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Applying palaeoecology to conservation: a long-term perspective for informed management of a fynbos nature reserve

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Applying Palaeoecology to Conservation: A long-term perspective for informed management of a fynbos nature reserve

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Abstract

This investigation proposes that long-term perspectives are essential in ecological conservation/restoration. Such a perspective is particularly important for fynbos, which has been substantially altered by an unspecified level of anthropogenic disturbance. Fossil pollen and micro-charcoal deposits are used to establish a proxy record for ecosystem state that can be applied to conservation. This is carried out at a nature reserve in the Langeberg Range, Western Cape, South Africa. Modern pollen-vegetation relationships are also examined to reduce inaccuracies in the fossil record. Three distinct phases are identified for the reserve over a period extending up to ~1000 years before present (BP). Phase 1a (pre-colonial settlement) was characterised by ~85-135% fynbos cover, relative to present cover, and greater than present afro-montane forest propagation. This may be a result of warm, mesic climatic conditions which occurred ~1000-600 years BP. Phase 1b saw fynbos proliferate to between ~135-225% of present cover, while afro-montane forest declined. This might be a result of cool, xeric conditions which occurred ~600-200 BP; conversely, the 'intermediate disturbance hypothesis' cannot be ruled out as a possible cause. Phase 2 appears to show colonial environmental degradation and fynbos decline (50-100% of present cover), initiating c. mid - late nineteenth century. In contrast, recent conservation efforts appear to have encouraged a return to conditions statistically analogous with those of phase 1a. Quantitative 'thresholds of potential concern' are defined for fynbos at 85-135% of present cover. Should fynbos cover breach these thresholds, this may indicate deviation from 'natural' conditions relative to present climate. However, given predicted future aridity, it is suggested that the full 'range of natural variability' exhibited by fynbos for the extension of the record might provide more appropriate parameters; 85-225% of present cover. Fire does not appear to be linked to fynbos proliferation/decline, but this could be a result of human perturbation.

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Introduction

The Cape Floral Region (CFR) is located in the Western Cape, South Africa. Its recent downgrading from floral kingdom status has done little to detract from the phenomenal levels of diversity and endemism contained in the unique CFRs borders. It covers ~90,000km², approximately four fifths of which is made up of the fynbos biome. The species diversity per geographical area of this region is unequalled anywhere in the world. It contains ~8,600 plant species, 5,800 of which are endemic. Comparisons of species diversity for a range of regions are shown in Table 1. It is of great concern therefore that the region is facing high species loss. 1400 plants feature on the Red Data list as endangered, and 29 of these are already known to have become extinct (Cowling, 1995). Thus, it is of high conservation priority.

Table 1: *Species Richness of the Cape Floral Region compared with other regions* (Bond, 1997)

Region	Area (10 ³ km ²)	No. of species	Species density (10 ³ km ⁻²)
<i>Mediterranean climate regions</i>			
Cape Floristic Region	90	8578	95.3
Cape Peninsula	0.47	2256	13.7
California Floristic Province	324	4452	13.7
SW Australia	320	3600	11.25
<i>Temperate Regions</i>			
British Isles	308	1443	4.7
Eastern N. America	3238	4425	13.7
<i>Tropical Regions</i>			
Malayan Peninsula	130	c.8000	61.5
Ivory Coast	320	c.4700	14.7

Establishing the true nature of fynbos ecology and biogeography is fundamental to its effective management and sustainability. The science of 'applied palaeoecology' seeks to reconstruct past ecological conditions, and provide a sound basis upon which to focus conservation strategy. In particular, the establishment of the 'range of natural variability' exerted by ecological variables is highly valuable, as this establishes parameters which, if surpassed, indicate deviation from the ecosystems 'natural' state (Birks, 1996; Froyd and Willis, 2008; Gillson and Duffin, 2007; Sweetnam, et al 1999; Willis, et al 2007; Willis and Birks, 2005). This however is problematic, as both pre- and post colonial anthropogenic perturbation has altered fynbos ecology and biogeography (Cowling, 1995; Crosby, 2004; Klutton-Broak, 1995; Meadows and Baxter, 2001; Smith, 1999). Moreover, the determination of reference conditions suitable to the present and future is dependent on identifying analogous climatic conditions in palaeoenvironmental records (Millar and Wolfenden, 1999).

The use of modern pollen samples in such studies can be viewed as essential, as it enables the reduction of inaccuracies in fossil pollen records caused by the differential representation of pollen between individual taxa (Ayyad, et al, 1992; Gillson and Duffin, 2007; Pardoe, 2001; Willis, et al, 2007; Wright, 1967). It also helps to disentangle the pollen signal of a subject plant community from the complex milieu of pollen in the fossil spectra. This is of particular importance to applied palaeoecologists, whom are often forced to sample from sedimentary records that are dislocated from the plant communities they wish to conserve (Froyd and Willis, 2008).

This study investigates the palaeoecology of a mountain fynbos nature reserve in the Langeberg Range, Western Cape, S.A. Modern pollen analogues are used to determine the relationship between pollen and parent vegetation, for both communities and individual taxa. This information is then applied in the interpretation of fossil pollen data obtained from a wetland core. Inferences relating to the proliferation and decline of fynbos, for a period of up to 1000 years, are used to determine quantitative objectives for the management of fynbos within the reserve. First however, literature relating to this investigation is discussed.

Fynbos, Palaeoecology and Conservation

Fynbos Composition, Diversity and Distribution

Fynbos consists of communities of grass-like plants, short shrubs and taller shrubs in varying combinations (DeBano, 1998). The main plant groups that make up fynbos are Proteas, Ericas, Restios and geophytes. The combination of these plant types in a species assemblage determines the type of fynbos vegetation. The five types are ericaceous, proteoid, restioid, dry and grassy fynbos. Ericaceous fynbos is found on the mid-upper slopes of the Langeberg range, and elsewhere in moist, cool environments. It is also characterised by high presence of Restionaceae, Bruniaceae, Paneaceae and Grubiaceae. Grassy fynbos is present in the foothills of the Langeberg, extending in a widening band from west to east (Cowling, 1995; Mucina and Rutherford, 2006).

Diversity in the Cape Floral Region is, at the local scale, high but not exceptional. At the regional scale however, its botanical diversity becomes phenomenal. Floristic dissimilarity occurs along transects ranging from hundreds of metres to hundreds of kilometres, with almost complete turnover of species/ vegetation types along geographical and environmental gradients. This type of diversity is known as 'beta diversity' (Mucina and Rutherford, 2006). The members of the plant groups described share similar growth forms, but are highly diverse along functional axis such as pollination and dispersal (Bond, 1997). The greatest proportion of endemics are found in mesic and wet habitats, particularly at high altitude, such as in the Langeberg (Macdonald and Cowling, 1993), where species are often endemic to a single peak or range (Cowling, 1995).

There are a number of factors that control the distribution of fynbos, which have also influenced its evolution and diversity. Nutrient poor soils in the area limit the colonization of the region by other vegetation types, allowing fynbos to proliferate since ~1.5 ma BP (Cowling, 1995). (It has been suggested that nutrient deficient soils have generated diversity as plants become more sensitive to nutrient

availability and specialization to nutrient niches causes speciation (Mucina and Rutherford, 2006)). Climate also plays an important role in distribution, and is an important determinant in the biogeography of fynbos type within the CFR. A palpable example of this is between the winter and all-year rainfall zones; although there are intricate localized variations. However, the hypotheses of climate and soil as controls on the development and distribution of fynbos are undermined by the successful transplantation of plants from other biomes to fynbos, and the success of invasive species (Bond, 1997). It is often suggested that the most dominant direct factor in both the distribution and biodiversity of fynbos is fire.

Fire and Fynbos

Fire has been a fundamental factor in the evolution of fynbos and its diverse plant communities. Before the twentieth century botanists viewed its effects as destructive, however modern ecology recognises its elemental role in the successional process of destruction, regeneration, growth, maturity and destruction again (Cowling, 1995). Burning serves a number of ecological roles. Fynbos contains many serotinous species that require fire for their seed to germinate. Some species may also benefit from the destruction of competitor species by fire. Moreover, the majority of the essential nutrients needed for new plants to grow are held in existing vegetation, which can be released by fire to facilitate new growth (Cowling, 1992; 1995; Bond, 1997; Debano, 1998).

Variables in the fire regime include the intensity of burning, season in which fire occurs, the fire-free interval (FFI) and the area burned. The combination of these variables means that each fire that occurs is different. These variables themselves are highly dependent on climate, available fuel and ignition source, among other influences. The high diversity of species functional types in fynbos ecosystems means that different species have varying optimum and least preferred fire types. It is this relationship between plant functional type and varying fire regime that contributed to the evolution of the unique and biologically diverse flora (Naveh, 1974; Cowling, 1995; Bond, 1997; Debano, 1998). Endemics are vulnerable to changing fire regimes, and therefore human impact or climate change could lead to extinctions (Bond, 1997; Cowling, 1992; MacDonald and Cowling, 1993).

Most fynbos land management and conservation plans incorporate some form of fire management. In fact, most management plans are fire-based (Cowling, 1995). Fynbos thrives on low frequency fires (>20 year FFI) which produce burns of low intensity. Cowling (1995) proposes that the optimum fire frequency for fynbos is 12-15 years. The ecological basis for this recommendation, and others offered, tends to be based on short-term (<50 years) observations. Considering fynbos has burned periodically over the last 100,000 years (DeBano, 1998) and that significant human disturbance occurred on the Western Cape before fynbos fire ecology was recorded or understood, it is conceivable that current burning regimes might not represent 'natural' conditions (discussed below). The proposition can also be made therefore that modern plant species assemblages may not represent natural conditions. Moreover, modern ecological studies often focus on organisms whose life-span is greater than the period being studied, and so can not represent ecosystems that are highly dynamic and have continually unique disturbance regimes (Whitlock, et al. 2003).

