The Reconstruction of Late Quaternary Vegetation and Climatic Patterns on the Cape West Coast, Using a Charcoal Sequence from Elands Bay Cave

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THE RECONSTRUCTION OF LATE QUATERNARY VEGETATION AND CLIMATIC PATTERNS ON THE CAPE WEST COAST, USING A CHARCOAL SEQUENCE FROM ELANDS BAY CAVE

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As I did stand my watch upon the hill.
I look'd toward Birnam, and anon.
methought,
The wood began to move.

Shakespeare, *Macbeth*

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ABSTRACT

A taxonomically well resolved sequence of charcoal spanning the past 40 000 years from the Elands Bay Cave was used in this thesis to achieve two main objectives: firstly to determine the plant communities which occurred in the past to compare these to extant communities, and secondly to predict past climates by using extant species-climate relationships. This quantitative approach in predicting past climates is novel in the western Cape.

Two scales of study were used, a local and a regional scale. The study area used in the local approach was a block of land in the surrounds of the cave where the present-day distributions of the species (that occurred in the charcoal) could be sampled. A larger study area including the whole of South Africa was also used as a study area so as to determine the distribution of species that do not occur on the Cape west coast today, and also to sample a wider suite of climatic conditions. A classification of the past, present and combined data was conducted in order to document the change in communities over time. Ordination techniques were used to asses the environmental variables controlling the distribution of species in the landscape.

The classifications highlighted the fact that communities have reshuffled over time, presumably tracking the changes in climatic conditions which have been noted as occurring over the past 40 000 years. These changed may have been influenced by a number of factors including; human disturbance, disturbance by large mammals, sea level changes and climatic change. It was found that no exact analogues of plant communities are present in the area today. The ordination identified climatic variables as contributing at least half of the variance which was accounted for by all of the measured environmental variables. Thus as the climatic variables contribute to controlling the distribution of species their use in reconstructing past climates was thus justified. Two new methods (a local and a regional approach) of climatic reconstruction were explored and the results compared. The local sale reconstruction of past climate does not indicate large changes in temperatures over time. This approach suggests that the maximum temperature increased by 1 % over time, and that minimum temperature decreased by 1 %. It also suggests an increasing number of growthdays (22 %), decreasing rainfall (38 %) and increasing radiation levels (11 %). The reconstructions using the regional scale approach suggest a relativley stable minimum temperature, but an increase in the maximum temperature (8.2 %). The approach suggests that the number of growthdays has decreased by 18 %, and that the rainfall decreased by 57 % over time. From these results it is clear that no one method of climatic reconstruction is likley to provide a definitive picture of past climates. Despite differences in the details of the reconstrucions, both methods suggested marked perturbations in climatic conditions at the Pleistocene / Holocene boundary. These quantitative estimates of past climatic conditions are novel in the fynbos biome and build on the narrative inferences that have been made.

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CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION

The overall aim of this dissertation was to explore the feasibility of reconstructing climatic conditions over the past 40 000 years on the Cape west coast using a charcoal sequence from the Elands Bay Cave (EBC). The specific objectives of the study were to:

- Determine whether past communities in the surrounds of EBC have present day analogues in the study area.
- Determine the community – environment relationships of the extant communities.
- Attempt a reconstruction of past climates using two methods – a local and a regional approach.

This thesis was based on a charcoal sequence which provided the platform from which all the research was conducted. The charcoal sequence was identified by Caroline Cartwright (British Museum, London) and was found in EBC. The vegetation and climatic reconstructions in this work are based on this sequence of charcoal which spans the last 40 000 years. In the introduction to this thesis I begin by describing the charcoal sequence in detail and them describing the local study area. As the thesis concerns past climates, current theories on the evolution of the Cape west coast climate are discussed. The hypothesis that the eastern section of the fynbos biome had a different past climate to the western section is discussed, including details of palaeoecological studies that have been conducted in each section.

Chapter 2 deals with the past and present vegetation in the local study area and the environmental correlates of the present communities. The present day distribution of the communities in the local study area is considered in an attempt to partition the variability in community and species distributions attributable to different environmental factors using Canonical Correspondence Analysis. This provides and objective criterion for judging the validity of attempting to reconstruct past climates by drawing analogies with present species distributions. The four main questions addressed in this chapter were:

1. Which communities, as based on the species identified in the charcoal, are present in the area today?
2. Which communities were evident in the past, from the fossil charcoal sequence?
3. What are the similarities between the fossil and present communities?
4. What environmental variates best explain the observed mosaic of woody species associations in the present landscape?

Chapter 3 deals primarily with the reconstruction of past climatic conditions using two methods of reconstruction. These two methods are compared. The main questions addressed were:

1. What are the distributions and corresponding climatic envelopes of each species found in the EBC fossil charcoal sequence on the Cape west coast study area?
2. What are the distributions and corresponding climatic envelopes of the species found in the EBC fossil charcoal sample in South Africa as a whole?
3. What are the past climatic conditions on the Cape west coast (>40 000 years – present) predicted using both the local and the regional approach?
4. How do the results of these two methods of climatic reconstruction compare?

The reconstructions are briefly discussed in an archaeological context, but further description of the results are beyond the scope of this thesis. Key questions and research approaches are summarized in Table 1.1.

The last chapter is a discussion which highlights the principle findings of the thesis, in particular comparing the two methods of climatic reconstruction. The fact that the results of the reconstructions of this thesis are quantitative as opposed to the narrative inferences (Cowling *et al.*, in press) that have been made in the area is also discussed.

TABLE 1.1: The key questions and research approaches used in this study.

QUESTION	**APPROACH**	**CHAPTER**
What is the relationship between the palaeo-communities, as represented in the fossil record, and the extant communities in the study area?	Comparison of multivariate classifications of palaeo, extant and combined data sets.	2
What are the community – environmental relationships of the extant vegetation in the study area?	Ordination (Canonical Correspondence Analysis) of extant and environmental variables in the study area.	2
What are the past climates on the Cape west coast?	Two approaches were used: 1. Local-scale species/climate relationships were used to infer past climatic conditions using a multiple regression approach. 2. Regional-scale (South Africa) species climatic envelopes were used to reconstruct past climates	3

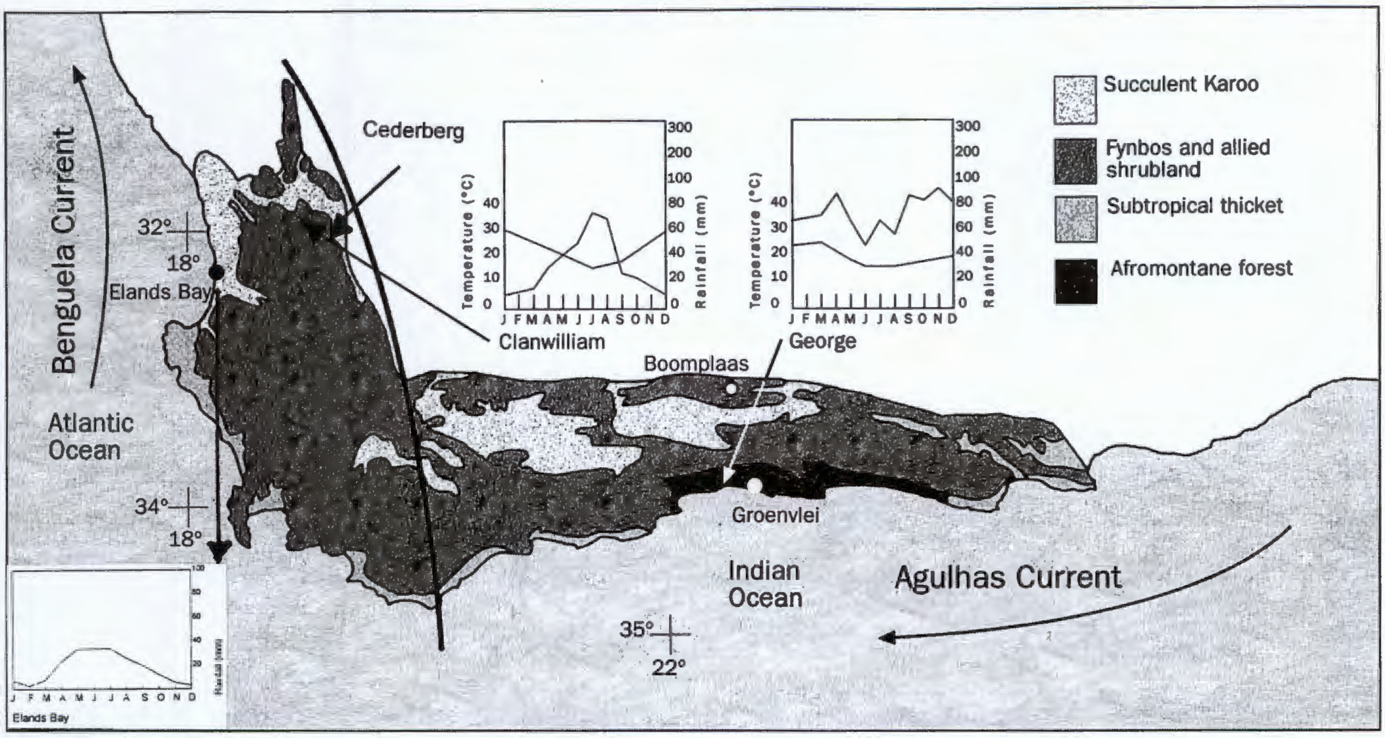

FIGURE 1.1: Map of south-western Africa showing distribution of major vegetation types, the location of the Agulhas and Benguela Currents, and the location of some places mentioned in the text. The bold line separates the western, and predominantly winter-rainfall region of the biome from the eastern, equinoctial (spring and autumn maxima) rainfall zone; Clanwilliam and George are representative climatic stations, respectively (Cowling *et al.*, in press).

1.2 THE ELANDS BAY CAVE CHARCOAL SEQUENCE

This work was based on the charcoal sequence identified by Caroline Cartwright (Department of Scientific Research, British Museum) excavated from EBC (Figure 1.1, 1.2, Plate 1.1). The archaeological remains were excavated by John Parkington and colleagues (Department of Archaeology, University of Cape Town). Over 7 600 fragments of wood were identified. The oldest sample dates from prior to 40 000 years ago while the most recent are about 350 years old. A selection of charcoal samples spanning the full sequence were radiocarbon dated by the Quaternary Dating Research Unit of the CSIR, Pretoria. Although the data spans a period of at least 40 000 years, the most accurate dating is for samples that are younger than 40 000 years. This is due to the limitations of the ^{14}C radiocarbon dating technique. A full description of the methodology used, including a discussion of the computerised database of anatomical characteristics, is given in Cartwright and Parkington (in press) and Parkington *et al.*, (in prep).

Detailed anatomical comparisons (up to 163) were made by Cartwright with over 350 reference specimens of woody taxa collected. The reference collection was compiled by collecting wood samples from the immediate environs of the site as well as further afield in the north-western, south-western, and southern parts of the fynbos biome (*sensu* Rutherford and Westerfall, 1986, Figure 1.1). Nomenclature was after Arnold and De Wet (1993). An attempt was made to cover large environmental gradients and varied substrata so as to lay some foundation for assessing possible variability introduced by micro-environments. The norm for identifying charcoal fossils is to identify them to genus level only. Many charcoal fragments in this sequence were identified to the species level. In some cases a qualified species determination was chosen to accommodate variability of preservation of the fragments. Where a fairly close match with reference material could be made the charcoal identification was annotated as 'cf.' with regard to a species. Where insufficient diagnostic anatomical structure was present the genus was qualified by 'sp.' This was a very precise and time consuming procedure which explains why it is not often used. The percentage (by weight in grams) of each species in the charcoal was determined (Appendix 1). This provides a rough estimate of the relative abundances of the taxa and a certain amount of inter-sample comparability. The charcoal that was identified by Caroline Cartwright was the remains of wood fires by the hunter-gatherers of the time. Fuelwood is chosen according to different characteristics, depending on what it is to be used for e.g. twigs for kindling and wood which releases slow heat for cooking (Eberhard, 1990; Davis and Eberhard, 1991; Archer, 1994). As a result it is necessary to be aware that the charcoal that is found in archaeological sites is biased in favour of the preferred fuel wood, which would presumably have been the wood in greatest abundance (February, 1994). To a certain extent the charcoal reflects the woody vegetation communities of the past, but it does not mirror the past vegetation. There are external factors such

PLATE 1.1: Elands Bay Cave: a view of the cave illustrating the Strandveld vegetation in the foreground.

as the ‘human choice’ of wood, and also the effect that man has had on altering the landscape which we know today. Although there are caveats, charcoal data is a useful tool for obtaining information about the past. Owing to the accuracy of the identification, this sequence provides the opportunity for palaeoenvironmental reconstruction that is unparalleled in the fynbos biome.

1.3 THE LOCAL STUDY AREA

1.3.1 Physiography and climate

The study area (Figure 1.2) chosen surrounding EBC represents steep enviornmental and topographic gradients that would provide a large number of different sites with a large range in environmental variables where plants could grow. This range of conditions was necessary in order to include the habitats of as many of the species in the charcoal sequence (particularly the species restricted to the Cape west coast) into the sample. The area is roughly 90 km x 125 km, (11 250 km^2 or 1 125 000 ha). EBC is situated on the western border of the study area. The northern and southern boundaries of the study area are the Olifants and Berg Rivers, respectively. These two rivers are the main perennial rivers in the western section of the fynbos biome and drain into the Atlantic Ocean. The eastern boundary of the study area is the crest of the Cederberg mountain range. The other mountain range in the area is the Piketberg range. EBC is situated near the coastal town of Elands Bay, approximately 180 km north of Cape Town. It is on a north-west-facing headland known as Cape Deseada or Baboon Point, approximately 100 – 200 m from the coastline. This distance is substantially less than what it was in the past as a result of rising sea levels since the LGM (Deacon and Lancaster, 1988) when it was predicted as being 110 m lower than it is today (Baxter, 1996). According to Parkington *et al.* (1981) accurate estimates of this rising sea level have been difficult to obtain, but it seems likely that between 17 000 and 12 000 years ago that the coastline advanced from 37 km to 12 km west of the cave. This translates to a rise of about 40 m in the sea level between 17 000 and 12 000 years ago. Baboon Point (Plates 1.2 a & b) lies at the southern end of the bay and about 2 km west of the mouth of the Verlorenvlei. This coastal lake drains into the sea near to the town of Elands Bay, and is fed by the Verlorenvlei River. The Verlorenvlei lake is about 13.5 km long and 1.4 km wide at its widest point, and its greatest depth is 5 m. The channel to the sea is only 2.5 m wide and sea water does not often enter the system. However, there are indications from between 4000 and 2000 years ago that the Verlorenvlei was not an intermittent estuary as it is today, but rather a marine lagoon which was open to the sea (Yates *et al.,* 1986; Grindley and Grindley, 1987). According to Baxter (1996) the early to mid – Holocene aquatic status of the Verlorenvlei embayment fluctuated as follows: i) an open estuary; ii) sheltered lagoon; iii) a terrestrial dune field; iv) an active estuary; v) a marine embayment. The micromammalian fossils from the EBC indicate a slightly higher proportion of riparian elements during the Terminal Pleistocene, possibly indicating that the Verlorenvlei extended closer to the cave than is presently the case (Avery, in prep).

The study area lies within the winter-rainfall region of the fynbos biome. Elands Bay itself, receives less than 200 mm of rain per annum and there is a 35 - 40 % variation of inter-annual precipitation (Schulze, 1997). According to Sinclair *et al.*, (1986), more than 80 % of the precipitation occurs between April and September. The cold Benguela current flows past the Cape

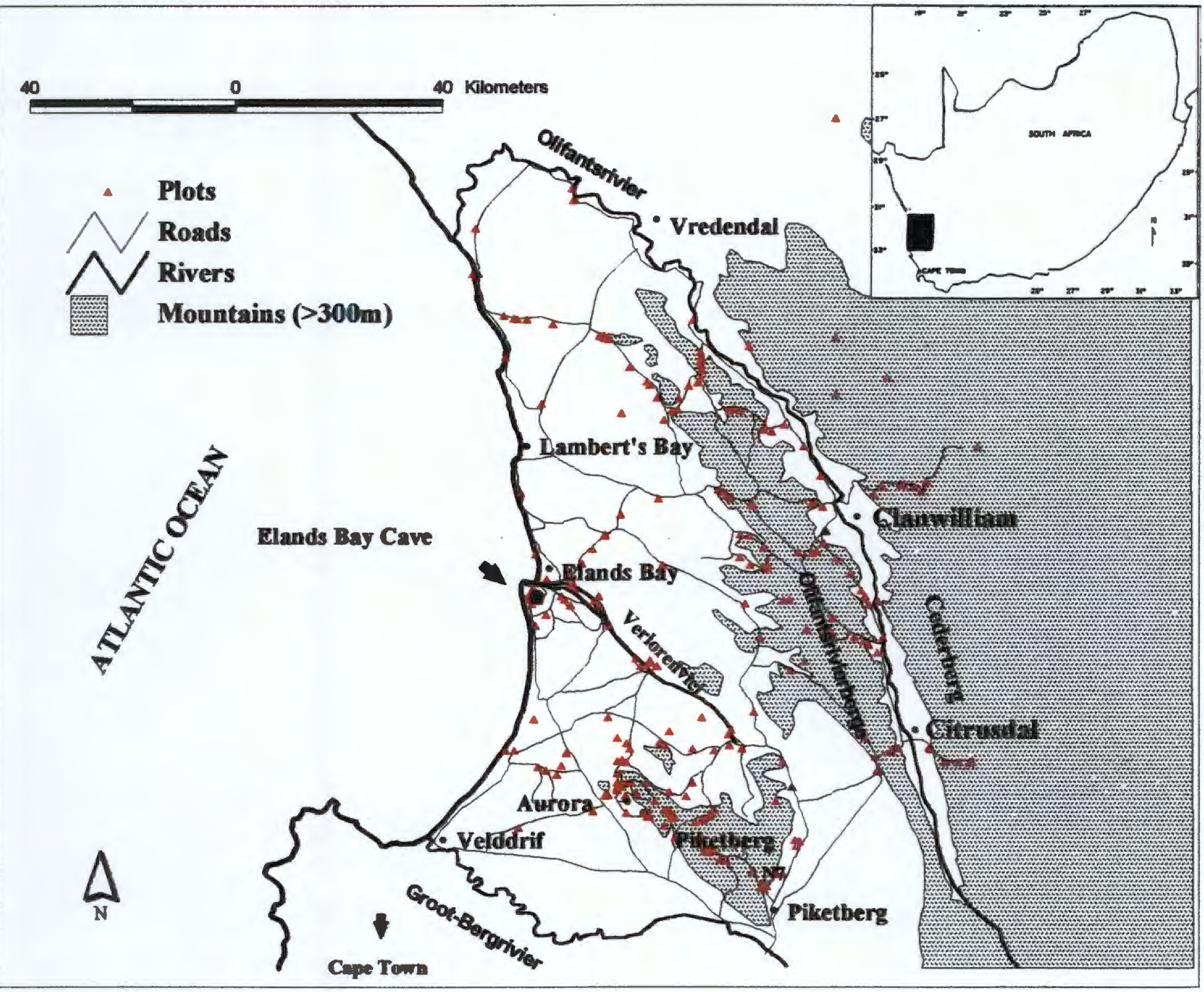

FIGURE 1.2: Map of the study area on the Cape west coast showing the location of plots, the roads which were used when sampling the area, the major towns, and the location of Elands Bay Cave.

west coast. The upwelling of cold water, mixed with the surface water of the warm inshore radiation, causes advection fog to be formed (Schulze, 1997). This fog may be an essential source of moisture for plants in low rainfall areas such as this. The Cape west coast is strategically placed to be able to reflect changes in the oceanic and atmospheric circulation patterns of the southern hemisphere.

From the coast inland, the study area is characterised by very sharp altitude, temperature, geological and rainfall gradients (Figures 1.2, 1.3, 1.4, 1.5) (Campbell, 1983; Deacon *et al.*, 1992). The shallow depth of moist flows and the marine clouds, and the steepness and height of the coastal escarpment, both contribute to these (Jury, 1993). These gradients occur all the way up the west coast of southern Africa (Jürgens *et al.* 1997). The topography varies from a level coastal plain to the broken, high altitude areas of the Cederberg mountain range. The altitude ranges from sea level to about 1 100 m above sea level in the mountains. The median annual rainfall as evidenced from rainfall stations varies from approximately 100 mm p.a. to 692 mm p.a. (at Algeria in the Cederberg). The minimum temperature of the coldest month ranges between 4.1 °C to 7.7 °C and the maximum temperature of the hottest month ranges between 26.1 °C to 34.6 °C .

The geology in the vicinity of EBC is predominantly Table Mountain Group (Cape Supergroup), Tertiary to Recent deposits and Malmesbury system shales. Baboon Point at EBC is composed of Table Mountain Sandstone. Much of the coastal plain is composed of Tertiary to Recent sands. The strip near the coast is composed of dune sand with marine shells, sand and

PLATE 1.2: a) A view from the EBC. The proximity of the shoreline to the cave can be seen. b) Baboon Point looking south from Elands Bay beach.

gravel. The mountainous areas (i.e. Cederberg and Piketberg) are composed of the Table Mountain Sandstone (1070 m deep) with bands of shale. This Table Mountain Sandstone is thrown into anticlinal ridges (Du Toit, 1939). The low-lying region between the Cederberg and the Piketberg (also known as the Swartland), is underlain by phyllitic shale, schist and greywacke of the pre-Cape Malmesbury System (Visser and Theron, 1973).

1.3.2 Flora and vegetation

The study area falls within the Cape Floristic Region (CFR) which is a highly distinctive phytogeographical unit recognized as a floral kingdom in its own right (Goldblatt 1978). This kingdom occupies an area of 90 000 km^2 in the extreme south-western and southern part of Africa where rainfall is predominantly in winter. The dominant vegetation in the CFR is fynbos, which contributes more than 80 % of the species. Other vegetation types represented in the Cape Floristic Region include subtropical thicket, succulent karoo and Afromontane forest (Cowling and Holmes, 1992). The region is characterised by very high levels of endemism (68% of species, 19.5% of genera and 6% of families) (Bond and Goldblatt, 1984).

The steep environmental gradients in the study area, which have already been mentioned, contribute to the high diversity of vegetation types represented in the study area (Figure 1.6). Two biomes (the fynbos and the succulent karoo biomes) occupy the bulk of the study area (Table 1.2) (Low and Rebelo, 1996). In addition to these, there are patches of Afromontane forest, mainly in the Cederberg and Piketberg mountains. The fynbos biome part of the study area comprises three vegetation types: sandplain fynbos, mountain fynbos and renosterveld. The succulent karoo biome

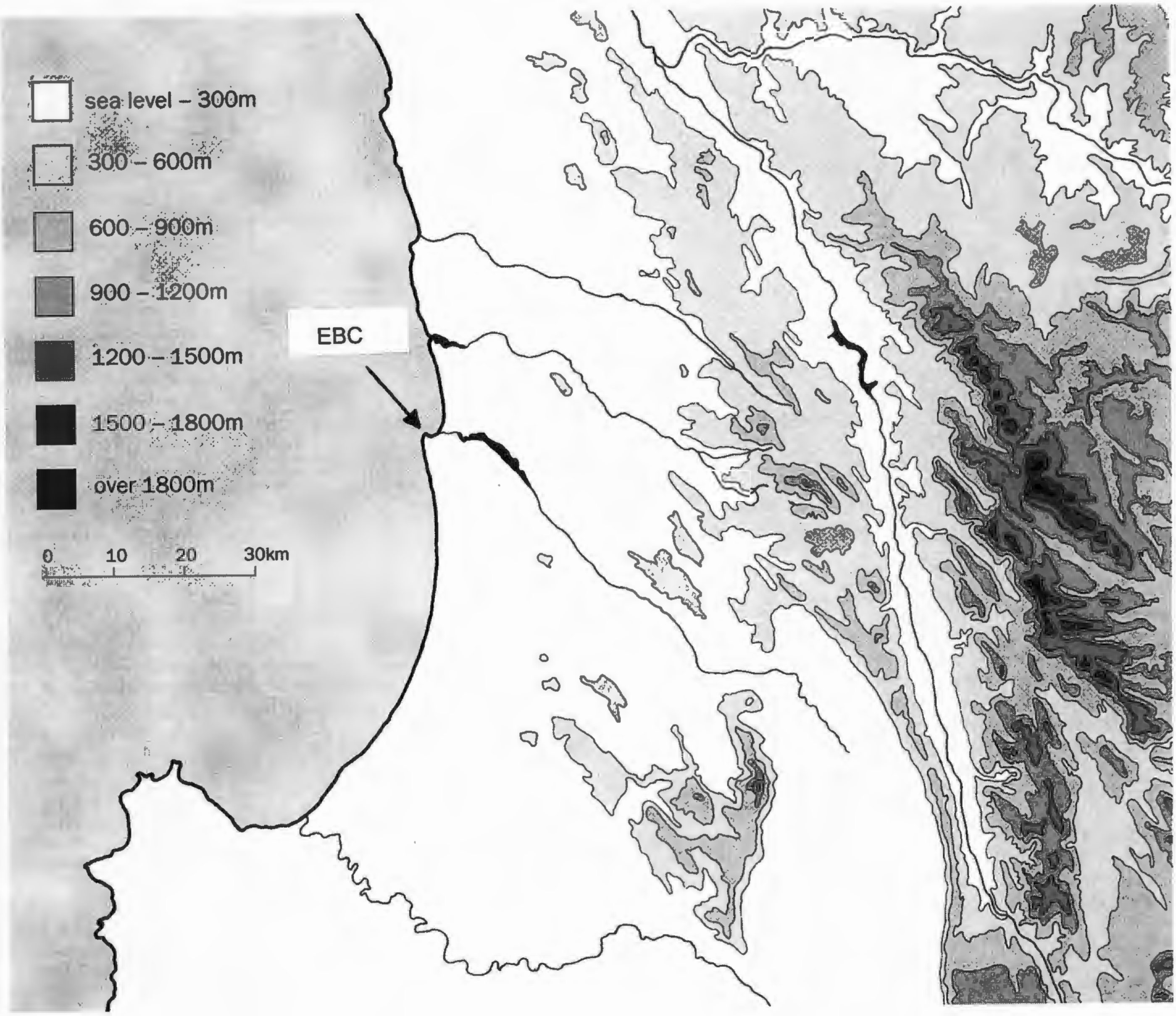

FIGURE 1.3: Topographic map of the local study area. The steep elevational gradients are evident. (with permission Parkington *et al.*, in prep).

