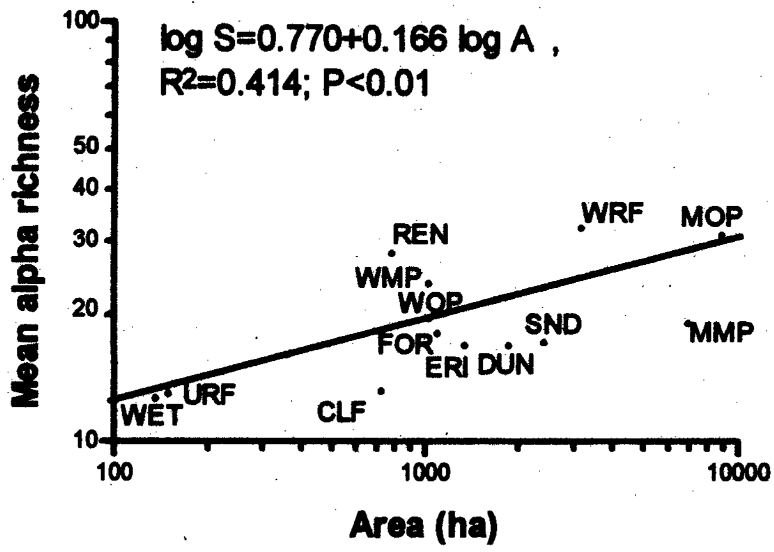


Figure 3.3 The relationship between mean alpha diversity and total area of each vegetation type on the Cape Peninsula.

Wilson, 1985; Magurran, 1988; Cowling, 1990) However, samples in this data set were not located in this way but mostly concentrated in sites for detailed phytosociological study (Chapter 1).

For this study samples were selected from the pool of 835 plots to cover one gradient in resource availability while controlling the value of other resource variables. For example, a series of plots was selected spanning an altitude gradient, while holding constant the other variables of soil fertility and radiation regime. Thus, beta diversity was computed along gradients of altitude (surrogate for rainfall and temperature), soil fertility and radiation. At intervals along each gradient a station was randomly selected such that a sample flora was compiled from three plots, selected from one geographic location within the same vegetation type. Turnover was then calculated both between stations and across the gradient as a whole (Fig. 3.4, 3.5 and 3.6) using the Biodiv 4.1 (Baev and Penev, 1993) package.

Of the several available methods of calculating beta diversity from a presence-absence data set, the Wilson-Shmida index was selected on account of its ability both to reflect the number of community changes along a gradient and its strength in fulfilling the criteria of additivity and independence from alpha diversity (Wilson and Shmida, 1984; Magurran, 1988). The Wilson-Shmida (1984) index (β) adds the number of species gained ($g(H)$) to the number of species lost ($l(H)$) along a habitat gradient (H), standardized by the average sample richness α. Thus,

$$\beta = [g(H) + l(H)]/2\alpha$$

When $\beta = 0$ there is no species change or "turnover" between stations; when $\beta = 1$ there is complete turnover. Consequently, $\beta + 1$ represents the number of distinct communities along the transect.

Patterns

Overall, there was a consistently high turnover along most gradients, summarised as follows:

(i) The highest turnover along altitudinal gradients was at low and moderate fertility sites, irrespective of radiation load (Fig. 3.4c), and lowest turnover at high fertility sites, especially at low altitude (Fig. 3.4a). The former gradient ranges from mesic oligotrophic fynbos through wet oligotrophic fynbos, and to ericaceous fynbos (dry, warm sites to wet, cool sites on shallow, nutrient-poor sands derived from Table Mountain Group sandstone); the latter sites represent forest and thicket, where the flora is small and comprises well-

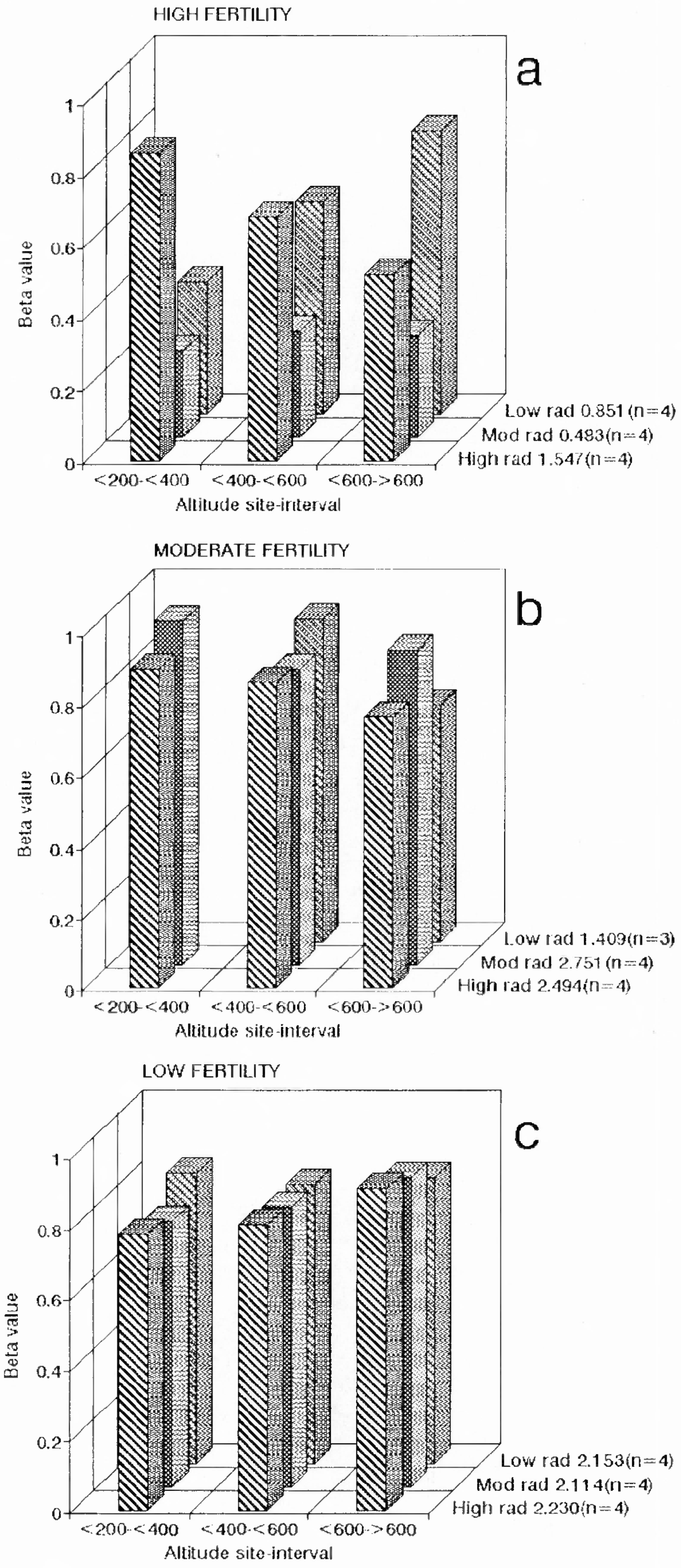


Figure 3.4 Turnover of species along altitudinal gradients on soils of (a) high fertility, (b) moderate fertility, (c) low fertility, for sites which have low (<2500 Joules cm^{-2} day^{-1}), moderate (2500-3000 Joules cm^{-2} day^{-1}) and high (>3000 Joules cm^{-2} day^{-1}) radiation loads. Each bar sysmbolizes turnover between two stations where a station denotes a cumulative sample of three plots within the same plant community. Total gradient beta value with number of stations (n) is given for each transect.

dispersed generalist trees and shrubs of tropical affinity (Campbell, 1986b; McKenzie *et al.*, 1977; Cowling *et al.*, in press; Midgely *et al.*, in press).

(ii) The highest turnover for all gradients (complete between some stations), was observed along a gradient of soil fertility within similar rainfall (altitude) and radiation regimes (Fig. 3.5). Rainfall and radiation did not appear to have an effect here i.e. turnover was more or less similar for all regimes. This gradient represents turnover from non-fynbos types at high soil fertility (forest and thicket, renoster shrubland), through proteoid fynbos on mesotrophic soils, to proteoid and ericaceous fynbos on oligotrophic soils. These patterns are consistent with high turnover values found along edaphic gradients in other fynbos regions (Cowling, 1990; Cowling *et al.*, 1992).

(iii) The turnover along gradients of radiation load (Fig. 3.6) was lowest on highly fertile sites irrespective of altitude, and highest on moderately fertile sites (dune asteraceous fynbos) as well as poorly fertile sites (mesic oligotrophic proteoid fynbos), especially between sites at the upper extreme of the radiation regime.

Gamma diversity

Approach and methods

In computing gamma diversity (compositional change between geographically distant sites of the same habitat) the same approach was adopted as for beta diversity. However, the determination of gamma diversity was problematic since the steep ecological gradients of the Cape Peninsula meant that it was very difficult to locate geographically distant sites within a similar habitat. Thus, there was a beta component to the gamma diversity computed here (*cf.* Cody, 1986). The high topographical and climatic variation across the Cape Peninsula means that there is a degree of isolation of communities even over small (several kilometres) distances. Therefore, to highlight the gamma component to diversity

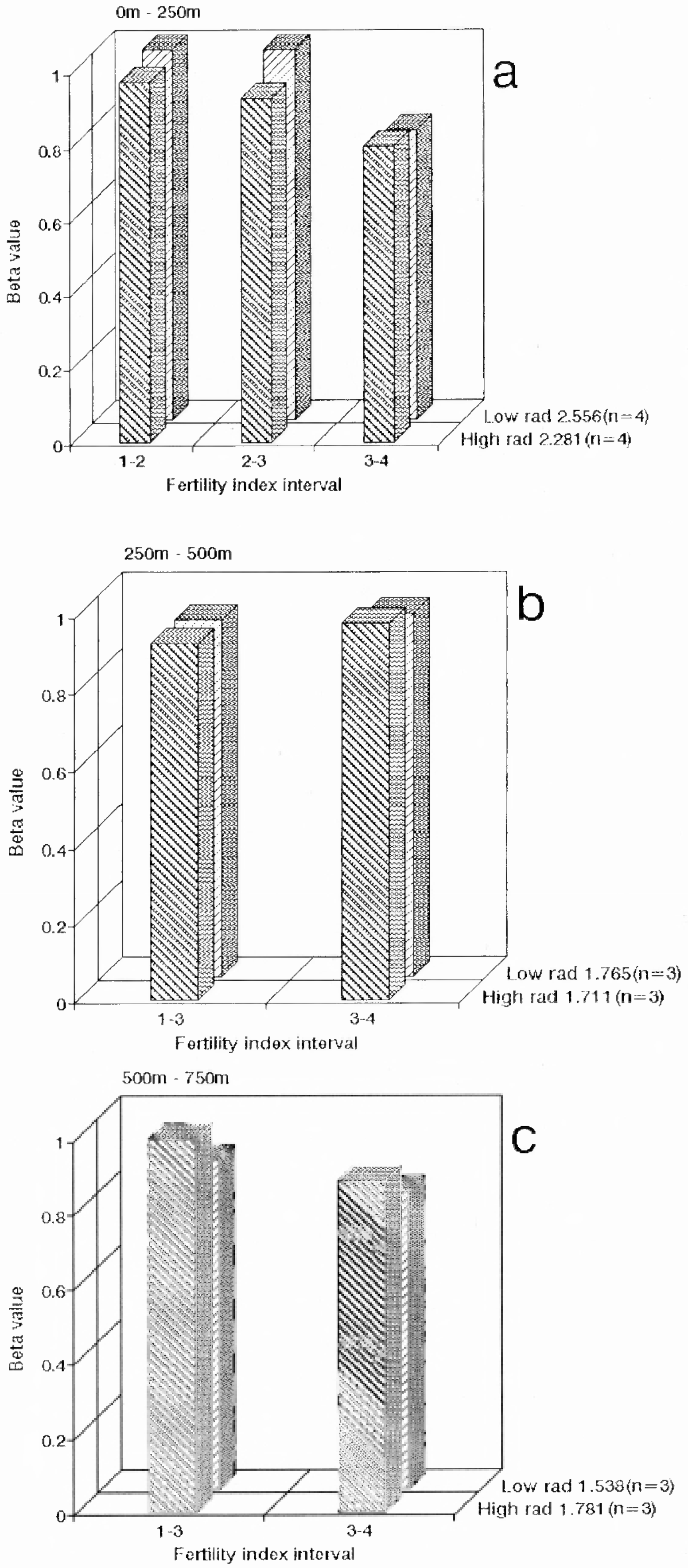


Figure 3.5 Turnover of species along fertility gradients of varying radiation loads (low = <2500) Joules cm^{-2} day^{-1}; high = > 2500 Joules cm^{-2} day^{-1}) and altitude (a) 0 m - 250 m; (b) 250 m - 500 m; (c) 500 m - 750 m. Each bar symbolizes turnover between two stations where a station denotes a cumulative sample of three plots within the same plant community. Total gradient beta value with number of stations (n) is given for each transect.