Palaeoecology and Conservation

There is increasing recognition of the importance of palaeoecological and historical information among conservationists and land managers (Birks, 1996; Froyd and Willis, 2008; Gillson and Duffin, 2007; Willis and Birks, 2005; Willis, et al., 2007). This is due, firstly, to the burgeoning need to understand species responses to changing environments, information on which is available through palaeoecological sources (Huntley, 1996). Secondly (and more important to the proposed purpose of this study), there has been a shift in the dominant paradigm in ecology from one that recognised the 'balance of nature', to an understanding of the 'flux of nature' and recognition of ecosystem dynamics (Fielder, et al. 1997). However, the conservation/land management and palaeoecological communities have been slow in unifying. Willis, et al. (2007) attribute this to perceptions of lack of spatial and temporal resolution, and improper, or lack of, application of palaeo-studies to the needs of conservationists. Moreover, palaeoecologists usually chose study sites on the basis of the highest quality available record, and conducting studies directly related to conservation often means sacrificing that preference.

The role of palaeoecology in conservation has been to determine 'natural', or 'baseline' ecological conditions. However this has been highly problematic (Froyd and Willis, 2008). First, this is due to the range of natural variation within a homeostatic ecosystem; there is no one clearly identifiable ecosystem state. Second, it is due to the undefined level of human operation in the landscape which inevitably altered ecosystems of the past away from 'natural' conditions. There have been a number of attempts to combat this issue. First, methods that aim to identify the type and range of variation that has occurred in an ecosystem have been used to identify dynamic 'baseline' conditions (examples given below). Second, 'natural' has widely been considered in the context of 'pre-industrial', and in the case of former colonial territories such as South Africa, 'pre-European settlement' (Christensen and Annels, 1985; Moore et al, 1999; Swetnam et al, 1999; Whitlock, et al. 2003). For further discussion of these issues, see Bradshaw, (1977); Froyd and Willis, (2008); Goldberg, (2007); and Appendix 1.

Palaeoecology in Practice

A traditional method of palaeoecological investigation involves the 'coring' of sediments from lakes or wetlands, and the analysis of its microfossil (and macrofossil) content (see Godwin, 1956). These often provide high resolution records with considerable temporal extension. This however is often not the case on the Western Cape, where the record tends to be poor, with shallow and weakly stratified sediments (Scott and Lee-Thorp, 2004). Although rare, high quality sedimentary records are available in the region. A number of successful studies of this nature have been carried out. Meadows and Baxter (2001) took a core from Klaarfontein Springs in the winter rainfall region of the W. Cape. The study involved a number of cores being taken representing the Late Holocene. Pollen analysis of the core representing the period c.AD1500-1830 showed clear evidence of colonial period environmental alteration. The data from strata lower in the core show fynbos elements well represented, including Proteaceae; Restionaceae; Rosaceae. Further up in the strata there is a marked decrease in fynbos and Poaceae which is representative of the colonial period. There is also a marked decline in the level of diversity in the pollen spectra recorded towards the surface. Similar results were obtained by Meadows, et al. (1996) using the same technique.

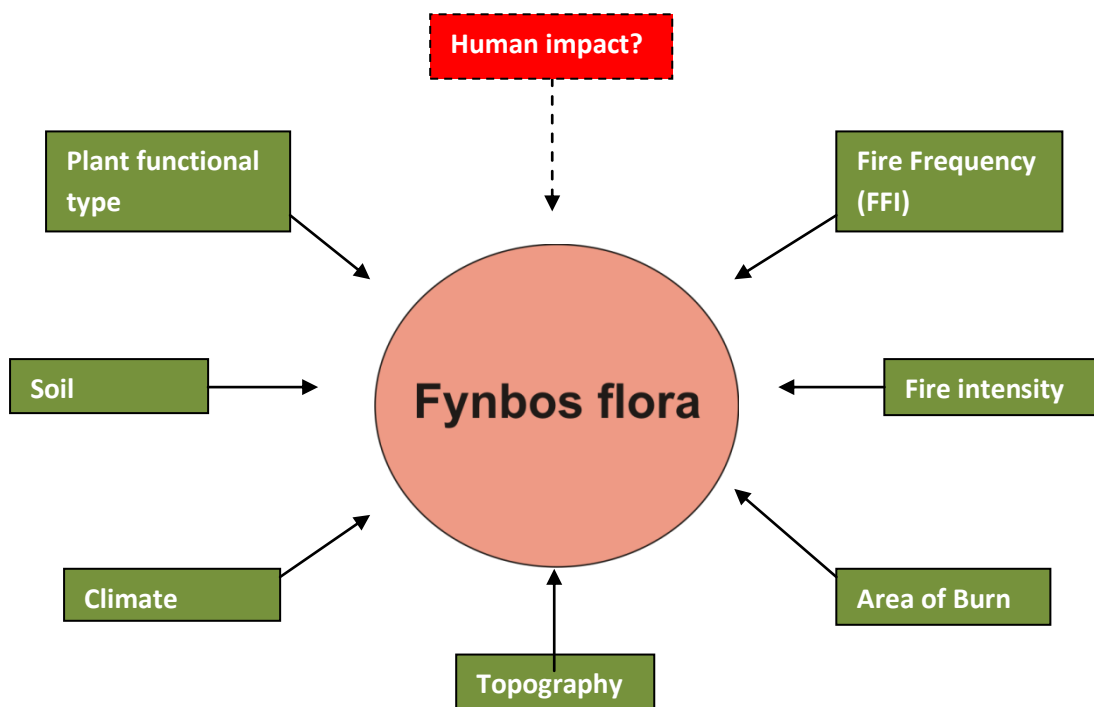
Scholtz (1986) conducted a palaeoenvironmental investigation using a three metre core sampled from the Norga peat, on a coastal platform west of George. The site is located in Knysna afro-montane forest, which lies within the same climate zone as the Langeberg range (Mucina and Rutherford, 2006). Pollen analysis was conducted by Scholtz in order to make inferences relating to ecological and climate history. Three phases were identified; 1) from 4000-2500 B.P. climate was equitable with adequate rainfall in summer. This favoured the proliferation of afro-montane forest, and thus fynbos cover was reduced; 2) from 2500-1800 B.P. climate became less favourable to forest cover, with conditions drying and cooling; 3) from 1800 B.P.-present climate became more mesic, allowing forests to propagate again. Conditions in the present climatic phase, Scholtz (1986) contends, were not as moist as the Holocene climatic optimum preceding 2500 BP.

An excellent example of the potentialities of applying palaeoecology to conservation comes from Kruger National Park, S.A. Gillson and Duffin (2007), used fossil pollen data (from cores) to infer a series of 'endpoints', or maximum and minimum levels of ecosystem variables that, if surpassed, indicate cause for concern. These are known as 'Thresholds for Potential Concern' (TPCs). The TPCs help land-managers identify changes that appear to be outside the limits of natural variation. For example, a TPC for woody taxa was established at 80%, meaning that the modern recorded levels of that vegetation type should not fall below 80% of 'highest ever cover' (Gillson and Duffin, 2007). Modern pollen data were also collected to apply greater spatial representation to the fossil pollen data. Similar applications have been made, most notably in N. America, using a technique that aims to identify the range of natural variability (RNV) of ecosystem variables (Swetnam, et al. 1999). Both the TPC and RNV techniques avoid the establishment of fixed 'baseline' conditions, and incorporate the concept of ecosystem 'flux' into preservation or restoration of ecosystems. They can also be applied to both fire and vegetation history.

Summary

In summary, fynbos flora is unique and highly diverse, and has been degraded and altered by human activity. Its conservation requires the identification of natural (pre-colonial) conditions. The issues of human impact and ecosystem flux mean that it is necessary to incorporate a palaeoecological perspective into management plans for both burning regimes and vegetation. Pragmatic applications of this sort have been uncommon; however recent development and use of the RNV and TPC techniques provide excellent examples of what can be achieved. A summary of the controls of, and impacts on, fynbos is provided in Figure 1.

Figure 1:



Pollen-Vegetation Relationships

Understanding modern pollen deposition has become increasingly valuable in palaeoecological studies (Ayyad, et al, 1992; Willis, et al. 2007). Comparisons between modern pollen-vegetation relationships and fossil pollen data for Pleistocene and Holocene sites are important to reduce inaccuracies and uncertainties in palaeoecological reconstructions associated with accurate spatial and plant population representation (Wright, 1967). These shortcomings have been a significant cause of the scarcity of applications of long-term ecology to conservation (Willis, et al, 2007). However, despite this recognition, our understanding of the relationship between vegetation and pollen deposition remains inadequate, particularly for individual taxa (Pardoe, 2001), and for Mediterranean-type environments (Ayyad, 1992).

There are a number of factors that contribute to the variance in patterns of pollen deposition and the pollen-vegetation deposition relationship. These include, varying pollen production and dispersal methods; transport; preservation; proximity to vegetation community, and the maturity of individual plants (Turner, et al 1989, Bunting, 2007). The complex mix of these variables that produce the pollen 'rain' means that any attempt to model the pollen-vegetation relationship has been highly problematic (Pardoe, 1996). These difficulties are increased in areas that have a high level of diversity and endemism. None the less, numerous studies have successfully identified patterns in pollen deposition that can highlight the under/ over-representation of certain taxa in the pollen rain, and serve as analogues in palaeoenvironmental studies.

Early critical analyses of palaeoenvironmental records in terms of patterns of pollen deposition have involved comparisons between closely sourced sedimentary records. Turner, et al (1989) studied fossil pollen from two monoliths taken 30cm apart from the same site, and used detrended correspondence analysis (DCA) to compare the pollen spectra. The results suggested some difference between the two monoliths. However, rather than recognising the taphonomic processes that caused the variance, Turner, et al (1989) attributed the results to either chance or differential pollen preservation. In using palaeo-records to investigate differences in pollen deposition, they were unable to analyse the pollen-vegetation relationship, and therefore restricted potential insights into the patterns or processes involved in pollen deposition.

The majority of modern pollen deposition studies have taken place in temperate and alpine environments of the northern hemisphere. Pardoe (1996) examined the relationship between pollen, individual taxa and whole plant communities on a glacier foreland in Southern Norway. She used moss polster samples in conjunction with vegetation survey data. Multivariate analysis revealed that the three major vegetation types being studied were well distinguished in the modern pollen samples. However, there was a great deal of variability within the vegetation groups between individual taxa, particularly the *Ericales* group. The study also attained information relating to micro-scale variation in pollen deposition. Previous studies typically used 5-10 sub-samples from moss polsters, but Pardoe (1996) concluded that at least 20 were needed to reduce micro-scale variability to acceptable levels (95% confidence) for the alpine environment.