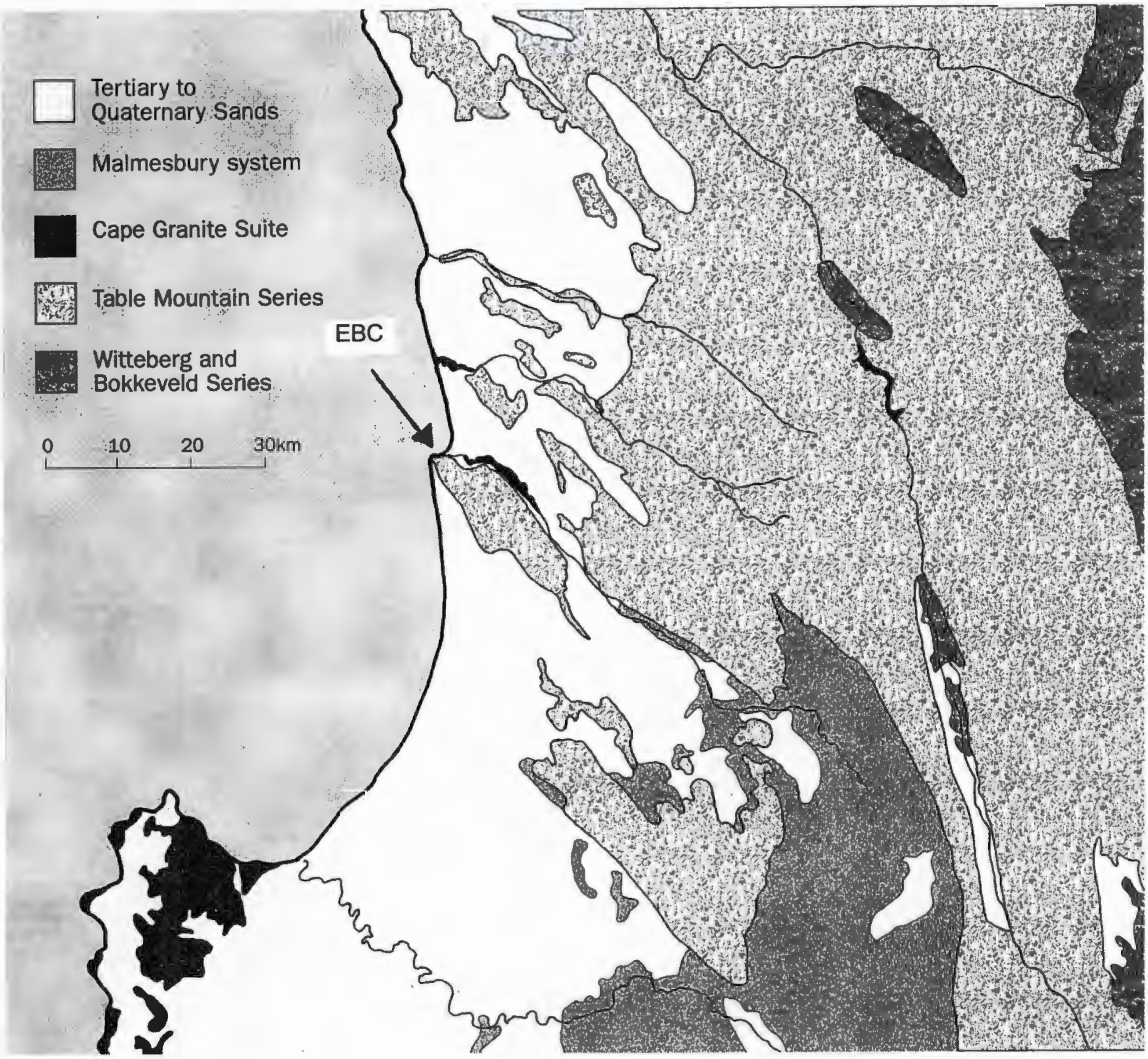

FIGURE 1.4: Map of the geology of the local study area (with permission Parkington *et al.*, in prep).

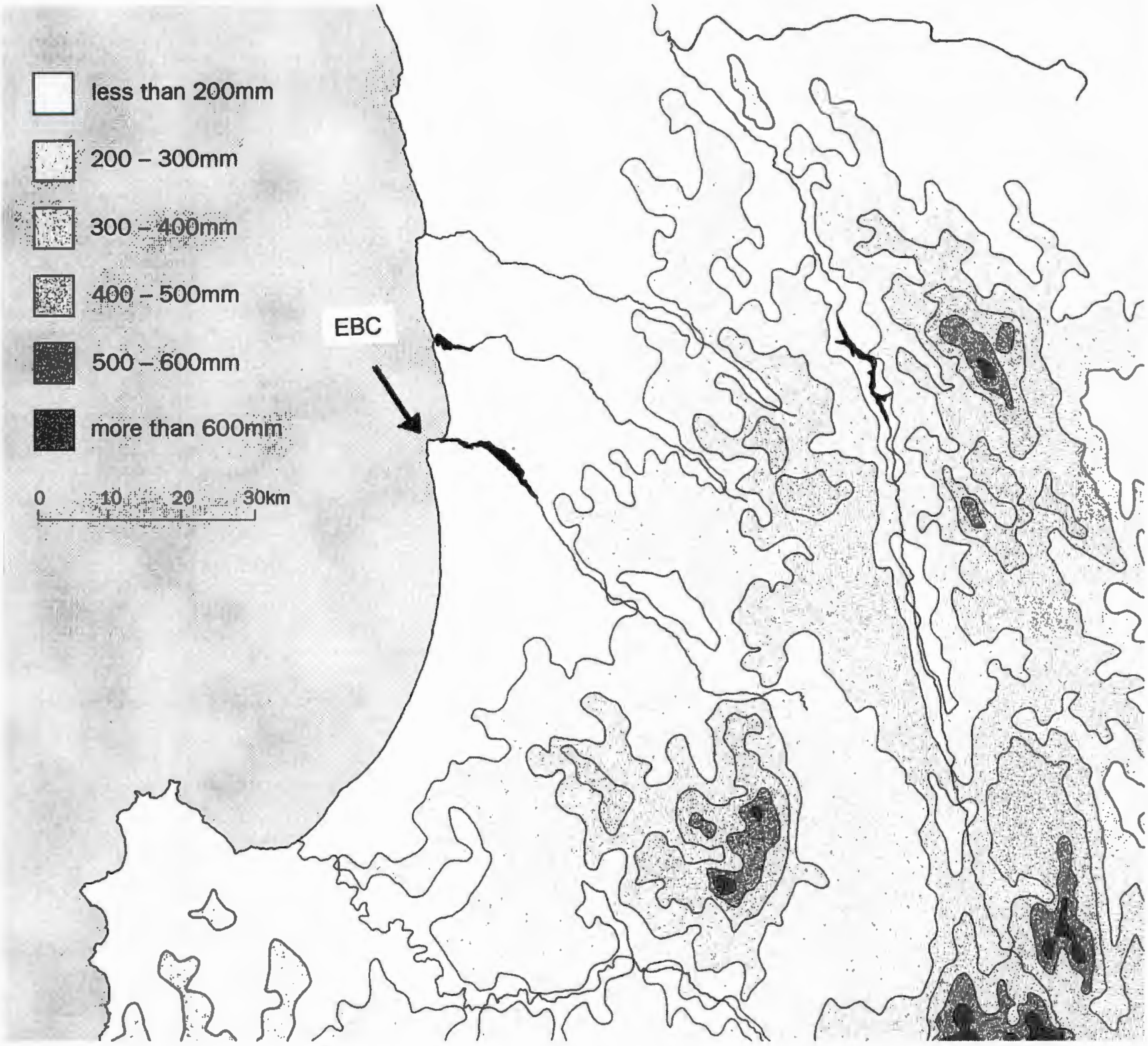

FIGURE 1.5: Map of the mean annual rainfall (mm) in the study area (with permission Parkington *et al.*, in prep).

is represented by the strandveld succulent karoo. The sandplain fynbos is found on flat areas with deep acidic sands that receive low rainfall. Mountain fynbos occurs in mountains where both rainfall and soils play important roles in determining community boundaries along altitude and aspect gradients (Cowling and Holmes, 1992). This vegetation type receives more rain than all the other types and is susceptible to fire (Low and Rebelo, 1996). West coast renosterveld has been found to occur in soils with a higher pH, coarser texture and low nitrogen and carbon content (Campbell, 1986) than those of fynbos. The soils (sandy loams and clayey subsoils) have also been found to be relatively shallow (Low and Rebelo, 1996). This vegetation type occurs in the interior at low altitudes and low rainfall (Campbell, 1986). The last vegetation type found in the study area, strandveld succulent karoo, is found predominantly in deep sands or shallow calcareous sand of the coastal forelands. It is found in areas of low rainfall and at low altitudes (0 -200m) (Boucher and Jarman, 1977). Sampling this diversity of vegetation types was necessary in order to include as many of the species represented in the charcoal sequence into the reconstruction of climates as possible and to cover a wide range of environmental gradients.

The vegetation types that occur in the immediate surrounds of the cave and are under strong edaphic control (Cowling *et al,* in press). Strandveld succulent karoo occurs on the deep calcareous sands below the cave. The shrub matrix (1.0 - 2.5 m) is composed of evergreen sclerophyllous species (*Euclea racemosa, Pterocelastrus tricuspidatus, Rhus* spp) of subtropical affinity, as well as drought deciduous shrubs with orthophyllous leaves (*Lycium* spp, *Zygophyllum morgsana*). The shrub interstices are mainly occupied by leaf succulent shrubs (e.g. *Ruschia, Cephallophyllum* and *Stoebaria,* in the Mesebryanthemaceae) of karroid affinity (Cowling *et al.,*

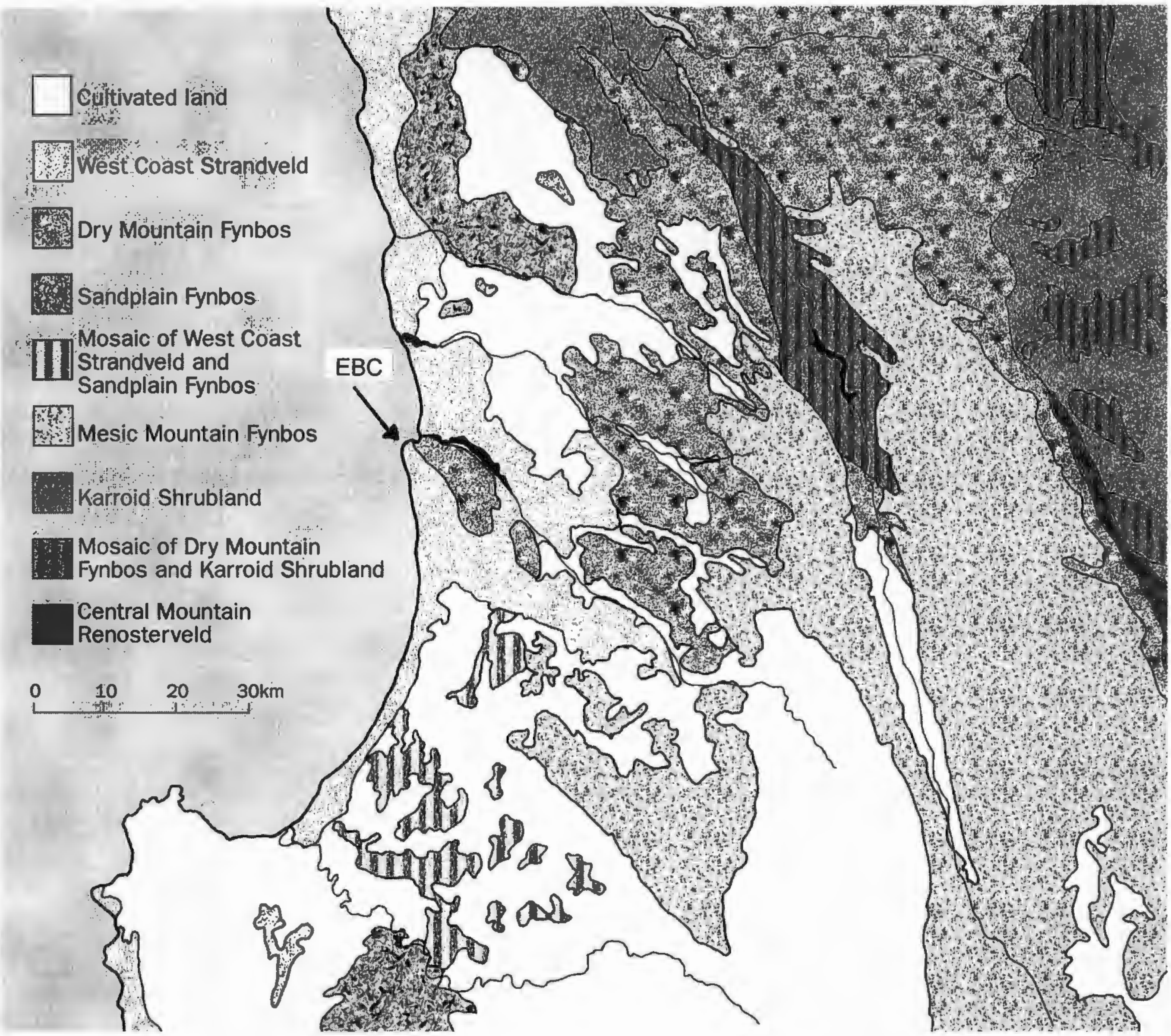

FIGURE 1.6: Map of the major vegetation types in the study area (with permission Parkington *et al.*, in prep).

TABLE 1.2: The major environmental correlates of the four main vegetation types that meet in the study area (adapted from Low and Rebelo 1996; R.M. Cowling pers comm).

VEGETATION	LOCATION	GEOLOGY AND SOIL	RAINFALL
Sandplain fynbos	Low-lying land between the coastal areas and the mountain ranges.	Deep, acidic, usually well drained sands mainly of Tertiary origin.	200 – 500 mm p.a.
Mountain fynbos	Along the Cape Fold Belt: including, the Cederberg and Piketberg mountain ranges.	Usually confined to soils derived from sandstones of the Cape Supergroup. Shallow, sandy soils to deeper stony colluvium.	200 - 2000 mm p.a.
West Coast Renosterveld	Western Cape forelands, from north of Piketberg to Somerset West. Mainly in low lying areas.	Confined largely to Malmesbury shales, Cape Granite Suite and Klipheuwel Formation shales. Relatively shallow, sandy loams and clayey subsoils.	300 - 600 mm p.a.
Strandveld succulent karoo	Coastal zone and immediate hinterland of the Cape west coast. From the Berg River mouth northwards to Port Nolloth.	Deep calcareous Quaternary sands or shallow calcareous sand over calcrete and dorbank.	50 - 300 mm p.a.

in press). Asteraceous shrubland is associated with the acid sand of the Table Mountain Sandstone of Baboon Point. Dominants include species of *Aspalathus, Eriocephalus, Ruschia,* and *Phylica.* Restionaceae are generally lacking in asteraceous shrubland and strandveld succulent karoo, but occur commonly in the sandplain fynbos where species such as *Wildenowia incurvata* and *Thamnochortus bachmanii* are often dominant. Patches of xeric thicket also occur in the area, especially on rocky sites. Dominants include *Rhus undulata, Maytenus oleoides* and *Diospyros glabra.* Other thicket species (*Euclea tomentosa, Rhus* spp) occur on leached sands together with

Leucadendron pubescens - dominated sandplain fynbos (Cowling *et al.*, in press). Patches of taller and more mesic thicket dominated by *Ficus cordata, Heeria argentea* and *Podocarpus elongatus* occur inland of EBC on outcrops of sandstone. This is possibly the lowest rainfall at which the genus *Podocarpus* is known to grow (Boucher and Moll, 1980).

1.4 THE EVOLUTION OF THE WEST COAST CLIMATE - TEMPORAL CONTEXT FOR THE EBC CHARCOAL SEQUENCE

The charcoal sequence from the EBC is important in terms of palaeoenvironmental reconstruction as it spans the last Glacial-Interglacial interface (± 13 000 years ago) and the Last Glacial Maximum (18 000 - 22 000 years ago). To briefly place this in the context of the past 100 Myrs (Table 1.3), the first angiosperms appeared in the fossil record of the south-western Cape 113 Myrs ago during the Mesozoic Era (Coetzee, 1993). At this time there were lush forests covering much of what is now the fynbos region and the climate was moist and subtropical (Coetzee, 1981; Linder *et al.*, 1992). The Cenozoic Era (65 Myrs to today), which succeeded the Mesozoic, comprises the Tertiary (65 Myrs to 1.6 Myrs ago) and Quaternary Sub-eras (1.6 Myrs to the present). It was during the Miocene of the Late Tertiary that the East Antarctica ice-sheet became established and by the Miocene/Pliocene boundary some five million years ago, this was twice its current size (Coetzee, 1983). These changes in Antarctica were probably the driving force behind the development of Mediterranean-type climates (and ultimately the vegetation patterns) in the southwestern Cape towards the end of the Pliocene (Deacon *et al*, 1992). It was during this time that southern oceanic currents took on their present form. After the northern hemisphere was glaciated (*circa* 3.2 - 2.5 Myrs ago) the symmetry of zonal climates was established and the position of the South Atlantic high pressure became fixed. This high pressure cell blocks frontal precipitation to the south-western Cape during summer which results in the distinctive annual climatic sequence of hot, dry summers alternating with cool, wet winters, characteristic of Mediterranean climates (Specht and Moll, 1983). At this time there was consistent upwelling of the cold Benguela Current (Figure 1.1) off the west coast of southern Africa, which exacerbated the aridity of the west coast (Siesser, 1980; Preston-Whyte & Tyson, 1988).

The Quaternary Sub-era, comprising the Pleistocene and Holocene Epochs (Table 1.3), began approximately 1.6 Myrs ago and was characterised globally by cycles of glacial and interglacial conditions which forced major vegetation changes (Scott *et al*, 1997). These approximately 100 000 year cycles were linked to changes in seasonal distribution of incoming solar radiation associated with perturbations of the earth's orbit around the sun (Tyson, 1986; Fairbanks, 1989; Cohen and Tyson, 1995). Approximately 90 000 years of these cycles are characterised by globally cooler and generally drier climates. These alternate with shorter, approximately 10 000 year, interglacial periods which are warmer and generally wetter (Deacon, 1983). These short warmer periods are difficult to analyse and raise important conceptual and factual questions, particularly in terms of vegetation / climate relationships (Webb III, 1986).

In South Africa there is evidence to suggest that during the last interglacial there were alternating periods of warm/wet, warm/dry and cold/wet conditions (Deacon and Lancaster, 1988). The last Glacial appears to have been cold and wet initially, but by the Last Glacial Maximum (LGM) was cold and very dry. Available sources of palaeoclimatic data indicate that significant

TABLE 1.3: The geological timetable with details of the Mesozoic and Cenozoic Eras (adapted from Saarnisto 1988; Campbell 1990; Cowling and Richardson 1996;). (ky = thousand years, Myr = million years)

Era	Sub-era	Epoch	Age
CENOZOIC	Quaternary	Holocene	10 ky
		Pleistocene	1.6 Myr
	Tertiary	Pliocene	
		Miocene	23.7 Myr
		Oligocene	
		Eocene	
		Paleocene	65 Myr
MESOZOIC	Cretaceous		144 Myr
	Jurassic		213 Myr
	Triassic		248 Myr

changes in both temperature and wetness occurred in southern Africa during the late Pleistocene and Holocene (Partridge *et al.*, 1990). These are likely to have been associated with dramatic changes in vegetation between the last Interglacial and Glacial (120 000 - 12 000 years ago), the LGM (22 000 and 18 000 years ago) and Holocene (10 000 years ago - present). It is this period of dynamic climate change that the EBC charcoal sequence spans.

1.5 PALAEOENVIRONMENTAL STUDIES IN THE EASTERN FYNBOS BIOME

Several different methods have been used to infer past climates in different parts of the world. An essential feature of all of these though, is that they provide a continuous signal suitable for time-series analysis (Bradley *et al.*, 1992). A review of the different methods and relevant literature is given in Bradley *et al.* (1992). In South Africa, the southern and western parts of the fynbos biome are the most intensively studied regions archaeologically, with cave sites along the coast having attracted a great deal of attention (Deacon and Brooker, 1975). However, there are other sites in South Africa not located in the fynbos biome that cover similar time periods (see Parkington *et al.*, in prep) to the EBC sequence. One such example is Rose Cottage Cave which is situated in the Free State (Plug and Engela, 1992; Wadley *et al.,* 1992; Scott *et al.,* 1995). Many studies have attempted to determine past climates, in particular past rainfall and temperature regimes in the fynbos biome (e.g. Avery, 1982; Klein & Cruz-Uribe, 1987; February, 1990; Jury, 1993; Scott, 1994; Miller *et al.*, 1995; Cowling *et al.*, in press).

Studies on past climates of the eastern section of the fynbos biome have suggested that drier and colder climates existed during the last Glacial than in the Holocene. These conclusions have been drawn from studies at sites such as Boomplaas (Deacon, 1979; Deacon *et al.*, 1983; Scholtz, 1986) and Groenvlei (Martin, 1959;1968) (Figure 1.1). The Boomplaas cave is situated in the Cango Valley of the southern Cape and contained a charcoal sequence which spans the last 80 000 years. Unlike the Elands Bay Cave sequence, the charcoal fragments from Boomplaas were not identified to species level. From the identifications made it was found that woody Asteraceae were dominant in the charcoal remains between 30 000 and 16 000 years ago. After this time the human occupants of the cave sampled thicket species, and, in the youngest samples in the sequence, *Acacia karoo* was commonly found. According to Scholtz (1986) the area was cold and dry between 26 000 to 18 000 years ago and became wetter around 17 000 to 14 000 years ago. Presently the area is dominated by thicket and dense shrubland, with fynbos of mesic south-facing slopes (Moffett and Deacon, 1977). Other lines of evidence provided by small mammals (Avery, 1982), larger mammals (Klein, 1978) and pollen (Deacon *et al.*, 1983; Scholtze, 1986) have also been used in the climatic reconstruction at this site. All the archaeological data indicate that the most extreme (cold and dry) environmental conditions of the last Glacial occurred about 18 000 years ago (LGM). They also indicate that temperature amelioration began about 14 000 years ago, and with this there was a corresponding increase in precipitation. The early-mid Holocene was relatively warm and temperatures have decreased over the past 2000 years.

The Groenvlei site (Figure 1.1) is a coastal lake situated within a forest zone in the eastern fynbos biome. The lake is shallow, slightly saline and eutrophic, and is one of seven similar lakes of Pleistocene origin in Knysna-Wilderness area (Martin, 1959;1968). The pollen evidence from Groenvlei indicates that before 7 000 years ago the area was covered by dry, open sclerophyllous heath (fynbos) dominated by Asteraceae, Ericaceae, Proteaceae and Restionaceae. After this there was an increase in tree pollen typical of those growing in the extant Afromontane forest (*Podocarpus, Olea, Apodytes* and *Zanthoxylon*), and a decrease in pollen of shrubs and herbs. Present-day vegetation near Groenvlei is Afromontane forest (Low and Rebelo, 1996). These vegetation changes reflect an overall trend toward moister conditions, with only minor superimposed oscillations (Street-Perrott and Perrott, 1993). These two archaeological studies (Boomplaas and Groenvlei), provide evidence for a trend of increasingly moist conditions the eastern section of the fynbos biome during the Holocene.

1.6 CLIMATES OF THE EASTERN VS. WESTERN SECTIONS OF THE FYNBOS BIOME

To date it has generally been inferred that past climates of the western section of the fynbos biome (comprising the area from Cape Augulas to the northern limit of the Cape Fold Belt) (Figure 1.1), resembled those of the eastern section (Klein, 1984; Scott, 1994). However, these two sections are under fundamentally different climatic controls (Campbell, 1983; Deacon *et al.*, 1992). Currently, the western part of the biome receives most of its rain from frontal depressions during the winter months. During summer, a ridge of high pressure (South Atlantic anticyclone) lies at about 37° S and effectively deflects the passage of fronts into the subcontinent. Winds associated with this high pressure system are shallow easterlies which are forced over the north-trending Folded Belt and reach the west coast as a dry and turbulent airstream (Deacon *et al.*, 1992). In the eastern part of the biome rain is received from three major sources: frontal depressions during winter; the ridging anticyclone, mainly in spring; and cut-off lows, mainly in autumn (Preston-Whyte & Tyson, 1988; Deacon *et al.*, 1992). The eastern part of the biome has spring and autumn rainfall peaks, and mid winter precipitation is relatively low (Figure 1.1). Moreover, owing to the unstable transitional nature of these rain bearing systems (Preston-Whyte & Tyson, 1988), annual rainfall is much less predictable in the east than in the west (Cowling and Holmes, 1992).

Therefore, the inference that climate changes in the eastern and western sections were the same probably reflects the lack of knowledge of these fundamentally different climatic controls (Cowling *et al*, in press). Furthermore, there is a paucity of suitably long palynological sequences in the western section of the biome (Deacon,1983; Scott *et al.*,1997). The EBC sequence is the only charcoal sequence in the western section of the biome that covers the LGM and the Pleistocene / Holocene boundary (Parkington *et al.*, in prep). Indeed, preliminary work conducted in the western section of the fynbos biome (Cowling *et al.*, in press) suggests that the past vegetation (and therefore climate) did not follow the same changes as in the eastern section (Martin, 1968; Deacon 1979; Deacon *et al.*, 1983). Palaeoecological evidence in the western-section of the biome reflect extensive change in temperature and humidity during the Late Quaternary (Coetzee, 1978). Deacon and Lancaster (1988) suggest that in the east, glacial periods were drier and colder than interglacials. In the west glacial conditions would have been wetter owing to an increased frequency of frontal rains, which would not have affected the east (Cockroft *et al.*, 1987). It would appear that these hypothesized differences in past climates of the eastern and western sections of the fynbos biome are not unique to this area. For example Tusenius (1986) found drier conditions in East Griqualand during the mid –Holocene, but others (Butzer, *et al.* 1978; Butzer, 1984; Beaumont, 1986) report wetter conditions during the same time from Gaap Escarpment and Kathu Pan.

1.7 PALAEOENVIRONMENTAL EVIDENCE FROM THE WESTERN FYNBOS BIOME

While the bulk of the archaeological evidence indicating Quaternary climate change for the western section of the fynbos biome has been obtained from the EBC area (Baxter, 1996; Parkington, in prep), other sites in the largely fynbos-clad Cederberg mountain range (Figure 1.2) have also provided important insights into past conditions (Meadows & Sugden 1991, 1993; Scott 1994). For instance, a deposit in a high-altitude marsh in the Cederberg spanning the past 14 500 years suggests that the environmental changes in the area were subtle rather than marked (Meadows and Sugden, 1991). This was inferred from the dominance of fynbos pollen throughout the sequence. In another study on the eastern, drier margin of the Cederberg, pollen remains spanning the past 20 000 years were identified from hyrax middens (Scott, 1994). This study indicated that the most prominent climatic changes occurred at around 13 000 years ago. During the LGM the vegetation was dominated by *Stoebe*-type shrubs (Asteraceae), *Cliffortia, Lobostemon* and Proteaceae. After this (during the Holocene) succulents (mainly

Mesembryanthemaceae) became more common, as did *Dodonaea* and *Olea*, components of contemporary thicket vegetation (Taylor, 1996). The increase in woody elements after 14 000 years ago was attributed to climatic amelioration after the LGM (Scott, 1994). This change in dominants to mesic species is similar to the results obtained from the Boomplaas site (Deacon, 1979; Deacon *et al.*, 1983) already mentioned. However, the increase in succulents is suggestive of both warmer and drier conditions (Cowling *et al.,* in press). Scott's (1994) results from the Cederberg could thus be used to infer the similarity between the past climates of the Cederberg mountain area with the eastern section of the biome (Boomplaas site). However, in a review of all the sites in the Cederberg, Meadows and Sugden (1993) conclude that there has been a transition from a high abundance of Proteaceae and *Widdringtonia cedarbergensis* to Asteraceous dominants. Inferences were made that the climatic conditions thus changed from being more moist (before 9 600 years ago) to the present more xeric environments.