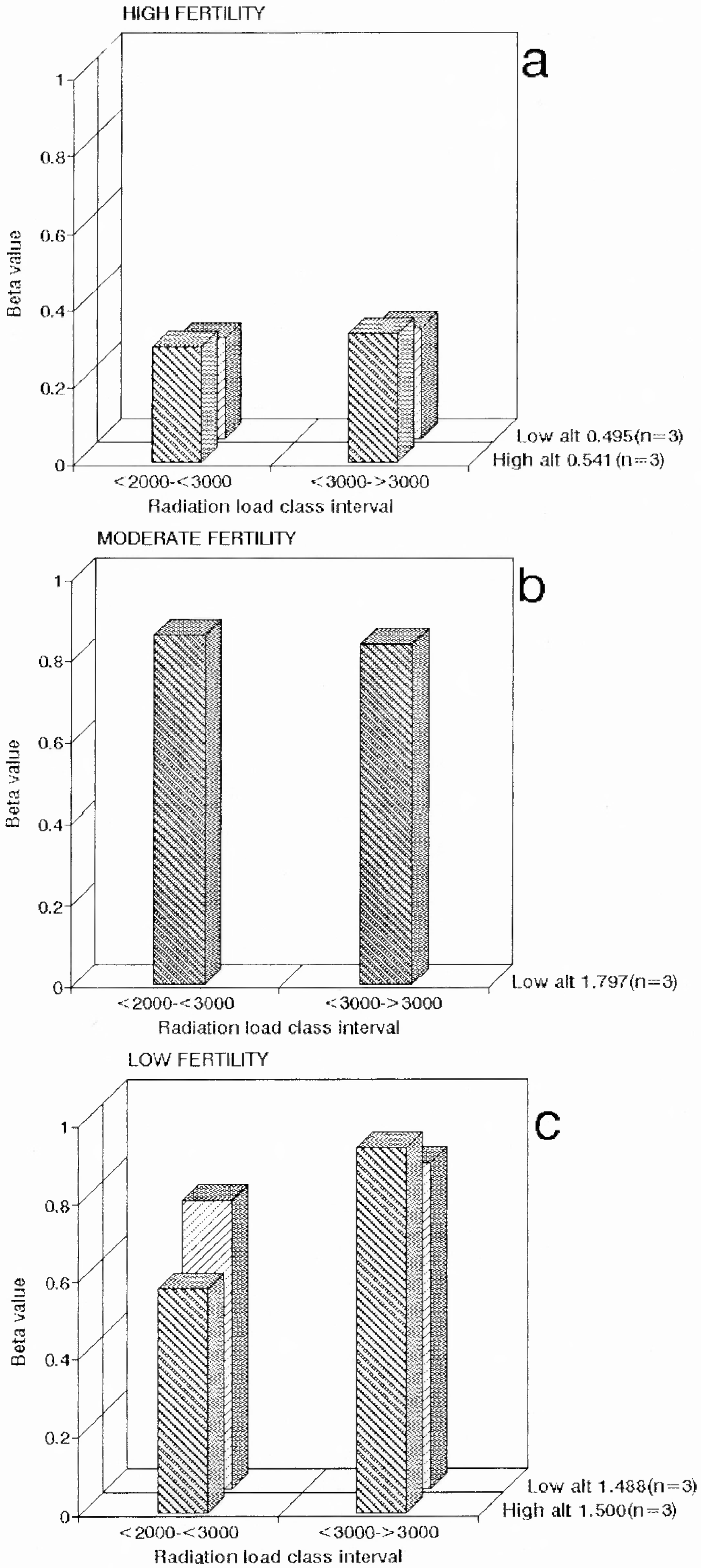


Figure 3.6 Turnover of species across radiation load gradients of (a) high, (b) moderate and (c) low soil fertility, and varying altitudes (low = < 500 m; high = > 500 m). Each bar symbolizes turnover between two stations where a station denotes a cumulative sample of three plots within the same plant community. Total gradient beta value with number of stations (n) is given for each transect.

the diversity was calculated between similar, disjunct sites relatively close together (*cf.* Cowling, 1990).

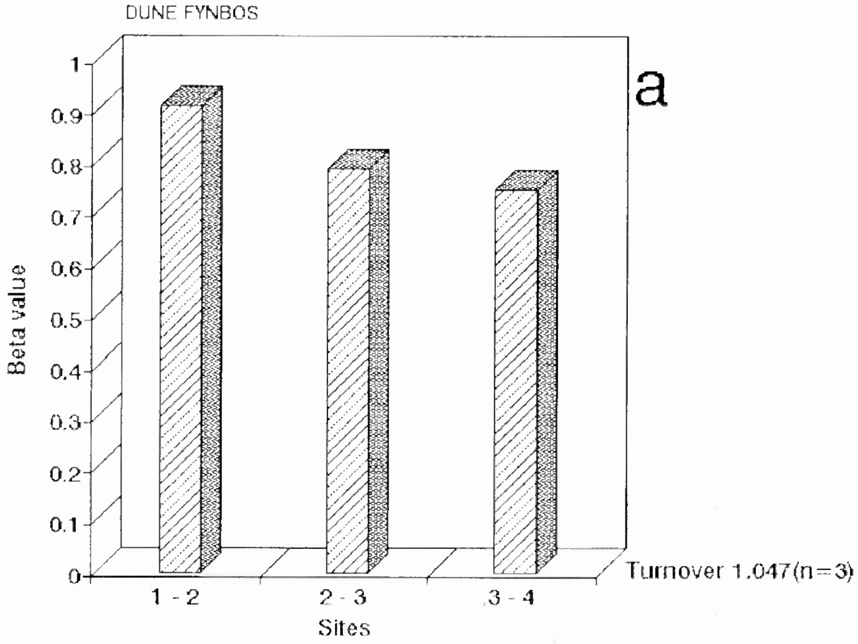
There were sufficient data for two comparisons: dune asteraceous fynbos (dry, moderately fertile conditions, low altitude) at four sites approximately 10 km apart along the west coast of the Cape Peninsula, and ericaceous fynbos (wet, infertile, high altitude) at three sites, 10 to 20 km apart.

Patterns

Turnover between similar habitats on the Cape Peninsula was exceptionally high with an average value of 0.803 (Fig. 3.7a) for dune asteraceous fynbos and 0.775 for ericaceous fynbos (Fig. 3.7b). Using the same approach as this study, Cowling (1990) recorded gamma values of 0.628 for dune asteraceous fynbos and 0.667 for ericaceous fynbos sites on the Agulhas Plain, 150 km to the southeast of the Cape Peninsula, and an average gamma-value of 0.300 for dune asteraceous fynbos in the southeastern Cape, 550 km east of the Cape Peninsula (Cowling *et al.*, 1992). Very high endemism on Cape Peninsula (Trinder-Smith *et al.*, 1996a) suggests that this high gamma diversity may be partly associated with *in situ* diversification of vicariant (ecologically equivalent) species. However, owing to subtle differences in environmental conditions between these geographically distant sites, there may also be a strong beta component, or habitat specialization, associated with turnover at this scale.

Rarity

The frequency distribution of species in the 835 plots sampled in the Cape Peninsula was plotted to assess the degree of rarity (Fig. 3.8). A very high proportion (54%) of the



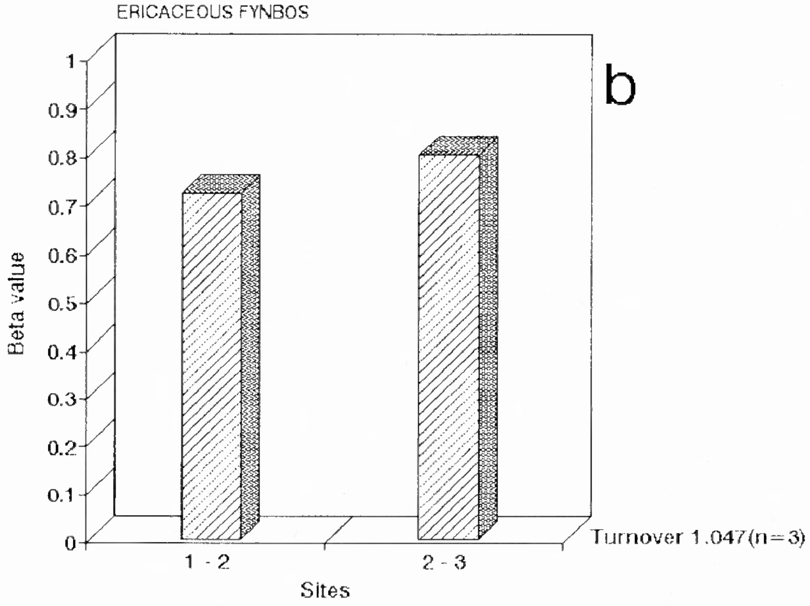


Figure 3.7 Gamma diversity of (a) dune asteraceous fynbos and (b) ericaceous fynbos across the Cape Peninsula from noth to south. Each bar symbolizes turnover between two stations where a station denotes a cumulative sample of three plots within the same plant community

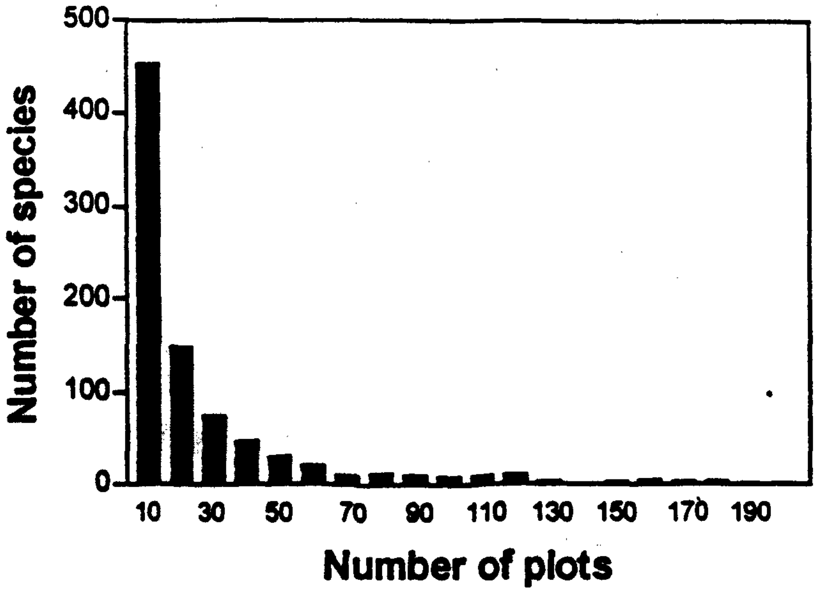


Figure 3.8 The frequency distribution of number of species with number of plot occurences recorded in the 835 plots sampled on the Cape Peninsula

species occurred in 10 plots or fewer, suggestion a high degree of rarity, at least in this data set. It appears that the Cape Peninsula flora includes relatively few widespread and abundant species and many range-restricted and rare species. Rarity may result as much from specialization associated with the wide range of microhabitats on the Cape Peninsula, as from the complex mosaic of distribution and abundance patterns resulting from fire related differential recruitment (Bond *et al.*, 1984; Cowling, 1987; Cowling and Gxaba, 1990; Bond and Van Wilgen, 1996).

The non-random location of plots on the Cape Peninsula (Chapter 1) is likely to result in the under-sampling of range-restricted rare species. This suggests that rarity is likely to be more pronounced in the Cape Peninsula flora than is evident in our data set, given the high beta turnover of the region. Indeed, Trinder-Smith *et al.*, (1996a) list 141 gazetted Red Data Book taxa, one of the highest concentrations of such taxa in the world.

General discussion

Regional richness and turnover

The Cape Peninsula is very rich in plant species at both a subcontinental and global scale, because of in the exceptionally high turnover within, and especially between, habitats which support moderately high numbers of species. Similar explanations have been invoked to explain the regional richness of other sites within the Cape Floristic Region (Kruger and Taylor, 1979; Cowling, 1990; Cowling *et al.*, 1992; Cowling *et al.*, in press). What is exceptional about the Cape Peninsula is the extraordinarily steep and long habitat gradients along which species are packed.

Correlative and experimental studies have suggested that the high beta diversity of fynbos results from a high level of habitat specialization of fynbos species, especially with regard to edaphic conditions (Cowling, 1983b; Cowling, 1990; Cowling *et al.*, 1992; Richards *et al.*, 1995). Research on the Agulhas Plain, some 150 km southeast of Cape Peninsula, has shown that physiological adaptation to different edaphic conditions (moisture and nutrients), rather than biological interactions between species, is the principle determinant of turnover (Mustart and Cowling, 1993; Richards, 1993; Richards *et al.*, 1995). Trinder-Smith *et al.* (1996a) have shown that both rare and endemic species on the Cape Peninsula, are often associated with one to a few vegetation types, suggesting a high degree of habitat specialization of these taxa.

Gamma diversity on the Cape Peninsula is very high and contributes substantially to the size of the Cape Peninsula's flora. Generally, gamma diversity is controlled by historical processes associated with the speciation of ecological equivalents along geographical gradients (Kruger and Taylor, 1979; Shmida and Wilson, 1985, Cody, 1986). With some

90 species endemic to the Cape Peninsula (Trinder-Smith *et al.*, 1996a), there is little doubt that the *in situ* diversification of a taxonomically and holographically non-random assemblage of lineages has contributed to the region's high gamma diversity. However, the high number of rare species, most of which are not Cape Peninsula endemics (Chapter 4), and the stochastic processes responsible for this rarity, is also a component of high gamma diversity. Finally as previously stated, it was not easy to separate the beta component of these gamma processes.

Implications for conservation of plant biodiversity

The patterns of diversity discussed here have three implications for biodiversity conservation.

(i) Because of high beta diversity, reserves should be located in landscapes that maximise environmental heterogeneity, especially edaphic heterogeneity. This will maximize species richness in the present and facilitate diversification of habitat specialists in response to future environmental changes (Graham, 1988). Such an strategy adopts a "coarse-filter" approach by conserving those habitats which maximise the plant species gene pool (Hunter *et al.*, 1988).

(ii) Because of high gamma diversity, geographically disjunct portions of the same habitat should be conserved, because a single portion of a habitat will not include all constituent species of that vegetation type. This action both maximises the conservation of extant biodiversity and allows for future diversification of ecologically equivalent taxa.