Pardoe (2001) built on the results of her earlier (1996) study, looking further into the representation of taxa in surface pollen spectra on alpine and sub-alpine glacier forelands in southern Norway. 16m² quadrats were established at a number of sites, and the vegetation within was surveyed. Note was taken of the taxa present, which were identified to the most specific level possible, and their total abundance was recorded. Where available, moss polsters were then collected from within the quadrats. In the analysis both total land pollen (TLP) and non-arboreal pollen sums were recorded to identify noise in the data. The results showed that if a species was present within the quadrat, its representation in the pollen spectra was markedly higher. However, the degree to which this representation was higher varied greatly both between and among taxa. A distinction was also made between entomophilous and anemophilous taxa in the pollen assemblage, with the former showing a strong pollen-vegetation correlation and the latter showing a weak correlation. The results conclusively highlight the complexities of pollen-vegetation relationships, and emphasize their spatial context.

While organizations such as the African Pollen Database have significantly advanced the available information on, and understanding of modern pollen deposition, studies in Mediterranean/ semi-arid environments have been relatively scarce. One example of the use of modern pollen samples in a Mediterranean environment comes from the Nile Delta, Egypt. Ayyad, et al (1992) analysed modern pollen in surface soil samples in conjunction with species lists for a 10m radius around the pollen sample site. The pollen data was subjected to DCA. The groupings that emerged from this were in general closely related to the vegetation groups from which they were derived. Ayyad, et al (1992) then tested their results against fossil

pollen for the area, which highlighted the potential for modern pollen studies as analogues in environmental reconstructions.

The inputs of pollen to a particular point may encompass a range of vegetation types from the landscape. Difficulty arises in the disentanglement of data from the subject community and others in the local area and wider region. In order to do this it is necessary to determine the area from which the pollen spectra obtained was derived. The widely used Prentice-Sugita model (Bunting, et al 2004; Brostrom, et al 2005; Sugita, 1994) assumes plants located further away from a sedimentary basin contribute less to the sites pollen rain. Moreover, beyond a certain distance the persisting vegetation becomes irrelevant (Sugita, 2004). David and Roberts (1990) delimited the pollen recruitment area for a lake in England. They compared historical land use/ vegetation data with sedimentary pollen records, and determined that significant inputs of arboreal and non-arboreal pollen came predominantly from within a 2km radius of the deposition site. This supported other previous work. The effects of fluvial inputs from the lake catchment however, remained unclear.

Relatively little work has been done on fluvial pollen transport. Brown, et al. (2007) carried out a dedicated monitoring programme in S.W. England over a two year period. The results supported the view that the majority of pollen and spores are transported in flood (91% in this case). The main control on waterborne pollen was determined to be catchment vegetation. Brown, et al, (2007) also identify four specific inputs to fluvial pollen; riparian components; overland flow (e.g. colluvial); bank erosion and suspension of stored pollen in flood events. Brown, et al, (2007) also note that fluvial inputs are significant in valley mires and alluvial wetlands. Bunting (2007) identifies five main complications in pollen recruitment within wetland sites (see Table 2).

Table 2: *Complications in pollen recruitment for wetland sites (Bunting, 2007).*

Complication:	Cause:
'Confusion'.	Presence of pollen originating from ambiguous groups that could exist within and beyond the wetland.
'Dilution'.	Local pollen dilutes the signal from the wider landscape.
'Filtration'.	Removal of pollen from the recruitment area transport system before deposition at the sampling point.
'Succession'.	Hydroseral succession causes variation in the effects of confusion, dilution and filtration.
Landscape morphology.	Landscape features such as basin shape or river course cause variation in the dryland landscape represented in the wetland pollen spectra.

In general, recent pollen analysis studies in N.W. Europe have been able to gain good taxonomic resolution due to the wealth of information available on pollen taxonomy. In South Africa however, taxonomic precision is somewhat more difficult due to the comparative scarcity of resources. Most studies in the region therefore have relied on identification of pollen to family (or possibly genus) level (see See Meadows and Baxter, 2001; Meadows, et al. 1996; Scott and Woodborne, 2007). It is often possible to determine the likely parent plant of a pollen group to genera or species level through knowledge of modern biogeographical distributions and

phytosociology. Some caution is necessary in this approach, but for the past c.500-1000 years these relationships are unlikely to have changed dramatically.

Conservation biologists tend to use genera and species level taxonomy in their approaches. The differential approaches to taxonomy used by palaeoecologists and conservationists may be a source of perceived incompatibility between the two scientific communities (Froyd and Willis, 2008; Willis, et al, 2007). However, information obtained relating to relative changes in botanical family representation is highly valuable and, at present, this remains the best practical means of investigating long-term ecology in the region. It is important to emphasise that any system of taxonomy, if used consistently, has the potential to reveal insights into vegetation changes through time that are highly valuable to conservationists. An explanation of the taxonomic classifications used in this investigation is provided in Table 3, along with a summary of each pollen groups inferred likely parent plants and their ecological significance.

Considering pollen analysis is a form of vegetation sampling, it should be able to provide some insight into past changes in biodiversity. However, problems arise due to the complexities of pollen-vegetation relationships. This is exacerbated by issues of taxonomic precision; although as discussed above, this problem is alleviated by use of consistent classifications. Most pollen analysis diversity studies have combated these problems by use of modern analogues. In general, measures of taxonomic richness have been applied, due to the unreliability of equitability measures for pollen data (Brown, 2001; Ludwig and Reynolds, 1988). However, diversity indices have been usefully applied to issue of vegetation community decline/ destruction at the landscape level (Moore, 1973).

Summary

Modern pollen studies offer valuable insights in to the interpretation of palaeoenvironmental records, and have emerged as a useful tool in environmental reconstruction. While most studies have remained at an inductive level, progress has been made resulting in an improved and firm understanding of pollen deposition patterns and processes for particular taxonomic groups. In large part however, our understanding of these issues in Mediterranean-type environments has lagged behind that of others; particularly the fynbos region. This lack of understanding is addressed by this investigation, which intends to facilitate a more critical approach to the analysis of the fossil pollen data.

The process of transport from plant to deposition site is an important determinant in the interpretation of fossil (and modern) pollen spectra. There are a number of modes of transport, and this process is complex. In general, an airborne pollen recruitment area of c.2km is likely, while fluviially transported pollen is should mainly be derived from the catchment vegetation. Once obtained, classification of pollen types can be problematic, particularly in the inadequately documented fynbos region. However, key fynbos families can be identified and valuable information can be obtained. Identification of landscape vegetation decline can be identified through analysis of diversity relative to time.

Table 3: Explanation of taxonomy and ecological significance (Adapted from Goldblatt and Manning, 2000; Mucina and Rutherford, 2006; Robertson, 2005; Scholtz, 1986, as well as field observations).

<u>Specified pollen taxon:</u>	<u>Possible parent plants inferred from modern ecology:</u>	<u>Ecological significance:</u>
Fynbos taxa:		
Restionaceae.	Spp. 224 in the SW CFR. Common and important taxa for the W'cliff area include; <i>Chondropetalum</i> , <i>Elegia</i> , <i>Restio</i> , <i>Thamnocortus</i> .	<ul style="list-style-type: none"> - The Restionaceae are a family of monocotyledonous plants, closely related to Poaceae; - They are a definitive characteristic of fynbos (>5-10% cover).
Erica.	Spp. 375 in the SW CFR. Common and important species for the W'cliff area include; <i>E. albens</i> , <i>E. longifolia</i> , <i>E. hispidula</i> , <i>E. longimontana</i> , <i>E. multumbellifera</i> , <i>E. versicolor</i> .	<ul style="list-style-type: none"> - Small to large shrubs, some herbs; - Fynbos vegetation dominated by Erica, such as at W'cliff, is known as ericaceous fynbos; - Present in a wide variety of habitat, but predominates in cooler and wetter areas.
Proteaceae.	Spp. 181 in the SW CFR. Common and important taxa for the Wildcliff area include; <i>Leucadendron eucalyptifolium</i> , <i>L. tinctum</i> , <i>Mimetites cucullatus</i> , <i>Protea aurea</i> , <i>P. cynaroides</i> , <i>P. nerifolia</i> , <i>P. nitida</i> .	<ul style="list-style-type: none"> - Mainly shrubs to small trees; - Proteoid fynbos predominates at drier sites, however Proteaceae is a common element in many fynbos types.
Rutaceae.	Spp. 87 in the SW CFR. Empleurum was common in the area around the sample site.	<ul style="list-style-type: none"> - Shrubs to small trees; - Wide range of habitats.
Rhamnaceae.	Spp. 61 in SW CFR.	<ul style="list-style-type: none"> - Shrubs and small trees; - Wide range of habitats.
Rosaceae.	Spp. 78 in SW CFR. Pollen is particularly likely to represent <i>Alchemilla capensis</i> .	<ul style="list-style-type: none"> - <i>A. capensis</i> is a herbaceous perennial common on moist montane slopes.
Asparagus.	Spp. 20 in SW CFR. Likely to represent <i>A. rubicandus</i> .	<ul style="list-style-type: none"> - <i>A. rubicandus</i> is common on sandy slopes.
Iridaceae.	Spp. 397 in SW CFR. Pollen for this group is most likely to represent the genus <i>Gladiolus</i> .	<ul style="list-style-type: none"> - Geophytes; - Wide range of habitats.
Rubiaceae:	Spp. 28 in SW CFR.	<ul style="list-style-type: none"> - Herbs and ericoid shrubs; - Wide range of habitats.
Geraneaceae:	Spp. 88 for SW CFR. Pollen	<ul style="list-style-type: none"> - Perennials, succulents and

	for this group likely represents the genus <i>Pelargonum</i> . <i>P. candicans</i> is an important plant in the W'cliff area.	shrubs; - <i>P. candicans</i> favours open landscapes.
Thymalaeaceae.	Spp. 70 in SW CFR.	- Mostly trees and shrubs.
Miscellaneous velt:		
Poaceae.	Many species.	- Ubiquitous.
Cyperaceae.	Spp. 161 in SW CFR.	- Particularly prevalent in ericaceous fynbos; - Also very common in the latter hydroseral stages in wetlands. - No distinction could be made between wetland and dryland Cyperaceae in pollen identification.
Asteraceae.	Spp. 506 in SW CFR. <i>Metalasia</i> is particularly common at W'cliff.	- Wide range of habitats; - Common element of fynbos, renostervelt and other vegetation types; - Particularly prevalent at drier sights; - Poor indicator as no differentiation can be made between the parent communities.
<i>Pteridium</i> .	Represents the species <i>Pteridium aquilinum</i> .	- Fynbos and forest margins.
Arboreal taxa:		
Podocarpaceae.	Likely to represent; <i>Afrocarpus falcatus</i> , <i>Podocarpus elongatus</i> , <i>P. latifolius</i> .	- Often found on mountain slopes near streams.
Cupressaceae.	Likely to represent <i>Widdringtonia nodiflora</i> .	- Rocky sandstone and clay slopes.
<i>Clusia</i> .	Spp. 16 in SW CFR.	- Shrubs and small trees common in a variety of habitats on montane forest margins.
Exotic taxa:		
<i>Pinus</i> .	<i>Pinus pinnaster</i> .	- Invasive; - Introduced to the region in the mid-nineteenth century.
<i>Acacia</i>	<i>Acacia mearnsii</i> .	- Highly invasive; - Introduced to the region in the mid-nineteenth century.
<i>Eucalyptus</i>	Could be confused with <i>Myrica</i> (native).	- Invasive weed Introduced in the mid-nineteenth century.