In terms of EBC, several lines of fossil evidence have been used in the reconstruction of past climates in the area. The faunal remains identified in EBC from the terminal Pleistocene included eland, elephant, quagga or Cape horse (*Equus capensis,* now extinct), black rhino and hippopotamus (Klein and Cruz-Uribe, 1987). Ten thousand years ago, large-medium bovids, equids and suids were significantly more numerous. Most of these species were grazers, which suggests that the local vegetation included more grass before 11-10 000 years ago. This inferred decrease in grass almost certainly reflects climatic change at the transition from the last Glacial to the Holocene. The proportions of steenbok to grysbok suggests that the regional vegetation was not only grassier in the late Pleistocene, but also that it contained a different mix of browser plants, which may have been more like the "typical fynbos" than "coastal strandveld" that surrounds the sites today (Klein and Cruz-Uribe, 1987). Hedgehogs (*Erinaceus frontalis*) were also found in the terminal Pleistocene, which strongly suggest that conditions were wetter with much more grass cover than today. Today hedgehogs are found only in regions with between 300 mm and 800 mm rainfall, compared to the estimated 200 mm at Elands Bay today (Parkington, 1981). Klein (1991) discussed measurements of Holocene and Pleistocene dune mole rat (*Bathyergus suillus*) distal humeri, which were interpreted as suggesting wetter conditions between about 13 000 and 10 000 years ago. The relationship between adult size and rainfall in dune mole rats is good, and this is presumably mediated by vegetation growth. Klein (1991) noted that EBC Terminal Pleistocene animals were much larger than their Holocene counterparts and implied a rainfall of more than 400 mm.

Pollen is a widely used source of information on past vegetation and climatic patterns (e.g. Opperman and Heyderych 1990; Meadows and Sugden 1991, 1993; Scott 1994; Meadows and Baxter, in prep.). EBC's pollen sequence provides a picture of changing vegetation patterns in the vicinity of the cave over a rather longer period than for other Quaternary pollen sites in the Western Cape (Meadows & Baxter, in prep). The variations in the pollen abundance suggest significant environmental changes during the sedimentary period from prior to 40 000 to about 11 000 years ago. Greater quantities of pollen from taxa such as Anacardiaceae, Celastraceae, *Celtis*, Ebenaceae, *Ficus*, Flacourtaceae, *Myrica, Olea, Podocarpus*, Santalaceae and Sapindaceae in the past all indicate an Afromontane forest and mesic thicket vegetation which points strongly to a cooler and moister conditions at this time. Between about 40 000 and 11 000 years ago the concentrations of total pollen reached a maximum, a phenomenon which is consistent with lower temperatures and greater moisture. Although pollen is often used in palaeoenvironmental reconstruction, identifications are often restricted to the level of family. The poor taxonomic resolution of pollen data means that it cannot be used conclusively to infer past environmental conditions.

Most studies (some already mentioned) which have used plant data to reconstruct past climates on the Cape west coast and elsewhere in the fynbos biome, are based on narrative accounts of the species - climate tolerances. The environmental tolerances or envelopes have not been accurate enough for quantitative climatic reconstruction. For instance, preliminary work has been done using the wood charcoal sequence from EBC to infer past climates (Cowling *et al.*, in press), but these have lacked rigor, and have not been based on detailed environmental envelopes of the species. In contrast, the inferences made in this thesis were not impeded by the lack of knowledge on the current species tolerance levels.

To conclude this introductory chapter, the overall aim of this thesis was to explore the feasibility of reconstructing climatic reconstructions over the past 40 000 years on the Cape west coast using an archaeological sequence from EBC. This approach represents a substantial advance relative to other, less rigorous approaches used in the past.

There were three main objectives in this thesis, to:

- Determine whether past communities in the surrounds of EBC have present day analogues in the study area.
- Determine the community – environment relationships of the extant community.

- Attempt a reconstruction of past climates using two methods – a local and a regional approach.

This thesis thus aims to makes use of the accurately identified EBC charcoal sequence spanning crucial time periods to reconstruct past climates. The methods used are novel and contribute new ways of predicting climates.

CHAPTER 2

THE CLASSIFICATION OF FOSSIL AND PRESENT WOODY PLANT COMMUNITIES AND THE ESTABLISHMENT OF PRESENT ENVIRONMENTAL CORRELATES OF COMMUNITIES.

2.1 INTRODUCTION

Species behave individualistically and understanding the historical development of assemblages is a difficult task (Davis, 1981). It has long been recognised that plant communities change over time (Woodward, 1987). The way communities change depends upon which aspect of the vegetation is monitored: individual plants, whole populations, or communities. Individual plants adjust their growth and reproductive rates; plant populations change in abundance, genetic composition and geographic distribution; and plant communities change in composition (Webb III, 1986). Thus communities do not change *en masse* but rather, as individual species migrate into them or become locally extinct. The individualistic concept (Gleason, 1926) is important in modeling the response of communities to environmental change. The implication of this individualistic response is that extant communities may not have existed in the past because of different environmental conditions. This effect becomes particularly marked over long time spans as environmental changes are more dramatic. As such, the recorded time series of vegetation and climate change over the past few centuries is not long enough to fully appreciate future changes. The Quaternary record, on the other hand, is a suitable time scale for testing hypotheses regarding climate-vegetation interactions (Prentice, 1986; Overpeck, 1992). The Quaternary vegetation history reveals that there has been long-term dynamism of distribution patterns of plants (Huntley and Webb III, 1988).

Obviously the amount of change in communities will depend, to some extent, on the characteristics of the species within the communities, especially life history characteristics, in particular longevity and regeneration requirements that determine persistence. For instance, relatively short-lived fynbos and karoo shrubs whose regeneration is sensitive to soil moisture and temperature conditions will show more turnover when compared with long-lived thicket species that regenerate in their own microclimates (Cowling *et al.*, 1997). In all communities there will also always be some species that are resilient to catastrophic weather events or climatic changes, and will persist under changed conditions (Diamond and Case, 1986). These plants do not necessarily thrive in the changed environment, but rather, simply persist under the changed conditions. "Persistors" are not the norm in plant communities and in general communities will change in accordance with climatic conditions. Interactions between species can also dramatically alter community structure. For instance plants may compete with each other for light, nutrients and water. Alternatively they may interact positively through the amelioration of harsh environmental conditions (Bertness and Leonard, 1997). In addition to these, plant - plant interactions, plants may interact with animals in a number of ways. For instance, species dependent on a specific pollinators will disappear if pollinators become extinct (Bond, 1994). These interactions provide opportunities for communities to achieve specific and different characteristics. Climatically induced changes will also depend to a large extent on the "neighbourhood" and in particular on the communities surrounding the community of interest. This neighbourhood provides the pool of species which might replace species that are unable to tolerate changed climatic conditions (Stacey and Taper, 1992). The concept of "tracking time" (Davis, 1986; Davis, 1989; Hengeveld, 1997) is a useful framework for understanding these migrations (Huntley and Webb III, 1988). The response of species to climatic change is to tend towards an equilibrium that has itself been shifted. Using the palaeorecord to understand how species behaved in the past can be pivotal in determining the rates of past climate change (Huntley, 1990; 1991). The palaeorecord provides the most secure documentation because the fossil indicators provide clear, quantitative responses of vegetation to climate change (Ritchie, 1986). It also provides compelling evidence that plant migrations can be rapid enough to track climate changes and that migrations can take place by means of sporadic long-distance leaps (Pitelka, 1997). Prentice (1986) notes that the time required for vegetation to change depends on the reproductive vigour of the invading species and how close the prevailing climate is to the optimum of the resident species. Different species have different tolerance levels, evolutionary histories, and dispersal abilities (Levin, 1988; Mackey, 1994). These dictate the tracking time (Hengerveld, 1997) and consequently the effect that changes in climate would have on the species.

Despite the inherently individualistic nature of changes which occur in communities at relatively short time periods, over longer time periods communities as units may possibly be characterised by certain tolerance levels or environmental envelopes (Box, 1981). These may then be used to make broad generalisation about climate change. However, to predict the effects of climate change we must understand mechanisms by which climate controls community distribution (Webb III, 1986). Identifying the climatic factors most important in limiting the distributions of plant species is the first step in the development of climatic envelopes and, consequently, past climatic conditions (Box, 1981).

The distributions of species are dictated by general climatic factors such as seasonal pattern of temperature, precipitation, solar radiation or wind; by physical features such as altitude, soil texture and soil depth; and by the chemical environment (e.g. the availability of inorganic and organic nutrients) (Diamond and Case, 1986). These factors all vary sub-continentally as well as on a meso- and micro-scale (Stephenson, 1990; Rutherford *et al.*, 1995, 1996; Schulze, 1997). Compositions of plant communities change along gradients of these environmental variables (Ter

Braak and Prentice, 1988). As the climate changed in the past so did the community structure and composition (Webb III, 1986). By understanding the most important environmental factors that define the distribution of the present day communities one can gain insight into the environmental conditions that changed past communities (e.g. MacDonald *et al.*, 1993; Jordan, 1997; Whitlock and Bartlein, 1997). It has been found that climatic variations beyond the Last Glacial Maximum were the primary cause of the regional changes in vegetation, and that non-climatic factors were secondary (Whitlock and Bartlein, 1997). There are three fundamental principles which constrain this inference process (Overpeck, 1992):

1. Climatic change of the magnitude of the past 18 000 years resulted in large changes in vegetation.
2. Plant taxa respond individualistically to climatic change. Vegetation regions, or biomes, commonly appear, change, and disappear through time as each taxon tracks its favoured climatic conditions.
3. Past climatic conditions in the past without modern analogues are likely to produce vegetation types without modern analogues.

Understanding more about how present-day species and communities function, especially their environmental relationships, is important if we are to use these to reconstruct past climatic conditions. This study records the change in community structure over time and relates the past communities to present day communities in the landscape. The important environmental relationships acting in the landscape today are identified. It is assumed that these would also have caused the community reshuffling or community shifts (Ladd, 1979) that occurred.

In this chapter, I describe in detail the past (based on a fossil charcoal sequence) and extant (based on contemporary samples using only those species in the fossil charcoals) vegetation in the Elands Bay study area. I also determine which environmental variables best explain the observed mosaic of species associations in the landscape. Four main questions addressed were:

1. Which communities, as based on the species identified in the charcoal, are present in the area today?
2. Which communities were evident in the past, from the fossil charcoal sequence?
3. What are the similarities between the fossil and present communities?
4. What environmental variates best explain the observed mosaic of woody species associations in the present landscape?

2.2 METHODS

2.2.1 Data collection

Sampling design

The methods of sampling and identification of charcoal fragments have already been described in Chapter 1. In terms of sampling the extant vegetation in the study area (described in Chapter 1), it was initially hoped that a "gradsect" approach could be used. This sampling approach is a directed transect sampling of vegetation which is intended to provide a description of the full range of floristic variation in a region (Austin & Heylingers, 1991). In essence, existing data are used to guide the *a priori* development of an economical and efficient sampling strategy. With this in mind, a geographical data base of the study area with all of the different combinations of pre-known environmental parameters, for which data exist, was produced using a geographical information system (Arc/Info and Arcview 3.0). Unfortunately, large scale agricultural disturbance (Plate 2.1a) of the natural plant communities in the sampling area meant that the correspondence between the occurrence of a particular suite of climatic parameters and the occurrence of the corresponding intact natural vegetation was low. In addition, cells containing unique sets of parameters were scattered throughout the landscape making *a priori* transect selection virtually impossible. This directed sampling protocol was therefore abandoned in favour of a strategy that attempted to cover the full range of environmental variation for each species as constrained by the availability of untransformed vegetation. Plots were sampled wherever there was natural untransformed (by agriculture) vegetation (Figure 1.2). Plots were also only located wherever there were species that were identified from the charcoal (e.g. Figure 2.1). A total of 259 plots were assessed. The size of the quadrats varied from 20 x 20 m to 80 x 80 m according to the vegetation structure (larger plots were sampled where the vegetation was structurally taller). In each plot the percentage cover of the woody species that were found in the EBC charcoal sequence were estimated, as was the total percentage cover of all species in the plot. This was done using a Braun-Banquet scale (Braun-Blanquet, 1951). This scale uses the following categories: 1 = 0 - 5 %; 2 = 5 - 10 %; 3 = 10 - 25 %; 4 = 25 - 33 %; 5 = 33 - 50 %; 6 = 50 - 75 %; 7 = > 75 %.

Measurements

For the local study, 27 species (Table 2.1), which had been identified in the EBC charcoal sequence were sampled in the extant landscape. Some of the species that were found in the charcoal samples in the cave do not occur in the study area today and could thus not be sampled. These included *Chionanthus foveolatus, Grewia occidentalis, Tarchonanthus camphoratus, Ficus sur*, and *Celtis africana*. *Salix mucronata* was identified in the charcoal samples, but was only found in the azonal riverine woodlands of the Olifants River and was, therefore, not sampled. In addition, two other species, *Erica caffra* and *E. verecunda,* were also not included because of their rarity in the contemporary vegetation.

In each sampled plot a number of site variables were measured (Table 2.2). Slope was measured using a Slope Meter (PM 5/66 & PM 5.66P Suunto Co.). The longitude and latitude for each plot were determined using a Magellan Global Positioning System. The rock cover was classed into three categories: the percentage of bedrock, boulders and pebbles. Boulders were defined as being loose rocks over 10 cm in diameter and pebbles as being rocks less than 10 cm in diameter. Bedrock was defined as rock that was not detached at all (i.e. exposed parent material).

A soil sample was collected from each plot, brought back to the laboratory, and then air-dried for further analysis. The soil samples were analysed for pH, colour and texture. For a few sites there was insufficient soil for samples due to the of high rock cover. The pH was determined using a 1M KCl suspension. The colour was determined using the Munsell system (Munsel

TABLE 2.1: The species used in the study, with their growth form, average height and distribution data from Jacobsen (1970), Bond and Goldblatt (1984), Coates Palgrave (1984), Pooley (1993), Rebelo (1995). * Not sampled in study area.

	SPECIES	EVERGREEN /DECIDUOUS	HEIGHT (M)	HABITAT	DISTRIBUTION IN S.A[1]
1	*Cassine peragua*	E	2 - 10 m	Forests or forest margins, dune scrub and dry rocky areas	Widespread in S and E. Cape to Natal and Swaziland.
2	*Celtis africana* *	D	< 40 m	Forests, riverine woodland and rocky outcrops	W. and E. Cape not along W. Coast, to tropical Africa.
3	*Chionanthus foveolatus* *	E	2 - 15 m	Forest and thicket	S.W. Cape and E. Cape – Natal and Transvaal.
4	*Colpoon compressum*	E	3 - 5 m	Coastal sand dunes, dune bush, lower slopes of mountains	S.W. Cape to E. Cape, Tranasvaal and North to Mozambique
5	*Diospyros glabra*	E	< 5 m	Mountain slopes, margins of forest, open grassland, sandy flats	S.W. Cape and W. Coast.
6	*Dodonaea angustifolia*	E	2 - 7 m	Forest margins, in scrub , coastal dunes and open woodland.	Widespread in S and W Cape – Natal to Tropical Africa.
7	*Erica caffra* *	E	2 - 4 m	In or near rivers	Widespread in S.W. Cape to E.Cape and Natal.
8	*Erica verecunda* *	E	< 1.8 m	900 - 1200 m	Widespread in mountains of W. Cape, Cederberg, Giftberg, Kouebokkeveld, Kamiesberg (Namaqualand)
9	*Eriocephalus africanus*	E	< 2 m	Asteraceous fynbos, dry nutrient poor soils	Widespread in S.W. Cape to Namaqualand
10	*Euclea racemosa* ssp *racemosa*	E	3 - 12 m	Coastal and dune forest	S.W. Cape and Namaqualand to E. Cape.
11	*Euclea tomentosa*	E	3 - 4 m	Arid areas, rocky mountain slopes, ravines and near water courses	S.W. Cape to W. Namaqualand.
12	*Euryops speciosissimus*	E	<2 m	Asteraceous fynbos, dry nutrient poor soils	W. Cape (Cederberg and Piketberg) to W. Karoo
13	*Ficus sur* *	E	< 35 m	Forests, riverine bush and wooded grassland	S. Cape to E. Cape to Tropical Africa (Arabia)
14	*Ficus cordata*	E	3 - 10 m	Rocky outcrops and woodlands	N. Cape to W. Cape including Namaqualand and Namibia.
15	*Grewia occidentalis* *	E	< 6 m	Evergreen forests, forest margins, open (dry) woodland / bush	Widespread in South Africa (E. Cape to Tropical Africa), excluding W. Cape and Karoo
16	*Halleria lucida*	E	2 - 20 m	Rocky outcrops, forests, forest margins and near streams.	W. Cape and E. Cape to Tropical Africa (Ethiopia)

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[1] Old provincial names used

TABLE 2.1: Continued.

	SPECIES	EVERGREEN /DECIDUOUS	HEIGHT (M)	HABITAT	DISTRIBUTION IN S.A
17	*Heeria argentea*	E	< 5 m	Rocky areas, on mountain slopes.	Widespread in S.W. and W.Cape
18	*Hymenolepis parviflora* *	E	1-3 m	Asteraceous fynbos and renosterveld.	S. and S.W. Cape to Namaqualand.
19	*Kiggelaria africana*	D	4 - 22 m	In or near forests.	S. W. (Namaqualand) and E.Cape to Tropical Africa (N. Kenya)
20	*Leucadendron pubescens*	E	0.6 - 3 m	Deep, sandy soils. Altitudes of 60 – 1700 m.	Widespread in W. and S.W. Cape to Natal (Ladismith)
21	*Maytenus heterophylla*	E	4 - 5 m	Variety of altitudes (up to 1900 m), many habitats.	Widespread in S.W Cape to Tropical Africa.
22	*Maytenus oleoides*	E	< 4 m	Mountain thickets on rocky outcrops.	Widespread in W. and S. Cape to Natal
23	*Myrsine africana*	E	< 3.5 m	Forest margins.	W. and E. Cape to tropical Africa (Azores, Asia)
24	*Olea europaea africana*	E	5 - 10 m	Forest margins, in bushveld, on rocky hillsides, often near water courses.	Widespread in S. and E. Cape
25	*Passerina glomerata*	E	< 2 m	Asteraceous fynbos, dry nutrient poor soils. Common in mountainous areas.	S.W. Cape - Namaqualand
26	*Podocarpus elongatus*	E	3 - 6 m	Near rivers, on mountain slopes, in sandy soils.	S and W. Cape
27	*Protea glabra*	E	< 5 m	Shallow sandstone soils / in cracks in rock slabs.	W. and S. Cape including Bokkeveld, Olifants River mountains, and Kouebokkeveld
28	*Pterocelastrus tricuspidatus*	E	5 - 25 m	Margins of forests, coastal areas, dune scrub.	S.W. Cape, S. Cape and E. Cape to Transvaal.
29	*Protea nitida*	E	< 5 m	Common in rocky areas, e.g. scree and talus slopes.	Widespread in S.W. Cape to Namaqualand.
30	*Rhus undulata*	E	< 5 m	In arid areas and forest.	Widespread in W. Cape and S.Cape.
31	*Ruschia maxima*	E	> 30 cm	Dry, rocky areas.	W. Cape from Cederberg to coast.
32	*Salix mucronata* *	D	< 25 m	Near watercourses.	Widespread in S.W. Cape
33	*Salvia africana-lutea*	E	< 2 m	Coastal dunes, arid fynbos and rocky slopes.	S.W. Cape (Namaqualand) to E.Cape
34	*Tarchonanthus camphoratus* *	E	< 5 m	Many areas (coast - high altitudes).	Widespread in S.W. and S. Cape, but not W. Coast.
35	*Zygophyllum morgsana*	E	< 1.5 m	Arid coastal areas associated with other succulent species.	S.W. Cape, W. Cape (Namaqualand and Namibia) and E. Cape

TABLE 2.2: Measured site variables and their units.

Factors measured in the field	Units	Abbreviation
Median height of vegetation	Meters	
Aspect	N, NE, NW, E, SE, S, SW, W.	
Slope inclination	Degrees	
Solar Radiation	Determined using slope and aspect (Schulze, 1997). Joules per m^2	rad
Rock cover: (bedrock, boulders and pebbles)	Percentage of each class	%bedk, %bould, %pebbs
Altitude (determined from 1:50 000 maps of the area).	Meters	alt
Geology	Seven classes, see text	geol
Soil factors: pH, texture and colour	See text	pH, %coarse, %medium, & fine, %clay, %silt

TABLE 2.3: The seven climatic variables used and their abbreviations.

Abbreviation	**Climatic parameter**
Marain	Mean annual rainfall (mmyr $^{-1}$)
Mwrain	Median winter rainfall (sum of rainfall for May-August in mm)
Mwrain%	Median winter rainfall as percentage of median annual rainfall
Growd	Optimum growth days.
Mhot	Maximum temperature of the hottest month (°C)
Mcold	Minimum temperature of the coldest month (°C)
Rad	Solar radiation (Jm $^{-2}$), determined using the slope and aspect measured in the field.

colour company, Inc., Baltmore 18, Md., USA). Particle size distribution analysis was conducted using the Bouyoucos particle size method (Rowell, 1994). A combination of sedimentation and sieving was used. Sedimentation for the separation of clay, silt and sand and sieving for the separation of sand into coarse, medium and fine fractions (Hartmann *et al.*, 1994; Rowell, 1994). The geology of the sample plots was determined from geological survey maps of the area which were digitised using Arc/Info (version 7.1) (Figure 1.4). The geology map produced was at a coarser scale than the coverage of the climatic parameters. This may have had an influence on my ability to asses the importance of geology in restricting the distribution of the species.

A total of seven climatic variables were also determined for each site (Table 2.3). The climatic variables were compiled using a number of existing data bases (Rutherford *et al.* 1995, 1996). These variables are spatially extrapolated using standard regression techniques, to cover the entire surface of South Africa. Each climatic grid consisted of a number of pixels which were 1 x 1 decimal degrees in size. Each decimal degree is approximately 1.5 km x 1.5 km in size. Thus the climatic data was at a resolution of 2.25 km^2 grids. Precipitation was described using median annual rainfall (marain), median winter rainfall (mwrain), and the percentage of the total rainfall occurring in winter (mwrain%). The temperature regime was described using the mean minimum temperature of the coldest month (mcold) and the mean maximum temperature of the hottest month (mhot). These variables have been used in other studies on predicting climates (e.g. Prentice *et al.*, 1992; Rutherford *et al.*, 1995, 1996). These latter two variables are important in the context of the Cape west coast as they describe the winter rainfall regime. Although seldom a limiting factor to vegetation development at the macro scale, estimated radiation was also included as it may have profound effects on vegetation at the meso-scale (Schulze, 1975; 1997). Finally, a derived climatic variable, optimum growth days, was included. The number of growth days is defined as the number of days when actual evapotranspiration is more than half the potential evapotranspiration for the topsoil horizon and when the mean temperature exceeds 24 °C (Schulze, 1997). These were calculated using daily soil water budgeting routines from actual soil properties and assuming vegetation hydrological characteristics (Rutherford *et al.*, 1995). These climatic variables are extrapolated (Shulze, R.E. CCWR, University of Pietermaritzburg, Natal). The climatic data, which were in the form of grids, were viewed and manipulated using Arcview 3.0 and Arc/Info (Version 7.1). These climatic coverages were overlaid with the distribution of each species in order to determine the climatic conditions that each species grows under. An example of the distribution of *Dodonaea angutifolia* (which was one of the species identified in the charcoal) can be seen in Figure 2.1. This type of species distribution coverage was overlaid with the climatic data bases.

2.2.2 Data analysis

Classification

Three data sets were classified using TWINSPAN (Two-Way Indicator Species Analysis) (Hill, 1979): the extant samples in the study area (259 plots); the fossil samples using the charcoal sequence (39 sequences, hereafter referred to as "plots"); and the combined fossil and the extant samples. There were thus effectively 39 'plots'. For the combined classification, the two data sets, fossil and extant, were merged. There were thus 298 "plots" in this analysis. The objective of this combined analysis was to identify community analogues between the present and past communities.

TWINSPAN is a widley used technique for vegetation classification (e.g. White *et al.*, 1985; Kent and Coker, 1992). The TWINSPAN method used for classification in this study relies on the concept of pseudospecies, whereby the presence of a species at different quantitative levels of abundance is used (Hill, 1979; Kent and Coker, 1992). Classifications are depicted in tabular and dendrogram forms. The communities that are produced by TWINSPAN are made by dividing the samples into groups by repeated dichotomization, and then doing the same for the species. In the TWINSPAN analysis, the default settings were used, except for the pseudospecies cut levels. In this study seven cut levels were used so as to standardise the three data sets to the Braun Blanquet scale. As the number of species used in the study was small compared to most vegetation surveys, all the species were made available for use as indicator species. The pseudospecies were not weighted. This was especially important for the charcoal data where presence of any species was significant.

Phytosociological tables were produced for each classification (Appendix 2, 3 and 4). Dendrograms with the indicator species for each community and the number of plots in each community are shown in Figures 2.1, 2.2, 2.3. Using the two-way phytosociological tables produced by TWINSPAN I extracted synoptic tables for each data set. The tables produced (Tables 2.4 - 2.6) summarised species fidelity to communities within each data set. Fidelity is rated on a 1 - 5 scale: 1 = 1- 20 % frequency; 2 = 21 - 40 %; 3 = 14- 60 %; 4 = 61 - 80 %; 5 = >81 %. The species with values greater than 1 in one or more communities were included in the synoptic tables.

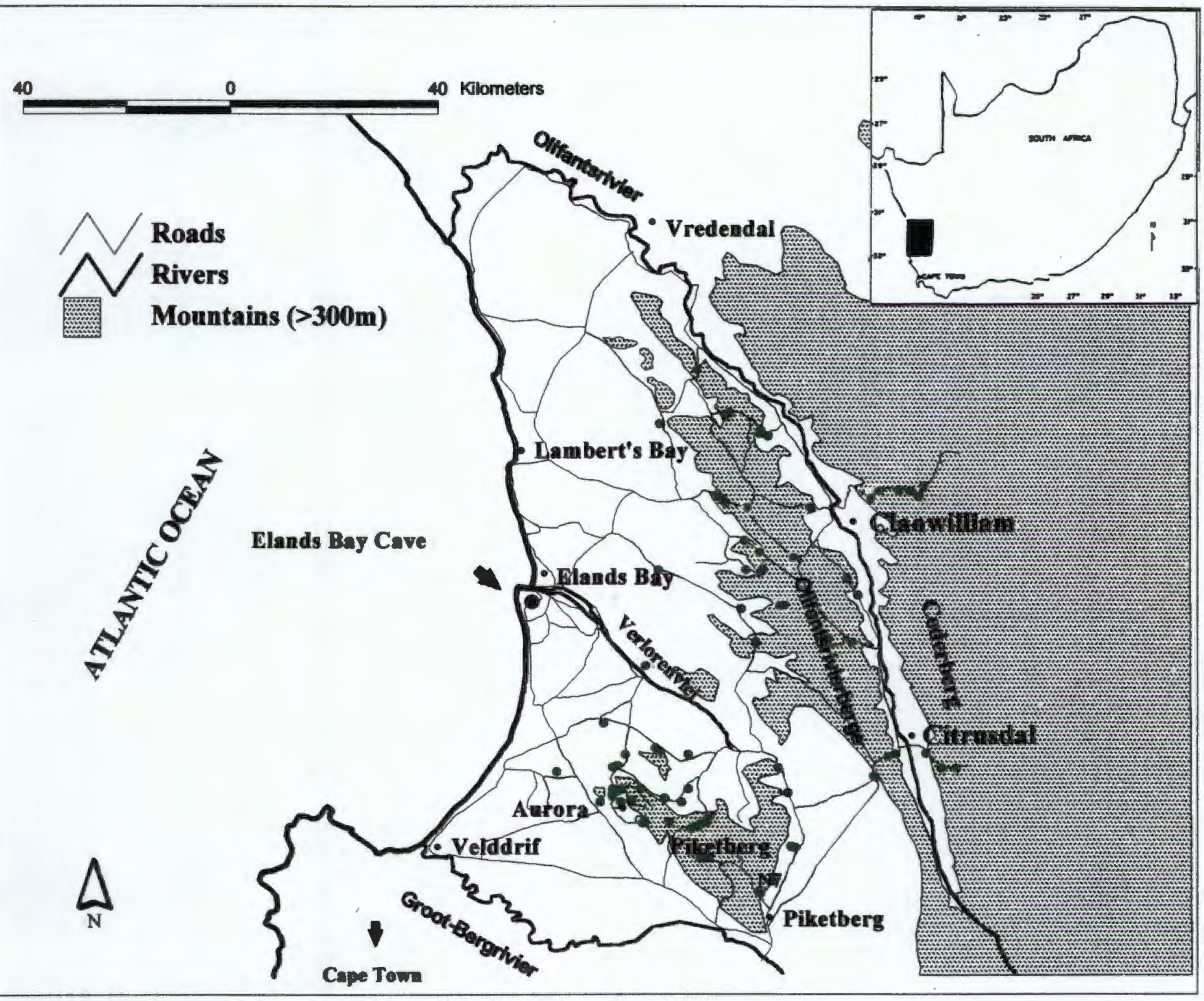


FIGURE 2.1: Map of the study area on the Cape west coast showing the location of plots in which *Dodonaea angustifolia* was sampled. The maps of each species distribution was overlaid with the climatic variable maps.