(iii) Since much of the Cape Peninsula's plant diversity is associated with species that are rare at both the local and regional scale, biological and ecological understanding of rarity must be recognised as a research priority. With several hundred species occurring in small populations, inappropriate fire regimes and the threat of invasive alien species could result in their extinction on the Cape Peninsula (Richardson *et al.*, 1996). The biological aspects of range-restricted rarity (local endemism), both on the Cape Peninsula (Trinder-Smith *et al.*, 1996a) and elsewhere (McDonald *et al.*, in press) hold important lessons for management aimed at conserving these species. There is an urgent need to gain an understanding of the biological aspects of different forms of rarity (Rabinowitz *et al.*, 1986) in the Cape Peninsula flora and to integrate this knowledge into spatially explicit management plans for the maintenance of plant biodiversity. The next chapter attempts to provide some further insights on biological and environmental correlates of rare (but not endemic or threatened) species on the Cape Peninsula.

CHAPTER 4

Do rare plants have different biological and habitat profiles compared to common ones? An analysis of the flora of the Cape Peninsula, South Africa.

Introduction

One of the main issues facing reserve managers is ensuring the maintenance of species diversity through selection and preservation of specific habitats. This includes the priority of the preservation of rare species, particularly if they are species of special appeal and considered to be threatened. Thus, prediction of the distribution patterns of individual and groups of species is an important part of an integrated approach to reserve management. The Cape Peninsula (471 km^2) includes some 2285 species, many of which are threatened (Trinder-Smith *et al.*, 1996a). Although it is expected that such a highly species-rich area should support a large number of both endemic (i.e. range restricted) and threatened (Red-Data Book) species (Prendergast *et al.*, 1993), the rank abundance relationship of species (Magurran, 1988; Gaston, 1994) follows a highly skewed log-normal curve, with relatively few 'common' species and a high number of rares (Chapter 3). A significant proportion of the species in this region can be regarded as 'rare', with over 50% of plant species occurring in 10 plots or less of the 835 phytosociological plots (Chapter 3), and a further 22% of these species occurring only once. This pattern is repeated elsewhere in mediterranean-type ecosystems where high diversity support a large number of rare and locally endemic species (Cowling and McDonald, in press). For example, on the Swan

Coastal Plain of southwestern Australia, within a total of 1097 species in 509 plots, 272 (25%) were only found once (Gibson *et al.*, 1994). Thus, rare species must be considered in any management strategy for such systems so that overall diversity can be maintained.

The phenomenon of rarity is both inconsistently defined and poorly understood, and remains a problem for conservation biologists (Rabinowitz *et al.*, 1986; Stacey and Taper, 1992; Gaston 1994). Rarity is a continuous variable with two dimensions: abundance (number of individuals in a given area) and geographic range, both which may vary over time. Therefore, a rare species does not necessarily imply that it is either endemic or endangered (Stacey and Taper, 1992), merely that is 'uncommon'. Rabinowitz *et al.* (1986) defined rarity in terms of geographic range, habitat specificity and local population size and used these characteristics to derive general conservation strategies for each case. Apart from this, the lack of research on rarity, particularly regarding plants, has resulted in a deficiency of knowledge relating to the traits of rare and common plant species (Gaston, 1994; Cowling and Samways, 1995). Most previous research has focused on range-restricted (i.e. endemic) species (McDonald *et al.*, 1995; Trinder-Smith, 1996a) or geographic distribution of rare species (e.g. Prendergast *et al.*, 1993). However, many rare species are neither range-restricted or threatened. For example, using Rabinowitz *et al.*'s (1986) categories of rarity traits, a non-habitat-specific species can occur over a wide geographic range but have small overall population size (i.e. uncommon everywhere). Furthermore, although attempts have been made to invoke mechanisms to describe patterns of rarity (Begon *et al.*, 1990), there has been no research which treats plant rarity as a continuous variable (Gaston 1994), and examining many species which may have few individuals locally but are nevertheless widespread regionally.

The relationship that species range is related to habitat is well documented, but directly relating species abundance or density with climatic and edaphic resource values is more problematic. The assumption that abundance is related to niche breadth (i.e. the range of available resources) is fraught with problems of sampling techniques and scale, and there is little evidence that rare plants have narrow resource niches (Gaston, 1994). Indeed, studies have shown that the relationship between abundance and niche breadth is inconsistent, demonstrating both positive (Hanski 1982; Bock and Ricklefs, 1983), negative (McCloskey, 1976; Seagle and MacCracken, 1986) relationships, or no significant relationship at all (Carnes and Slade, 1982; Shenbrot *et al.*, 1991).

Species biology (e.g. dispersal ability), which has been shown to limit range size (Kunin and Gaston, 1993; Gaston, 1994), may also be a strong determinant of population size. In the Cape Floristic Region it has been suggested that range-restricted and Red Data Book taxa are associated with particular lineages and specific biological traits (McDonald *et al.*, 1995; Trinder-Smith *et al.*, 1996a, and others, see Cowling and McDonald (in press) for review). Most of these species are non-sprouting shrubs with relatively large, ant-dispersed seeds, and many others are geophytes. These species are particularly vulnerable to certain management regimes. For example, ant dispersed (myrmecochorous) species are vulnerable to invasive ant species which displace their dispersers (Bond and Slingsby, 1983); low, non-sprouting species are excluded by alien invasive trees and shrubs (Richardson and van Wilgen, 1986); pollinator-specific geophytes are affected by habitat fragmentation which reduces the population of the pollinators (Johnson and Bond, 1992); and large seeded and slow-maturing species are eliminated by controlled, high frequency, low intensity burns (Bond *et al.* 1990; van Wilgen *et al.* 1992).

It is possible that there is no specific explanation for the low abundance of some species. It merely may be a temporarily low number of individuals if the population fluctuates stochastically, or a mathematical artifact of the distribution of species as a whole (Preston, 1948; Hanski and Gilpin, 1991). This mathematical explanation is supported by the lack of any general theory predicting rarity and suggests that either rare species are subject to the same processes that act on widespread and common species, requiring no specialised management strategies, or that the biological attributes and abiotic requirements of each species, require individual examination.

The Cape Peninsula offers an exceptional site for the study of rarity since the region supports an exceptionally high number of rare species available for analysis. However, although the Cape Peninsula has a large number of endemics (Trinder-Smith *et al.*, 1996a) the majority of rarer species found in this study have a wide geographic distribution throughout the Cape Floristic Region, thus making it an ideal site for studying the phenomenon of these widespread, but rare species. This study had two main objectives:

1. To determine the relationship between rarity status and biological traits
2. To determine whether rare plants have different environmental requirements from common ones.

Methods

Data selection

Data were drawn from a phytosociological data base and associated environmental factors (Chapter 1). This was modified because the non-random, clumped distribution of the plots throughout the Cape Peninsula necessitated a stratification of the data to avoid bias of over-represented vegetation types. The number of plots selected for each vegetation type was proportional to its area on the Cape Peninsula. Also, because analysis of the phenomenon of rarity within fynbos was the objective here, forest plots, which were significantly over-represented in the data set, were removed. Within each vegetation type, a proportional number of plots were selected randomly, with a resulting subsample of 254 plots and 636 species.

The definition of rarity is somewhat problematic and varies in type (abundance or range), dimension (space and time) and magnitude (Rabinowitz *et al.*, 1986; Begon *et al.*, 1990; Gaston, 1994). In an effort to establish a standardized definition of abundance, Gaston (1994) proposed using a cut-off point at the first quartile (i.e. lower 25%) of the frequency distribution of species abundances, depending on sample design. The highly skewed frequency distribution of the species on the Cape Peninsula (Chapter 3) resulted in an unusually high number of species with only one or two occurrences. This study approximated Gaston's (1994) definition of a "rare" species, using a cut-off of 22% (139 species), because this proportion captured all those species with a single occurrence in the data set. Those species occurring two or more times in the data set are referred to as "non-rare" or "common". Where the numbers of rare species (single occurrence in the whole data base) within quadrats were used needed for analyses, a density value was calculated by correcting for plot size (i.e. number of rares per hectare). Alternatively, where it was not possible in the analyses to use this binary classification, rarity was treated as a continuous variable, thus "abundance" refers to the number of plots within a given habitat or data set, in which a species occurs. For example, a species which occurs in only five plots in the data set is less "abundant" than one which occurs in ten plots.

In these analyses, range was not considered, and a rare species was therefore solely defined as having low abundance in the data base. By virtue of its sampling method (Chapter 1), the database samples did not include many of the very rare species, only capturing 36% of all Cape Peninsula species. Thus, although this study attempted to deduce general causes of rarity, it did not include most of those species considered be extraordinarily rare or even 'threatened' (i.e. Red Data Book taxa) on the Cape Peninsula (Trinder-Smith *et al.*, 1996a). Thus rarity should be examined through demographic research.

Biotic and abiotic attributes

To test for any relationship between the biological attributes and rarity each species was assigned a categorical value representing growth form, post-fire regeneration strategy and dispersal mode (Trinder-Smith, 1995):

1. Growth form: low shrub (0-1 m); medium shrub (1-2 m); tall shrub (>2 m)
2. Regeneration strategy: non-sprouter (reseeder); resprouter.
3. Dispersal mode: passive; wind; ant (myrmecochorous).

For each classification a two-way contingency table was constructed and χ^2 statistic calculated to test the null hypothesis that rarity and non-rarity are independent of biological attributes.

In order to determine the effect of environmental factors on the density of rare species, mean number of rare species per plots was calculated, and compared to the following environmental variables: aspect (ASP), altitude a surrogate of temperature (ALT), drainage (DRA), soil fertility (FER), radiation load (RAD), rainfall (RAI), rock cover (ROC) and slope (SLO) (see

Chapter 1 for details). The hypothesis that rarity was independent of the level of an environmental factor was tested using one-way ANOVA.

In order to test whether abundance was a function of resource availability, the range of values of all measured environmental factors in multivariate space for a particular species was calculated (Green, 1971; Carnes and Slade, 1982; MacNally, 1989). Because of the mathematical problems of using the mathematical range of environmental variables for abundance analysis, several studies have used canonical niche estimates as summary values (Gaston, 1994). Green (1971) defined "niche breadth" as the standard deviation of discriminant scores along axes, or the multidimensional volume bounded by the mean square of displacements of all sites occupied by one species (MacNally, 1989). Carnes and Slade (1982) verified the use of the standard deviation about the species centroid as a preferable measure of niche width, as opposed to the variation of species scores from the discriminant space origin, as used by Dueser and Shugart (1978). Root mean squared values can be extracted from Canonical Correspondence Analysis (CCA) analysis and a summary value for niche breadth can be obtained from the root mean square standard deviation across the first four axes (ter Braak, 1990). To over-come the problem of the positive relationship between sample size (*n*) and standard deviation, ter Braak (1990) suggests that for a presence-absence data set, such as was used here, the standard deviation should be divided by *sqrt(1-1/n)*. For this analysis, single occurrences were removed from the data set and discriminant score was produced using CANOCO (ter Braak, 1991).

Species distribution models

SELECTION OF A MODEL

Generalised linear models using presence-absence data, were used to develop predictive correlations of species and environmental relationships. Assuming independence of observations, it is likely that the data will follow a binomial distribution (Nicholls 1991a, Crawley 1993). The procedure for model fitting was according to Nicholls (1991a) and Crawley (1993), whereby using forward stepwise regression selection, variables were sequentially added using the computer package GLIM (Baker, 1987), to find the most parsimonious model. Where variables were continuous (e.g. altitude), both linear and quadratic functions were tested to account for possible curvature of the response variable. Those variables which accounted for the most significant change in the deviance were retained in the model to which each further variable was added. The final explanatory variance was calculated as a measure of the strength of the model (for details of method see example in Appendix II).

SELECTION OF SPECIES

The high number of rare species in the data set (Chapter 3) presented a problem in that modelling requires a reasonable representative sample. Those species which were well represented in this data set often occurred in a high number of habitats and consequently, had low predictive characteristics. To unravel these attributes, the species were sorted with respect to both number of plot occurrences (abundance) and habitat specificity. A further categorisation of constancy within a habitat is also required to adequately describe species fidelity (Shimwell, 1971; Kent and Coker, 1992). Classification (Chapter 2) using TWINSPAN (Hill, 1979) produced surprisingly low numbers of preferential species, largely owing to the low degree of constancy of fynbos species. For example, although a species may have only occurred in one habitat it was not found in quantity at most sites within that habitat, exhibiting therefore high fidelity but low constancy. For this reason a fidelity-constancy index was formulated to select a range of species suitable for modelling.

There appeared to be several categories of species distributions within and across habitats. Three main groups of fidelity were categorised here approximating to Braun-Blanquet's (1951) categories of fidelity.

(i) species which are generalists occurring throughout all, or most habitats (Braun-Blanquet's (1951) class 2).

(ii) species which occur commonly within several habitats (Braun-Blanquet's (1951) class 3).

(iii) species which occur in one habitat only (Braun-Blanquet's (1951) class 1).

In addition, within each of these habitats a species can be also classified according to its degree of constancy. The constancy (*C*) of a species (*i*) can be considered to be the average proportion of the number of species occurring in a habitat,

$$C_i = \frac{\sum\left(\frac{S_i}{N_j}\right)}{V_i} \qquad (1)$$

where S_i is the number of species (*i*) occurring in the *j*th vegetation type, N_j is the number of plots in the *j*th vegetation type, and V_i is the number of vegetation types containing the *i*th species.

Crudely, the fidelity of a species to a particular vegetation type can be considered to be the inverse of the total number of vegetation types in which that species occurs (*1/V*$_i$), that is, the more habitats, the lower the fidelity a species exhibits to any one of them. Combining this function with equation 1, an expression combining constancy and fidelity can be derived.

$$F_i = \frac{\sum\left(\frac{S_i}{N_j}\right)}{V_i^2} \quad (2)$$

For example, a species that occurs in all plots in all habitats has a lower fidelity than a species with occurrences in only one habitat. Similarly, a species which occurs in several plots in several habitats has a greater fidelity than a species with fewer plots in the same habitat. A species which occurs in all plots within a habitat has a fidelity of 1.0 and is independent of the number of plots in the vegetation type (N_j). Given these fidelity scores, a range of 19 species were selected for linear modelling to represent variation in abundance, fidelity and biological attributes (Table 4.1).