Aims and Objectives

This research aims to establish proxy records for ecosystem state that can be applied to ecosystem conservation and/ or restoration. This will be achieved by testing the following hypothesis:

H₁: Fynbos vegetation has declined, not proliferated, over time.

H₂: Fynbos vegetation has proliferated, not declined, over time.

H₃: Fynbos vegetation has neither declined nor proliferated over time.

H₄: Fynbos vegetation has both declined and proliferated, periodically, over time.

In order to test these hypotheses, the following objectives have been identified:

- Examine key modern pollen-vegetation relationships;
- Critically analyse fossil pollen data using results of the modern pollen vegetation relationship study;
- Establish vegetation history through analysis of fossil pollen;
- Establish fire history through analysis of micro-charcoal deposits;
- Establish changes in diversity of fossil pollen through time;
- Determine 'RNV' and 'TPC.'

Study Area

The study was carried out at Wildcliff, a mountain fynbos nature reserve in the Langeberg range, approximately 17 km N.E. of the town of Heidelberg, Western Cape (Figure 2) (a history of settlement in the region is provided in Appendix 1). Altitude in the reserve, centred around 33°57'S, 21°2E, ranges between 290-1130m (Rollinson, 2008) and accommodates a complex mix of gentle to very steep slopes. The underlying geology of the mountain ridges and slopes is made up of erosion resistant Ordovician quartzite sandstone of the Table Mountain Group, while the valley floors are relatively soft shale of the Bokkevelt group. Fynbos type corresponds to this geological pattern through the medium of the associated soils (Mucina and Rutherford, 2006).

The climate of the area corresponds to the climatic zone of the Western Cape that receives rainfall distributed throughout the year. Mean annual precipitation for the area is 320-1,440 mm (mean 675 mm), and peaks slightly in winter but lowers slightly in summer (December- February). Mean daily maximum and minimum temperatures range from 26.6°C to 4.0°C for January and July, respectively. There is a frost incidence of 3-20 days per year (Mucina and Rutherford, 2006). Climate also plays an important role in fynbos type distribution, forming part of the complex mix of distributional controls on CFR vegetation types.

Ericaceous sandstone fynbos predominates at Wildcliff as sandy colluvium derived from quartzite sandstone ridges has spread across shale valley floors allowing sandstone fynbos communities to persist there, as well as on the slopes. In the wider local area the general characteristic of sandstone fynbos is for ericaceous and

restioid fynbos to predominate at higher altitudes, with moderately tall to tall proteoid cover on lower slopes. Shale fynbos is also noted to be situated in the local area, and is characterised by tall, dense proteoid and ericaceous composition in wetter areas, and graminoid fynbos in drier areas (Mucina and Rutherford, 2006).

There are also a number of non-fynbos vegetation types present both in and around Wildcliff. First, another constituent vegetation type of the fynbos biome, renostervelt, can be identified. This is a fire prone (and adapted), Asteraceae dominated shrubland, with an understory of Poaceae. Restionaceae cover is less than in fynbos, and it occurs in drier areas (but wetter than that of succulent karoo shrublands) (Mucina and Rutherford, 2006).

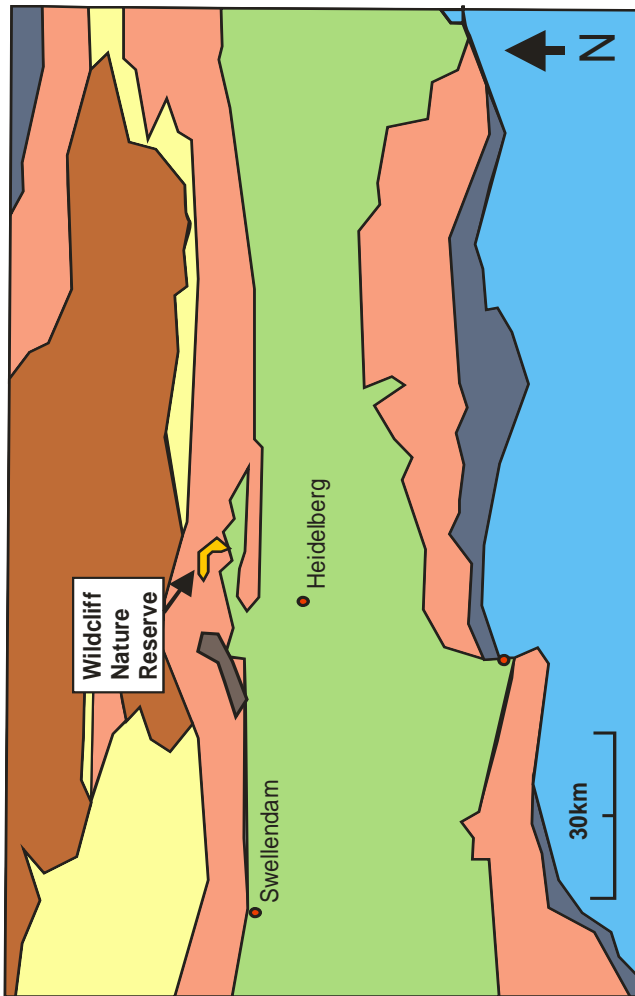
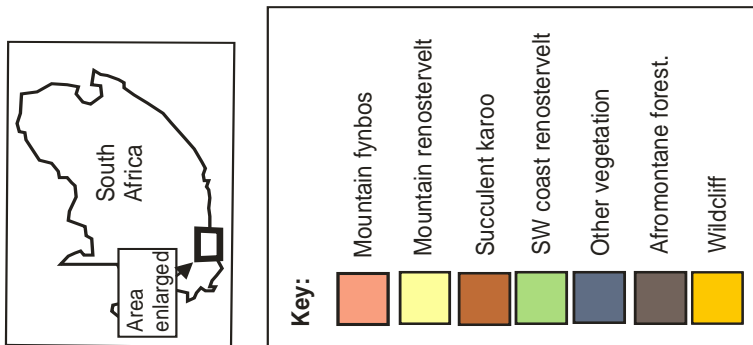


Figure 2: Regional vegetation types



Knysna-Amatole afromontane forest persists in the cooler and wetter kloof areas. Invasive *Pinus pinnaster* and *Acacia mearnsii* are dominant in the reserve and wider area. These arboreal types were introduced into the region by European colonial settlers from the mid-nineteenth century onwards (Cowling, 1992; Scholtz, 1986). Furthermore, the reserve is also situated on former farmland, and a small area remains Poaceae pasture. The general vegetation types observed at Wildcliff are shown in Figures 3 and 4.

A core was extracted at the location S33°57.865' E021°02.123 from a permanent wetland situated within Poaceae pasture in the southern part of the reserve. Juncaceae-type rushes were common at the site. The quadrats for the modern pollen samples were located to the north of this, in a valley above and perpendicular to the south part of the reserve. However the eastern end of this valley was fairly open, meaning that the core site and modern pollen sites were not divided communities. Quadrats 1 and 2 were located on rocky, north facing sandstone slopes with gradients of 22° and 14°, respectively. Quadrat 3 was located at the bottom of the valley adjacent to a stream and had a 0° gradient (Figure 4). The sites correspond to the coordinates S33°56.347, E21°01.427; S33°56.347, E21°01.304; S33°56.273, E21°01.224; respectively. Figures 3-4 and Plates 1-4 show the sample sites and a map of the reserve.

Figure 3: Key for Wildcliff maps (Following page).

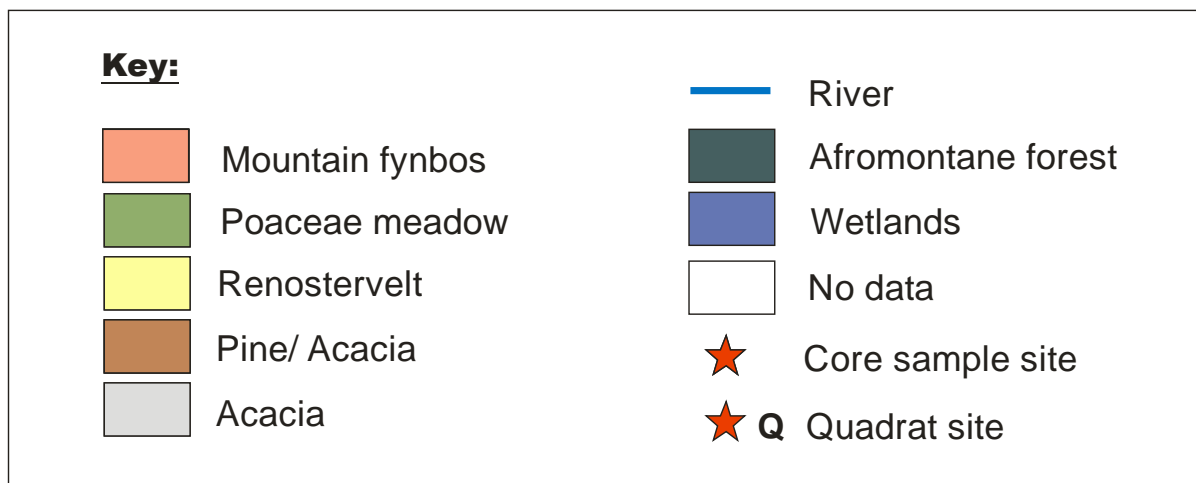


Figure 4: Maps of Wildcliff North (above) and Wildcliff South (below) showing vegetation types and sample sites. The two areas are linked where the arrow indicates.