TWINSPAN has been criticised by van Groenewoud (1992) as giving erratic results, especially after the first division in complex models. In his study van Groenewoud (1992) found that the first few divisions were reasonably accurate, but with increasing divisions there was a corresponding increase in misclassification of sample points. I used the third level of division as the cut-off. According to van Groenewoud (1992) this is still a relatively 'safe' level of division which is likely to produce few misclassifications.

Multivariate Direct Gradient Analysis

Ordination is an indirect gradient analysis tool for exploratory analysis of community data with no prior information about the environment (Ter Braak and Prentice, 1988). Understanding the relationships between species and environments is a fundamental ecological objective. Multivariate methods have therefore been adopted and adapted to best organise samples on the basis of the site attributes (Jackson and Somers, 1991). Canonical Correspondence Analysis (CCA) (Ter Braak, 1991) is a direct gradient analysis technique that is an elegant extension of the indirect gradient analysis technique, Correspondence Analysis (CA). It is a good ordination technique and is commonly used for organising environmental and species data (Kent and Coker, 1992). The method uses multiple regression to select the linear combination of environmental variables that explains most of the variation in the species scores on each axis (Kent and Coker, 1992). CA and a related ordination technique, Detrended Correspondence Analysis (DCA), have both been criticised in the literature (Kent and Coker, 1992) and it is necessary to guard against the acceptance of DCA as an ecological panacea (Jackson and Somers, 1991). In CCA the resulting ordination is a product of the variability of the environmental data as well as the variability of the species data. CCA has all the advantages and none of the disadvantages of DCA, and is most suitable where a good set of environmental and species data are available (Kent and Coker, 1992).

Two CCA's were run using the ordination programme, CANOCO (Ter Braak, 1991) in order to analyse the species - environmental relationships in this study. The first CCA was run using the entire set of environmental variables (those measured in the field plus extrapolated climatic variables). The second was run using only the climatic variables. My rationale for conducting these two separate ordinations was to resolve how much of the variation in community distributions could be accounted for by climate alone, as well as by all measured environmental variables. Latitude and longitude were included as covariables in both CCAs. The results of the first CCA on all of the environmental variables indicated that geology and soil colour did not have a large influence the distribution of the communities, these variables were, therefore, excluded in subsequent analyses. One of the factors that may have caused geology not to be a major determinant of the species distribution was the low resolution of the geology data. Another reason is that fire can restricts the distribution of larger trees (Bond, 1997) and this would confine trees to afromontane patches in ravines.

2.3 RESULTS

2.3.1 Extant communities

The classification of extant vegetation in the study area resolved eight communities at the third level of division (Figure 2.2). Four categories were formed at the second level of division and eight at the third level. Data are summarised in Table 2.4 which shows frequency data for species in each of the communities. For data on the percentage cover of the species in each community, see Appendix 2. For a general description of each species' growth form, distribution and preferred habitat, see Table 2.1. The environmental attributes for each community are presented in Table 2.5.

1. *Heeria argentea - Maytenus oleoides* community

Dominant and frequent species in this community include *Heeria argentea, Maytenus oleoides, Diospyros glabra,* and *Protea nitida* (Table 2.4). *Heeria argentea* occurs predominantly in thicket clumps, interspersed in fynbos. This community occurs at altitudes between 150 - 1 100 m, in areas receiving between 296 - 696 mm of rainfall per annum, and receiving relatively low levels of radiation (Table 2.5). The community is also associated with a high cover of bedrock (up to 70 %) and soils with pH values ranging between 4 - 6. It is found in isolated patches (Plate 2.1b) and includes many Afromontane forest species such as *Halleria lucida, Podocarpus elongatus* and *Kiggelaria africana* (Taylor, 1996). The community resembles the Michell Thicket described by Campbell (1985). The Michell Thicket is confined to mountains of the western fynbos biome, especially on scree slopes. The high percentage cover of *Protea nitida* is characteristic of the 'Waboomveld' community described by Taylor (1996) and the Brandwag talus asteraceous fynbos, also 'Waboomveld' described by Campbell (1985).

2. *Olea europaea - Maytenus heterophylla* community

Dominant and frequent species in this community include *Maytenus heterophylla, Olea europaea-africana, Myrsine africana, Dodonaea angustifolia, Cassine peragua* and *Eriocephalus africanus* (Table 2.4). The community is associated with a relatively wide range of sites, ranging in altitude from 50 - 1000 m, and having relatively low soil pH values of 4 - 7, and high radiation levels (Table 2.5). The rainfall ranges between 210 - 559 mm p.a. The soils

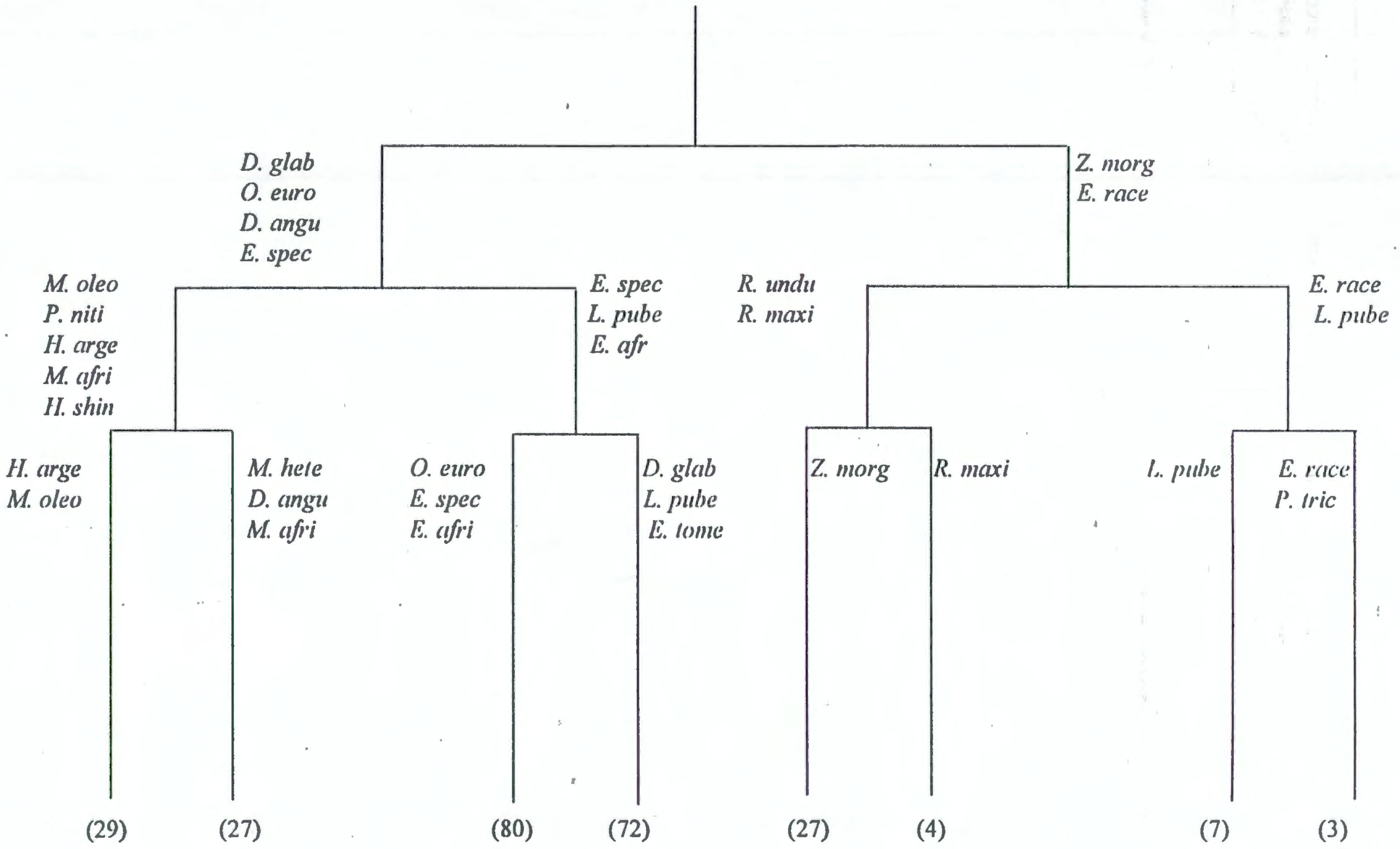


FIGURE 2.1: TWINSPAN classification of extant communities. See Table 2.4 for complete names of species.

TABLE 2.4: Synoptic table for eight extant plant communities. 1 = Heeria - Maytenus, 2 = Olea – Maytenus, 3 = Rhus – Euclea, 4 = Diospyros - Leucadendron, 5 = Rhus - Zygophyllum, 6 = Ruschia - Eriocephalus, 7 = Zygophyllum - Euclea and 8 = Zygophyllum - Leucadendron community.

Community	1	2	3	4	5	6	7	8
Number of plots	49	60	69	30	18	5	15	13
Heeria argentea	4	1	1	1			1	
Maytenus oleoides	4	1	1	1				
Protea nitida	4	1		1				
Myrsine africana	3	3	1		2			
Colpoon compressum	2	1	1				1	
Maytenus heterophylla	1	3	1	1	1		1	
Protea glabra			1					
Halleria lucida	1	1						
Cassine peragua	4	1	4					
Olea europaea	3	4	2					
Euryops speciosissimus	1	4	2	1		1		
Diospyros glabra	4	3	3	4	1		1	
Dodonaea angustifolia	2	3	2	2				
Hartogiella schinoides	2	2	1					
Kiggelaria africana	1	2	1					
Podocarpus elongatus	1	1	1				1	
Euclea tomentosa	1	1	3	2	1		1	
Passerina glomerata	1	1	2	3				
Eriocephalus africanus	1	4	2	1	2	3		
Leucadendron pubescens	1	1	1	4				2
Pterocelastrus tricuspidatus	1	1	1	1			2	
Ruschia maxima	1	1	1		2	5		
Ficus cordata		1	1		2			
Euclea racemosa	1	1	1		1		5	2
Rhus undulata	3	4	5	1	5			2
Salvia africana-lutea		1	2		2		1	1
Zygophyllum morgsana		1	1	1	5	3	5	5

TABLE 2.5: The environmental variables associated with each of the extant communities sampled in the local study area. Communities are those described in the text. The abbreviations for the environmental variables are shown in Tables 2.2 and 2.3.

Community		radiation (Jm^{-2})	bedrock (%)	pH	altitude (m)	% sand	mhot (°C)	marain (mm)	growday (days/yr)
1 *Heeria-Maytenus*	max	380	70	6	1100	99	31.1	696	23
	min	140	0	4	150	78	26.1	296	11
2 *Olea-Maytenus*	max	380	80	7	1000	110	32.7	559	27
	min	110	0	4	50	75	28.1	210	11
3 *Rhus-Euclea*	max	495	80	8	800	99	33.5	514	26
	min	135	0	3	45	84	27.5	142	12
4 *Diospyros-Leucadendron*	max	380	70	9	700	100	32.6	577	29
	min	220	0	4	20	80	28.3	57	12
5 *Rhus-Zygophyllum*	max	410	70	8	300	100	32.4	317	22
	min	185	0	4	40	86	28	128	14
6 *Ruschia-Eriocephalus*	max	380	30	6	300	92	34.6	362	30
	min	220	0	5	10	87	28.2	106	15
7 *Zygophyllum-Euclea*	max	335	10	8	200	102	30.4	243	19
	min	230	0	5	3	87	28.2	114	9
8 *Zygophyllum-Leucadendron*	max	310	40	8	250	99	30.2	312	18
	min	250	0	5	3	84	27.1	64	13

are shallow and the bedrock cover is often high (up to 80 % cover). The community contains some dry asteraceous fynbos elements (Campbell, 1985). Taylor (1996) describes a 'scree and sand' community from the Cederberg mountains that resembles this community.

3. *Rhus undulata - Euclea tomentosa* community

Dominant and frequent species in this community include *Rhus undulata, Euclea tomentosa, Olea europaea-africana, Cassine peragua, Euryops speciosissimus* and *Diospyros glabra* (Table 2.4). *Protea glabra,* which is restricted to this community, is common in shallow sandstone soils or cracks in rock slabs in the dry, north-trending mountains of the fynbos biome (Rebelo, 1996). The community is associated with low to mid-altitude (45 - 800 m), relatively xeric sites with rainfall ranging from 142 - 514 mm p.a. The soil pH has a wide range from 3 - 8. This is one of the most well represented communities (found in 69 out of 259 plots) in the present study area (Plate 2.2a). Most of the species comprising this community are tall shrubs with trees being the exception (*Kiggelaria africana* and *Olea europaea-africana*) (Table 2.1). Taylor (1996) describes a community with a similar composition (*Olea europaea-africana - Myrsine africana* community) which occurs on sandy flats in the mid-altitudes of the Cederberg mountains.

4. *Diospyros glabra - Leucadendron pubescens* community

Dominant and frequent species in this community are *Diospyros glabra, Leucadendron pubescens, Passerina glomerata* and *Euclea tomentosa* (Table 2.4). The community is associated with low to mid-altitude (20 - 700 m), xeric sites (57 - 577 mm p.a.) and deep sands with pH ranging from 4 - 9 (Table 2.5). *Leucadendron pubescens* is an important proteaceous element which suggests an affinity between this community and proteoid fynbos defined by Cowling and Holmes (1992). Proteoid fynbos is defined as having > 10 % cover of mid- to tall

PLATE 2.1: a) A view of the Piketberg illustrating the large tracts of agricultural land and natural vegetation in the mountainous areas. b) A patch of forest / thicket (*Heeria argentea - Maytenus oleoides* community), typical of those found in the Piketberg and Cederberg mountain ranges.

non-sprouting, proteoid shrubs. Similar proteaceous communities are represented in the sand plain fynbos vegetation of the west coast (Low and Rebelo, 1996).

5. *Rhus undulata - Zygophyllum morgsana* community

Dominant and frequent species in this community include *Zygophyllum morgsana, Rhus undulata* and *Euclea racemosa* (Table 2.4). The community is characterised by a high percentage cover of *R. undulata*. The community is associated with low lying (40 - 300 m), xeric conditions (128 - 317 mm p.a.). It occurs on deep coastal sands with pH values between 4 - 8. Elements of this community occur in Strandveld Succulent Karoo of the Cape west coast (Low and Rebelo, 1996).

6. *Ruschia maxima - Eriocephalus africanus*

Dominant and frequent species in this community include *Ruschia maxima, Eriocephalus africanus* and *Zygophyllum morgsana* (Table 2.4). These species are all relatively low growing shrubs (Table 2.1). *R. maxima* is a robust leaf succulent while *Z. morgsana* has semi-succulent leaves. These communities occur near to the coast (10 - 300 m) where bedrock cover is low (0 - 30 %), sands are deep and pH values are moderately high (5 - 6). The succulent elements suggest an affinity with Succulent Karoo vegetation.

7. *Leucadendron pubescens - Zygophyllum morgsana* community

Dominants in this community include *Leucadendron pubescens, Zygophyllum morgsana, Euclea racemosa*, and *Salvia africana-lutea* (Table 2.4). The community has a high percentage cover of *L. pubescens* (Plate 2.2b). It is associated with low-lying (3 - 200 m) coastal environments and soils which often have relatively high pH values (5 - 8). The rainfall ranges between 114 - 243 mm p.a. and the bedrock cover is low (0 - 10 % cover). The

PLATE 2.2: a) *Rhus undulata - Euclea tomentosa* community, which is dominant in low rainfall, lowland areas. b) *Leucadendron pubescens- Zygophyllum morgsana* community. Note the high cover of *L. pubescens.*.

community represents the driest extension of Sand Plain Fynbos (Low and Rebelo, 1996) in the study area.

8. *Zygophyllum morgsana - Euclea racemosa* community

Dominants include *Euclea racemosa, Pterocelastrus tricuspidatus, Zygophyllum morgsana,* and *Ruschia maxima* (Table 2.4). The community is associated with xeric (64 - 312 mm p.a.), low- lying sites (3 - 250 m) with relatively high pH values (5 - 8) (Table 2.5). The bedrock cover is relatively low, between 0 - 40 % cover. Most of the component species are characteristic of Strandveld Succulent Karoo (northwards) and coastal thicket (southwards) of the Cape west coast (see also Boucher and Jarman, 1977) (Plate 2.3a).

2.3.2 Fossil communities based on charcoal data

Classification of the vegetation data from the charcoal sequence resolved seven communities at the third level of division (Figure 2.3). Data are summarised in Table 2.6 which shows the frequency data for each species in all communities. The "plots" which classify into each community and the time period that each community covers are listed in Table (2.7).

1. *Podocarpus elongatus - Halleria lucida* community

Dominant and frequent species in the community include *Halleria lucida, Kiggelaria africana, Podocarpus elongatus, Celtis africana* and *Olea europaea-africana* (Table 2.6). *Salix mucronata* and *Ficus sur* are also common species in this community. These two species are generally considered to be riverine woodland species and this affinity between the Afromontane and the riverine species is salient. A similar with a similar composition, the

Michell Thicket, is found on the lower slopes of the Cederberg (Campbell (1985). *Cassine peragua* and *Dodonaea angustifolia*, two other species which occur in this community, are relatively common in the charcoal sequence, occurring in 39 % and 46 % of the "plots" respectively. Communities similar to these that occur on the middle slopes of the Cederberg have been recorded by Taylor (1996).

2. *Podocarpus elongatus - Ficus cordata* community

Dominant and frequent species in this community include *Ficus cordata, Maytenus heterophylla, Diospyros glabra, Euclea tomentosa, Kiggelaria africana, Podocarpus elongatus, Celtis africana, Grewia occidentalis, Hartogiella schinoides* and *Myrsine africana* (Table 2.6). *M. africana* is relatively uncommon in the charcoal sequence, only occurring in 5 % of the samples. *E. tomentosa* and *D. glabra* are two of the most common species in the charcoal samples (occurring in 69 % and 64 % of the intervals respectively), and are also common in this community. *M. heterophylla*, *H. schinoides* and *F. cordata* are also relatively common in this community occurring in 44%, 28% and 18 % of the "plots" respectively. Today, *Ficus cordata* is a common tree in rocky crevices and slopes (Plate 2.3b). Communities with similar dominants (*Olea europaea -africana, Cassine peragua, Hartogiella schinoides* and *Diospyros glabra*) have been recorded in the Cederberg mountains (Taylor, 1996).

3. *Olea europaea-africana - Protea glabra* community

Dominant and frequent species in this community include *Olea europaea-africana, Maytenus heterophylla, Leucadendron pubescens, Protea glabra* and *Diospyros glabra.* The three proteoid species which are associated with this community in the charcoal sequence are *Leucadendron pubescens, Protea nitida* and *P. glabra.* The indicator species for the community, *O. europaea-africana*, occurs in 46 % of the charcoal samples. Twelve "plots" are associated with this community which is the largest number of plots for any community in the fossil sequence. The occurrence of *P. nitida* is characteristic of the extant 'Waboomveld' community (Plate 2.4a) and the high cover of *P. glabra* is characteristic of one of the communities found on rock slopes and platforms described on the relatively xeric lower to mid slopes of the Cederberg (Taylor, 1996). *Leucadendron pubescens* is very common on sandy flats and valleys of the coastal forelands inland of EBC (Rebelo, 1995), as well as on the relatively xeric low-mid slopes of the Cederberg (Taylor, 1996).

4. *Cassine peragua - Heeria argentea* community

Dominant and frequent species in this community include *Cassine peragua, Maytenus oleoides, Heeria argentea, Euclea tomentosa* and *Diospyros glabra* (Table 2.6). This, essentially mesic thicket / asteraceous fynbos (Plate 2.4) community, is also associated with a relatively high number of plots (11 out of 39 plots). *Euryops speciosissimus*, occurred in 26 % of the samples. *Hymenolepis parviflora* and *M. oleoides* were both identified in 18 % of the samples and *Tarchonanthus camphoratus* in 13 % of the samples. A community with similar dominant elements is described by Taylor (1996), as a 'scree and sand community'. *H. argentea* and *M. oleoides* are common components of Mitchell Thicket, a community characteristic of the north-trending folded belt of the western, winter-rainfall fynbos biome (Campbell, 1985).

5. *Pterocelastrus tricuspidatus - Salvia africana-lutea* community

Dominant and frequent species in this community include *Hymenolepis parviflora, S. africana-lutea, Euclea tomentosa* and *Pterocelastrus tricuspidatus. E. tomentosa* is the most commonly occurring species in the charcoal samples, occurring in 69 % of the samples. *P.*

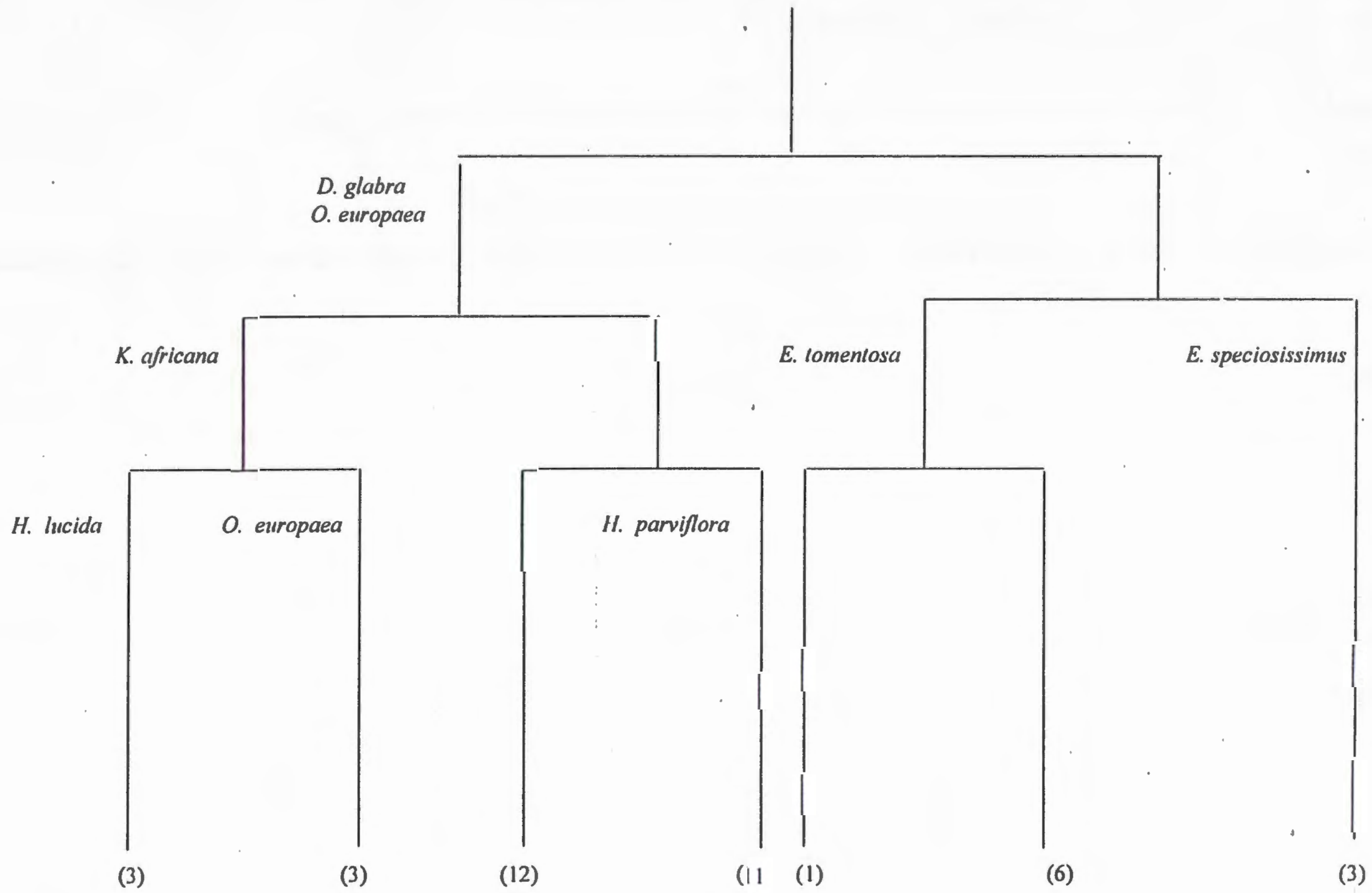


FIGURE 2.2: TWINSPAN classification of charcoal assemblages from EBC. Each "plot" is a sample of charcoal. The indicator species for each division in the dendrogram are indicated, as are the number of samples representing each final community.

TABLE 2.6: Synoptic table for seven charcoal communities. 1 = Podocarpus - Halleria, 2 = Podocarpus- Ficus 3 = Olea - Protea, 4 = Cassine - Heeria, 5 = Pterocelastrus - Salvia, 6 = Zygophyllum - Ruschia and 7 = Euryops - Eriocephalus community.

Community	1	2	3	4	5	6	7
Number of plots	3	3	12	11	1	3	6
Halleria lucida	5						
Ficus sur	5						
Salix mucronata	5						
Kiggelaria africana	5	5					
Podocarpus elongatus	5	5					
Celtis africana	5	5					
Grewia occidentalis	2	4					
Myrsine africana		4					
Chionanthus foveolatus	2						
Ficus cordata		5	2				
Olea europaea	5	5	5				
Hartogiella schinoides	4	4	2	2			
Maytenus heterophylla		5	5	1			
Colpoon compressum			2				
Leucadendron pubescens			3				
Protea glabra			3				
Protea nitida			1				
Erica verecunda			1				
Erica caffra			1				
Dodonaea angustifolia	4	5	3	4			
Tarchonanthus foveolatus	2			2			
Diospyros glabra	2	5	5	5			
Cassine peragua	2		2	5			
Maytenus oleoides				4			
Heeria argentea				4		2	2
Hymenolepis parviflora			1	3	5		
Salvia africana-lutea			1	1	5		
Euryops speciosissimus				3		5	1
Euclea tomentosa		4	5	5	5		5
Eriocephalus africanus						4	
Passerina glomerata						2	
Pterocelastrus tricuspidatus			2	1	5	4	2
Rhus undulata						2	2
Ruschia maxima						2	4
Zygophyllum morgsana							5
Euclea racemosa							1

TABLE 2.7: Corresponding dates in the charcoal sequence for communities derived from the fossil charcoal data.