Results

Generally, rare plants were distributed with the same frequencies as non-rares, with regard to biological attributes (Tables 4.2-4.4). Rare plants were over-represented only among medium shrubs (30.6%) and forbs (29.2%)(Table 4.2). Arranged crudely in descending order of size class, there was little relationship between abundance and height, with the exception of a trend for more rare than common forbs (Fig. 4.1). Otherwise the proportion of rares to non-rares remained around 20% for all biological attributes (Tables 4.2 - 4.4).

Table 4.1. Attribute, fidelity index and explained variance of species selected for modelling. n_{tot} = number of species occurrences in the total data set which was used for the models; n_{sub} = number of species occurrences in subset of stratified plots used for rarity analysis; E.V. = explanatory variance of model; Fid. index = fidelity index.

Species	n_{tot}	n_{sub}	Fid. index	E.V.
Erica hispidula	52	6	0.04	0.386
Erica plukenetii	157	101	0.02	0.164
Anthospermum aethiopicum	121	40	0.02	0.045
Indigofera incana	12	2	0.23	0.621
Protea lepidocarpodendron	71	56	0.02	0.223
Asclepias cancellata	6	0	0.02	0.526
Osmitopsis astericoides	14	1	0.02	0.447
Mimetes fimbriifolius	13	8	0.01	0.272
Elegia stipularis	68	48	0.09	0.538
Chondropetalum ebracteatum	43	2	0.09	0.665
Hypodiscus wildenowia	21	16	0.02	0.356
Hypodiscus aristatus	112	42	0.02	0.249
Ursinia nudicaulis	26	0	0.46	0.744
Senecio crassulaefolius	2	1	0.05	0.170
Euphorbia caput-medusae	8	1	0.16	0.496
Bobartia gladiata	86	39	0.02	0.146
Aristea africana	40	24	0.13	0.601
Haemanthus coccineus	10	5	0.01	0.287

More frequently-occurring species generally occupied a larger number of vegetation types (Fig. 4.2) but these were the minority of the species in the data set. Over 85% occupied three vegetation types or less. The distribution of rare species between vegetation types varied significantly with proportionally more rare species in sand plain fynbos (17.5%), renosterveld (15.6%), mesic proteoid fynbos (13.3%) and wet oligotrophic fynbos (12.3%) (Table 4.5). The average density of rare species per plot varied across the range of environmental variables, with a trend towards more rare species on poorly drained, nutrient-poor soils (Fig. 4.3).

Table 4.2. The association between number (percentage) of rare species (one plot occurrence in data set, n = 254) and growth forms. $\chi^2 = 8.49$; df=5; $P > 0.1$. Low shrub = 0-1 m; medium shrub = 1-2 m; tall shrub = > 2 m.

Abundance	Growth form					
	Tall shrub	Medium shrub	Low shrub	Graminoid	Forb	Geophyte
Non-rare	28(82.3)	25(69.4)	230(80.1)	113(81.9)	81(70.8)	20(80.0)
Rare	6(17.6)	11(30.6)	57(19.9)	25(18.1)	35(29.2)	5(20.0)

Table 4.3. The association between the number (percentage) of rare species (one plot occurrence in data set, n = 254) and regeneration strategy. $\chi^2 = 0.704$; df = 1; $P > 0.40$.

Abundance	Regeneration strategy	
	Non-sprouter	Resprouter
Non-rare	290(77.1)	207(79.9)
Rare	86(22.9)	52(20.1)

Table 4.4. The association between the number (percentage) of rare species (one plot occurrence in the data set, n = 254) and dispersal mode. $\chi^2 = 1.14$; df = 2; $P > 0.5$.

Abundance	Dispersal mode		
	Passive	Wind	Ant
Non-rare	343(77.1)	90(79.6)	64(82.1)
Rare	102(22.9)	23(20.4)	14(17.9)

Table 4.5. The association between the number (percentage) of rare species and vegetation type (n= 254). $\chi^2 = 22.57$ df = 7 $P<0.01$. DUN = dune asteraceous fynbos; ERI/URF = ericaceous fynbos and upland restioid fynbos; MMP/MOP = mesic mesotrophic and oligotrophic proteoid fynbos; REN = renosterveld; SND = sand plain proteoid fynbos; WMP = wet mesotrophic proteoid fynbos; WOP = wet oligotrophic proteoid fynbos; WRF = wet restioid fynbos.

Abundance	Vegetation type							
	DUN	ERI/ URF	MMP/ MOP	REN	SND	WMP	WOP	WRF
Non-rare	199 (95.2)	135 (93.8)	365 (86.7)	81 (84.4)	33 (82.5)	109 (93.2)	100 (87.7)	229 (92.0)
Rare	10 (4.8)	9 (6.2)	56 (13.3)	15 (15.6)	7 (17.5)	8 (6.8)	14 (12.3)	2 (8.0)

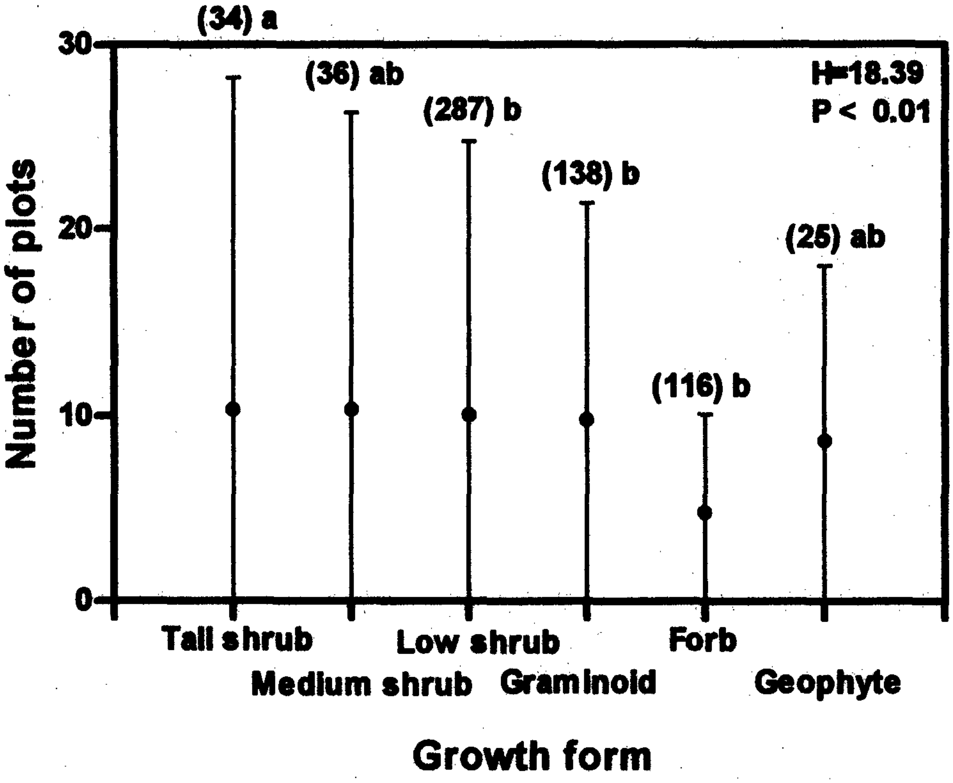


Figure 4.1 Mean number of plots occupied by species with different growth forms. Numbers in brackets indicate number of species; error bars = SD; graminoids = perennial species of Restionaceae, Poaceae, Cyperaceae and Juncaceae. Species with different labels are significantly different at the 0.05 level (non-parametric multiple comparison test of rank sums (Zar, 1984)).

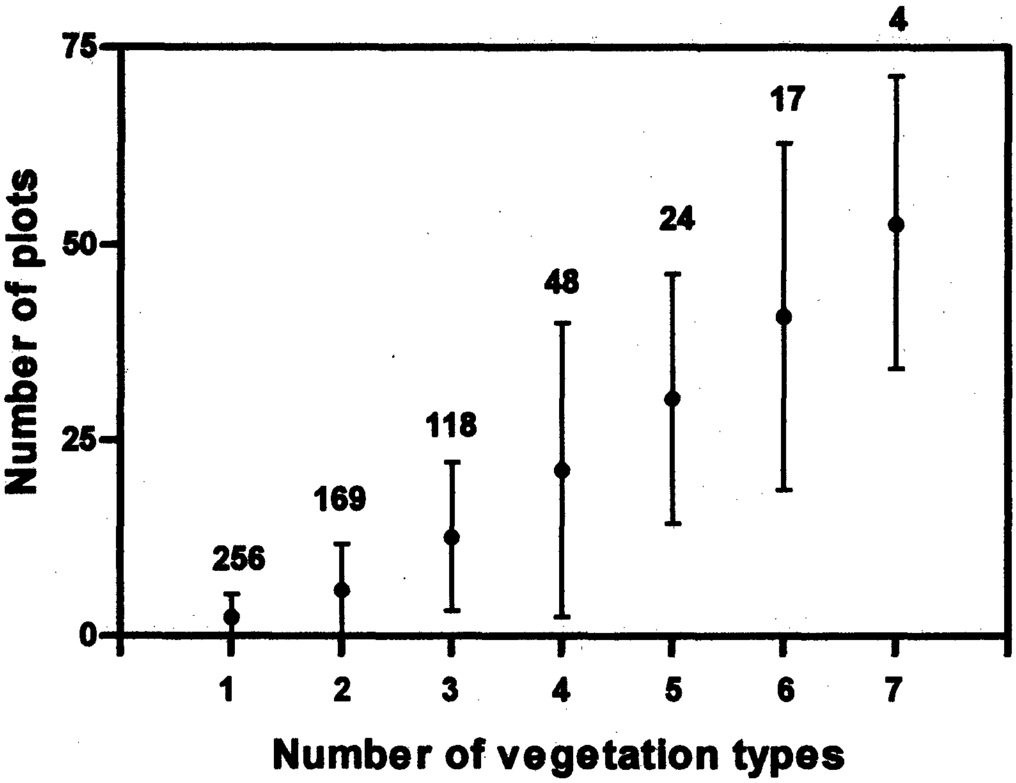


Figure 4.2 The relationship between mean number of species occurrences and number of occupied vegetation types. Labels indicate number of species.

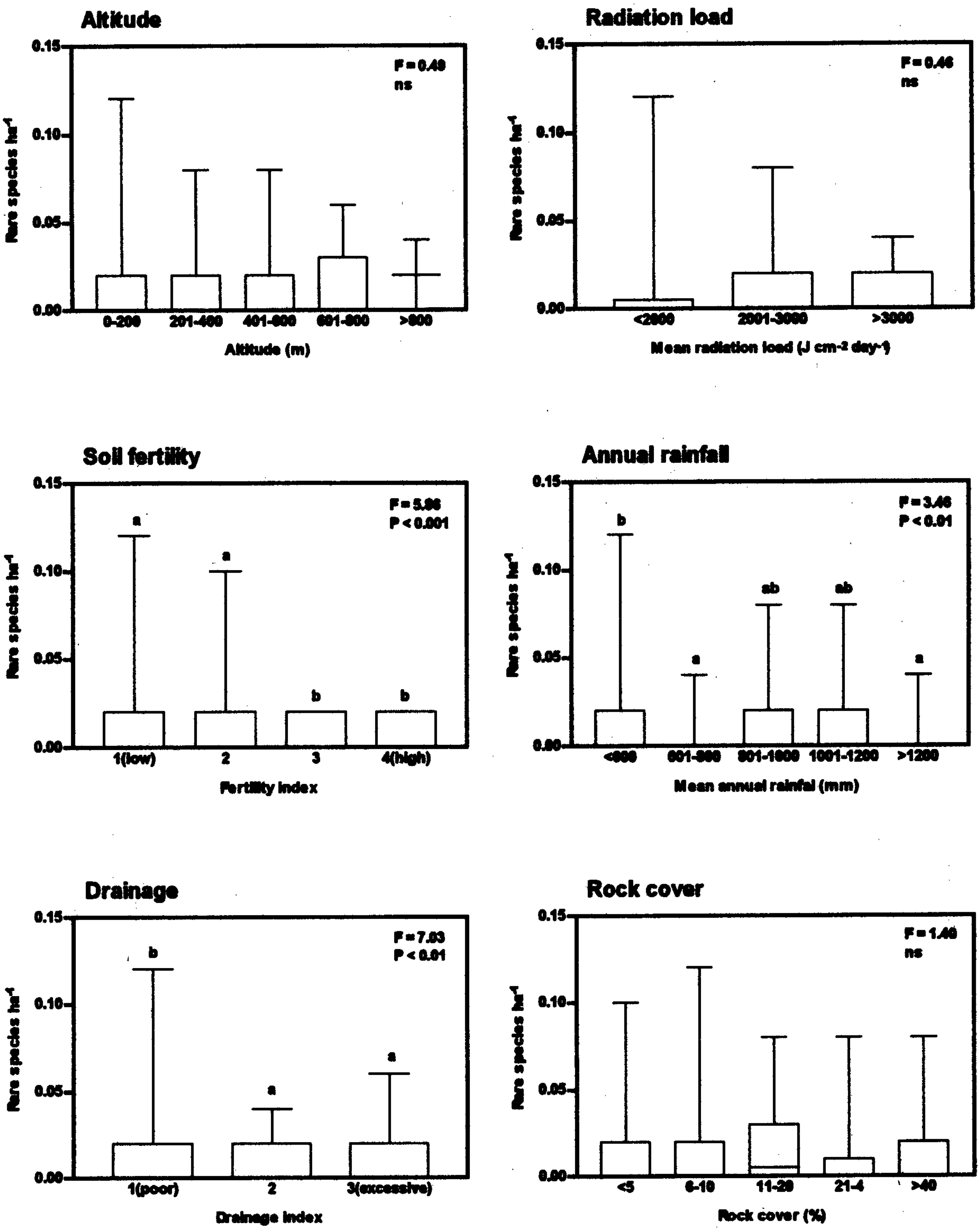


Figure 4.3 The mean and standard deviation of the plot density of rare species across environmental gradients. Groups with the same label are not significantly different at the 0.05 level (Tukey multiple range test).