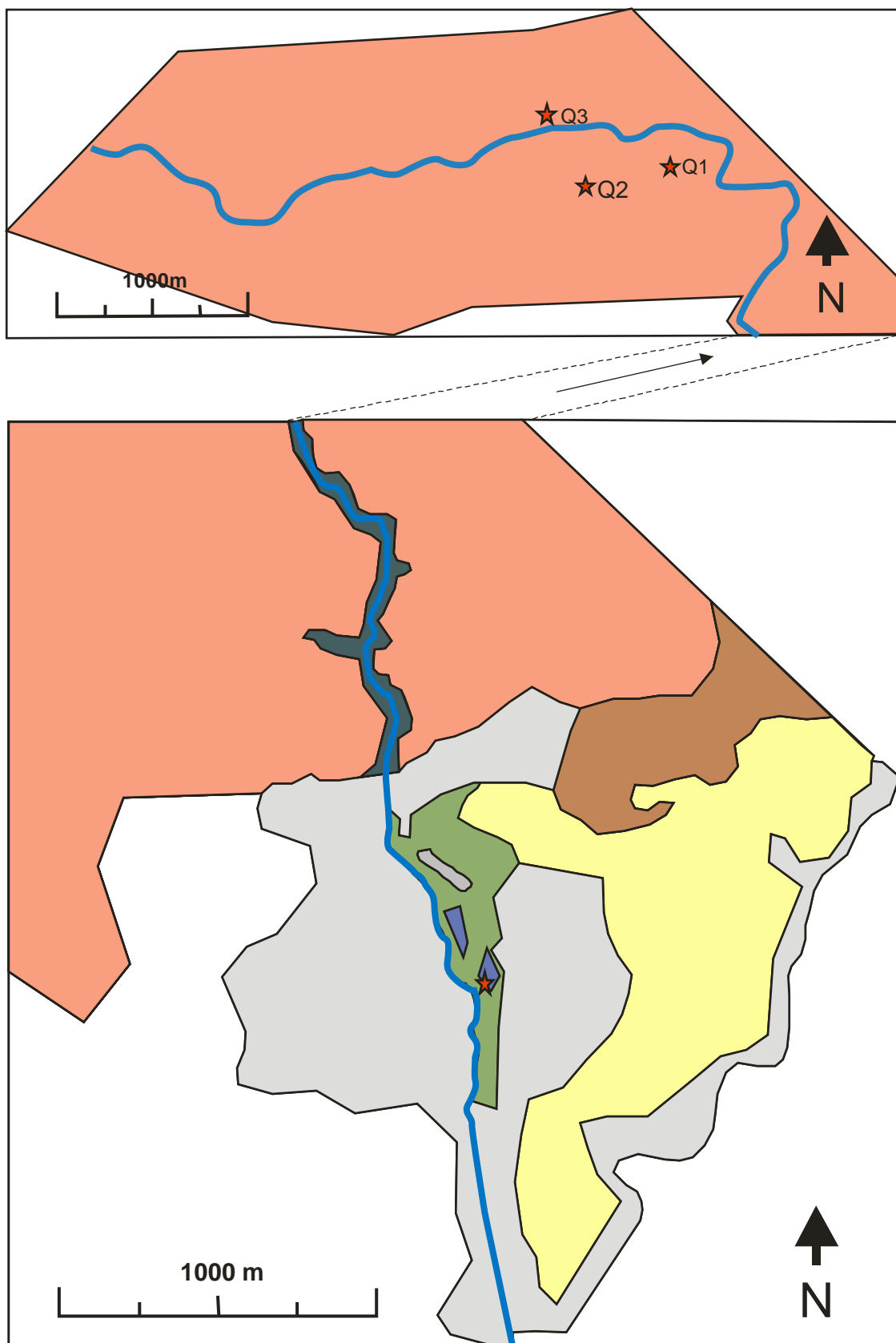


Plate 1: Stellite image of Wildcliff (Google Earth, 2009).

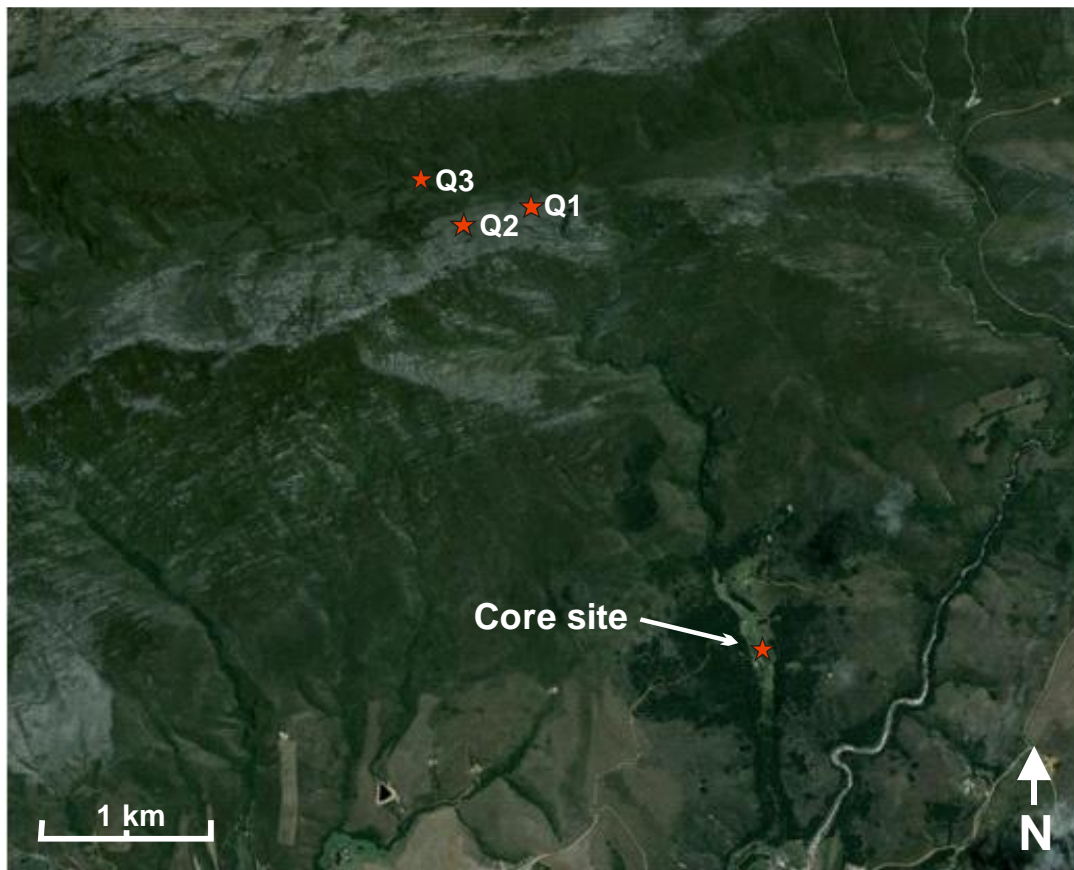


Plate 2: Overview of Wildcliff South and surrounding landscape.