Fossil communities	Dates	"Plots"
1. *Podocarpus elongatus - Halleria lucida*	> 40 000 yrs ago	37 - 39
2. *Podocarpus elongatus - Ficus cordata*	40 000 - 20 000	34 - 36
3. *Olea europaea-africana - Protea glabra*	17 800 - 10 400	22 - 33
4. *Cassine peragua - Heeria argentea*	9 900 - 7 910	11 - 21
5. *Pterocelastrus tricuspidatus - Salvia africana – lutea*	3 90	4
6. *Euryops speciosissimus -Eriocephalus africanus*	4 370 – 320	1, 2, 6, 7, 8, 9
7. *Zygophyllum morgsana - Ruschia maxima*	4 370 – 320	3, 5, 10

tricuspidatus (26 %) *H. parviflora* (18 %), and *S. africana-lutea* (13 %) occur far less frequently in the charcoal sequence. *E. tomentosa* and *P. tricuspidatus* are commonly found today in coastal calcareous areas. *H. parviflora* and *S. africana-lutea* are typical of drier, asteraceous fynbos and karroid shrubland of the lower slopes of the Cederberg mountains (Campbell, 1985; Taylor, 1996), and coastal hills of the study area.

6. *Euryops speciosissimus -Eriocephalus africanus* community

Dominant and frequent species in this community include *Euryops speciosissimus, Eriocephalus africanus, Passerina glomerata* and *Pterocelastrus tricuspidatus* (Table 2.6). Shrubs typical of asteraceous fynbos (*Euryops speciosissimus, Passerina glomerata and Eriocephalus africanus*) are particularly common in this community.

PLATE 2.3: a) Strandveld Succulent Karoo near to Elands Bay, with Bobbejaansberg in the background. b) *Ficus cordata* growing in a rocky outcrop on the lower slopes of the Cederberg mountains.

PLATE 2.4: a) *Protea nitida*, a dominant in the *Heeria argentea - Maytenus oleoides* community. b) Asteraceous fynbos, dominated by *Euryops speciosissimus*, *Eriocephalus africanus* and *Passerina glomerata*.

7. *Zygophyllum morgsana - Ruschia maxima* community

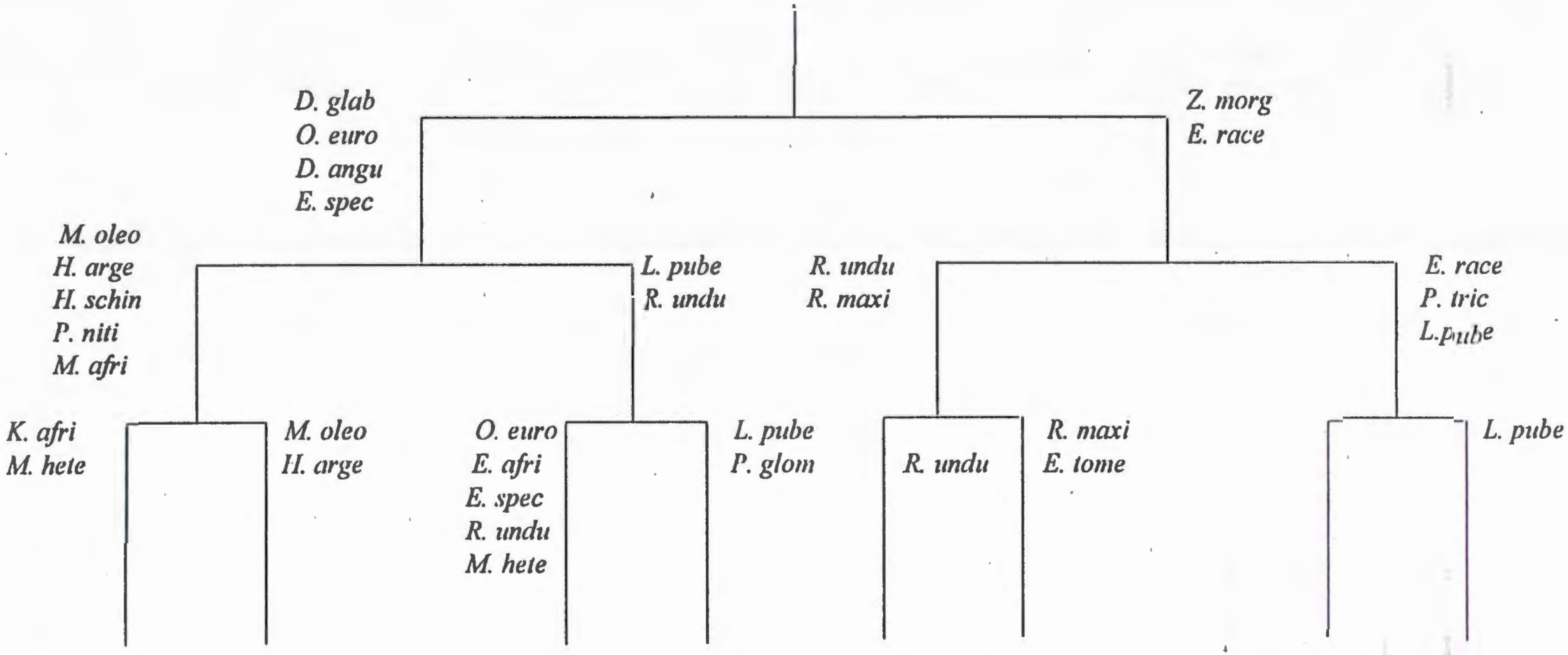
Dominant and frequent species in this community include *Zygophyllum morgsana, Ruschia maxima* and *Eriocephalus africanus.* This community is composed of species which are characteristic of the driest environments in the study area. *Ruschia maxima* is a robust leaf succulent typical of dry rocky sites while *Zygophyllum morgsana* is a species that is particularly common in Strandveld Succulent Karoo (Acocks, 1953; Low and Rebelo, 1996). Both these species were identified in 13 % of the charcoal samples. *Rhus undulata,* a species typical of xeric thicket in the north-western fynbos biome, occurs in 8 % of the charcoal samples.

2.3.3 Combined data

Classification of the combined data set identified eight communities at the third level of division (Figure 2.4). Four communities were formed at the second level of division. The eight communities identified at the third level of division were named A, B, C, D, E, F, G and H. This different nomenclature was used because these do not represent real communities in the true sense of the word. Data are summarised in Table 2.8, which shows the frequency data for each species in all communities. In the description, I emphasize the representation of plots from the fossil and extant data sets in each combined community.

Community A

The dominant and frequent species in this community included *Kiggelaria africana, Maytenus heterophylla, Podocarpus elongatus* and *Halleria lucida.* Most of these species are typical Afromontane taxa (e.g. *Podocarpus elongatus, Kiggelaria africana* and *Halleria lucida*). One proteoid shrub, *Protea glabra,* was also a frequent component of the community. *Ficus sur*



Total plots in community	**(15)**	**(67)**	**(126)**	**(34)**	**(29)**	**(8)**	**(15)**	**(4)**
Plots from charcoal	1(3) 2(2) 3(2)	4(11)	3(10) 7(3) 2(1)	5(1)	6(1)	6(4)	6(1)	
Plots from extant	2(8)	1(45) 4(4) 2(6) 3(1)	3(59) 2(46) 1(4) 4(2) 6(1)	4(24) 3(9)	5(18) 8(9) 7(1)	6(4)	7(14)	8(4)

FIGURE 2.3: TWINSPAN classification of combined data (i.e. extant samples and from fossil charcoal plots). Full names of species given in Table 2.8. The total number of plots in each community are indicated (plots), as are the number from the fossil and the extant data.

TABLE 2.8: Synoptic table for combined data sets (extant and fossil samples).

Community Number of plots	A 15	B 67	C 126	D 34	E 29	F 8	G 15	H 4
Hartogiella schinoides	5	3	1					
Olea europaea-africana	4	2	3					
Kiggelaria africana	4	1	1					
Maytenus heterophylla	4	1	2	1	1		1	
Podocarpus elongatus	3	1	1				1	
Halleria lucida	2	1						
Celtis africana	2		1					
Eriocephalus africanus	2	1	3	1	1	2		
Protea glabra	2		1				1	
Ficus cordata	1		1		1			
Ficus sur	1							
Chionanthus foveolatus	1							
Grewia occidentalis	1							
Salix mucronata	1							
Myrsine africana	3	3	1		1			
Dodonaea angustifolia	4	2	3	2				
Cassine peragua	2	1	1					
Heeria argentea		4	1			1	1	
Maytenus oleoides	1	4	1	6				
Protea nitida	1	3	1	1				
Rhus undulata	2	2	4	3	4	1		2
Euryops speciosissimus	1	2	3	1				
Diospyros glabra	2	4	3	4	1		1	
Leucadendron pubescens		1	1	4	1			5
Passerina glomerata	1	1	1	3				
Euclea tomentosa	1	2	2	3	1	3	1	
Ruschia maxima			1		2	5		
Euclea racemosa	1	1	1		1		5	4
Zygophyllum morgsana		1	1	1	5	4	5	4
Pterocelastrus	1	1	1	1	1		2	
Salvia africana		1	1	1	1		1	2
Colpoon compressum	1	1	1				1	
Hymenolepis parviflora		1	1	1				
Tarchonanthus	1	1	1					
Erica verecunda			1					
Erica caffra			1					

and *Salix mucronata,* both riverine woodland species, were also frequent components of this community. As a general trend this community is characterised by species which grow in moist, cool environments. Seven of the fossil "plots" were associated with this community. In the fossil sequence three of these were from the *Podocarpus elongatus - Halleria lucida* community. Two "plots" are from the *Podocarpus elongatus - Ficus cordata* community of the fossil sequence and two from the *Olea europaea-africana- Protea glabra* community. Eight of the extant plots from the *Olea europaea-africana – Maytenus heterophylla* community were associated with this community.

Community B

The dominant and frequent species in this community included *Maytenus oleoides, Heeria argentea, Protea nitida* and *Hartogiella schinoides*. This community was represented by a large number of plots, 67 out of 298 plots sampled in total. Of these 11 were from the fossil data set, all members of the *Cassine peragua- Heeria argentea* community. The bulk of the plots (43) were from the extant *Heeria argentea – Maytenus oleoides* community.

Community C

The dominant and frequent species in this community included *Olea europaea-africana, Euryops speciosissimus, Maytenus heterophylla, Olea europaea* and *Rhus undulata.* Two of these species are asteraceous shrubs, namely, *Eriocephalus africanus* and *Euryops speciosissimus*. This community is very well represented, including 126 plots. Of these 14 are fossil "plots". The majority (10) of these were from the *Olea europaea - Protea glabra* community. Plots from the extant communities that fell into this combined community were predominantly from the *Rhus undulata – Euclea tomentosa* community (97) and the *Olea europaea-africana – Maytenus heterophylla* community (46).

Community D

Dominant and frequent species in this community included *Leucadendron pubescens, Passerina glomerata, Diospyros glabra* and *Rhus undulata*. Only one "plot" from the fossil data was included in this community, a member of the *Pterocelastrus tricuspidatus- Salvia africana-lutea* community. Two extant communities (*Diospyros glabra – Leucadendron pubescens* and *Rhus undulata – Euclea tomentosa*) contributed plots (24 and 9 respectively) to this combined community.

Community E

Dominant and frequent species in this community included *Rhus undulata, Zygophyllum morgsana* and *Ruschia maxima*. This community is represented by 29 plots, which is almost 10 % of all the plots sampled. One fossil "plot" a member of the *Euryops speciosissimus - Eriocephalus africanus* community, was included in this community. The *Rhus undulata – Zygophyllum morgsana* extant community contributed 18 plots and the *Zygophyllum morgsana – Euclea racemosa* community contributed 9 plots.

Community F

Dominant and frequent species in this community included *Euclea tomentosa, Ruschia maxima* and *Zygophyllum morgsana*. This community comprised only 8 out of 298 (3 %) plots. Of these four were fossil "plots", all included in the *Euryops speciosissimus - Eriocephalus africanus* community and four were from the extant *Ruschia maxima – Eriocephalus africanus* community.

Community G

The dominant and frequent species in this community were *Zygophyllum morgsana, Euclea racemosa* and *Pterocelastrus tricuspidatus*. This community was found in 5 % of the combined plots, one of which was from the fossil "plots"- a member of the *Euryops speciosissimus - Eriocephalus africanus* community. The remaining 14 plots were from the *Zygophyllum morgsana – Euclea racemosa* extant community.

Community H

The dominant and frequent species in this community included *Leucadendron pubescens, Euclea racemosa, Zygophyllum morgsana* and *Salvia africana lutea*. This community, which only comprised 1 % of the plots, included no fossil "plots". All of the plots were from the *Zygophyllum morgsana – Leucadendron pubescens* extant community.

2.3.4 Multivariate Direct Gradient Analysis

CCA of full set of environmental variables

The CCA, using the full set of environmental variables, is shown in Figure 2.5. For this biplot, the communities illustrated correspond to the eight extant communities identified in the classification (Table 2.4). The canonical coefficients and the t-values of regression coefficients are presented in Table 2.9. The t-values have exploratory use only as they only approximate the exact t-tables. When the t-value of the variable is less than 2.1, then the variable does not contribute much to the fit of the species data. FR Explained is the fraction of variance that an ordination axis explains in the species-environment biplot (Ter Braak, 1991). Axis 1 essentially indicated a gradient of increasing altitude, bedrock, decreasing radiation and decreasing % sand in the soil. Axis 2 indicated a gradient of decreasing maximum temperature, and decreasing winter rainfall. There were several strong correlations between the species and the environmental variables and the first two axes (Table 2.10).

Axis 1 and axis 2 accounted for 48 % (eigenvalue = 0.2097) and 25 % (eigenvalue = 0.1088) of the total variance accounted for (10.4%), respectively (Table 2.9 & Table 2.11). Axis 1 and 2 accounted for 4.3 % and 3 % of the total variance in the species distribution (Table 2.11). Determining variance accounted for by each axis is a better measure of the species-environment relationship than the 'species-environment correlation' (McCune, 1997). The highest canonical coefficients for axis 1 were for altitude (r=0.69), bedrock (r=0.43), median winter rainfall (r=0.37), radiation (r=-0.21), minimum temperature (r=0.18), and median annual rainfall (r=0.16). The r-values (canonical coefficients) quoted do not have the same statistical properties as regression coefficients. In particular, canonical coefficients have a larger variance than regression coefficients (Ter Braak, 1991). The highest canonical coefficients for axis 2 were for growthdays (r=-0.92), maximum temperature (r=-0.76), and pH (r=0.33) (Table 2.9). The t-values indicate the significance of the environmental variables. The variables that accounted for the most variance in the ordination were highly significant (T > 2.1).

There were strong correlations (Table 2.10) between radiation (rad) and altitude (alt), and radiation and annual rainfall (marain). Most of the soil factors (i.e. % coarse, % medium and % fine sand) were also highly correlated with each other, which was expected. Altitude was positively correlated with maximum temperatures and bedrock. Bedrock was also negatively correlated with radiation. Median annual rainfall was negatively correlated with growthdays and minimum temperatures. Altitude was directly correlated with median

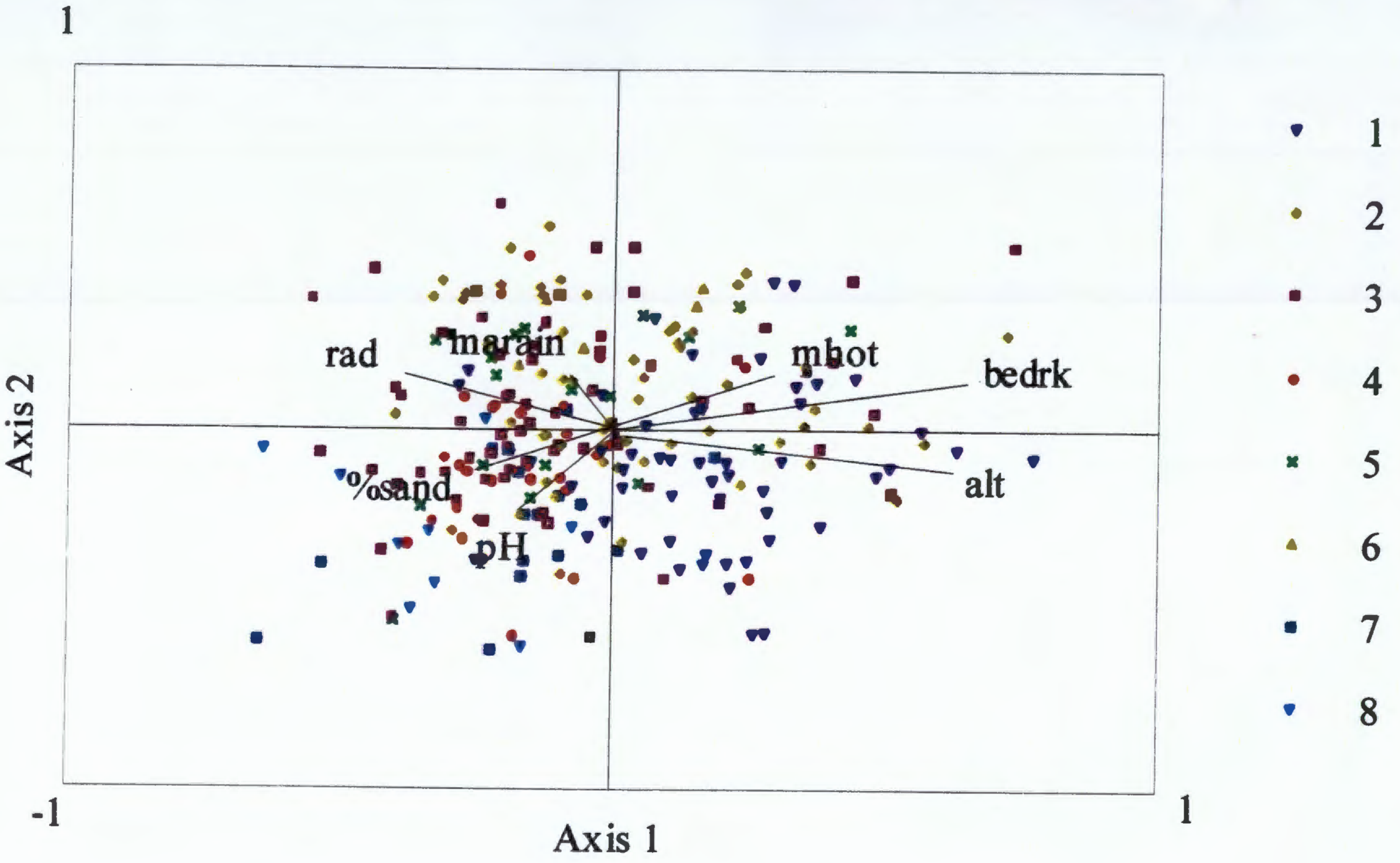


FIGURE 2.5: A labelled biplot of communities and the full set of environmental variables with CCA axis 1 and 2. The abbreviations for the variables are shown in Tables 2.2 and 2.3. The plots have been labelled according to communities: 1) *Heeria - Maytenus* 2) *Olea - Maytenus* 3) *Rhus – Euclea* 4) *Diospyros - Leucadendron* 5) *Rhus - Zygophyllum* 6) *Ruschia - Eriocephalus* 7) *Zygophyllum – Euclea 8) Zygophyllum - Leucadendron.*

TABLE 2.9: (a) Canonical coefficients for standardised variables (using all the environmental variables). (b) t-values of regression coefficients for axis 1 and 2 of the CCA. FR explained: is the fraction of variance that an ordination axis explains in the species - environment biplot. The highlighted t-values represent t- values > 2.1, a critical value. The abbreviations of the environmental variables are shown in Tables 2.2 and 2.3.

		(a) Canonical coefficients for standardised variables		(b) t-values of regression coefficients	
	CCA Axis	1	2	1	2
	FR Explained			0.324	0.168
1	rad	**-0.209**	0.2189	**-3.5199**	2.0815
2	bedrk	**0.4281**	0.276	**6.2401**	**2.2717**
3	bold	0.0949	-0.1146	1.5667	-1.068
4	pebs	-0.0578	**0.3094**	-0.7993	**2.4167**
5	ph	-0.274	**-0.3511**	**-3.561**	**-2.5772**
6	alt	**0.6927**	**-0.4628**	**8.6223**	**-3.2537**
7	%sand	0.0889	**-0.3394**	0.6638	-1.4319
8	%clay	0.0307	-0.1358	0.3056	-0.7634
9	%silt	0.1008	**0.3871**	1.0843	**2.3519**
10	%coarse	0.1038	0.2541	1.2041	1.6653
11	%med	0.1107	**-0.5568**	0.8733	**-2.4815**
12	%fine	-0.0874	-0.43	-0.6257	-1.7379
13	mcold	**0.3426**	0.0253	**2.883**	0.1203
14	mwrain	**0.3701**	-0.0591	**3.4509**	-0.311
15	mhot	0.049	**0.7554**	0.3935	**3.4267**
16	growd	**0.1533**	**0.9203**	1.1448	**3.8825**
17	marain	**0.155**	0.3561	1.4812	1.9212

TABLE 2.10: Correlation coefficients between all environmental variables. Highlighted values are the variables that were most highly correlated. The abbreviations of the environmental variables are shown in Tables 2.2 and 2.3.

	marain	growd	mhot	mwrain	Mcold	%fine	%med	%coarse	%silt	%clay	%sand	alt	ph	pebs	bold	bedrk	rad
rad	0.08	0.10	0.02	-0.15	0.05	0.04	0.02	-0.07	0.04	0.04	0.09	-0.18	-0.03	-0.05	0.07	**-0.23**	1.00
bedrk	-0.08	-0.28	**0.27**	0.26	-0.02	**-0.26**	0.22	**0.23**	0.04	-0.06	**-0.30**	**0.24**	-0.08	0.06	-0.12	1.00	
bold	0.04	0.19	0.04	0.06	**-0.25**	0.17	-0.02	-0.01	-0.17	-0.02	0.14	-0.04	**-0.20**	-0.14	1.00		
pebs	**0.29**	**-0.45**	0.16	0.22	-0.06	**-0.39**	0.10	0.08	-0.05	0.18	**-0.55**	0.07	-0.06	1.00			
pH	-0.22	-0.23	**-0.23**	-0.01	**0.63**	-0.15	-0.12	-0.02	**0.41**	-0.10	-0.16	-0.03	1.00				
alt	-0.03	-0.16	**0.27**	0.33	-0.07	-0.07	0.20	-0.01	0.11	-0.10	-0.18	1.00					
%sand	-0.40	**0.85**	-0.22	-0.24	-0.18	**0.76**	-0.15	-0.10	-0.13	-0.32	1.00						
%clay	**0.63**	-0.27	-0.09	-0.21	-0.15	**-0.26**	-0.05	-0.08	0.30	1.00							
%silt	-0.16	-0.13	-0.06	-0.04	**0.52**	-0.09	0.00	-0.02	1.00								
%coarse	-0.10	-0.12	-0.20	**0.49**	-0.15	-0.23	-0.31	1.00									
%med	-0.09	-0.15	**0.81**	-0.09	-0.05	-0.30	1.00										
%fine	**-0.35**	**0.83**	-0.18	-0.19	-0.21	1.00											
mcold	**-0.33**	-0.25	-0.17	-0.24	1.00												
mwrain	-0.08	-0.23	-0.06	1.00													
mhot	-0.10	-0.15	1.00														
growd	**-0.37**	1.00															
marain	1.00																

winter rainfall (mwrain). The most important variables determining the distribution of species in the landscape are illustrated in the sample-environmental variable biplot (Figure 2.5). The *Heeria - Maytenus* community (1) and *Olea - Maytenus* community (2) were associated with the high altitude, high annual rainfall and high bedrock sites. The *Rhus - Euclea* community (3), the *Diospyros - Leucadendron* community (4) and the *Rhus - Zygophyllum* community (5) were all associated with a high number of growthdays and high radiation. The *Zygophyllum - Leucadendron* community (8) was distinct in that it occurred in association with soils of high pH.

TABLE 2.11: Eigenvalues, species environment correlation, and cumulative percentage variance of species data and species-environment data for the four CCA axes of the full data set.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.205	0.141	0.094	0.051
Species-environment correlation	0.768	0.591	0.541	0.446
Cumulative % variance of species data	4.3	7.3	9.3	10.4
of species-environment relationships	28.3	47.7	60.7	67.7

This community occurred in areas where the minimum temperature was highest, (i.e. temperatures are moderate). The last two communities (*Rhus - Zygophyllum* and *Zygophyllum - Euclea*) (6 & 7) were also predominantly located to the left of axis 1, which indicates that they occur on sites with lower median annual rainfall, high number of growthdays, high radiation, low altitude and low % cover of bedrock. The environmental variables that best determined the distribution of plant assemblages are altitude, bedrock, pH, median annual rainfall, number of growthdays and radiation.

CCA using the reduced set of environmental variables

The reduced set of environmental variables included only the four climatic variables (maximum temperature, minimum temperatures, median annual rainfall and number of growthdays) which are used in the climatic reconstruction described in the following chapter. The first axis of the CCA explained 52 % (eigenvalue=0.143) and the second axis, 31 % (eigenvalue=0.087) of the total variance accounted for (5.8 %) respectively (Table 2.12 and Table 2.14). The highest canonical coefficients for axis 1 were for median annual rainfall (r=0.93), maximum temperature (r=-0.59) and minimum temperature (r=-0.3). For axis 2 these were for median annual rainfall (r=-1.17) and maximum temperature (r=-0.87). The t-values indicate all environmental variables that were significant (T > 2.1) and these correspond to the highest canonical coefficients (Table 2.12).

The correlation coefficients (Table 2. 13) indicate the correlation between median annual rainfall and the temperature variables (mhot and mcold). These variables are negatively correlated with rainfall indicating that with increasing rainfall there is a decrease in maximum temperatures as well as a decrease in minimum temperatures. Growthdays is positively correlated with maximum temperatures, and thus indicates that with increasing optimum growthdays there is a corresponding increase the maximum temperatures.

The plots from the CCA did not separate evenly along the axes (Figure 2.6). Community 1 (*Heeria - Maytenus* community) was separated out along the gradient of high median annual rainfall (marain). It was also associated with a low number of growthdays (growd) and the lower maximum temperature values (mcold). Community 2 (*Olea* - *Maytenus* community) and 3 (*Rhus* - *Euclea* community) were dispersed along Axis 1, which as mentioned was associated with increasing minimum temperatures. Communities 4 (*Diospyros* - *Leucadendron* community), 5 (*Rhus* - *Zygophyllum* community) and 6 (*Rhus* - *Zygophyllum* community) are located on the left hand side of Axis 2, and were thus associated with a high number of growthdays, a low minimum temperature and high maximum temperatures. Communities 7 (*Zygophyllum* - *Euclea* community) and 8 (*Zygophyllum* – *Leucadendron* community) are predominantly associated with high minimum temperature and high maximum temperatures.

TABLE 2.12: Canonical coefficients for standardised variables and t-values of regression coefficients of reduced environmental data set. The abbreviations of the environmental variables are shown in Tables 2.2 and 2.3.