Similarly, the average density of rare species varied between vegetation types (Kruskal-Wallis $H = 26.77$ $P<0.001$), although non-parametric multiple comparison testing of rank sums (Zar, 1984) showed significantly higher density of rare species in sand plain proteoid fynbos, and a significantly lower value for mesic proteoid fynbos (Fig. 4.4).

Using the collective score of root mean square of species scores of CCA, a marked inverse correlation was demonstrated between niche breadth and abundance ($r_s = -0.651$ $P<0.001$) (Fig. 4.5). Thus, rare species are generally distributed throughout a range of habitats on the Cape Peninsula, and not necessarily restricted by narrow environmental niches.

The generalised linear models produced values of explanatory power ranging from 4.5% to 74.4% (Table 4.1), but there was no relationship between this and species abundance ($r_s = -0.426$, $P > 0.5$) (Fig. 4.6), suggesting that rarer species are just as readily modelled as more common ones. The relationship between species' resource range and degree of species' habitat specialization is demonstrated by the log-log correlation between explained variance of the models and species fidelity ($r^2 = 39.5$, $P < 0.01$) (Fig. 4.7). Predictably, therefore, highly habitat-faithful species had the greatest explained variance, with habitat generalists producing the poorest models. *Anthospermum aethiopicum*, the outlier in Fig. 4.7, is a very common (second in this data set) generalist species but exhibited low explained variance for the fidelity value.

Although there was no significant correlation between number of species plot-occurrences and species fidelity index ($r_s = 0.118$ $P > 0.5$) (Fig. 4.8), rarer species displayed the greatest range of fidelity. A few abundant species are found in many habitats (see Fig. 4.2 and 4.8), but most are generalists occurred in a few plots. There is a lack of moderately

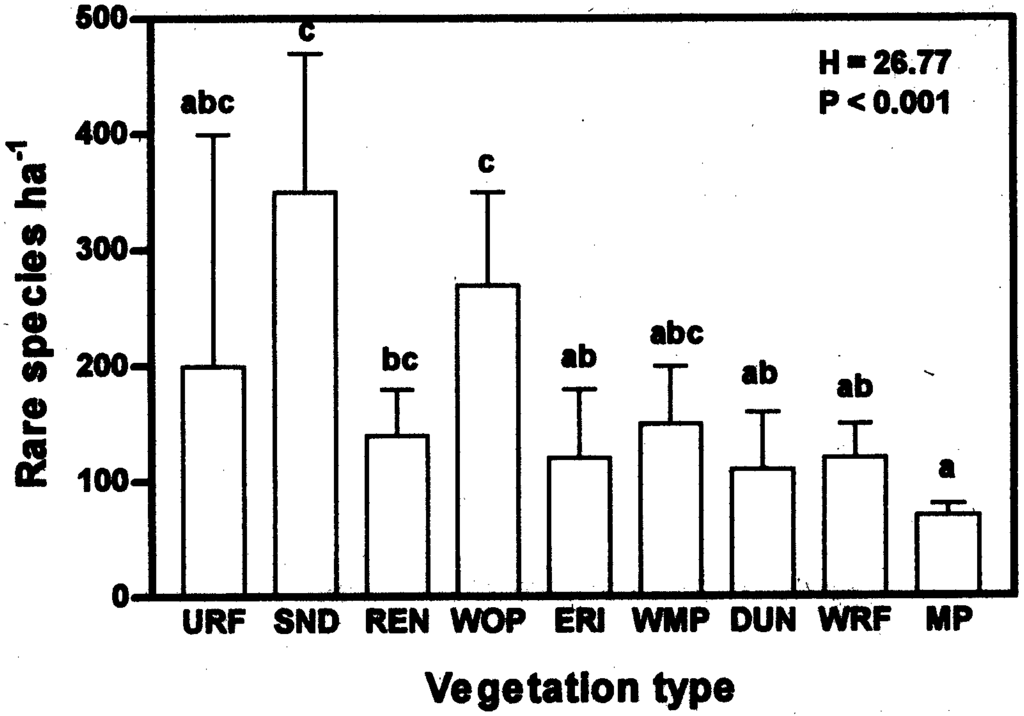


Figure 4.4 the mean and standard deviation of rare species density across environmental gradients. Groups with the same label are not significantly different at the 0.05 level (non-parametric comparison testing of rank sums (Zar, 1984)).

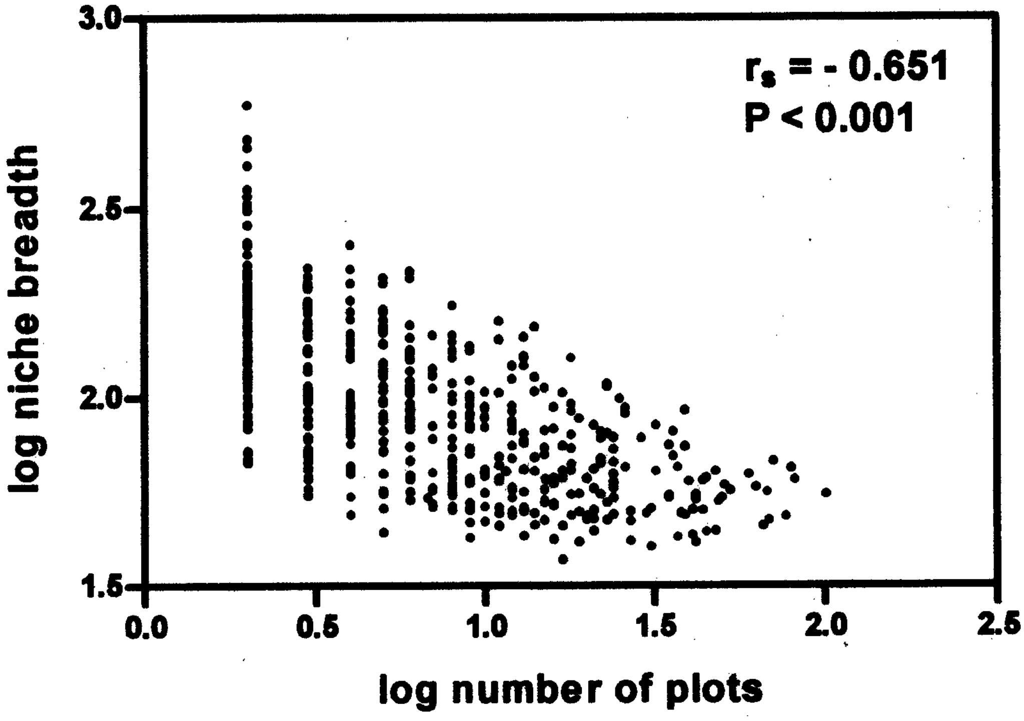


Figure 4.5 The relationship between niche breadth and number of species occurrences. r_s = Spearman rank correlation coefficient.

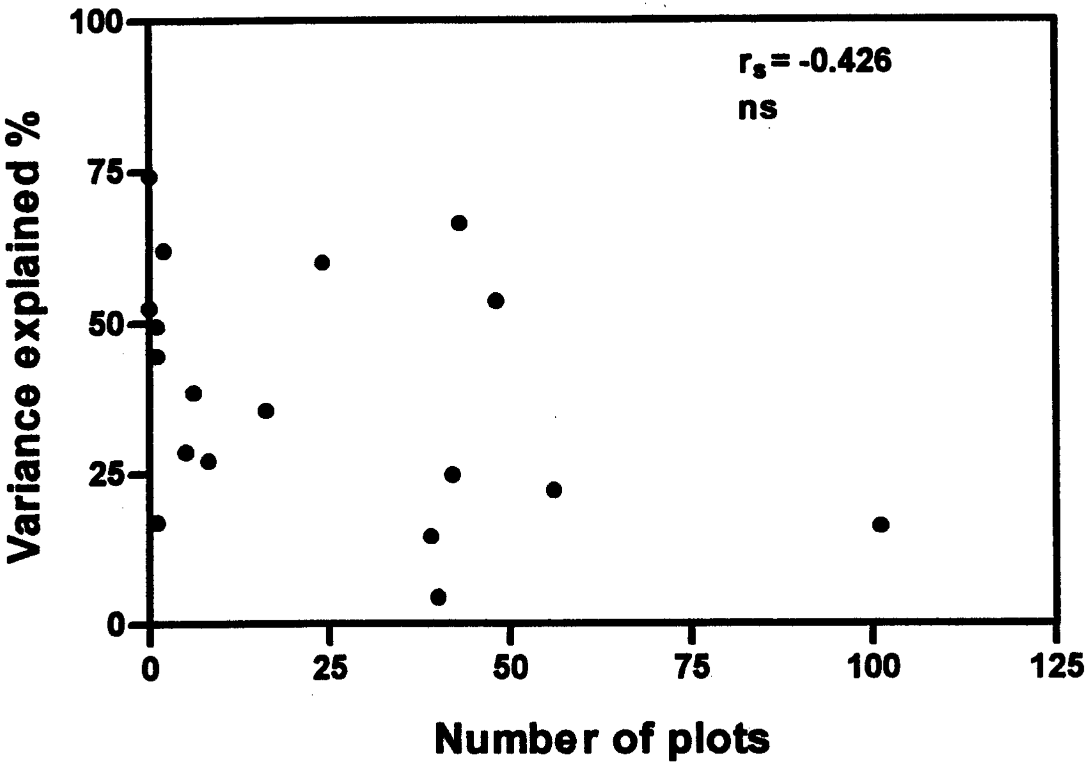


Figure 4.6 The relationship between number of species occurrences and explained variance in species-environment models (r_s = Spearman rank correlation coefficient).

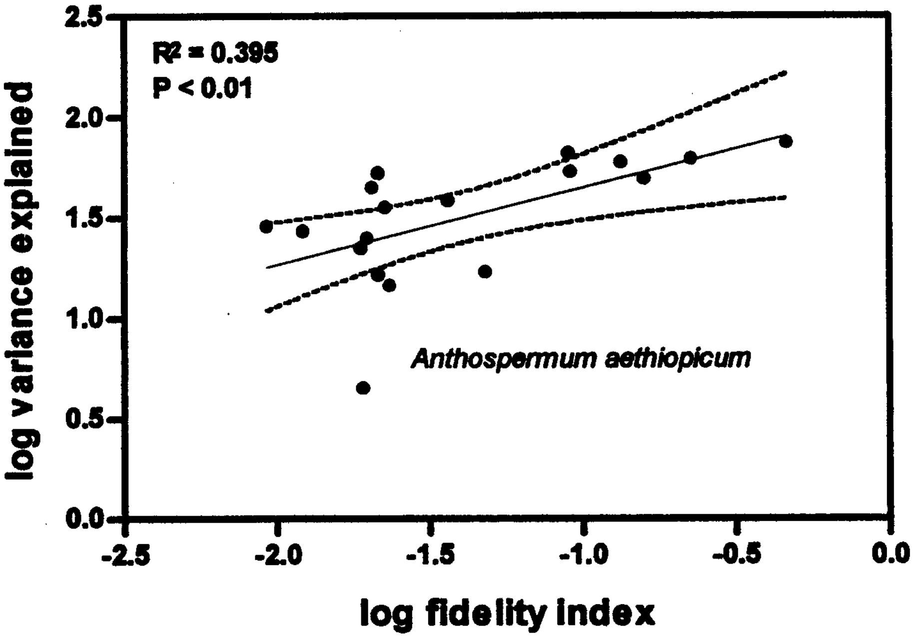


Figure 4.7 The relationship between fidelity index and explained variance in species-environment models. 95% confidence limits shown.

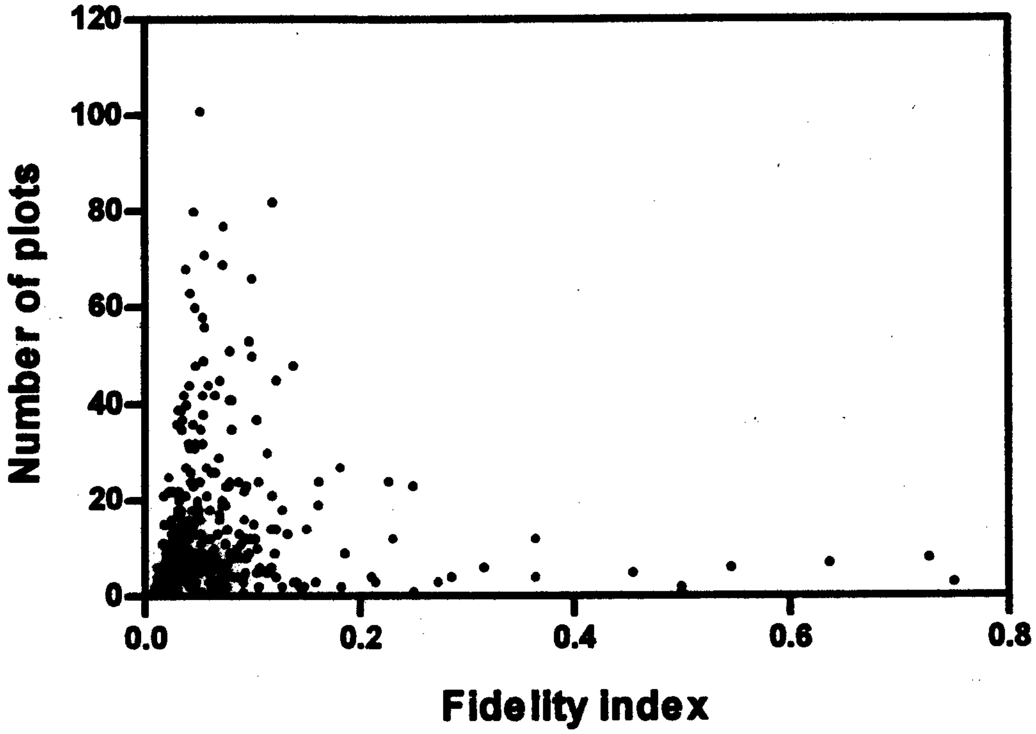


Figure 4.8 The relationship between fidelity index and number of species occurrences.

abundant species which have moderate fidelity values (Fig. 4.8).