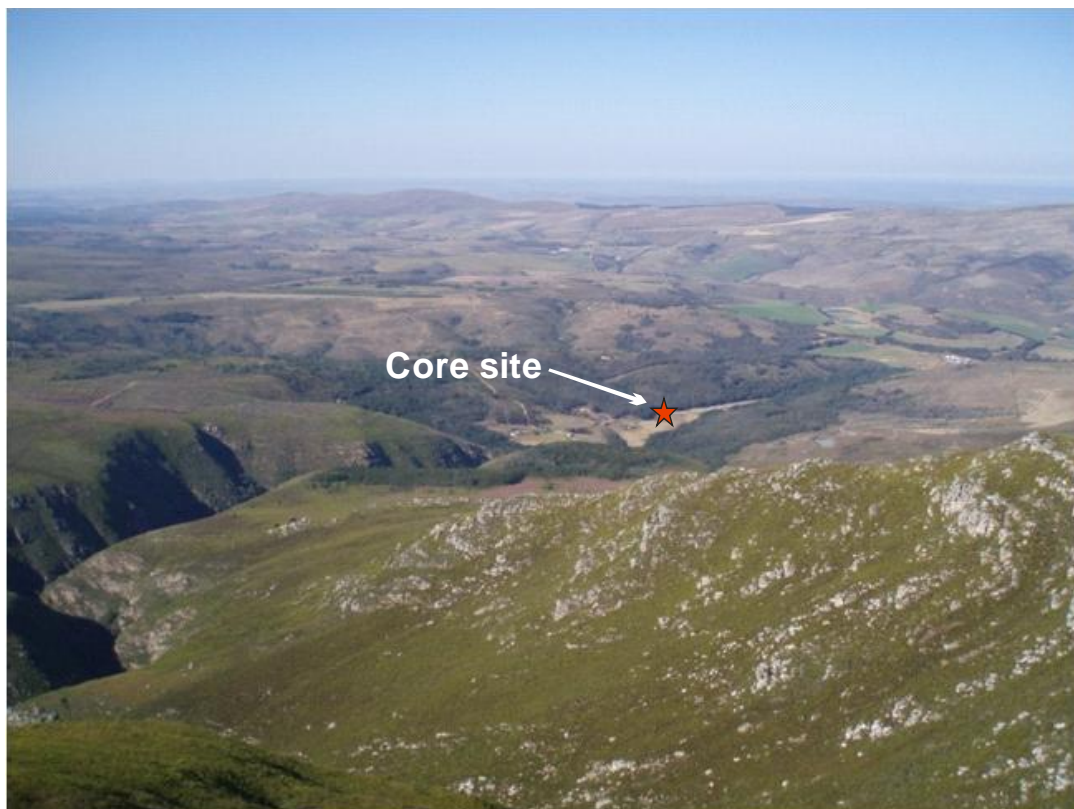
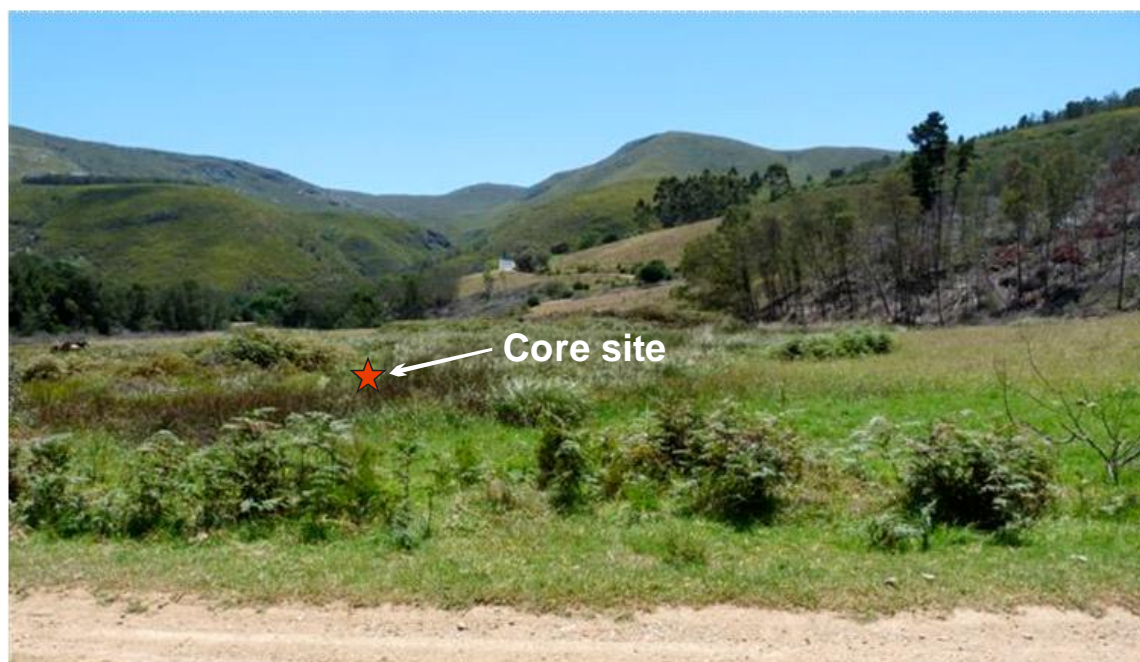


Plate 3: Wildcliff North valley (looking west), where quadrats were located.



Plate 4: Meadow and wetland (Wildcliff South), where core was extracted.



Methods

A 1 m sediment core was extracted from a wetland (Figures 3-4; Plates 1, 2 and 4) using a Hiller borer. The core was transferred immediately to plastic tubing and wrapped in cellophane to prevent contamination by modern pollen rain. The core was then sub-sampled under controlled conditions at 4cm intervals using a knife. At least 1cm³ of sample was taken at each interval. The lithology was described according to the Troels- Smith (1955) system.

It was deemed that the nature of this study did not necessitate costly radiometric dating techniques, as it is not focused directly on chronology. However, it is certainly beneficial to gain some perspective of time scales, and this is done by identifying the emergence of European colonial ecological impact in the stratigraphy through its fossil pollen spectra via introduced taxa.

For the modern pollen-vegetation relationships investigation, three 5m X 5m quadrats (Figure 3-4; Plates 1, 3) were selected that were judged by eye to represent a range of vegetation cover in the landscape. Clearly in a community as diverse as mountain fynbos this is not wholly representative of the entire population; however it will include a range of the important and common taxa. All taxa were identified to the most specific level possible (usually genus; except for the Restionaceae). While it may only be possible to identify pollen to family level, possessing more detailed taxonomy may be useful in making inferences based on the known phytosociology of the area. Percent cover for all taxa was then estimated. One surface soil sample of approximately 1cm³ was collected from each quadrat at random. This was often selected on the basis of availability of bare surface soil, which was associated with animal/human pathways. Thus, humans or animals could have acted as agents of pollen transport.

Both surface and core samples were processed in the laboratory at a later date. A sample of 1cm³ was combined with one Lycopodium tablet of concentration 1858 and dissolved in 10% HCl. The solutions were centrifuged and decanted, and the pollen pellet was washed in 10% KOH and placed in a water bath for 20 minutes. The samples were then sieved through 180µ mesh and washed with water until no longer dark in colour. HF treatment was used to dissolve the SiO₂ content. Next, acetolysis was applied to dissolve the remaining organics. Finally, aqueous safranin was added to the samples, which were then dehydrated and mounted on slides in solution with silicon oil. A more detailed account of these methods can be found in Moore and Webb (1978).

Analysis of the samples was carried out using a Zeiss high powered microscope at X400 resolution. Test counts showed that a count of 150 for pollen was sufficient to provide a representative sample of the pollen spectra. Attempts were made to identify every pollen grain to family level, however only approximately 65-70% have been identifiable in this way, and the remainder have been placed in other artificial groupings. Identification was facilitated by use of lists of likely taxa compiled by field survey and literature sources, and use of APD (2009) pollen catalogues as well as identification texts (notably, Scott, 1982).

The core samples were also analysed for the total abundance of micro-charcoal particles. The original objective was to focus on macro, meso and micro-charcoal

content, however processing for the former two types was not possible. Analysis of micro-charcoal content can nonetheless facilitate insights into fire history.

Pollen-Vegetation Relationships: Key Characteristics

Results

Before analysing the fossil pollen data, it is necessary to establish the key trends in over/ under-representation of plant groups using the modern analogues. The Czeknowski coefficient (see Kent and Coker, 1992) showed a partial correlation between vegetation and pollen for quadrats 1, 2 and 3 (see Table 4). The mean value for the three quadrats is 0.54, where 0 represents complete dissimilarity, and 1 represents total similarity. Thus, the quadrat data for vegetation and pollen can be said to show a mean similarity of 54%. Clear distinctions can be made between groups of plants that are under or over-represented. In general, fynbos is underrepresented, while miscellaneous taxa are overrepresented. However, there is significant variation in the degree of under/ over-representation of individual taxa between the different quadrats. Figures 5 to 10 show the relative proportions of vegetation recorded at each quadrat, and the corresponding pollen identified. Only taxa that represented $\geq 5\%$ of the total vegetation/pollen recorded are shown. The key findings are presented in Table 5.

Simpson's Diversity Index (SDI) was applied to the vegetation and pollen data (Table 4) in order to test the representation of plant diversity in pollen spectra. SDI takes into account not only the taxonomic richness of a given sample, but the relative quantities of those taxa. This index produces a value between 0 and 1, where 1 is perfect diversity, and 0 is a homogenous community (Ludwig and Reynolds, 1988). It is usually applied at the species level, but can theoretically be applied to any taxonomic system. Pollen diversity appears to broadly reflect vegetation diversity at the scale tested (i.e. 5X5 m quadrats). The mean SDI score for all quadrats was 0.79 and 0.77 for vegetation and pollen, respectively. However, there was variation in the accuracy of diversity representation between the quadrats.

Discussion

As in most palynology studies, there is likely to be a bias towards those taxa that are well dispersed by wind, and produce large amounts of pollen. However, numerous modern pollen studies have shown that a combination of key taxa is adequate to represent a vegetation community (see Ayyad, et al. 1992; Meadows and Sugden, 1991; Pardoe, 1996; 2001; Scott and Cooremans, 1992). Caution is needed in the interpretation of results due to variation in the degree of under/ over-representation of individual taxa, and this is exacerbated by the small sample size (Pardoe, 1996). This means that clearly quantifiable assertions cannot be made. However, as the general trends of plant representation in the pollen rain are consistent, a broad understanding of how the different plant groups are represented has been attained. The underrepresentation of fynbos taxa suggests that these plants are underestimated in the fossil pollen spectra. In contrast, the overrepresentation of miscellaneous taxa suggests this group is overestimated in the fossil pollen spectra, and could distort the proportional representation of fynbos plants. This agrees with

wider knowledge of the miscellaneous group, which recognises its abundance and ubiquity in many environments (Bunting, 2007; Godwin, 1956; Meadows and Baxter, 2001; Scholtz, 1986). Overall however, the majority of the pollen rain was of fynbos origin, and only a small proportion belonged to the miscellaneous group. It should be noted that the exclusion of taxa below 5% of the total pollen sum may create a bias towards plants with high pollen production or anemophilous dispersal methods.

The Prentice-Sugita model assumes vegetation closer to a sample site will be more dominant in the pollen rain than that which is further away from the sample site (Brostrom, et al. 2005; Bunting, et al, 2004; Sugita, 1994). Thus, it could be conceived that the pollen diversity statistics are predominantly a product of the quadrat vegetation. However, while this may be true for the data obtained on taxonomic representation, it may not be so for diversity. This is because those taxa constituting less than 5% of the total pollen were excluded from the taxonomic representation results, filtering more distal parent plants. As the diversity results take into account all pollen grains, they are likely to represent parent plants in the landscape that are more distal and exerting a weak pollen signal. Thus, the level of diversity expressed in the pollen rain is a function of wider inputs at the landscape level.

Table 4: *Statistical values for quadrat sites:*

Site No.	Czeknowski coefficient value:	SDI score (Vegetation):	SDI score (Pollen):
1	0.59	0.72	0.65
2	0.54	0.85	0.79
3	0.48	0.78	0.86
Mean=	0.54	0.79	0.77

Figure 5: Chart showing % vegetation cover for quadrat 1.