		(a) Canonical coefficients for standardised variables		**(b) t-values of regression coefficients**	
CCA Axis		1	2	1	2
FR Explained				0.5173	0.3149
1	mcold	**-0.3029**	0.0956	**-2.0533**	0.4088
2	mhot	**-0.5972**	**-0.8731**	**-4.3265**	**-3.9887**
3	growd	-0.1850	-0.2925	-1.5827	-1.5781
4	marain	**0.9293**	**-1.1706**	**6.5888**	**-5.2343**

TABLE 2.13: Correlation coefficients between reduced set of environmental variables. Highlighted values being most highly correlated. The abbreviations of the environmental variables are shown in Table 2.3.

	marain	growd	mhot	mcold
mcold	**-0.4523**	0.0047	-0.0125	1
mhot	**-0.3244**	**0.6666**	1	
growd	-0.0563	1		
marain	1			

TABLE 2.14: Eigenvalues, species environment correlation, and cumulative percentage variance of species data and species-environment for the four CCA axes for the reduced data set.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.143	0.087	0.034	0.012
Species-environment correlation	0.665	0.490	0.398	0.272
Cumulative % variance of species data	3	4.9	5.6	5.8
of species environment relationship	51.7	83.2	95.6	100

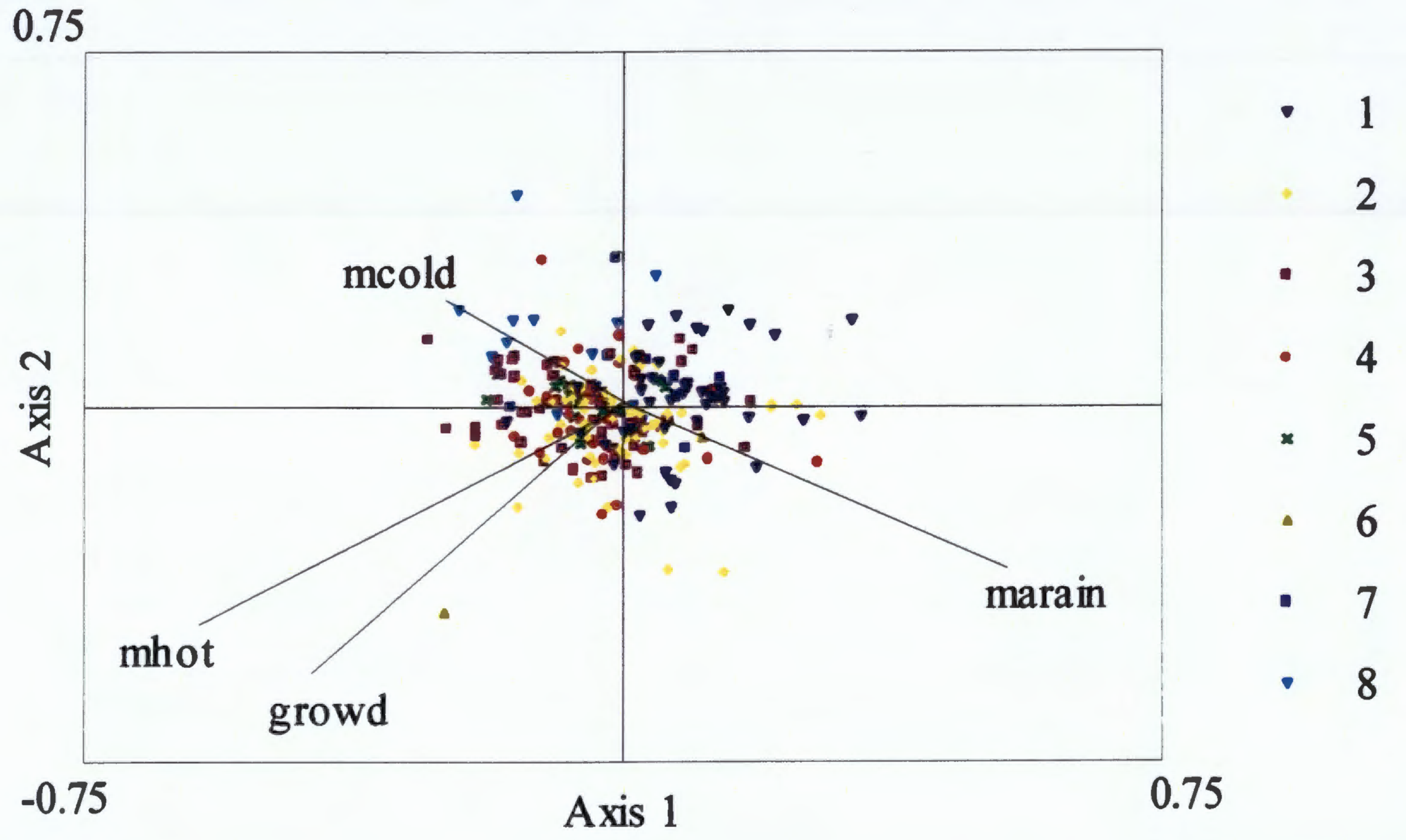


FIGURE 2.6: A labelled biplot of communities and the reduced set of environmental variables with CCA axis 1 and 2. The abbreviations for the variables are shown in Tables 2.2 and 2.3. The plots have been labelled according to communities: 1) *Heeria - Maytenus* 2) *Olea - Maytenus* 3) *Rhus - Euclea* 4) *Diospyros - Leucadendron* 5) *Rhus - Zygophyllum* 6) *Ruschia - Eriocephalus* 7) *Zygophyllum – Euclea* 8) *Zygophyllum – Leucadendron*.

2.4 DISCUSSION

Eight contemporary communities were identified on the basis of the woody species that occurred in the fossil charcoal. These were: *Heeria argentea - Maytenus oleoides* community (1), *Olea europeaea-africana - Maytenus heterophylla* community (2), *Rhus undulata - Euclea tomentosa* community (3), *Diospyros glabra - Leucadendron pubescens* community (4), *Rhus undulata - Zygophyllum morgsana* community (5), *Ruschia maxima - Eriocephalus africanus* community (6), *Zygophyllum morgsana - Leucadendron pubescens* community (7) and *Zygophyllum morgsana - Euclea racemosa* community (8). These communities occurred under a wide range of environmental and climatic conditions, from the coast to the Cederberg and Piketberg mountain ranges.

In contrast, the classification of the EBC charcoal sequence resolved seven communities which occurred at different stages and for differing lengths of time over the past 40 000 years (Table 2.7). These communities frequently have different dominant elements in comparison to the extant communities. The communities were (from oldest to most recent) : *Podocarpus elongatus - Halleria lucida* community (1), *Podocarpus elongatus - Ficus cordata* community (2), *Olea europaea - Protea glabra* community (3), *Cassine peragua -Heeria argentea* community (4), *Pterocelastrus tricuspidatus - Salvia africana lutea* community (5), *Zygophyllum morgsana - Ruschia maxima* community (6) and *Euryops speciosissimus - Eriocephalus africanus* community (7).

The classification of the combined data sets (fossil and extant) also resolved eight communities. Of these, the fossil "plots" classified predominantly (36 out of 39) into four of the combined communities: A, B, C and F (Figures 2.1, 2.2 and 2.3). Communities A, B and C were dominated by; proteaceous species, riverine species, Afromontane elements, and other mesic elements. Community F was dominated by xeric elements including *Zygophyllum morgsana, Ruschia maxima* and *Rhus* *undulata*. Thus the communities from the fossil charcoal sequence grouped essentially into four communities, three being the most mesic communities, and one being a xeric community. The remaining three fossil "plots" classified into communities D, E and G (Figure 2.4).

Thus, while some of the fossil communities are represented in the study area today, some are not. This can be attributed to the reshuffling that occurred over time. As already discussed, species all behave individualistically which means that communities generally do not remain intact over time. In this study, some of the dominant species of the past remain only as relicts in the present study area. For example, Afromontane species such as *Podocarpus elongatus* (Boucher and Moll, 1980) and *Kiggelaria africana,* which were dominant in charcoal communities 1 and 2, are today largely confined to mesic sites of Cederberg and Piketberg mountain ranges. We can assume that these species must have occurred nearer to the cave in the past as they are currently too far away to have been sampled by the resident hunter gatherers of EBC.

Clearly the communities in the EBC study area have not always been structured as they are today. This is likely to have been primarily due to the interaction between climatic (or other environmental) changes over time, and the individualistic responses species to these changes. The individualistic nature of species is evident from the fact that while I have categorised the species identified into communities, these communities are not clearly distinct in terms of species composition. Some species transcend several communities (e.g. *Pterocelastrus tricuspidatus* and *Euclea tomentosa*) while others are dominant in only very restricted time periods (e.g. *Halleria lucida* and *Zygophyllum morgsana*) (Appendix 1). Putative climatic changes on the Cape west coast during the Quaternary (February, 1990; Avery, 1990; Meadows and Sugden, 1991; Jerardino and Yates, 1996; Meadows *et al.*, 1996; Cowling *et al.,* in press) are likely to have provided a target for the vegetation to track. Factors such as soils, fire regimes (Bond, 1997; Cowling *et al.*, 1997), anthropogenic factors, topographic diversity and life-cycle characteristics (Ritchie, 1986), are assumed to have played secondary roles in this restructuring of communities. However, the selective sampling of wood by the inhabitants of EBC, which may have changed in response to the requirements of different occupants over time, may have played an important role in characterising the fossil communities. I attempted to accommodate for this by sampling, for the extant communities, species present only in the fossil charcoals. However this approach could not accommodate for differences in proportions of species in the sequence, as determined by fuelwood characteristics. Correcting for this bias is a topic for future research. Whatever the exact nature of the environmental changes, it can be assumed that these changes on a large time scale are likely to have caused species to respond by changing in abundance and by migrating but not by speciating (Bartlein, 1988; Huntley and Webb III, 1988; Pitelka, 1997). Speciation is unlikely to have been a major factor as the process is too slow in the context of the Quaternary time period.

Thus in the past there were communities that were very different to those that occur in the area today. They are essentially different associations of the same species found in the local study area that have been reshuffled at various stages over time. The implication of this is that communities can only be used in a narrative way to reconstruct past climates (e.g. Wadley *et al.*, 1992; Cowling *et al.*, in press). In order to make reconstructions more quantitative it is necessary to consider species level processes as is done in Chapter 3.

The significance of climatic factors in controlling species and community distribution is illustrated by the results from the CCAs. The direct gradient analysis, which included all the environmental variables, accounted for 10.4 % of the total variance in species distribution. While this may not seem like a lot, it must be remembered that the objective in any ordination is not to account for 100 % of the variance, as much of the variance is due to noise in the data or environmental factors not included in the analysis. This noise is usually unavoidable in CCA (McCune, 1997) and explaining even a low percentage of the variance can be informative (Ter Braak, 1992). The most important variables in this study were altitude (often a surrogate for temperature and rainfall), radiation or energy regime, maximum temperature of the hottest month, median annual rainfall, growthdays, bedrock cover, pH of the soil and percentage of sand in the soil (Figure 2.5 and Table 2.9). These particular climatic variables still accounted for about half (5.8 % of total) of the variance that all the measured environmental variables explained. Thus climatic factors play a significant role in controlling species distribution today and would probably also have done so in the past.

From this chapter it is clear that communities have changed over the past 40 000 years on the Cape west coast. It would appear that climatic factors (i.e. temperature and rainfall) have had an influence in on this change. Because of the individualistic nature of species, these changes have not only been a shift of one community to the next, but also a change in actual composition over time. The result of this is that there are no exact analogues of past communities in the extant vegetation. Due to the lack of exact community analogues it is necessary to conduct reconstructions of past climates based on species level changes.

CHAPTER 3

RECONSTRUCTING QUATERNARY CLIMATES FROM FOSSIL CHARCOAL DATA: QUANTITATIVE ESTIMATES BASED ON SPECIES-CLIMATE MODELS OF EXTANT DISTRIBUTIONS.

3.1 INTRODUCTION

Reconstructing past climates on the basis of plant (or animal) species which occurred in an area is essentially the corollary of predicting how species might respond to climate changes. Both endeavours require an intimate understanding of all the factors which affect species distributions; not only climate. The confidence which we have in our reconstructions or predictions will vary greatly depending on how much of the variability in species distribution can be accounted for by climate. A strong correlation between climate and species means that reconstructions will be robust, a poor correlation means that they will be weak. In Chapter 2, the relative contributions of a range of climatic and other environmental factors in determining species distributions were investigated using a multivariate direct gradient technique. Despite the fact that only a relatively small proportion of the variance was attributable to climatic variables, this is still considered significant. There are two assumptions which are less easy to test. Firstly, it must be assumed that climate is not just correlated with species distribution, but that it is a causal factor dictating where species occur. In addition, it is necessary to assume that the climatic tolerances of species have remained unaltered through the course of time (Chaloner, 1991).

The need for using palaeobotanic and other palaeoecological data in conjunction with palaeoclimatic data, has been recognised as a tool which can provide predictions of past and future climates (Schneider, 1992). In this study present climates and species distributions are used in conjunction with fossil evidence to reconstruct past climates. To do this I have attempted to develop climatic envelopes of fossil species using extant distributions and associated climatic thresholds. Essentially, climatic envelopes are defined as "boundaries within which a vegetation or plant type is expected to occur" (Box, 1995). The envelope is defined by upper and lower limits for selected variables. A basic assumption for each climatic envelopes is that a plant or vegetation types will not grow at a place if the local values of any climatic envelope variables is outside the limit of the envelope (Box, 1981). By combining the envelopes of the component species, plant communities can also be represented by climatic envelopes.

This chapter deals with the determination of the climatic conditions of late Quaternary (prior to 40 000 years ago - late Holocene) on the Cape west coast using two methods. In the first, a multiple regression approach was used to model climate as a function of extant species distributions in the Cape west coast study area. These climate models were then used to "reconstruct" the past climates (local approach) (Draper and Smith, 1981). Following this, a reconstruction based on climatic and species distribution data from South Africa as a whole was carried out (regional approach). These two approaches should be viewed as complimentary. The local scale reconstruction is statistically more rigorous; limits potential error due to topographic or landscape fragmentation effects on species migrations mentioned in the previous chapter; and avoids variation in species responses to climate which might exist between widely separated populations of plants. The advantage of the regional approach is that a wider range of potential climatic conditions is sampled; the spatial scale of the species distribution data are more compatible with that of the extrapolated climatic data; and in addition, most of the species in the charcoal samples could be included in the analysis. These two approaches provide two very different methods of reconstructing past climates. The combination of these two approaches provides rigorous quantitative estimates of past climatic variables. This is in stark contrast to earlier reconstructions which were based on vague inferences (Cowling *et al.*, in press; Klein & Cruz-Uribe, in prep).

The main questions that are addressed in this chapter were:

1. What are the distributions and corresponding climatic envelopes of each of the species found in EBC fossil charcoal samples in the Cape west coast study area?
2. What are the distributions and corresponding climatic envelopes of the species found in EBC fossil charcoal samples in South Africa?
3. What are the past climatic conditions on the west coast (> 40 000 BP - present) reconstructed using both the local and regional approach?
4. How do these two methods of reconstruction compare?

3.2 METHODS

3.2.1 Local scale reconstruction

The local-scale study area was defined and described in Chapter 1, and the sampling method used for determining the species distribution patterns and the climatic variables used in the reconstructions were described in Chapter 2 (Table 2.3). The species that were available for use in the analysis are listed in Table 3.1.

Data analysis

Multiple regression methods (Dixon 1992; Genstat 5 Committee, 1994) were used to derive models for reconstructing climate on the basis of species present in an area or in a particular time period. A separate linear regression model for each climatic variable was built. The standard form for these models was:

$$Y_{kj} = \alpha_{ko} + \sum_{i=1}^{I} \alpha_{k\alpha} X_{ij} + \sum_{i=i'}^{I} \alpha_{kii'} X_{ij} X_{i'j} + e_{kj}$$

for $k = 1 \ldots K$ and $j = 1 \ldots J$; where Y_{kj} is the observed value of the k^{th} climatic variable in the jth plot; j denotes an arbitrary plot; J is the total number of plots; k is an arbitrary climatic variable; K is the total number of climatic variables; i is an arbitrary species; i' is another arbitrary species different from species i; I is the total number of species; $X_{ij} = 1$ if species i is present in plot j and $X_{ij} = 0$ if it is not; and e_{kj} is the random error of observations. The α's are the regression coefficients.

Each model includes a constant, terms for the main effects of the species and the pairwise interactions between the species, and a term accounting for random error. Not all species were useful in predicting all climatic variables. "All Subsets Regression" (Dixon, 1992) was used to select a set of species for each climatic variable model. The interaction terms were included in the model to account for the effect that a combination of two species might have on predicting a climatic variable. A separate climatic model, based on a selected subset of species, was created for each climatic variable. In this way independence of the climatic reconstructions was facilitated.

After selecting the best species subset, the models were used to predict the average values of the climatic variables at each of seven time intervals, based on the species present in the charcoal during that interval. Not all of the species included in the best model chosen for each climatic variable were necessarily present in the charcoal analysed. Predicted values for each of the seven time intervals were graphed with the 95 % confidence limits (Figure 3.1). The rationale behind these seven intervals was that the EBC charcoal sequence was not continuous. There were times when there was an occupational hiatus which mean that no wood was burnt (Parkington, 1981). Intervals were thus

TABLE 3.1 The List of species found in the Elands Bay Cave charcoal samples, and which were used in the different sections of this thesis. Widespread = Species that are widespread in South Africa. Endemic = Species that are endemic to the Western Cape Region (winter-rainfall region of the fynbos biome). Regional refers to data from ACKDAT, Local refers to extant data.

Regional	Local	Endemic	Widespread	Species	Height
✓	✓		✓	*Cassine peragua*	2 - 10 m
✓				*Celtis africana*	< 40
✓				*Chionanthus foveolatus*	2 - 15
✓	✓		✓	*Colpoon compressum*	3 - 5
✓	✓		✓	*Diospyros glabra*	< 5
✓	✓		✓	*Dodonaea angustifolia*	2 - 7
				Erica caffra	2- 4
				Erica verecunda	< 1.8
✓	✓		✓	*Eriocephalus africanus*	< 2
✓	✓	✓		*Euclea racemosa*	3 - 12
	✓	✓		*Euclea tomentosa*	3 - 4
	✓	✓		*Euryops speciosissimus*	< 2
✓	✓		✓	*Ficus cordata*	< 35
✓				*Ficus sur*	3 - 10
✓				*Grewia occidentalis*	< 6
✓	✓		✓	*Halleria lucida*	2- 20
✓	✓		✓	*Hartogiella schinoides*	< 5
	✓	✓		*Heeria argentea*	< 5
		✓		*Hymenolepis parviflora*	1- 3
✓	✓		✓	*Kiggelaria africana*	4 - 22
✓	✓	✓		*Leucadendron pubescens*	0.6 - 3
✓	✓		✓	*Maytenus heterophylla*	4 - 5
✓	✓	✓		*Maytenus oleoides*	<4
✓	✓		✓	*Myrsine africana*	<3.5
✓	✓		✓	*Olea europaea-africana*	5- 10
	✓	✓		*Passerina glomerata*	< 2
	✓	✓		*Podocarpus elongatus*	3 - 6
	✓	✓		*Protea glabra*	< 5
✓	✓		✓	*Protea nitida*	< 5
✓	✓		✓	*Pterocelastrus tricuspidatus*	5 - 25
✓	✓		✓	*Rhus undulata*	< 5
	✓	✓		*Ruschia maxima*	> 0.3
✓			✓	*Salix mucronata*	< 25
✓	✓		✓	*Salvia africana lutea*	< 2
✓			✓	*Tarchonanthus camphoratus*	< 5
✓	✓		✓	*Zygophyllum morgsana*	< 1.5
Total = 25	**Total** = 27				

selected to reflect these breaks in the sequence. The time span that each calculated interval represents, the species in each interval and the median date for each time interval are listed Table 3.2.

3.2.2 Regional scale reconstruction

The regional study area incorporates distribution and associated climatic data for the whole of South Africa (excluding Lesotho and Swaziland). The species distribution data were derived from the ACKDAT database (O'Callaghan, 1994). This data set comprises comprehensive plant abundance records of a total of about 12 000 species at over 3 500 sites well distributed throughout South Africa. These records were collected by the government botanist, John Acocks, between 1925 - 1979. Of the 36 species that were identified from the EBC charcoal sequence, 31 of these were used in this regional study (Table 3.1). There were five species that were not sampled by Acocks but which were found in EBC charcoal namely: *Erica caffra, E. verecunda, Ruschia maxima, Podocarpus elongatus*, and *Euclea tomentosa*. The climatic variables used are described in Chapter 2 (Table 2.3). As described previously (Chapter 1) the charcoal remains in EBC were sampled from 39 contexts in sequence. Within each interval a number of species were identified. Once again, I consolidated the 39 intervals into seven groups, determining the climatic envelopes for each species and then reconstructing the climatic conditions at each of the seven intervals (Table 3.2). Thus the overall change in climate from prior to 40 000 years ago to the late Holocene, at seven intervals, was reconstructed.

Data analysis

The climatic data, which were in the form of grids, were viewed and manipulated using Arcview 3.0 and Arc/Info (Version 7.1). Using these Geographical Information Systems, the climatic variables were overlaid with the distribution data (e.g. Figure 2.1) for each species and from this the climatic limits of the species were determined. Then, using the groupings of species in each interval (Table 3.2), the climatic intersections of the species in each group were determined in order to identify a climatic envelope to the group as a whole. The intersections were determined using the minimum value of the maximum values and the maximum value of the minimum values of the climatic envelopes of all the species. These intersection values at each interval were then graphed as climatic ranges (Figure 3.1). The past climatic conditions were thus resolved at seven intervals of time from > 40 000 years ago to the late Holocene.

3.3 RESULTS

3.3.1 Local approach

The amount of variance in the climatic variables that is accounted for by the models, as well as the regression coefficients for the models, are presented in Table 3.3. The variables where the highest proportion of variance was accounted for by the models were the two rainfall variables: marain (median annual rainfall - r^2 =66.3 %) and mwrain% (percentage winter rainfall - r^2 =67 %). For all climatic variables, the models account for at least 29 % of the variance The list of species in Table 3.3 is ordered from those species most frequently used in predicting climatic variables (top), to those least frequently used in the models (bottom). There were thus a few species which were used in predicting all five climatic variables. In addition, there were some species that were not used at all, and these are listed below all of the species interactions. Twenty four different species interaction terms were also used in the models, thus taking into considerations co-occurrence of the species in determining the appropriate climatic variables. The values of past climatic variables predicted using the models, along with the 95 % confidence intervals, are illustrated in Figure 3.1. The actual predicted values with their corresponding standard errors are presented in Table 3.4. The graphs of the temperature variables, mcold (median temperature of the coldest month) and mhot (median temperature of the hottest month) (Figure 3.1a and 3.1b), do not indicate a dramatic overall change in the temperatures between the Pleistocene and the Holocene. The model predicted (Figure 3.1a) a relatively stable median temperature of the coldest month, except for a marked drop from around 6.6 °C to 4.6 °C between 10 700 and 9 000 years ago. One possible explanation for this drop in temperature is that it indicates perturbations associated with that the change from Pleistocene (full glacial) to Holocene (inter-glacial) some time between 13 600 and 9 000 years ago. However, in this case, the perturbation occurs slightly later than in most of the other climatic variables. In the case of median temperature of the hottest month (Figure 3.1b), there was a slight increase between 40 000 and 19 000 years ago when the median maximum temperature reached its highest value (around 31 °C).. This was followed by a decline in temperatures around 13 000 years ago, when it dropped to a median value of 29.4 °C. Temperatures increased steadily from this point till the late Holocene (350 years ago). Over the entire time sequence the percentage increase in temperatures was less than 1 %, and the increase in temperature from 13 000 years ago was around 5 %.

The predicted number of optimum growth days (Figure 3.1c) prior to 40 000 years ago was 15.5 days p.a. The model predicted that this increased slightly to around 18.2 days p.a. at 19 150 years ago. The predicted growth days also suggests that the Pleistocene / Holocene boundary occurred

TABLE 3.2: A list of all the fossil charcoal species found in each time interval described for the EBC sequence. This list excludes those species not present in the ACKDAT data base (see text). Also shown is the length and median age of each time interval.

Interval	Species		Time span (years ago)	Median age (years ago)
1	*Euclea racemosa*	*Pterocelastrus tricuspidatus*	320 - 1 400	860
	Zygophyllum morgsana	*Euryops speciosissimus*		
	Rhus undulata	*Eriocephalus africanus*		
2	*Euclea racemosa*	*Eriocephalus africanus*	3 290 - 4 370	3 830
	Zygophyllum morgsana	*Salvia africana-lutea*		
	Pterocelastrus tricuspidatus	*Hymenolepis parviflora*		
	Passerina glomerata	*Heeria argentea*		
	Euryops speciosissimus			
3	*Euclea racemosa*	*Maytenus oleoides*	7 910 - > 8 800	8 350
	Pterocelastrus tricuspidatus	*Diospyros glabra*		
	Euryops speciosissimus	*Cassine peragua*		
	Salvia africana-lutea	*Tarchonanthus camphoratus*		
	Hymenolepis parviflora	*Dodonaea angustifolia*		
	Heeria argentea	*Hartogiella schinoides*		
4	*Ficus cordata*	*Diospyros glabra*	> 9 000 - 10 700	9 850
	Olea europaea-africana	*Maytenus oleoides*		
	Colpoon compressum	*Heeria argentea*		
	Hartogiella schinoides	*Hymenolepis parviflora*		
	Maytenus heterophylla	*Salvia africana-lutea*		
	Dodonaea angustifolia	*Pterocelastrus tricuspidatus*		
	Tarchonanthus camphoratus	*Euclea racemosa*		
	Cassine peragua			
5	*Colpoon compressum*	*Leucadendron pubescens*	12 500 - 13 600	13 000
	Hartogiella schinoides	*Protea glabra*		
	Maytenus heterophylla	*Protea nitida*		
	Dodonaea angustifolia	*Pterocelastrus tricuspidatus*		
	Cassine peragua	*Euclea racemosa*		
	Diospyros glabra			
6	*Kiggelaria africana*	*Hartogiella schinoides*	17 800 - >20 500	19 150
	Celtis africana	*Maytenus heterophylla*		
	Grewia occidentalis	*Dodonaea angustifolia*		
	Myrsine africana	*Diospyros glabra*		
	Ficus cordata	*Euclea racemosa*		
	Olea europaea-africana			
7	*Halleria lucida*	*Salix mucronata*	> 40 000	40 000
	Chionanthus foveolatus	*Hartogiella schinoides*		
	Kiggelaria africana	*Dodonaea angustifolia*		
	Celtis africana	*Tarchonanthus camphoratus*		
	Grewia occidentalis	*Cassine peragua*		
	Ficus sur	*Diospyros glabra*		

TABLE 3.3: The contribution of individual species and combinations of species in explaining the variance in the multiple regression models. The regression coefficients and standard error values for each species that was used to predict the climatic variables are indicated. Species and interactions (combinations of species) are ordered from the most used to the least frequently used in the models (abbreviations in Table 2.3).

	mcold	Marain	growd	mwrain%	rad	mhot
Multiple regression r^2(%)	44.10	66.30	38.8	67	26.90	36.60
Species (abbreviation)						
Heeria argentea (ha)	0.22 (0.08)	185.70(26.50)			-10.47(8.83)	-0.47 (0.23)
Euclea racemosa (er)	0.30 (0.10)	-8.30 (17.50)	-1.81 (1.02)	-11.90 (10.60)		-0.70 (0.24)
Protea nitida (pn)		140.00 (25.20)	-3.68 (0.75)	83.20 (15.10)	-28.29 (8.24)	-0.64 (0.20)
Salvia africana-lutea (sa)		-17.00 (15.10)	-1.32 (0.60)	-3.91 (0.60)	-14.71 (9.68)	
Zygophyllum morgsana (zm)	0.23 (0.08)	-71.50 (13.70)	-3.14 (0.84)	-46.95 (8.27)		
Colpoon compressum (cc)		23.40 (21.40)	-2.87 (0.91)	8.70 (13.00)	-20.00 (12.50)	
Dodonaea angustifolia (da)	-0.10 (0.07)	105.60 (16.50)	1.58 (0.58)	66.64 (9.98)		
Eriocephalus africanus (ea)		44.00 (15.10)	1.71 (0.59)	30.03 (9.11)		0.25 (0.16)
Hartogiella schinoides (hs)	-0.33 (0.10)	25.20 (22.00)		14.40 (13.40)		
Leucadendron pubescens (lp)	0.23 (0.08)	-15.70 (13.20)		-16.19 (9.18)		
Maytenus oleoides (mo)		23.40 (14.90)		19.63 (9.42)		-0.61 (0.19)
Passerina glomerata (pg)	-0.25 (0.01)	22.60 (13.90)		7.20 (10.40)		
Euryops speciosissimus (es)	-0.15 (0.07)		1.09 (0.47)			0.58 (0.16)
Pterocelastrus tricuspidatus (pt)	-0.32 (0.12)		1.41 (0.85)		-4.10 (16.10)	
Rhus undulata (ru)			-0.18 (0.54)			0.48 (0.15)
Ficus cordata (fc)			1.95 (0.78)			0.67 (0.29)
Halleria lucida (hl)	0.14 (0.25)		-7.80 (1.54)			
Kiggelaria africana (ka)			1.33 (0.64)			0.67 (0.23)
Cassine peragua (cp)					-72.50 (15.40)	
Maytenus heterophylla (mh)					-10.68 (8.54)	
Myrsine africana (ma)			-0.45 (0.49)			
Olea europaea-africana (oe)	-0.18 (0.07)					
Protea glabra (pgl)	-0.09 (0.19)					

TABLE 3.3: Continued.

	mcold	marain	Growd	mwrain%	rad	mhot
Multiple regression R^2(%)	44.1	66.3	38.8	67	26.9	36.6
Species						
da & ea		-53.90 (23.10)	-1.96 (0.88)	-37.10 (13.90)		
da & hs		-68.50 (35.00)		-53.40 (21.90)		
da & ha		-100.90 (34.30)		-57.80 (20.60)		
da & pn		-72.60 (30.20)		-43.10 (18.10)		
ea & hs		82.00 (36.00)		57.40 (21.70)		
hs & pg	0.25 (0.28)			30.60 (25.70)		
ha & pn		-121.80 (30.80)		-73.50 (18.50)		
ha & zm		-260.00 (83.20)		-154.60 (49.90)		
mo & zm		8.20 (48.70)		36.70 (32.10)		
cc & da			2.41 (1.58)			
cc & mh					-73.80 (34.50)	
cc & sa					103.20 (45.80)	
er & zm			1.76 (1.39)			
ha & ka						-1.44 (1.16)
hl & pn			6.89 (2.74)			
hl & pg	-1.91 (0.48)					
hs & pgl	-1.78 (0.40)					
lp & pg				21.10 (17.60)		
mo & sa				-59.30 (25.10)		
mh & sa					-45.30 (18.80)	
oe & pg	0.26 (0.17)					
pn & pt					-43.10 (23.90)	
pn & ru			2.57 (1.07)			
ru & zm			1.95 (0.969)			
Species not used in models						
Diospyros glabra (dg)						
Podocarpus elongatus (pe)						
Ruschia maxima (rm)						
Euclea tomentosa (et)						

TABLE 3.4: Values of the climatic variables and the standard error (SE) at each time interval (1-7) predicted using regression models derived from species distribution – climate data for the local study area (see text).