Discussion

While range-restricted and threatened (Red Data Book) species are often habitat specialists, and associated with a particular suite of biological attributes (Trinder-Smith 1996a; McDonald *et al.*, 1995), this is not the case for the generally rare species as defined in this data set. Analysis of rarity and species biology showed no strong relationships, with the possible exception of the plant height (biomass), despite speculation that rarity would favour certain attributes (Trinder-Smith, 1996a). That larger species are rarer has been suggested before, particularly for animals (May, 1978; Griffiths, 1986) However, a hump-backed relationship between body-size and abundance has also been proposed (Brown and Maurer, 1987; Gaston and Blackburn, 1995). More typically, however, there is no general relationship between abundance and body mass across a wide range of organisms (Gaston, 1994).

There is little relationship between rarity and environmental factors. However, there was a slightly higher density of rare species on poorly drained, nutrient-poor, wetter sites; these are also associated with a higher number of endemics (Trinder-Smith, 1996a). As can be expected, more common species occupy a greater variety of vegetation types, but so do those which are less abundant. Most species occupy only a few habitats and true generalists are few; only 3.3 % of all species in the data set were found in six or more vegetation types. Although it has been shown that within fynbos, Red Data Book species, (most of which are endemics on the Cape Peninsula (Trinder-Smith, 1996a), are habitat specialists (Cowling and Holmes, 1992b; Linder *et al.*, 1993; McDonald and Cowling, 1995), community fidelity of Cape Peninsula species does not provide an indication of rarity. Rather, the total resource range, as plotted in multidimensional space, suggests that rarer species generally occupy a wider niche, than more abundant species (see also McCloskey, 1976; Seagle and MacCracken, 1986). Therefore, although somewhat counter-intuitive, it is proposed that rare plants are rare not because of the restrictions of habitat. Rather, this study has shown that they occupy a variety of vegetation types and are associated with a wide range of resource levels, but not as frequently occurring across vegetation types as some more abundant species. The conflict between these two results may be because in fynbos, the floristic community (i.e. vegetation type) definition is not necessarily in phase with all environmental variables which dictate a particular species distribution (see Chapter 2). This result also reflects the remarkably low number of abundant species in the Cape Peninsula flora. Most species tend to occur only in several plots throughout a range of vegetation types. It is the lack of very common species which is surprising.

If rare species are not limited by habitat then there must be an alternative explanation to account for their distribution. It has been proposed that rarity is a fundamental mathematical artifact of species distribution, where the log-normal abundance distribution is a result of random distribution of species in a patchy resource environment (Preston 1948; Colinvaux, 1973). Owing to its pronounced environmental heterogeneity, the Cape Peninsula offers a wide range of potential habitats (Chapter 3), and can harbour a wide range of habitat specialists. Situated on the boundary of east and west fynbos species pools, many taxa may be outside their optimal conditions, and hence climatically "residual" species.

Alternatively, rarer species may be out-competed following disturbance (Gaston, 1994). The unexplained variation of many of low-fidelity species could be related to species sensitivity to a variable fire regime. For example, true generalists, occurring throughout many vegetation types and in high concentrations are, by definition, unlikely to be as site- or fire-dependent as specialists. However, the abundance of species within a habitat which seem to be sometimes locally common and at other times sparse or absent, might be influenced directly by fire regime effects (e.g. Bond *et al.*, 1984), or indirectly through being outcompteted by another species which thrives on that fire/habitat combination (Bond *et al.*, 1990). Consequently, a non-equilibrium situation is maintained by variable fire regimes resulting in pulses in the abundance of species (Bond *et al.*, 1984). The species which is rare as a result of the last fire, may be the dominant species following the next. Thus, species fire-attributes should be considered to prevent local extinction of these fire-sensitive plant populations.

The higher concentration of less abundant species in sand plain proteoid fynbos and mesic proteoid fynbos coincides with a over-representation of threatened species in these habitats (Trinder-Smith *et al.*, 1996a). The location of these communities at low altitude has meant that the component species are susceptible to pressures of both urbanization and invasive plant species, and these areas have been dramatically reduced in size in historic times (Richardson *et al.*, 1996; Trinder-Smith *et al.*, 1996a). This may have therefore inflated the proportion of rare species in these habitats.

Notwithstanding the above, rarity has demonstrated little useful pattern at the phenomenon level. It is the modelling of the distribution of individual species, rare or otherwise, that presents the best predictive power. Predictably, those species with the greater degree of habitat specificity (i.e. fidelity) produced the most resolved predictive models. These were, however, correlated with habitat requirements and not the biology of those species. For management, this means that there is no difference between management strategy for rarer plants and common ones, other than maintaining a suite of habitats across the environmental gradients under variable fire regimes (see Chapter 3). However, maintaining a data bank of threatened species locations would enable predictive modelling to produce expected (probability) distribution maps for individual species and groups of species (Nicholls, 1991b). This would allow particular habitats to be prioritorized for conservation.

This study has highlighted the inadequacies of the data set for such a study. GLIM is a powerful method of predicting species distribution, especially those with specific habitat requirements. But stronger patterns may be detected with additional factors included in the data set. There is a noticeable lack of time series data, specifically concerning fluctuations in species abundance and fire history. One of the major benefits of GLIM is its ability to use ranked categorical data (e.g. age of vegetation, last fire intensity and season), and inclusion of such variables in the model may reveal more characteristics of rarity. Furthermore, the phenomenon of rarity has been assumed to be a continuous variable for these analyses, and the sampling method employed here, combined with the infrequent distribution of extremely rare (Red Data) species, has resulted in what may be the omission of highly significant data points. Some aspects of the biology, were not measured here and such attributes, such as competitive ability which may be independent of growth form and dispersal mode, may influence species regeneration potential.

Conclusions

There is no clear biological profile for widespread, rare species although there is a degree of habitat preference, and species with a wide niche breadth are rare. Further examination of the distribution of rare species should prioritise those habitats and locations on the Cape Peninsula which capture higher densities of diversity. General patterns of rarity found here suggest that although preservation of certain habitats will maintain the populations of certain rare species, there is no overall strategy directed at rare plants as a whole: hence, rare species are not essentially different from common ones. Thus, conservation of the habitat is the most effective way to preserve diversity (Rabinowitz, 1986). Fluctuation in population size may be due to fire-related stochasticity (Bond *et al.* 1990) and this requires further investigation. If there are species that require priority conservation status, management can be assisted by modelling at the species level, where given a large enough sample size, habitat requirements can be identified and consequently targeted for protection.

CHAPTER 5

Conclusions

If we are to conserve hotspots of diversity, such as the Cape Peninsula then every effort should be made to understand enough of the biology and ecology of the species and vegetation systems involved, to manage effectively. This study has attempted to describe patterns of species distributions and their respective determinants in an effort to aid management strategies for the area. Although detailed conclusions are incorporated into each chapter, several key components have been extracted from the analyses and are summarised here along with suggested guidance for future research.

Explanation of biological pattern is rarely perfect. Unexplained variance may result from the stochastic nature of natural systems or from the omission of explanatory variables which have been overlooked or are impractical to include. Therefore, the accurate description of phytosociology of fynbos has been traditionally time-consuming and problematic, largely on account of the nature of variable disturbance in such a fire-prone system. Nonetheless, the analyses in Chapter 2 demonstrated that the combination of standard phytosociological techniques and rapid, user-friendly field description may have produced a system of vegetation unit description applicable for reserve managers. Using listed suites of species in combination with broad environmental components which describe the habitat, restricts the vegetation identity problems encountered as a result of post-fire re-mixing of species composition.

The Cape Peninsula is rich in plant species at both a subcontinental and global scale, because of the exceptionally high turnover within and between habitats in a highly environmentally heterogeneous area. These patterns described in Chapter 3 have a clear lesson for conservation, that is, in order to maintain the area's biodiversity, it is not enough to conserve a particular 'representative' habitat, but proposed reserves must encompass environmental gradients at different geographic locations across the Cape Peninsula. Because gamma diversity may be related to area then further habitat fragmentation may necessitate active management of individual species.

Rare species (excluding range-restricted and Red Data Book species) are key contributors to this high diversity and therefore required enquiry. However, they do not exhibit strong biological attributes or environmental correlates. Rare plants can occupy as diverse a range of habitats as common ones. Therefore, their low abundance must be attributed to other factors not examined here. In terms of management requirements rarer plants are little different from common ones. Although this particular field requires more research, the results so far suggest that the best conservation policy is to preserve appropriately managed habitats. The identification of these areas can be aided with the use of suitable models (e.g. GLIM) for selected priority species.

The nature of the data prevented certain analyses and distorted the pattern. The data set was unbalanced in its representation of the Cape Peninsula's complex flora; some vegetation types were overlooked or at most, poorly represented and a more stratified sampling technique using the gradsect approach (Austin and Heyligers, 1991), would have been more desirable. However this study capitalised on a wealth of phytosociological data already collected on the Cape Peninsula, and only limited attempts were made to fill in the gaps in the distribution of sample plots. In addition, analysis of rare plants is inherently problematic, and in order to compile an accurate species model, more data points would be essential, especially considering that the Red Data Book species cannot be expected to be covered by such a sampling technique.

Perhaps the most noticeable component missing from the data set is that of fire history. Both the nature of last fire (for species models) and vegetation age (for phytosociological time-series analysis) would greatly enhance the descriptive characteristics of this study and possibly improve the predictive quality of the findings.

Nonetheless, this thesis has outlined fundamental patterns which could be used in assisting management of this area. It is hoped that despite the increasing pressures of development, and changing political priorities, such an internationally recognised centre of diversity will be maintained indefinitely.

REFERENCES

Adamson, R.S. (1927) The plant communities of Table Mountain. I. Preliminary account. *Journal of Ecology* **15**, 278-309.

Anonymous (1992) *Yearly weather report 1991*. Pretoria: Weather Bureau, Department of Environmental Affairs publication.

Arnold, T.H. and De Wet, B.C. (1993) Plants of southern Africa: names and distribution. *Memoirs of the Botanical Survey of South Africa* **62**.

Arroyo, M.T.K., Cavieres, L., Maticorena, C. and Munoz-Schlick, M. (1995) Convergence in the mediterranean floras in central Chile and California: insight from comparative biogeography. In *Ecology and biogeography of mediterranean ecosystems in Chile, California and Australia* (M.T.K. Arroyo, M. Fox and P. Zedler, eds.) pp. 43-88. Berlin: Springer-Verlag.

Austin, M.P. and Heyligers, P.C. (1991) New approach to vegetation survey design: gradsect sampling. In *Nature Conservation: cost effective biological surveys and data analysis.* (C.R. Margules and M.P. Austin eds.) Australia: CSIRO.

Baev, P.V. and Penev, L.D. (1993) *Biodiv: Program for calculating biological diversity parameters, similarity, niche overlap and cluster analysis.* Sofia: Pensoft.

Baker, R.J. (1987) *GLIM version 3.77 Reference Manual* (2nd edition) Oxford: Numerical Algorithms Group.

Begon, M., Harper, J.L. and Townsend, C.R. (1990) *Ecology: Individuals, Populations and Communities* (2nd edition) Oxford: Blackwell Scientific.

Bock, C.E. and Ricklefs, R.E. (1983) Range size and local abundance of some North American songbirds. *American Naturalist* **122**, 295-299.

Bond, P. and Goldblatt P. (1984) Plants of the Cape Flora. *Journal of South African Botany* supplement number 13.

Bond, W.J. (1981) *Vegetation gradients in southern Cape mountains*. Unpublished M.Sc. thesis, University of Cape Town.

Bond, W.J. (1983) On alpha diversity and richness of the Cape flora: a study in southern Cape fynbos. In *Mediterranean-type ecosystems: the role of nutrients*. (F.J. Kruger, Mitchell D.T. and J.U.M. Jarvis eds) pp. 337-356. Berlin: Springer-Verlag.

Bond, W.J. (1988) Proteas as 'tumble weeds': wind dispersed through air and over soil. *South African Journal of Botany* **54**, 455-460.

Bond, W.J., Vlok, J. and Viviers, M. (1984) Variation in seedling recruitment of Cape Proteaceae after fire. *Journal of Ecology* **72**, 209-221.

Bond, W.J., Le Roux, D. and Erntzen, R. (1990) Fire intensity and regeneration of myrmecochorous Proteaceae. *South African Journal of Botany* **56**, 326-330.

Bond, W.J., and Slingsby, P. (1983) Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *South African Journal Science* **79**, 231-233.

Bond, W.J. and Van Wilgen, B.W. (1996) *Fire and plants*. London: Chapman and Hall.

Bond, W.J., Vlok, J. and Viviers, M. (1984) Variation in seedling recruitment of Cape Proteaceae after fire. *Journal of Ecology* **72**, 209-221.