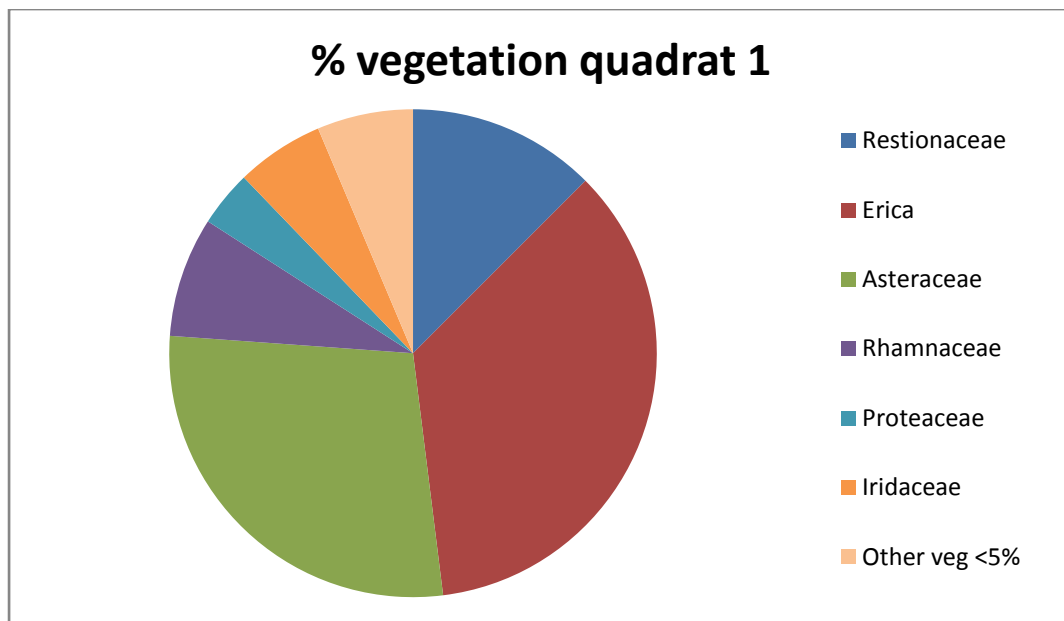


Figure 6: Chart showing % pollen for quadrat 1.

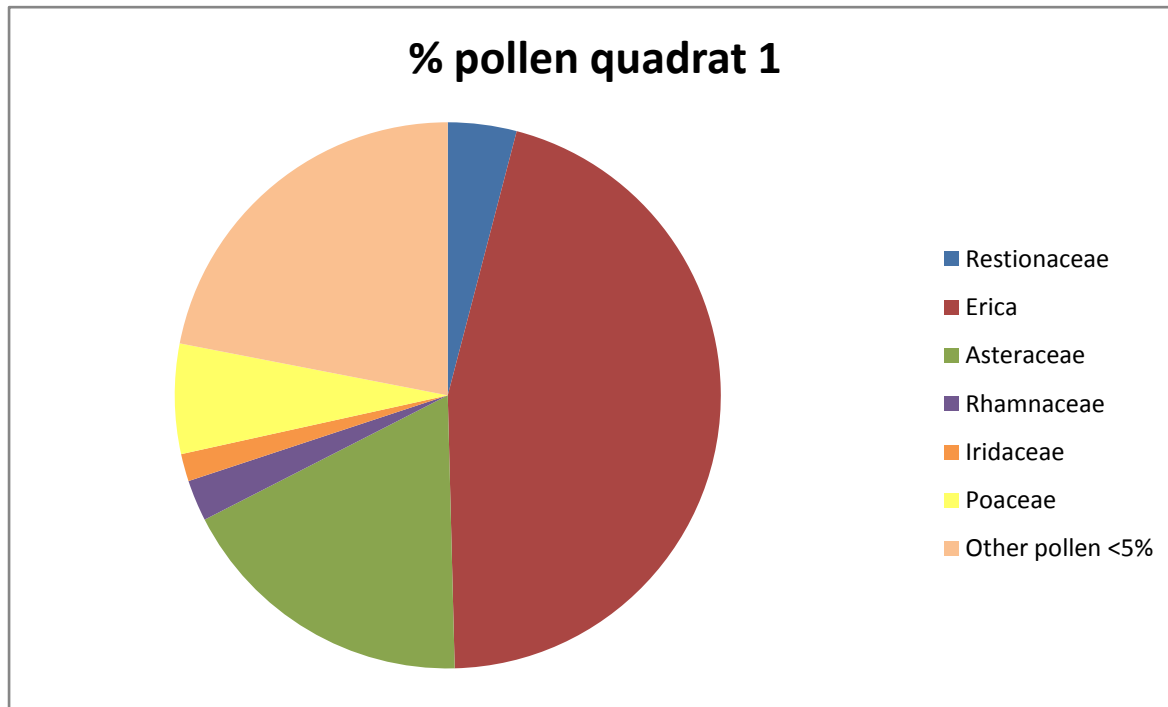


Figure 7: Chart showing % vegetation for quadrat 2.

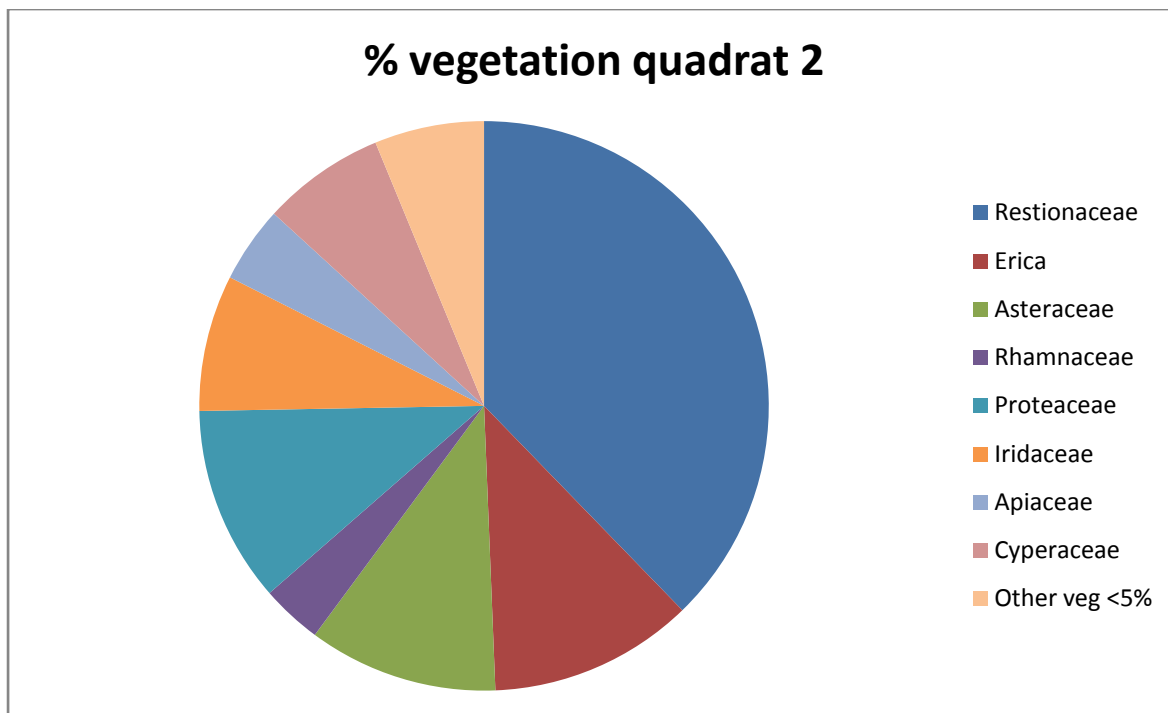


Figure 8: Chart showing % pollen for quadrat 2.

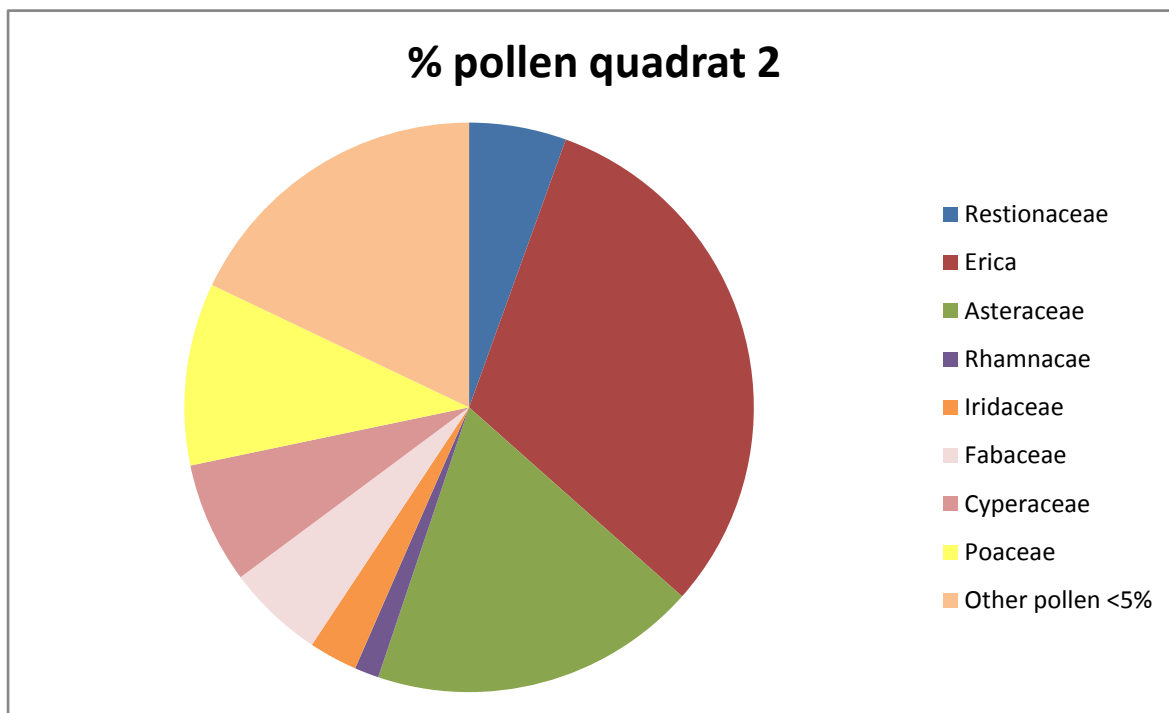


Figure 9: Chart showing % vegetation for quadrat 3.