Interval	Median years	Predicted mean value of climatic variables ± Standard Error (S.E.)											
		Marain	S.E.	mhot	S.E.	mcold	S.E.	rad	S.E.	mwrain %	S.E.	Growd	S.E.
7	>40 000	429.1	24.72	29.91	0.28	6.83	0.31	261.94	9.47	56.75	4.36	15.54	2.36
6	19150	356.5	26.53	31.06	0.36	6.82	0.15	193.30	31.43	56.75	3.48	18.14	1.34
5	13050	662.2	37.74	28.46	0.21	6.66	0.31	91.70	63.16	45.02	4.78	12.47	1.06
4	9850	555.0	52.05	29.66	0.39	4.64	0.48	91.70	63.16	41.26	7.35	14.04	1.53
3	8355	492.4	25.92	29.39	0.24	6.45	0.13	198.30	24.62	47.66	7.12	19.09	1.05
2	3830	191.7	79.68	30.03	0.25	6.46	0.20	268.40	19.72	58.11	7.64	17.88	1.30
1	860	265.0	21.32	29.82	0.28	6.75	0.16	290.00	15.41	62.037	4.23	19.02	1.45

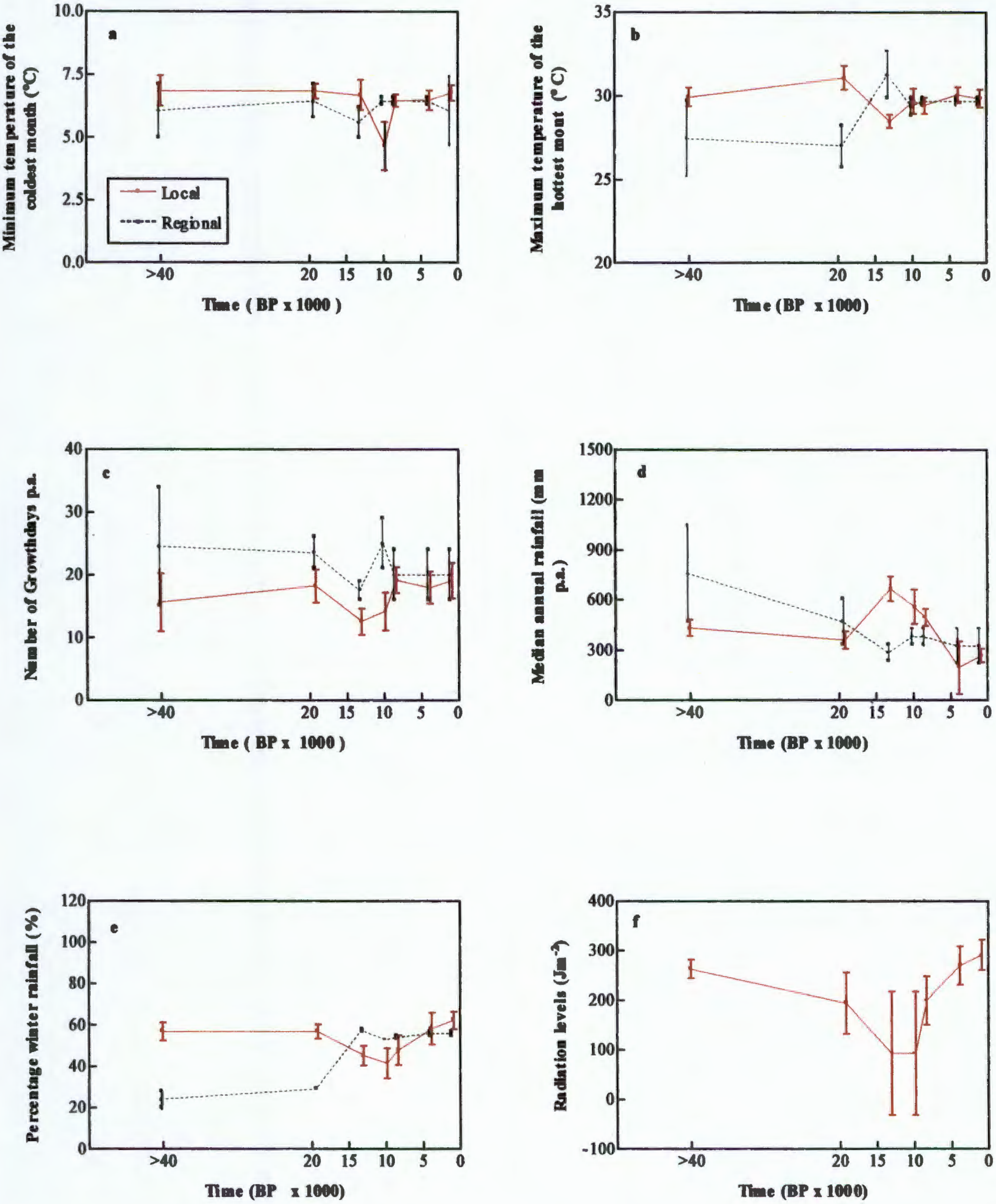


FIGURE 3.1: Climatic reconstructions from prior to > 40 000 years ago to the late Holocene. "Local" refers to predictions made using the local approach (3.3.1 above); "Regional" refers to predictions made on the using the regional approach described in 3.3.2 above. a) Median minimum temperature of the coldest month; b) Median maximum temperature of the hottest month; c) Growthdays; d) Median annual rainfall; e) Percentage winter rainfall; f) radiation (local approach only). The x axis for the regional results has been slightly offset (300 yrs) to prevent the graphs from overlapping.

around 13 000 years ago. This prediction is indicated by a significant lowering of the number of growthdays to 12.4 days p.a., followed afterwards by a general increase up until present times. In total, over the past 40 000 years, the number of growthdays has increased by 22 %. Much of this increase occurred after 13 000 years ago, when the number of growthdays increased by 52.5 %.

In terms of rainfall patterns, predicted values for median annual rainfall (Figure 3.1d) indicated a general decrease in rainfall over time. The model suggested that between 40 000 and about 19 150 years ago, the annual rainfall decreased from 429 to 356 mm p.a. There appeared to be a peak in rainfall between 13 600 and 12 500 years ago (635 mm p.a.). Once again this oscillation can be interpreted as indicating the transition from Pleistocene and Holocene somewhere around 13 600 -12 500 years ago. Following this peak, there was a very rapid decrease in the median annual rainfall to the present predicted value of about 265 mm. Today the rainfall in the Elands Bay area is approximately 200 mm p.a. The model suggested that from 40 000 years ago to present times, the median annual rainfall decreased by 38 %, and from 13 000 years ago to the present, it decreased by 60 %. The percentage winter rainfall indicated slight general increase in between 40 000 years ago and today. This general increase was, however, punctuated by a fairly dramatic drop around the time of the Pleistocene / Holocene boundary (13 600 years ago) which corresponds with a general increase in annual rainfall (Figure 3.1d).

The predicted radiation levels (Figure 3.1f) prior to 40 000 years ago were around 261 Jm^{-2}. Following this, the model predicted that they dropped to a low of about 97.1 Jm^{-2} between 12 500 and 9 000 years ago. This low corresponds with higher annual rainfall. After 9 000 years ago (early Holocene) the model suggested steadily increasing radiation levels to a present day, 290Jm^{-}

². Thus, overall there was only a slight (11 %) increase in suggested radiation levels from 40 000 years ago to the present although between 13 600 years ago and the present day there was a 216 % increase.

3.3.2 Regional approach

The climatic reconstructions based on the regional data are also presented in Figure 3.1 and the actual predicted values and their corresponding ranges are presented in Table 3.5. Once again, the two temperature variables that were considered were the minimum temperature of the coldest month and the maximum temperature of the hottest month (Figure 3.1a and 3.1b). In the case of median minimum temperatures, the reconstructed values have oscillated around 6 °C. Prior to 40 000 years ago the predicted value was 6 °C. Thereafter, it increased slightly until 20 000 years ago. Following this, it decreased to the lowest predicted median minimum temperature of around 5.6 °C, at 13 600 years ago (possibly related to the Pleistocene/Holocene interphase). The model predicts that it then increased again to a high of about 6.5 °C, between 9 000 and 3 290 years ago after which time it returned to the pre 40 000 years ago 6 °C. It is evident from the ranges of the values that these minimum temperatures were highly variable, especially between 1 400 - 320 years ago (late Holocene), where they ranged between about 4.7 °C and 7.4 °C. Overall, however the prediction is that there has not been a dramatic change in minimum temperature regimes over the past 40 000 years, with the exception of the period centered on 13 000 years ago.

In contrast, there was a marked increase in maximum temperature of the hottest month from prior 40 000 years ago to present times (Figure 3.1b). The predicted median maximum temperature increased from around 27.5 °C at 40 000 years ago to 29.7 °C, 860 years ago. Again, the most dramatic change (when the temperature increased from 27.1 to 31.3 ° C) occurred at around 13 000 years ago, indicating the change from glacial to interglacial (Holocene) conditions. During the Holocene, the temperatures remained steady and high at a median of 29.7 °C. The magnitude of the ranges relative to the actual temperature changes in maximum temperatures were low in comparison to the ranges for the minimum temperatures. Overall this graph shows a general increase of 8.2 % in maximum temperatures between 40 000 years ago and the late Holocene.

In terms of number of growth days (Figure 3.1c) it would appear that there has been a general decrease from around 24.5 days p.a., 40 000 years ago, to around 20 days p.a. in the late Holocene. Once again there is an oscillation between 13 000 years ago and 9 850 years ago which is probably linked to the change from full glacial - interglacial conditions. From 9 850 years ago (Holocene) the number of growth days are remarkably constant.

In the case of median annual rainfall, the predicted values decreased from a high of about 759 mm p.a. (> 40 000 years ago) to a low of 285 mm p.a. (13 000 years ago) (Figure 3.1d). Prior to 40 000 years ago the model predicts that the rainfall ranged between 473 and 1046 mm p.a. Although this range is high, the minimum range value is still greater than the median values predicted for the Holocene (<12 500 years ago). The median annual rainfall decreased most markedly from the late Pleistocene to the early Holocene. The model predicts that rainfall at the LGM (18 000 - 22 000 years ago) was around 467 mm p.a. Median annual rainfall values during

TABLE 3.5: Values of the climatic variables and the ranges (maximum and minimum) at each time interval (1-7) predicted using species-climatic envelopes from the regional study area (see text).

Interval	Median years	Marain			mhot			mcold			growd			mwrain %		
		Max	Median	min	max	Median	min	max	median	min	max	median	min	Max	median	min
7	>40 000	1046	759.50	473	29.70	27.45	25.20	7.10	6.05	5.00	34	24.50	15	28	24.0	20
6	19 150	605	467.50	330	28.30	27.05	25.80	7.10	6.45	5.80	26	23.50	21	29	29.0	29
5	13 050	330	285.00	240	32.70	31.30	29.90	6.20	5.60	5.00	19	17.50	16	58	57.5	57
4	9 850	432	381.00	330	29.90	29.40	28.90	6.60	6.45	6.30	29	25.00	21	53	53.0	53
3	8 355	432	381.00	330	29.90	29.70	29.50	6.60	6.45	6.30	24	20.00	16	53	54.0	55
2	3 830	432	326.50	221	29.90	29.70	29.50	6.60	6.45	6.30	24	20.00	16	57	56.0	55
1	860	432	326.50	221	29.90	29.70	29.50	7.40	6.05	4.70	24	20.00	16	57	56.0	55

the Holocene were generally low and there was not much variability. Thus, there is an overall drop in annual rainfall of 57 % from the earliest interval in the sequence (> 40 000 years ago) to the most recent part. The graph of percentage winter rainfall over time (Figure 3.1e) had the smallest ranges (relatively speaking) of all the climatic variables. Prior to 40 000 years ago, 24 % of the median annual rainfall fell in winter and this increased to a peak of 57.5 % 13 000 years ago. After this the model predicts that it decreased slightly till 9 850 years ago and then increased again until early in the last millenium (late Holocene) when the percentage winter rainfall was 56 %. Over the whole time covered by the sequence, the percentage winter rainfall increased overall by 133 %.

3.4 DISCUSSION

Perhaps the most significant climatic event evident in the reconstructions presented above, is the transition between the full glacial conditions of the late Pleistocene to the interglacial conditions of the current Holocene. This is indicated by oscillations or perturbations in all of the climatic variables between 13 600 years ago and 8 350 years ago (Figure 3.1). Globally, amelioration of glacial climatic conditions started between 10 000 and 12 000 years ago (Deacon *et al.,* 1992). The early Holocene was characterised by several climatic anomalies. One of the most severe and widely documented of these was the Younger Dryas (YD) period, a period of rapid cooling which occurred around 10 000 years ago (Fairbanks, 1989; Stocker and Wright, 1991; Zahn, 1992; Scott *et al.*, 1995; Hughen *et al.*, 1996). Evidence of the YD has been found in many parts of the world (Jouzel *et al,* 1987; Fairbanks, 1989; Roberts *et al.,* 1993; Hughen *et al.*; 1996), with the most evidence being found in Greenland and the North Atlantic. In Africa evidence for the YD has been found in East Africa (Roberts *et al.,* 1993). This has, however, been disputed by Scott *et al.*, (1995) who argue that the cooling of the northern hemisphere during the YD had no distinct counterpart in the interior of Southern Africa, or at least that an effect was not large enough to show up clearly in the fossil pollen record. The only evidence from this study for climatic cooling associated with the YD period could possibly be the marked decrease in minimum temperatures, recorded in the local approach, between 10 700 and 9 000 years ago (Figure 3.1a). However, this is far from conclusive. The time intervals used are too large to be able to reflect changes over such short time periods and there is a poor synchrony between the results from the local and regional scale climatic changes at this time. Thus, this study does not confirm that the YD had an effect on the climates of the Cape west coast.

The regional and local approach produced different reconstructions of past climates. In terms of the minimum temperature of the coldest month, both time series followed the same general trend, although the perturbation associated with the transition between Pleistocene and Holocene occurred slightly later according to the local approach. In contrast, the predictions for median temperature of the hottest month indicated very different results. The regional method predicted a peak at around 13 000 years ago, while the local method indicates the highest temperaturest about 19 150 years ago, and a dramatic drop about 13 000 years ago. The regional method also predicted that the late Pleistocene was colder (median maximum temps of 27 °C) than the Holocene (median maximum temp of 29 °C) which is opposite to the predictions based on the local approach. Both methods indicate similar temperatures for the Holocene period, with median temperatures being around 29 °C for both methods. The temperature figures from the regional study therefore support other results from the Cape west coast that temperatures were lower during the late Pleistocene, and that they increased towards the beginning of the Holocene (Deacon and

Lancaster, 1988). However, there is a large amount of variability associated with predictions in the Pleistocene. In contrast, the local approach supports the work by Meadows and Sugden (1991, 1993) which suggests that climates may have changed little over the past 14 000 years in the western fynbos biome.

Although the temporal resolution of this data is not directly comparable to Baxter's (1996) comprehensive reconstruction (Baxter, 1996 Table 9.1) it is still important to consider major similarities and differences in the trends (Figure 3.1). In terms of rainfall (Figure 3.1d) the local approach indicates a similar pattern although it appears to be shifted to the right on the time axis by a period of about 5000 years (i.e. a high at 13 000 BP rather than Baxter's (1996) 18 000 BP high). The regional approach agrees with Baxter's (1996) 18 000 BP high and more or less decreasing rainfall trend over time. In terms of temperature (Figure 3.1b) the local approach differs quite noticeably from Baxter's (1996) trend. While Baxter (1996) suggests a low temperature at about 18 000 BP followed by increasing temperatures, the local approach indicates a high at about 20 000 BP followed by a decrease. However it is possible that this decline in temperature could have occurred in the approximately 2 000 year period between 20 000 BP and 18 000 BP. Baxter's (1996) work provides a clear precedence for such dramatic change over equivalent periods of time. The reconstruction based on the regional approach correspond more closely with Baxter's (1996) low temperature at 18 000 BP and ensuing increase.

The trend in growth days is more or less the same for both approaches, however, the local approach generally predicts fewer growth days over the entire sequence. In terms of median annual rainfall, both approaches indicate a marked decline between 40 000 years ago and today confirming several earlier studies (Parkington, 1981; Klein, 1991; Meadows and Sugden, 1991). However, as with the maximum temperature predictions discussed above, the direction of the oscillations associated with the transition between the Pleistocene and the Holocene seem to be opposite. The local approach suggest that the seasonality has changed little over the past 40 000 years, while the regional approach indicates a marked increase in the proportion of rainfall occurring in winter.

It is far from simple to explain these differences in predictions using the different approaches. Many factors may have contributed. Firstly, slightly different sets of species were used in the different approaches (Table 3.1) and this effect would have been further amplified by the inclusion of species interactions and the use of "all subsets regression" in the local approach. Secondly, the regional approach was based on wider distributions ranges and consequently greater climatic ranges than the local approach. Thirdly, in the local approach the climatic variables were sampled at a larger spatial scale (1.5 km x 1.5 km) than were the species distributions (between 20 m x 20 m and 80 m x 80 m). It is possible that this resolution of the climatic variables may have been too coarse for the local approach.

The hypothesis that the eastern and western sections of the fynbos biome are under fundamentally different controls and would thus have had different past climates (Cowling *et al.*, in prep), is supported by this study. The eastern section appears to have been cold and dry during the LGM and terminal Pleistocene according to evidence from Knysna and the Boomplaas cave in the Cango Valley (Martin 1968; Deacon, 1979; Deacon et al., 1983; Scholtz, 1986). In contrast this study generally supports the suggestion that the western section of the fynbos biome was wetter during the LGM and terminal Pleistocene than today (Parkington, 1981; Klein 1991; Meadows and Sugden, 1991; Baxter, 1996; Meadows and Baxter, in prep).

Attention has been drawn to the need for a multidisciplinary study on the past climates of the western section of the fynbos biome (Parkington, 1981; Meadows and Sugden, 1991; 1993; Cowling *et al.*, in press). The inferences regarding past climates in the western section of the fynbos biome, and elsewhere, to date have been narrative, and not quantitative estimates as in this study. According to the results of this study there have been marked changes in the temperature, rainfall and related climatic variables over the past ~ 40 000 years. Thus, this study has confirmed narrative inferences and provided more quantitative estimates on the past climatic conditions on the western section of the fynbos biome.

The two methods used to reconstruct past climates provide support for using present day species distributions to predict past climates. Previous estimates, which were not based on quantitative estimates of past climates of the Cape west coast, were confirmed using a more rigorous approach. The quantitative predictions made in this study suggest that Pleistocene climates were fundamentally different between the eastern and western parts of the fynbos biome. However, similar quantitative estimates do not exist for the eastern part of the biome were reconstructions are based on narrative inferences of taxon - climate relationships. The two methods did not provide identical estimates, but did follow the same general trends. The methods lend new insight into reconstructing past climates using palaeobotanical data, thus linking the present to the past.

CHAPTER 4

DISCUSSION OF PRINCIPLE FINDINGS

4.1 DISCUSSION

The climatic conditions on the Cape west coast have altered over the past 40 000 years. This study addressed the feasibility of reconstructing these climatic changes using a charcoal sequence spanning the past 40 000 years. In contrast to the more narrative approaches of climatic reconstruction which have previously been made (e.g. Cowling *et al.*, in press), I used a quantitative approach. This quantitative approach provides two rigorous methods of inferring past climates on the basis of present climatic and vegetation data. Although detailed discussions have been incorporated into each chapter, several key components have been extracted from the analysis and summarized here, along with suggested guidance for future research.

The specific aims addressed were:

- To determine whether past communities in the surrounds of the EBC have present day analogues in the study area.
- To determine the community - environmental relationships of the extant communities
- To attempt a reconstruction of past climates using two methods - a local and a regional approach.

The three classifications conducted on the fossil species, present vegetation and a combined data set, clearly indicates that community structure has changed over the past 40 000 years. The communities have been reshuffled in such a way that no exact analogues of the past communities exist in the study area today. Among other things these changes in composition were influenced by species tracking the climatic changes in an individualistic manner (Webb III, 1986; Davis, 1986; Huntley and Webb III, 1988; Huntley, 1991; Hengeveld, 1997). As communities have altered so dramatically over time, using these as units for reconstruction of past climates is not feasible. Using the components of communities (extant species) to determine climatic conditions is more appropriate and was thus adopted here.

Being able to explain the causes of species distribution in the extant study area is essential before climatic reconstructions on the basis of species present could be made. Using species environmental ordinations, the most significant variables controlling geographical distributions of species were identified. These included altitude, rainfall, temperature, growthdays, pH and bedrock. Of these the climatic variables, and surrogates for climatic variables (e.g. altitude), were found to play a significant role in species distribution. These results provided a sound reasoning for using species distributions in reconstructing the following climatic variables: maximum temperature of the hottest month; minimum temperature of the coldest month; median annual rainfall; percentage winter rainfall; and number of growthdays.

The use of two methods of climatic reconstruction proved valuable in that results could be compared and in this way validated to a certain extent. The local method was based on a multiple regression technique using present day species - climatic correlates in the local study area. The regional method adopted a similar approach, but used present day climatic envelopes derived from nation-wide species distribution data. In my opinion both methods are rigorous and can be confidently used in other studies of climatic reconstruction.

There are, however, certain aspects of the data which, had they been better, could have improved the confidence in the reconstrucitons. Firstly the climatic variables should idealy have been at a finer resolution. In this study the climatic data were extrapolated over the landscape, and thus were not as precise as would have been desirable. However, this lack of precision could not be avoided as no other climatic data are presently available at such a large scale. Secondly, there are limitations in obtaining accurate climatic envelopes of the species. While the sample size used in this study was more than adequate, large scale landscape transformations by human activities (e.g. agriculture) have occurred. This has had the effect of restricting the distribution of species, thereby narrowing the range of potential climatic conditions under which the species can exist, resulting in a weakening of the correlation between climate and species distribution.

The predictions from the regional method correspond most closely with other narrative inferences (Cowling *et al.*, in press) of climatic changes on the Cape west coast over the past 40 000 years. In my opinion the predictions from the regional approach are more satisfactory than those of the local approach. I attribute this to the fact that the regional study is based on a larger study area (national) and a more complete range of climatic conditions. In addition, the climatic data used was possibly more appropriate for interpretations at this scale. Although both methods have advantages and disadvantages, and predicted subtle differences in trend, the overall trends predicted were similar. Both illustrated increasing temperatures, decreasing rainfall, increasing percentage winter rainfall and an increasing number of optimum growthdays over the past 40 000 years on the Cape west coast. In addition both methods resolved marked climatic perturbations at about 13 000 BP.

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APPENDIX 1:

Relative importance of fossil charcoal in samples from Elands Bay Cave. See text for derivation of importance values. Nomenclature according to Arnold and de Wet (1993). *Age of sample interpolated (see overleaf).

Sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13
Sample size (*n*)	500	100	100	200	104	150	100	200	150	150	100	100	100
Sampl e mass (g)	52.32	10.74	9.28	21.64	10.24	12.12	11.32	18.63	16.23	14.84	10.14	11.63	10.77
Age (BP)	320	500	1400	3290	3780	3780	3940	4160	4370	4370	7910	7910	8500*
Euclea racemosa	0.244												
Rhus cf. *Undulata*	0.168	0.14	0.17										
Ruschia maxima	0.186	0.22	0.02				0.06	0.14					
Zygophyllum morgsana	0.152	0.18				0.28	0.34		0.373				
Lycium sp.		0.09			0.067			0.11		0.04			
Ruschia sp.			0.11		0.173	0.187	0.02	0.24	0.253	0.28	0.03		0.09
Eriocephalus cf. *aromaticus*			0.15		0.096								
Aspalathus sp.				0.04		0.08							
Passerina glomerata					0.154								
Chrysanthemoides sp.						0.1							
Euryops cf. *speciosissimus*			0.25		0.135					0.147	0.11	0.115	0.06
Hymenolepis cf. *parviflora*				0.05									
Salvia africana-lutea				0.13									0.03
Phylica sp.					0.096	0.033							
Heeria argentea								0.04	0.027	0.073	0.1	0.074	0.03
Maytenus cf. *oleoides*												0.098	0.19
Cassine cf. *peragua*											0.21	0.216	0.14
Diospyros cf. *glabra*											0.22	0.192	0.16
Dodonaea angustifolia													
Hartogiella schinoides													
Tarchonanthus camphoratus													
Maytenus cf. *heterophylla*													
Olea europaea ssp. *africana*													
Ficus cf. *Cordata*													
Colpoon compressum													
Protea cf. *glabra*													
Leucadendron cf. *pubescens*													
Euryops sp.													
Cliffortia sp.													
Erica cf. *Verecunda*													
Erica cf. *Caffra*													
Protea cf. *nitida*													
Rhus sp.		0.08	0.11	0.22		0.18	0.32			0.28	0.28	0.28	0.12
Euclea tomentosa		0.26		0.28		0.107	0.2	0.4	0.107			0.048	0.08
Pterocelastrus tricuspidatus	0.204		0.16	0.24					0.193	0.187			0.05
Kiggelaria africana													
Podocarpus cf. *elongatus*													
Celtis africana													
Grewia cf. *occidentalis*													
Passerina sp.													
Myrsine africana													

APPENDIX 1: Continued.