Braun-Blanquet J. (1951) *Plant Sociology: The study of Plant Communities*. New York: McGraw-Hill.

Brown, J.H. (1988) Species diversity. In *Analytical biogeography. An integrated approach to the study of animal and plant distributions*. (A.A. Myers and P.S. Giller eds.) pp. 57-89. London: Chapman and Hall.

Brown, J.H and Maurer, B.A. (1987) Evolution of species assemblages: effects of energetic constraints and species dynamics on diversification of the North American avifauna. *American Naturalist* **130**, 1-17.

Campbell, B.M. (1985) A classification of the mountain vegetation of the fynbos biome. *Memoirs of the Botanical Survey of South Africa* **50**, 1-121.

Campbell, B.M. (1986a) Montane plant communities in the fynbos biome. *Vegetatio* **6** 3-16.

Campbell, B.M. (1986b) Vegetation classification in a floristically complex area: the Cape Floristic Region. *South African Journal of Botany* **52**, 129-140.

Campbell, B.M. and Moll, E.J. (1977) The forest communities of Table Mountain, South Africa. *Vegetatio* **34** 105-115.

Carnes, B.A. and Slade, N.A. (1982) Some comments on niche analysis in canonical space. *Ecology* **63**, 888-893.

Cody, M.L. (1986) Diversity, rarity and conservation in mediterranean-climate regions. In *Conservation biology. The science of scarcity and diversity*. (M.E. Soule ed.) pp. 122-152. Sunderland, Massachusetts: Sinauer Associates.

Cody, M.L. (1993) Bird diversity components within and between habitats in Australia. In *Species diversity in ecological communities: Historical and geographical perspectives*. (R.E. Ricklefs and D. Schluter eds.) pp. 350-363. Chicago: University of Chicago Press.

Colinvaux, P.A. (1973) *Introduction to Ecology*. New York: Wiley.

Cowling, R.M. (1983a) Diversity relations in Cape shrublands and other vegetation in the southeastern Cape, South Africa. *Vegetatio* **54**, 103-127.

Cowling, R.M. (1983b) Phytochorology and vegetation history in the south eastern Cape, South Africa. *Journal of Biogeography* **10**, 393-419.

Cowling, R.M. (1987) Fire and its role in coexistence and speciation in Gondwanan shrublands. *South African Journal of Science* **83**, 106-112.

Cowling, R.M. (1990) Diversity components in a species-rich area of the Cape Floristic Region. *Journal of Vegetation Science* 1 699-710.

Cowling, R.M., Campbell B.M., Mustart, P., McDonald, D.J., Jarman, M.L. and Moll, E.J. (1988) Vegetation classification in a floristically complex area: the Agulhas Plain. *Journal South African Botany* **54**, 290-300.

Cowling, R.M. and Gxaba, T. (1990) Effects of a fynbos overstorey shrub on understorey community structure: implications for the maintenance community-wide species richness. *South African Journal of Ecology* 1, 1-7.

Cowling, R.M. and Holmes, P.M. (1992a). Flora and Vegetation. In: *The ecology of fynbos - nutrients, fire and diversity*. (R.M. Cowling ed.) pp. 23-61. Cape Town: Oxford University Press.

Cowling, R.M. and Holmes, P. (1992b) Endemism and speciation in the lowland flora from the Cape Floristic Region. *Biological Journal of the Linnean Society* **47**, 393-419.

Cowling, R.M, Holmes, P.M., and Rebelo, A.G. (1992) Plant diversity and endemism. In: *The ecology of fynbos - nutrients, fire and diversity*. (R.M. Cowling ed.) pp. 206-225. Cape Town: Oxford University Press.

Cowling, R.M. and Macdonald, I.A.W. and Simmons, M.T (1996) The Cape Peninsula, South Africa: Physiological, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation* **5** 527-550.

Cowling, R.M. and McDonald, D.J. (in press) Local endemism an plant conservation in the Cape Floristic Region. In *Mediterranean-type ecosystems. Land Degradation.* (P.W. Rundel, G. Montenegro and F. Jaksic eds.) Berlin: Springer Verlag.

Cowling, R.M., Richardson, D.M., Schulze, R.E., Hoffman, M.T., Midgley, J.J. and Hilton-Taylor, C. (in press) Species diversity at the regional scale. In *Vegetation of Southern Africa*. (R.M. Cowling and D.M. Richardson eds.) Cambridge: Cambridge University Press.

Cowling, R.M. and Samways M.J. (1995) Endemism and biodiversity. In *Global biodiversity assessment* (V.H. Heywood ed.) pp. 174-191 Cambridge: Cambridge University Press.

Crawley M.J. (1993) *GLIM for ecologists*. Oxford: Blackwell Scientific Publications.

Deacon, H.J. (1983) An introduction to the fynbos region, timescales and palaeoenvironments. In: *Fynbos palaeoecology: a preliminary synthesis*. (H.J. Deacon, Q.B. Hendley and J.N.N. Lambrechts eds.) pp. 1-20. Pretoria: South African Scientific Programmes Report **75**.

Deacon, H.J., Dury, M.R. and Ellis, F. (1992). Selective regime and time. In: *The ecology of fynbos - nutrients, fire and diversity*. (R.M. Cowling ed.) pp. 6-22. Cape Town: Oxford University Press.

Diamond, J.M. (1988) Factors controlling species diversity: overview and synthesis. *Annals of the Missouri Botanical Garden* **75**, 117-129.

Dueser, R.D. and Shugart H.H. (1978) Microhabitats in a forest- floor small-mammal fauna. *Ecology* **59**, 89-98.

Du Toit, A.L. (1954) *The Geology of South Africa*. London: Oliver and Boyd.

Esler, K.J. and Cowling, R.M. (1990) The effects of density on the reproductive output of *Protea lepidocarpodendron*. *South African Journal of Botany* **56**, 29-33.

Gaston, K.J. (1994) *Rarity*. London: Chapman and Hall.

Gaston, K.J. and Blackburn, T.M. (1995) Rarity and body size: some cautionary remarks. *Conservation Biology* **9**, 210-213.

Gauch, H.G. (1982) *Multivariate analysis in community ecology*. Cambridge Studies in Ecology. Cambridge: Cambridge University Press.

Gibson, N., Keighery, B.J., Keighery, A.H., Burbridge, A.H. and Lyons, M. (1994) *A floristic survey of the southern Swan Coastal Plain*. Perth: Department of Conservation and Land Management, Heritage Council of W.A.

Glyphis, J., Moll, E.J. and Campbell, B.M. (1978) Phytosociological studies on Table Mountain, South Africa: 1. The Back Table. *Journal South of African Botany* **44**, 281-289.

Goldblatt, P. (1978) An analysis of the flora of southern Africa: its characteristics, relationships and origins. *Annals Missouri Botanic Gardens* **75**, 1-34.

Graham, R.W. (1988) The role of climatic change in the design of biological reserves. The paleoecological perspective for conservation biology. *Conservation Biology* **2**, 391-394.

Green, R.H. (1971) A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. *Ecology* **52**, 543-556.

Griffiths, D. (1986) Size-abundance relations in communities. *American Naturalist* **127**, 140-607.

Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**, 107-45.

Hanski, I. (1982) Dynamics of regional distribution:the core and satellite species hypothesis. *Oikos* **38**, 210-221.

Hanski, I. and Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**, 3-16.

Hill, M.O. (1979) *TWINSPAN - a Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attribute.* Ithaca, New York: Section of Ecology and Systematics, Cornell University.

Hill, M.O. and Guach, H.G. (1980) Detrended correspondence analysis, an improved ordination technique. *Vegetatio* **42**, 47-58.

Johnson, S.D. and Bond, W.J. (1992) Habitat dependent pollination success in a Cape orchid. *Oecologia* **91**, 455-456.

Joubert, C. and Moll, E.J. (1992) A phytosociological study of Signal Hill, Cape Town, utilizing both perennial and ephemeral species. *Bothalia* **22**, 255-282.

Kent, M and Coker, P. (1992) *Vegetation Description and Analysis*. London: Belhaven Press.

Kruger, F.J. (1974) *The physiography and plant communities of Jakkalsrivier catchment.* M.Sc. thesis. University of Stellenbosch.

Kruger, F.J. (1979) South African heathlands. In *Heathlands of the World. A. Cescriptive Studies.* (R.L. Specht, ed.) pp. 19-84. Amsterdam: Elsevier

Kruger, F.J. and Taylor, H.C. (1979) Plant species diversity in Cape fynbos: gamma and delta diversity. *Vegetatio* **47**, 85-93.

Kunin, W.E. and Gaston, K.J. (1993) The biology of rarity: patterns, causes and consequences. *TREE* **8**, 298-301.

Laider, D., Moll, E.J., Campbell, B.M. and Glyphis, J. (1978) Phytosociological studies on Table Mountain, South Africa: 2. The Front Table. *Journal of South African Botany* **44**, 291-295.

Le Maitre, D.C. (1987) Effects of season of burn on species populations and composition of fynbos in the Jonkershoek valley. *South African Journal of Botany* **53**, 284-292.

Levyns, M.R. (1964) Migrations and origin of the Cape Flora. *Transactions of the Royal Society of South Africa* 37 85-107.

Linder, H.P., Meadows, M.E. and Cowling, R.M. (1992) History of the Cape Flora. In *The ecology of fynbos - nutrients fire and diversity*. (R.M. Cowling ed.) pp. 113-134. Cape Town: Oxford University Press.

Linder, H.P., Vlok, J.H., McDonald, D.J., Oliver, E.G.H., Boucher, C., van Wyk, B.E. and Schutte, A. (1993) The high altitude flora and vegetation of the Cape Floristic Region, South Africa. *Opera Botanica* 121, 247-261.

Luckhoff, C.A. (1951) *Table Mountain*. Cape Town: A.A. Balkema.

MacNally, R.C. (1989) The relationship between habitat breadth, habitat position, and abundance in forest and wood land birds along a continental gradient. *Oikos* 54, 44-54.

Magurran, A.E. (1988) *Ecological diversity and its measurement*. London: Croom Helm.

Manders P.T. (1990) Fire and other variables as determinants of forest/fynbos boundaries in the Cape Province. *Journal of Vegetation Science* 1, 483-490.

Marloth, R. (1903). Results of experiments on Table Mountain for ascertaining the amounts of moisture deposited from south-east clouds. *Transactions of the South African Philosophical Society* 14, 403-409.

Marloth, R. (1905) Results of further experiments on table mountain for ascertaining the amounts of moisture deposited from the south-east clouds. *Transactions of the South African Philosophical Society* 16, 97-105.

May, R.M. (1978) The dynamics of and diversity of insect faunas. In *Diversity of insect faunas*. (L.A. Mound and N. Waloff eds.) *Symposium of the Royal Entomological Society of London* 9 pp 188-204. Oxford: Blackwell Scientific Publications.

McCloskey, R.T. (1976) Community structure in sympatric rodents. *Ecology* 57, 728-739.

McDonald D.J. (1987) Ordination by detrended correspondence analysis (DCA) of the vegetation of Swartboschkloof, Jonkershoek, Cape Province. *Bothalia* **17**, 121-129.

McDonald D.J. (1993a) The vegetation of the southern Langeberg, Cape Province 1. The plant communities of the Boosmansbos Wilderness Area. *Bothalia* **23** 129-151.

McDonald D.J. (1993b) The vegetation of the southern Langeberg, Cape Province 2. The plant communities of the Marloth reserve. *Bothalia* **23**, 153-174.

McDonald D.J. (1993c) The vegetation of the southern Langeberg, Cape Province 3. The plant communities of the Bergfontein, Rooiwaterspruit and Phesantefontein areas. *Bothalia* **23** 239-263.

McDonald, D.J. and Cowling, R.M. (1995) Towards a profile of an endemic mountain fynbos flora: implications for conservation. *Biological Conservation* **72**, 1-12.

McDonald, D.J., Cowling, R.M. and Boucher, C. (1996) Vegetation-environment relationships on a species-rich coastal mountain range in the fynbos biome (South Africa). *Vegetatio* **123**,165-182.

McDonald, D.J., Juritz J.M, Cowling, R.M. and Knotterbelt W.J. (1995) Modelling the biological aspects of local endemism in South African fynbos. *Plant Systematics and Evolution* **195**, 137-147.

McKenzie, B., Moll, E.J. and Campbell, B.M. (1977) A phytosociological study of Orange Kloof, Table Mountain, South Africa. *Vegetatio* **34**, 1-53.

Midgley, J. and Seydack, A. and Van Wyk, G.F. (in press) *Forest Biome*. In *Vegetation of Southern Africa*. (R.M. Cowling and D.M. Richardson eds.) Cambridge: Cambridge University Press.

Moll, E.J. and Romoff, N. (1983). Evidence of mist trapping by *Thamnocortus punctatus* Pillans at Pella in the southwestern Cape Province. *South African Journal of Science* **79**, 432-437.

Moll, E.J. and Campbell B.M. (1976). The ecological status of Table Mountain. In: *Table Mountain: a conservation and management report.* Unpublished report, Department of Botany, University of Cape Town.

Mueller-Dombois, D. and Ellenberg, H. (1974) *Aims and methods of vegetation ecology.* New York: Wiley.

Mustart, P.J. and Cowling, R.M. (1993) The role of regeneration stages in the distribution of edaphically restricted fynbos Proteaceae. *Ecology* **74**, 1490-1499.

Myers, N. (1990) The biodiversity challenge: expanded hot-spot analysis. *The Environmentalist* **8**, 1-20.

Nicholls, A.O. (1991a) An introduction to statistical modelling using GLIM. In *Nature Conservation: cost effective biological surveys and data analysis.* (C.R. Margules and M.P. Austin eds.) pp. 191-201. Australia: CSIRO.

Nicholls, A.O. (1991b) Examples of the use of generalised linear models in analysis of survey data for conservation evaluation. In *Nature Conservation: cost effective biological surveys and data analysis.* (C.R. Margules and M.P. Austin eds.) pp. 54-63. Australia: CSIRO.

Oliver, E.G.H., Linder, H.P. and Rourke, J.P. (1983) Geographical distribution of present day Cape taxa and their phytogeographical significance. *Bothalia* **18**, 1-10.

Prendergast, R., Quinn, R.M., Lawton, J.H., Eversham, C. and Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335-337.

Preston, F.W. (1948) The commoness and rarity of species. *Ecology* **29**, 254-83.

Preston-Whyte, R.A. Tyson, P.D. (1988) *The atmosphere and weather of southern Africa.* Cape Town: Oxford University Press.

Rabinowitz, D., Cairns, S. and Dillon, T. (1986) Seven forms of rarity and their frequency in the flora of the British Isles. In *Conservation biology: The science of scarcity and diversity*. (M. Soule ed.) pp. 182-204. Sunderland, Massachusetts: Sinauer Associates Inc.

Richards, M.B. (1993) *Soil factors and competition as determinants of fynbos plant species distributions in south-western Cape, South Africa.* M.Sc. thesis. University of Cape Town.

Richards M.B., Cowling R.M. and Stock, W.D. (1995) Fynbos plant communities and vegetation - environment relationships in the Soetanysberg hills, Western Cape. *South African Journal of Botany* **61**, 298-305.

Richardson, D.M and van Wilgen, B.W. (1986) Effects of thirty-five years of afforestation with *Pinus radiata* on the composition of mesic mountain fynbos near Stellenbosch. *South African Journal of Botany* **52**, 309-315.

Richardson, D.M., van Wilgen, B.W., Higgins, S.I., Trinder-Smith, T.H., Cowling, R.M. and McKelly, D.H. (1996) Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodiversity and Conservation* **5**, 607-647.

Ricklefs, R.E. (1987) Community diversity: Relative roles of local and regional processes. *Science* **235**, 167-71.

Ricklefs, R.E. and Schluter, D. (1993) Species diversity: regional and historical influences. In *Species diversity in ecological communities: historical and geographical perspectives*. (R.E. Ricklefs and D. Schluter eds.) pp. 350-363. Chicago: University of Chicago Press, Chicago.

Rosenzweig, M.L. (1992) Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy* **73**, 715-730.

Rosenzweig, M.L. and Abramsky, Z. (1993) How are diversity and productivity related. In *Species diversity in ecological communities: historical and geographical perspectives*. (R.E. Ricklefs and D. Schluter eds.) pp. 52-65. Chicago: University of Chicago Press.

Seagle, S.W. and MacCracken, G.F. (1986) Species abundance, niche position, and niche breadth for five terrestrial animal assemblages. *Ecology* 67, 816-818.

Snow, C. (1985) *Mist interception by three species of mountain fynbos*. Unpublished M.Sc. thesis. University of Cape Town.

Shenbrot, G.I., Rogovin, K.A. and Surov, A.V. (1991) Comparative organization of desert lizard communities in Middle Asia and Mexico. *Oikos* 41, 157-168.

Shimwell, D.W. (1971) *Description and Classification of Vegetation*. London: Sidgewick and Jackson.

Shmida, A. and Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography* 12, 1-20

Stacey, P.B. and Taper, M. (1992) Environmental variation and the persistence of small populations. *Ecological Applications* 2, 18-29.

Swift, L.W. (1976) Algorithm for solar radiation on mountain slopes. *Water Resources Research* 12, 108-112.

Takhtajan, A. (1986) *Floristic regions of the world*. Berkeley: University of California Press.

Taylor, H.C. (1969) *A vegetation survey of the Cape of Good Hope Reserve*. Unpublished M.Sc. thesis. University of Cape Town.

Taylor, H.C. (1978) Capensis. In: *Biogeography and ecology of southern Africa*. (M.J.A. Werger ed.). The Hague: Junk.

Taylor, H.C. (1996) Cederberg vegetation and flora. *Strelitzia* 3.

ter Braak, C.J.F. (1990) *Update notes: Canoco version 3.1*. Wageningen: Agricultural Group.

ter Braak, C.F.J. (1991) *CANOCO - a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis and redundancy analysis (version 3.12)*. Wageningen: Agricultural Mathematics Group.

Theron, J.N. (1983). Geological setting of the fynbos. In *Fynbos palaeoecology: a preliminary synthesis*. (H.J. Deacon Q.B. Hendley Q.B. and J.J.N. Lambrechts eds.) pp. 21-34. Pretoria:South African Scientific Programmes Report 75, CSIR.

Theron, J.N., Gresse, P.G., Siegfried, H.P. and Rogers, J. (1992). *The geology of the Cape Town Area*. Pretoria: Department of Mineral Affairs, Government Printers.

Tilman, D. and Pacala, S. (1993) The maintenance of species richness in plant communities. In *Species diversity in ecological communities: historical and geographical perspectives*. (R.E. Ricklefs and D. Schluter eds.) pp. 13-25. Chicago: University of Chicago Press.

Tinley, K.L. and Heydorn, A.E.F. (1980). *Estuaries of the Cape. Part I. Synopsis of the Cape coast - natural features, dynamics and utilization*. Stellenbosch: CSIR.

Trinder-Smith, T.H. (1995) *Flora of the Cape Peninsula: Endemism, threatened plants and conservation in perspective*. Unpublished M.Sc. thesis. University of Cape Town.

Trinder-Smith, T.H., Cowling, R.M. and Linder, H.P. (1996a) Profiling a besieged flora: endemic and threatened plants of the Cape Peninsula, South Africa. *Biodiversity and Conservation* **5**, 575-590.

Trinder-Smith, T.H., Lombard, A.T. and Picker, M.D. (1996b) Reserve scenarios for the Cape Peninsula: high-, middle- and low-road options for conserving the remaining biodiversity. *Biodiversity and Conservation* **5**, 649-670.

Turner, B.R. (1987) *Research report on sedimentology and depositional environments of the Graafwater and Peninsula formations in the Cape Peninsula, South Africa.* CSIR-FRD unpublished report, University of Cape Town.

UCT (1994) *Policy for multipurpose use of the Cape Peninsula. Volume 1. Main Report.* Cape Town: University of Cape Town.

van Wilgen, B.W. (1996) Management of the natural ecosystems of the Cape Peninsula: current status and future prospects. *Biodiversity and Conservation* **5**, 671-684.

van Wilgen, B.W., Bond W.J. and Richardson, D.M. (1992) Ecosystem management. In: *The ecology of fynbos - nutrients, fire and diversity*. (R.M. Cowling ed.) pp. 345-371. Cape Town: Oxford University Press.

Werger, M.J.A. (1974) On concepts and techniques applied in the Zurich-Montpellier method of vegetation survey. *Bothalia* **11**, 309-323.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* **21**, 213-251.

Whittaker, R.H. (1977) Evolutions of species diversity in land communities. *Evolutionary Biology* **10**, 1-67.

Williamson, M. (1988) Relationship of species number to area, distance and other variables. In *Analytical biogeography. An integrated approach to the study of animal and plant distributions*. (A.A. Myers and P.S. Giller eds.) pp. 91-115. London: Chapman and Hall.

Wilson, M.V. and Shmida, A. (1984) Measuring beta diversity with presence-absence data. *Journal of Ecology* **72**, 1055-1064.

Wright, D.H., Currie, D.J. and Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. In *Species diversity in ecological communities: historical and geographical perspectives*. (R.E. Ricklefs and D. Schluter eds.) pp. 66-74. Chicago: University of Chicago Press.

Zar, J.H. (1984) *Biostatistical Analysis* (2nd edition). Englewood Cliffs: Prentice-Hall.

APPENDIX I

Phytosociological table of fynbos shrublands on the Cape Peninsula.

Table 1

Due to the dimensions of this phytosociological table only the top right-hand corner is shown here. The complete tables are on the enclosed disk in three softare formats, one file per table (e.g. TABLE1.WK1): Lotus/Quattro Pro (*.wk1); Excel (*.xls). The data are arranged in four tables; two representing fynbos communities and two tables containing forest, thicket, remosterveld and dune fynbos (see Chapter 2).

Aspect (o True)	270	250	45	207	225	225	225	225	180	180	115	135	90	270	315
Altitude (m)	505	40	140	120	200	200	140	120	210	65	6	3	5	6	5
Radiation load (J cm-2 day-1)	3051	2759	3051	2165	2704	2900	1906	2349	3001	3001	3015	3010	3051	3051	3051
Fertility index	4	3	4	4	4	4	4	4	4	2	2	2	2	2	2
Mean annual rainfall (m)	10	7	9	7	9	9	9	9	9	6	6	6	6	6	6
Drainage index	3	2	1	1	3	3	1	1	1	3	2	2	3	2	3
Rock cover (%)	0	10	5	20	0	0	15	25	0	0	0	0	0	0	0
Slope (o)	30	2	4.83	5	27	10.66	4.66	3.66	30	5.66	32	35	31	22	29
Releve	708	80	323	331	174	175	324	325	330	806	831	836	829	881	834
Veg Type	SND	SND	SND	SND	SND	SND	SND	SND	SND	SND	SND	SND	SND	SND	SND
Berzelia abrotanoides															
Carpacoce vaginellata															
Ischyrolepis cincinnata															
Pentaschistis curvifolia			1	1				1							
Willdenowia glomerata															
Elegia neesii															
Ischyrolepis capensis										1					
Pentaschistis colorata															
Restio quinquefarius															
[illegible]															
Acrolophia capensis									1						
Adenandra uniflora															
Agathelpis dubia															
Agathosma hookeri															
Amphithalea ericifolia															
Anthospermum bergianum															
Aristea africana															
Aspalathus cymbiformis															
Aspalathus linguiloba															
Bobartia filiformis															
Chironia decumbens															
Cliffortia subsetacea															
Corymbium africanum subsp. scabridum															
Crassula fascicularis															
Dilatris corymbosa															
Elegia cuspidata															
Elegia stipularis															
Erepsia bracteata															
Erica calycina															
Erica imbricata															
Euphorbia genistoides															
Euphorbia silenifolia															
Ficinia bulbosa										1					
Ficinia pinguior															
Ficinia secunda										1					
Gnidia imbricata															
Gnidia subulata															
Hypodiscus willdenowia										1					
Ifloga ambigua															
Lachnaea densiflora															
Lampranthus [illegible]															
Leucadendron laureolum															
Lightfootia longifolia															
Liparia parva															
Lobelia coronopifolia															
Lobelia setacea															
Metalasia brevifolia									1						
Metalasia cephalotes															
Osteospermum polygaloides															
Petalacte coronata															

APPENDIX II

Example of variable selection for generalised linear model for *Chondropetalum ebracteatum*.

For presence-absence data as used in this analysis, it was assumed that the data followed a binomial distribution and a logistic regression (Nicholls, 1991b; Crawley, 1993). Using the logit function the probability (*p*) of a species occurring on a site is

$$p=e^{l}(e^{l}+1)$$

where *l* is the linear predictor calculated from the model.

To construct the model, each variable is initially added singly to the null model to establish any significant change in deviance (Table 1). Continuous variables are squared to test for a curved response. The significance of the change in deviance is tested assuming that it follows a χ^2 distribution. Each of the significant variables is then added cumulatively to the model to asses significant deviance change (Table 2). Finally, the estimated parameters (Table 3) are entered into the linear equation to calculate *l*. The overall change in deviance is used to calculated the proportion of explained variance, that is the change in deviance divided by the deviance of the initial null model. In this example the model explained 66.5 % of the variance.

$$l=-10.27+0.01105.ALT-0.01003.SLO+0.03029.ROC$$

Thus for a site at 800 m with a 5° slope and 10% rock cover, $l = -1.629$ and the probability of occurrence $p = 0.235$. In this model there were no significant categorical variables. When these occur a separate coefficient for each category is calculated (Crawley, 1993).

Table 1. The change in deviance from a model for *Chondropetalum ebracteatum* from the mean of variables added singly. Significance is measured from the χ^2 distribution at 5% (*) and 1% (**) levels. For abbreviations see text.

Model	Residual deviance	Change in degrees of freedom	Change in deviance	Significance
Mean	338.84			
ASP	279.90	-3	-58.88	**
ALT	136.34	-1	-202.50	**
ALT+ALT^2	130.94	-2	-5.4	ns
RAD	338.69	-1	-0.15	ns
FER	260.55	-3	-78.29	**
RAI	291.89	-1	-46.95	**
RAI+RAI^2	257.99	-2	-33.90	**
DRA	334.24	-2	-4.61	ns
ROC	330.40	-1	-8.45	**
SLO	306.66	-1	-32.18	**

Table 2. The change in deviance from a model for *Chondropetalum ebracteatum* from the mean of variables added cumulatively. Significance is measured from the χ^2 distribution at 5% (*) and 1% (**) levels.

Model	Residual deviance	Change in degrees of freedom	Change in deviance	Significance
Mean	338.84			
ALT	136.34	-1	-143.62	**
FER	132.56	-3	-3.8	ns
ASP	135.03	-3	-1.3	ns
RAI	135.93	-1	-0.4	ns
RAI+RAI^2	135.65	-2	-0.7	ns
SLO	122.58	-1	-13.8	**
ROC	113.38	-1	-9.2	**

Table 3. The estimated parameters and approximate standard errors for the *Chondropetalum ebracteatum* model.

Variable	Parameter estimate	Standard error	Student's t statistic
Mean	-10.27	1.508	6.81
ALT	0.0110	0.0016	6.88
SLO	-0.1003	0.0311	3.23
ROC	0.0302	0.0103	2.93