14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
32	100	100	150	104	100	200	400	163	100	100	500	200	70	100	200
3.3	10.66	12.14	16.44	10.24	12.53	26.85	47.64	18.54	13.95	15.33	62.84	26.65	10.23	13.43	28.25
8860	9000*	9000*	9000*	9510	9600	9950	9950	10460	10660	10660	10700	12450	1300*	1300*	1300*
				0.096											
0.156	0.04	0.05	0.055												
	0.02		0.045		0.044	0.015	0.015	0.018							
		0.03						0.074			0.067				
						0.14	0.07							0.01	
0.125		0.08	0.05				0.08								
	0.19	0.12	0.15	0.212	0.155										
	0.12	0.1	0.085	0.163	0.102	0.09	0.025					0.085			0.13
0.469	0.18	0.14	0.135	0.173	0.237	0.12	0.235	0.172	0.08	0.13	0.16	0.11	0.214	0.13	
	0.17	0.16	0.15	0.125	0.194	0.24	0.18	0.092	0.14	0.12	0.124		0.171	0.12	
	0.06		0.06	0.048			0.015					0.065			
	0.02				0.04	0.05	0.09								
						0.06	0.08	0.135	0.19	0.16	0.148	0.11	0.2	0.11	0.19
								0.147	0.12	0.14	0.162	0.105	0.143	0.1	0.06
									0.12	0.16	0.124				
									0.09			0.06			0.04
												0.045	0.043	0.15	0.07
													0.043	0.1	0.2
								0.086				0.045			0.01
									0.05					0.04	
															0.07
0.219	0.03	0.09	0.09	0.029	0.061	0.08	0.055	0.061		0.08	0.04	0.095	0.057	0.15	0.1
	0.14	0.18	0.135	0.067	0.123	0.18	0.11	0.16	0.12	0.18	0.126	0.125	0.086	0.07	0.09
				0.058					0.04			0.055			0.02
												0.05			

APPENDIX 1: Continued.

30	32	32	33	34	35	36	37	38	39
120	100	100	30	200	200	150	600	340	200
13.53	11.73	12.24	6.1	32.15	28.44	18.45	72.97	45.64	27.16
13260	13260	13600	17800	20500	2100*	?	>40000	>40000	>40000
0.05	0.21								0.02
0.1		0.14	0.2	0.16	0.09	0.05	0.053		
				0.02	0.04	0.065	0.11	0.041	
0.04	0.06				0.03	0.1	0.017	0.012	
							0.04		
0.17	0.25	0.18	0.23	0.1	0.1	0.06			
0.11	0.18	0.18	0.2	0.06	0.07	0.1	0.083	0.106	0.06
			0.167	0.18	0.125	0.12			
0.15	0.2	0.08							
0.18									
		0.07							
		0.06							
		0.04							
0.07	0.04	0.1		0.04	0.1	0.05	0.007		
0.04			0.1	0.07	0.06				
0.05									
				0.1	0.12	0.115	0.123	0.212	0.15
				0.16	0.09	0.105	0.137	0.144	0.18
				0.07	0.07	0.085	0.113	0.118	0.2
				0.02	0.02		0.013		
		0.13					0.033	0.053	0.05
					0.065	0.1			
							0.037	0.112	
							0.02	0.023	0.01
									0.025
									0.01
							0.077	0.071	0.14
							0.107	0.082	0.11
0.02	0.06	0.02	0.1	0.02	0.02	0.05	0.03	0.026	0.045

APPENDIX 2:

Phytosociological table produced from the classification of the extant vegetation.

```
              111           1 111112  1111222    11222111111111122222222222111111112222111111112
              6688026667777888880006999186881309000021672234011379909002667889999900001122233113677890013334777791
              3537246794789014580680047628697539147956456731957163550011169691267945670902358048826852811490345748

 2 colp comp  --------4-242-33-2233---------------2-------------------------3-----------------------------2--2----  0000
15 mayt hete  ------------------------------------------532333-------------------------33--222-23-22233323-2-24332  0000
17 myrs afri  --22222---2-32-2---22-2--3--2---2222-33---32-2-23------2-2----------3-----22--------22--22-344253335  000100
10 nall luci  -------------------------------------22---------------------------------------2-------------------2-  000101
11 hart schi  ---44-------2-23-3---------------2223332---343332--------------2-------------22---------3-----224--3  000101
12 heer arge  5463475645554774353535342-4432---323334------------542----------------------------------------------  000101
16 mayt oleo  323543343443443534333-2-342-22-----2-3--4-2222222--2--------------------------22---------------2----  000101
21 prot niti  -3-32-4-33--3--32-2---423523325542223-233532-342243-2-------------------2----2---2----------------3-  000101
13 kigg afri  --------------------------------------2---------2-----------3-322-2-2-32------225-34423333----3---22  00011
18 olea euro  4343-2--33-53-34---32433453------2---22-------3----22-3-2345433434444434444333264-3333434332--2233--  00011
20 podo elon  55544-------------------2---------------------------6-4343------------------222---------------------  00011
27 prot glab  -------------------------------------------------------------1-323211-------------------------------  0000
 1 cass pera  ------------------------------------------3--2---------------------------------------------------3--  0010
 3 dios glab  -3322433322-23-3-2-22-332----2-2--322222432222-22--222-2322---22----2---2-2--22-2--22--2---322--3-22  0010
 4 dodo angu  ---------------------3-433-32--33----2--3---3---3-2332--------22---3-2332-2--32-2-2-32232--22322-322  0010
 8 eury spec  --------322------------3-33--------2----------3--5433-2-32-322233333243332322----33-2-322---4--2---2  0010
19 pass glom  -----2-----------2-------43-------------------------------------------------------------2-----------  0011
 5 erio afri  -----------4------------2--463--------------------33332433-2-334222322---333232------3-2----3322-222  010
 7 eucl tome  -------------------2--2223---------2---------------22---------------------2-------------------------  011
 9 ficu cord  ------------------------------------------------------22--------------------------------------------  011
14 leuc pube  -----------------------2---------------------------24-----------------------------2-2--2-2-2-2------  011
23 rhus undu  -33--4--24-33-2----3-42223------------4-432-2-2-3-3-2-2222-2-323----33--23-3---3344334--23-344433433  011
25 salv afri  --------------------------------------------------------2--------------------------------2----------  10
 6 eucl race  -------------------------3----------------------2--------------------------2--------------2--------2  11
22 pter tric  -------------------------------2-3--3-42--------2---2-----------------------------------------------  11
24 rusc maxi  -----------------------------------------2----------------------------------------------------------  11
26 zygo morg  -----------------------------------------------------------------------------------------------2----  11

              0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
              0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
              0000000000000000000000000000000000000000000000000111111111111111111111111111111111111111111111111111
              0000000000000000000000000001111111111111111111111000000000000000000000000000000000000000000111111111
              0000000000000000000001111110000001111111111111111000000000111111111111111111111111111111111000000000
              0000011111111111111110000110001110000000011111111001111111000000000000000000000111111111111000000000
```

Appendix 2. Continued

```
               222122122    1111         111111          11   11 22222  11111122  11111221112    1 1  11122   12
               3339449054499111111355559912223611223345576723668522244453337881122346682358852377171151225544425222
               9678123395968123845334591291235338692670627050255156707681278042317652978091213803716975043712392028

  2 colp comp  ---------------------------23-------------------------------3---------------------------------------  0000
 15 mayt hete  3322223------2------------------------------------3-322-----2------------23--------------------3----  0000
 17 myrs afri  343232-2---------------------------------------------43---2-----------------------------------------  000100
 10 hall luci  -24-------------------------------------------------------------------------------------------------  000101
 11 hart schi  4242--244--------------------------------------------2----------------------------------------------  000101
 12 heer arge  -----2-----------------7------------------------------------------------------------2---------------  000101
 16 mayt oleo  222-----------------------------243---3-42----3---22-2223-----------------------------3-2-----------  000101
 21 prot niti  2-----------------------------------------------------------------------------3--3---44-------------  000101
 13 kigg afri  --------------------------------------------------------------------------4224----------------------  00011
 18 olea euro  ----------222232---4-4---33443-4---3--5-5--4-4-----------------2-----433----------------------------  00011
 20 podo elon  ------------------------5232------------------------------------------------------------------------  00011
 27 prot glab  ----------------------------------------------------------------------------------------------------  0000
  1 cass pera  -322-----------4-----------------------------------2-3----------------------------------------------  0010
  3 dios glab  -2-----2-4223--------------2----24----245-----3--42333-332-23--233---3-2232222-------33322--43422564  0010
  4 dodo angu  222-22-2---5-3---23-334-24333-2-23-------6-----------2--4233222---------------3752242-533-----------  0010
  8 eury spec  2----2422-625------3-43---324342334-------42--42------2----------------4-2-3--4-423------3-------3--  0010
 19 pass glom  -42-------4------3855454-3---4--235433-33----3---3---3------------------------3-4544-4-----------625  0011
  5 erio afri  3-2-323-2743254-4---33-3-34-43------------------3-2-232-4----2-----2-------------2-34---32----------  010
  7 eucl tome  --2--3---232323423-3--3-2244-2--3223243533--3----4---22----------------------2-----3--4-22-233422---  011
  9 ficu cord  ---222-----------------------------2--------44433----2------2---------------------------------------  011
 14 leuc pube  ---------------------4---------------------------3---2---232---22-------------445-343-3-432256343335  011
 23 rhus undu  335233342---2-3233432423323333234456436346235144433323277-4243323532333233322------3----------4-----  011
 25 salv afri  ----------------------------2--23----------3-----4332323-2-3---22--2-22232332-----------------------  10
  6 eucl race  ---------------------------------------------------2------------------------------------------------  11
 22 pter tric  ------------------------2-----------------------------------2---2----------------------2------------  11
 24 rusc maxi  ----3---4-----------------------------------------2-------------------------------------------------  11
 26 zygo morg  ----------------2----------------------3-------3----2-23-3---2233-----------------------------523---  11

               0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
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               1111111110000000000000000000000000000000000000000000000000000000000000000000001111111111111111111111
               1111111110000000000000000000000000000000000000001111111111111111111111111111100000000000111111111111
               0001111110000000000000000000000011111111111111111000000000000000011111111111110000000111100000000111
               01100011100000000111111111111111000000000000111110000001111111111000000000111100000011    00011111000
```

Appendix 2. Continued

```
                      111111  111121211212222  2      22222211122 1112 11
              34445 1145447836565625455454544  3    3123535554445 4451 23
              40482602916813714430925674894685441237914382065233584704980

 2 colp comp  --------------------------------4--------------------------  0000
15 mayt hete  ------------------------32------------5--------------------  0000
17 myrs afri  ----------------2----32-2----------------------------------  000100
10 hall luci  -----------------------------------------------------------  000101
11 hart schi  -----------------------------------------------------------  000101
12 heer arge  -------------------------------3---------------------------  000101
16 mayt oleo  2----------------------------------------------------------  000101
21 prot niti  -----------------------------------------------------------  000101
13 kigg afri  -----------------------------------------------------------  00011
18 olea euro  -----------------------------------------------------------  00011
20 podo elon  -------------------------------3---------------------------  00011
21 prot glab  -----------------------------------------------3-----------  0000
 1 cass pera  -----------------------------------------------------------  0010
 3 dios glab  33-453332----------------------4---------------------------  0010
 4 dodo angu  -----------------------------------------------------------  0010
 8 eury spec  ------------------------------2----------------------------  0010
19 pass glom  4-363------------------------------------------------------  0011
 5 erio afri  -------------------2--23-2-2-23----------------------------  010
 7 eucl tome  3--2----------34---------2-----------------222-------------  011
 9 ficu cord  --------------3--2-----32----------------------------------  011
14 leuc pube  57543-------------------------------------------------33543  011
23 rhus undu  3---3---232232545333232353--------------------3-------22---  011
25 salv afri  --------33--------------22-----5--------------4--------2---  10
 6 eucl race  --------------------3----------54277766434323-2--------4-22  11
22 pter tric  --------------------------------24-82----------------------  11
24 rusc maxi  ------------------2422-44352234----------------------------  11
26 zygo morg  --------534533554244432333223--222-63373534-4342333444442-3  11

              00000000111111111111111111111111111111111111111111111111111
              11111111000000000000000000000001111111111111111111111111111
              11111111000000000000000000111110000000000000001111111111111
              11111111000000000011111111000110111111111111110000000011111
              11111111000000111100011111      000000011111110111111100111
              00000111001111       00111      00111110000111 0000111
```

APPENDIX 3:

Phytosociological table produced from the classification of the fossil charcoal species.

```
              33333332233222222312211111111         1
              789456269017842353701568931244692781350

 3 Kigg afri  343333---------------------------------  000000
 4 Podo elon  333323---------------------------------  000000
 5 Celt afri  333222---------------------------------  000000
 6 Grew occi  1--11----------------------------------  000001
 7 Myrs afri  ----23---------------------------------  000001
 1 Hall luci  111------------------------------------  00001
 2 Chio fov   --1------------------------------------  00001
 8 Fics ur    223------------------------------------  00001
 9 Sali mucr  323------------------------------------  00001
10 Ficc ord   ---333-------3-333---------------------  0001
11 Olea euro  232223332333333333---------------------  0001
13 Hart shin  11--13-2-12-------2-12-1---------------  0001
14 Mayt hete  ---332333343333333-22------------------  00100
12 Colc comp  -------21----2-------------------------  001010
21 Leuc pube  ------3-33-13--------------------------  001011
22 Prot glab  ------2123313--------------------------  001011
23 Prot niti  ------1--------------------------------  001011
24 Eric vere  --------2------------------------------  001011
25 Eric caff  ------2--------------------------------  001011
15 Dodo angu  31-112-----333233-3333333--------------  00110
16 Tarc cam   1------------------22-1-1--------------  00110
18 Dios glab  2--32233-3-332333333333333335----------  00110
17 Cass pera  --1----2323-------2213333333-----------  00111
19 Mayt oleo  ------------------3--33333-2-----------  00111
20 Heer arge  ------------------2-2-2--1323--1--1---2  01
26 Hyme parv  --------------1---1111--1----2---------  10
27 Salv afri  --------------2-2-----1--1---3---------  10
29 Eury spec  ---------------------22--3321--3----433  10
31 Eucl tome  ---22--321-223333333333232-1-433435----  10
28 Erio afri  ------------------------------------32-  110
30 Pass glom  -------------------------------------3-  110
32 Pter tric  -------212---1---------2-2---3-3---33-3  110
33 Rhus undu  --------------------------------3--33--  111
34 Rusc maxi  --------------------------------32331--  111
35 Zygo morg  ------------------------------4535-3---  111
36 Eucl race  -----------------------------------4---  111

              000000000000000000000000000001111111111
              000000111111111111111111111110000000111
              000111000000000000111111111110111111
                    00000111111100000000111 000001
                    01111001111100011111    00111
                            01111   00001
```

APPENDIX 4:

Phytosociological table produced from the classification of the combined (extant and fossil) data.

```
               222221221112222    1               111     1111111111222222222      122222222222  1 1 122222222222222
               9998999977901336688026667777888888900016999000022234700111333113688077777778677351419137888888889999
               6785084535488583537246794789012458006864179147956731439567679791869312456780903575514319123467891236

  2 colp comp  ---3-------------------4-242-3-3-2-233-------2------2-------------------------------------3---2-----  0000
 12 heer arge  ---------------54634756455547744353353---2323334----------------432-32-33--3344-----4---------------  0000
 17 myrs afri  -----23423325----22222---2-32--2--2-223---222-3332-252-2-3433----2-2--------------------------------  0000
 20 podo elon  444---34-----2255544--------------------52--------------------------------------------------------4-  0000
 10 hall luci  222-------2---2-------------------------------22----------24----------------------------------------  00010
 11 hart schi  22-3322424-3322---44-------2-2-3-3--------222333-343243322244---------3-32-2-------------------2----  00010
 16 mayt oleo  --------------23235433434434432534233344-3--2-3-22222-22-2222----22-3444444-----3-------------------  00010
 22 prot niti  ----------3--2--3-32-4-33--3--232-42--53-32223-232-3--4232--25443324-----------54---2-----------2---  00010
 28 chio fov   --2-------------------------------------------------------------------------------------------------  000110
 29 celt afri  444---33------------------------------------------------------------------------------------------3-  000110
 30 grew occi  2-----2-------------------------------------------------------------------------------------------2-  000110
 31 fics ur    334-------------------------------------------------------------------------------------------------  000110
 32 sali mucr  434-------------------------------------------------------------------------------------------------  000110
  1 cass pera  --2342------------------------------------------3--2------32--------44443442-4-------4-3------43----  000111
 33 tarc cam   2-------------------------------------------------------------------------23-----------3------------  000111
 36 hyme parv  ----------------------------------------------------------------------2-2-22-----------22-----------  000111
  3 dios glab  3--4--33-32-222-3322433322-23--3-23-22-4-2-322222222-2-2222---3---2-44444444-462334-3--4443444-44442  0010
  4 dodo angu  42----232-22232-----------------------3323----2---3-22---3222---32-3--444444---353-34--4344444----25  0010
 13 kigg afri  454---443-232-2--------------------------------2---------2----------------------------------------4-  0010
 15 mayt hete  ---45243-433222---------------------------------53232-33--323--------------3-------2--2344444444444-  0010
  8 eury spec  -----------22----------322----3-------3-----2-------223-----2--5----3433----442-----3--------------2  001100
 18 olea euro  34344-3423-4-324343-2--33-53-334--3-325--42---22----2-3----------------------------2323-444444344432  001100
 34 eric vere  ----------------------------------------------------------------------------------------------3-----  001100
 35 eric caff  ------------------------------------------------------------------------------------------------3---  001100
 19 pass glom  -----------2--------2---------3--2----4-------------------42--4-------------------------------------  001101
  5 erio atri  --------2-2-232-----------4--------------2----------2------23---463---------------75---------------3  00111
  9 ficu cord  -----244---------------------------------------------------------------------------------444-----44-  010
 14 leuc pube  --------------------------------------------------------------------------------3---2-------24444---  010
 21 prot glab  ---24--------22-----------------------------------------------------------------------------24343---  010
  7 eucl tome  ---4--3---------------------------2-2-3-22--2--------------2--------23444344----4-2224-444443332-432  011
 24 rhus undu  -----2--43323---33--4--24-33-2----2-3-3432-----42-2-342--3353-----------------------22--------------  011
 26 salv afri  ---------------------------------------------------------------------2-2----------------3--3--------  011
  6 eucl race  ------------2-------------------------3------------------2----------------------------2-------------  1
 23 pter tric  ---3------------------------------------2-3--3-4--------22-----------3---3--4--2-2--------2---23----  1
 25 rusc maxi  ----------------------------------------------------------------------------------------------------  1
 27 zygo morg  ----------------------------------------------------2-----------------------------------------------  1

               0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
               0000000000000000000000000000000000000000000000000000000000000000000000000000000000111111111111111111
               0000000000000001111111111111111111111111111111111111111111111111111111111111111111000000000000000000
               0001111111111110000000000000000000000000000000000000000000000000000001111111111111000000000000000000
                  0011111111110000000000000000000000011111111111111111111111111111000000000000111000000000000000001
                    0001111111000001111111111111111110000000000000000000000111111100000000111   001111111111111110
```

Appendix 4. Continued

```
              11111111111111111111111122222222222             1111112222222222211111111222222 11111222        1111
              1123345666667777788888990000111225112222344556773467882222344442689999900012273336945623455557991112
              0412409123890267912789050124129011381579067682256558455678001272661267956702365897389263934593282893

 2 colp comp  --2------------------3-----------------------------3-----------3----------------2-------------------  0000
12 heer arge  -------------------------------------------------------------2------------------------------7-------  0000
17 myrs afri  ---234--------23----2---2--32--22--------------------------4323------------2----4-------------------  0000
20 podo elon  --2-------------------4-34------3-------------------------------------------2-----------------2---3-  0000
10 hall luci  ----------------------------------------------------------------------------------------------------  00010
11 hart schi  -----------------------------------------------------------2------2---------------2-4---------------  00010
16 mayt oleo  2---------------------------------24-----234332-------22---2--2-----------------------3-------------  00010
22 prot niti  -----------------------------------------------5--------------------------2--3-2-------------3------  00010
28 chio fov   ----------------------------------------------------------------------------------------------------  000110
29 celt afri  ----------------------------------------------------------------------------------------------------  000110
30 grew occi  ----------------------------------------------------------------------------------------------------  000110
31 fics ur    ----------------------------------------------------------------------------------------------------  000110
32 sali mucr  ----------------------------------------------------------------------------------------------------  000110
 1 cass pera  ---------------3---------------------------------------2---3----------------------------------------  000111
33 tarc cam   ----------------------------------------------------------------------------------------------------  000111
36 hyme parv  ----------------------------------------------------------------------------------------------------  000111
 3 dios glab  -22-32223----22--222-2--2322-2-222243----32533-3---3--233233------2-------2-----2-------2------3----  0010
 4 dodo angu  -23323----2---33----22-2--3----2--23--------4-6----22------222-3--2---32332--22-2--------334-24---3-  0010
13 kigg afri  25----4---3--44-322-23-3--323----4--------------------------------22-2--32--------------------------  0010
15 mayt hete  2---323---3---23----2--2--3-3-33-------------------2--3-3-22222----------------2--3-----------------  0010
 8 eury spec  --2------23-2-2-23-4-223-322--232-33---------4----2-------2--2243233333433322443444225436-43-2-5--33  001100
18 olea euro  644-2--4443343334--33334-23432443------34-55-------------------45343444434433----------42-4---323-33  001100
34 eric vere  ----------------------------------------------------------------------------------------------------  001100
35 eric caff  ----------------------------------------------------------------------------------------------------  001100
19 pass glom  ----------------------------------23---43--3---------------3--------------------------554545453----4  001101
 5 erio afri  -----3---------2----332-4322--333-----------4---2----32-2--3322423422232---323--3-3324--433-32324443  00111
 9 ficu cord  ----------------------2-2------------4-24----4----32-3-----222--------------------------------------  010
14 leuc pube  ---322----2---2-----------2-22-----------------------------2------------------------------4---------  010
21 prot glab  ----------------------4-34------3-------------------------------------------2-----------------------  010
 7 eucl tome  --4----------------------------2-232-3-3--33--3------------2-32-----------------------233--3--233242  011
24 rhus undu  3334343-33433334-222422-22-3323-2-445536476474632344343323333323233----3--23-324423-2453-2423-223333  011
26 salv afri  ------3-22-23----322-----2--22----3------3------2-----332323--22------------------------------------  011
 6 eucl race  -------------------------------------------------------2-------------------2------------------------  1
23 pter tric  ---------------------------------------------------2---------------------------------4--------------  1
25 rusc maxi  -----------------------------------------------2------2-----3----------------------442--------------  1
27 zygo morg  -----------------------------3-----------3--------3-2---2-----2----------------------------------2--  1

              0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
              1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111
              0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
              0000000000000000000000000000000000000000000000000000000000000001111111111111111111111111111111111111
              1111111111111111111111111111111111111111111111111111111111111110000000000000000000000000111111111111
              0000000000000000000000000000000000111111111111111111111111111110000000000001111111111000000000000000
```

Appendix 4. Continued

```
              12   111       11          1    2222   11222111211112111 11111111122   222221222222   222   2  112
              866990121132377122223445444234556555 1133126556455564455 44444457845365666665445336  3255  13  231
              04035564452380170028448201296301323760217390670423445915823467801335716156786942482794081341359804

 2 colp comp  ------------------------------------------------------------------------------------------4-------  0000
12 heer arge  --55422-------------------------------------------------------------------2------2-----------3----  0000
17 myrs afri  ---------------------------------------------2--3-2-2---------------------------------------------  0000
20 podo elon  ----6----------------------------------------------------------------------------------------3----  0000
10 hall luci  --------------------------------------------------------------------------------------------------  00010
11 hart schi  --------------------------------------------------------------------------------------------------  00010
16 mayt oleo  ---2------------2---2-----------------------------------------------------------------------------  00010
22 prot niti  ----2------3--------------------------------------------------------------------------------------  00010
28 chio fov   --------------------------------------------------------------------------------------------------  000110
29 celt afri  --------------------------------------------------------------------------------------------------  000110
30 grew occi  --------------------------------------------------------------------------------------------------  000110
31 fics ur    --------------------------------------------------------------------------------------------------  000110
32 sali mucr  --------------------------------------------------------------------------------------------------  000110
 1 cass pera  --------------------------------------------------------------------------------------------------  000111
33 tarc cam   --------------------------------------------------------------------------------------------------  000111
36 hyme parv  --------------------------------3-----------------------------------------------------------------  000111
 3 dios glab  ---222-2--------25643-453432-444-2--333223-----------2---------------------------------------4----  0010
 4 dodo angu  2-33322-23-375423----------------------23---------------------------------------------------------  0010
13 kigg afri  --------------------------------------------------------------------------------------------------  0010
15 mayt hete  ---------------------------3-----------------3-2------------------------------------5-------------  0010
 8 eury spec  -4-33--3---4-4-3-3--------------------------------------------------------------------------------  001100
18 olea euro  --422---------------------------------------------------------------------------------------------  001100
34 eric vere  --------------------------------------------------------------------------------------------------  001100
35 eric caff  --------------------------------------------------------------------------------------------------  001100
19 pass glom  -4------3833-444-6254363----3-33------------------------------------------------------------------  001101
 5 erio afri  23-33342------3-3---------------------------3-22----2-----------------------22--------------------  00111
 9 ficu cord  --------------------------------------------32-----2----------------3-----------------------------  010
14 leuc pube  ---24-33---44543433555437564-3-3-322---222---------------------3------------------------------5433  010
21 prot glab  -----------------------------------------------------------------------------------4--------------  010
 7 eucl tome  ---22--23-2---3-2---3-2--332445452-2-----------2--------------------3425446----2-4----2-----------  011
24 rhus undu  3-4-2---344---3-----3--3----3433--------2324353333532233----2-2232--54-4-------------------------2  011
26 salv afri  -------------------------------44------232---2-2-----334-------------------------------------5---2  011
 6 eucl race  ------------------------------------------35-----------2-----------------------22-766333774445-224  1
23 pter tric  ----2---------------------------4--------2-4------------------------------------448------22-------  1
25 rusc maxi  ------------------------------------------24444322---------------------4-345322-------------------  1
27 zygo morg  2--------------------------2-53--3-----3-344334334422534423444543333553456-2-23-26637544-323322-34  1

              00000000000000000000000000000000000000000011111111111111111111111111111111111111111111111111111111
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              00000000111111111111111111111111111111111100000000000000000000000000000111111110000000000000001111
              1111111100000000000000000000111111111111110000000000011111111111111111100001111000000000000001
              11111111000000000111111111110000011111111100111111111000000000000000111        00011111111111
              001111110001111110000000111100001000111111  000011111000111111111111              00000011111
```