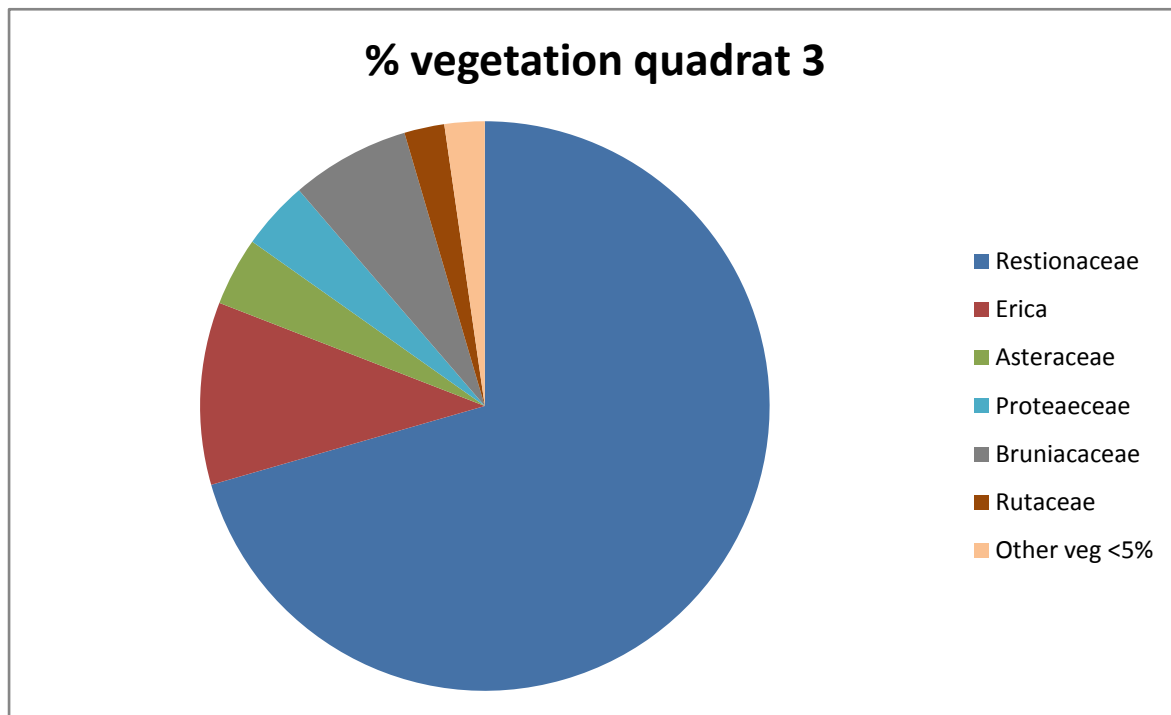


Figure 10: Chart showing % pollen for quadrat 3.

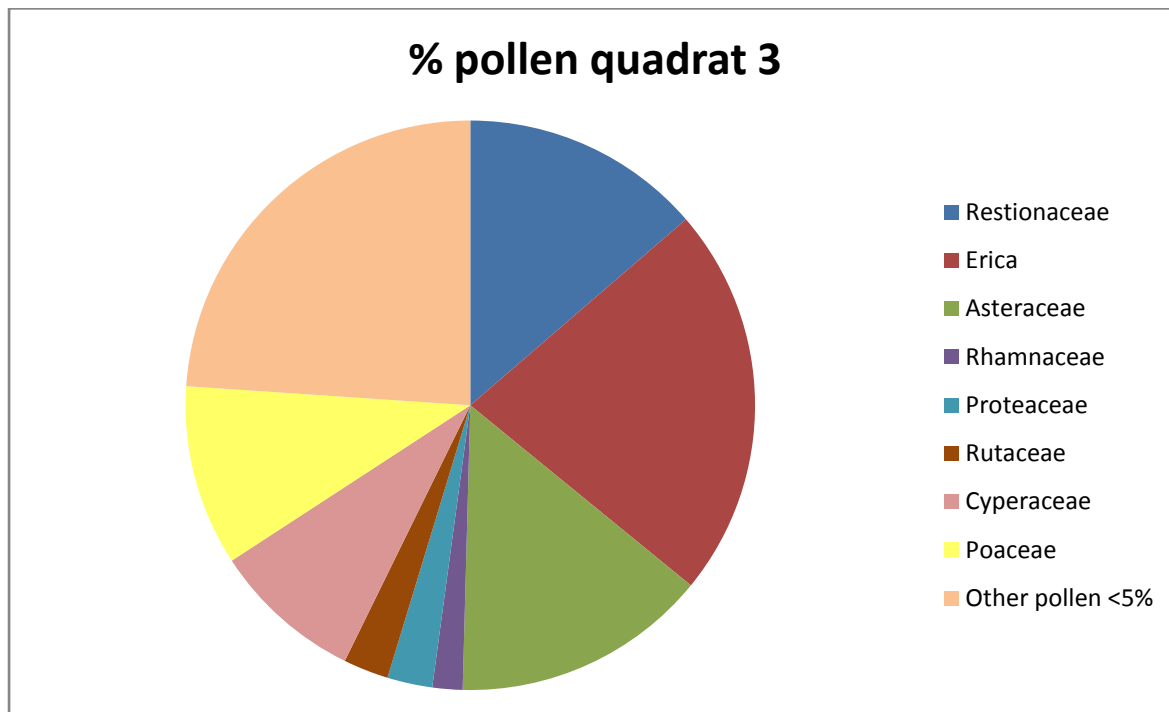


Table 5: Key modern pollen-vegetation relationships.

Taxon:	Modern pollen-vegetation relationship:
Restionaceae	This group of plants can be dramatically underrepresented in the pollen rain (by a factor of ~3- 6). The abundance of Restionaceae in the local landscape might thus be underestimated in the fossil pollen spectra.
<i>Erica</i>	In general, <i>Erica</i> seems to be overrepresented in the pollen rain. Quadrats 2 and 3 (Figures 7, 8 and 9, 10, respectively) show the proportion of pollen to vegetation to be over two times greater. However the inverse of this relationship is noted for Quadrat 1 (Figures 5, 6). This suggests the fossil pollen spectra may overestimate the proportion of <i>Erica</i> in the local landscape.
Asteraceae	In general, Asteraceae can be overrepresented in the pollen rain (by \leq a factor of 3). However this varies, and for quadrat 1 (Figures 5, 6), pollen is over representative of vegetation. This suggests local landscape Asteraceae may be overestimated by the fossil pollen spectra, but some caution is needed in this assertion due to variance between the sites.
Rhamnaceae	Rhamnaceae can be under represented in the pollen rain (by a factor of 2-4). Thus, the fossil pollen spectra may underestimate its persistence in the local landscape.
Proteaceae	Proteaceae showed a very weak vegetation-pollen correspondence where Proteaceae vegetation was present quadrats 1 and 2 (Figures 5, 6 and 7, 8, respectively), no pollen signal was recorded. For quadrat 3 (Figures 13; 14), Proteaceae vegetation was underrepresented in the pollen rain. This suggests the fossil pollen spectra underestimate the persistence of

	Proteaceae in the local landscape.
Iridaceae	Iridaceae can be significantly underrepresented in the pollen rain (by \leq a factor of 3), suggesting the fossil pollen data underestimate its presence in the local landscape.
Rutaceae	Rutaceae vegetation was only present for quadrat three (Figures 9, 10), and showed an accurately representative vegetation- pollen relationship. However, the amount of data obtained for this taxon may be too small to make reliable generalisations.
Cyperaceae	Cyperaceae pollen is recorded for quadrats 2 and 3, but a parent plant is not recorded (Figures 7, 8 and 9, 10, respectively). This suggests the amount of Cyperaceae in the local landscape is significantly overrepresented in the fossil pollen spectra.
Poaceae	Poaceae can also be over represented in the pollen rain. No parent Poaceae is recorded for quadrat 2, but it composed 10% of the pollen rain (Figures 7, 8). This suggests its presence in the local landscape is over represented in the fossil pollen data.

Fossil Pollen Results

Core Lithology (Table 6)

The core lithology is characterised in Table 6. Full listings using the Troels-Smith (1955) system are provided in Appendix 2.

Table 6: Core lithology description (using Troels-Smith, 1955). Sediments are described from the bottom- up for clarity. (Also see Figure 11 for lithology diagram).

Unit:	Characteristics:
Unit A (96-80 cm)	Contained equal proportions of Argilla (clay) and Grana saburralia (0.6- 2.0mm sand). The sediments were dark (Nigror 4), almost completely homogenous, totally inelastic and fairly wet (Siccitas 3). Any organics were hardly discernable.
Unit B (79-70 cm)	Composed of three parts Grana saburralia to one part Grana glareosa minora (2-6mm gravel). The larger clast sizes in this unit are indicative of a higher energy depositional environment, such as fluvial (flood plain) sedimentation. The sediments were light in colour, and are likely to be derived from the quartzite sandstone slopes surrounding the site. Stratification, elasticity and organic content were again very low, and the sediments were fairly wet.
Unit C (68-41 cm)	Contained equal proportions of Argilla and Grana saburralia. The sediments were fairly dark (Nigror 3), and stratification, elasticity and humicity were again very low for this fairly wet sediment.
Unit D (40-17 cm)	A significant change occurs at unit D this unit. The sediments are composed entirely of Argilla. Larger material is absent, suggesting that fluvial deposition reduced in significance, or another local factor influenced the sedimentation regime (such as land use change). The sediments in this unit were totally homogenous, inelastic and fairly wet. No humus was detectable.
Unit E (16-0cm)	Unit E was similar to unit D. It is composed of Argilla, although this was lighter in colour, presumably because its organics were less well decomposed. The unit was unstratified and inelastic. It was slightly drier than lower layers, and some humus was detectable.

In summary, the five units A-E (described in Table 6) can be broadly categorised into two groups:

- 1) The lower strata (96-41 cm) that contained larger material (sand and gravel), possibly associated with fluvial transport;
- 2) The upper strata (40-0 cm) that contained only fine material (clay) associated with a different sedimentation regime.

Chronology

Exotic pollen indicating the onset of the colonial period is detected at a depth of 36cm in the core pollen spectra. These taxa- *Acacia mearnsii*, *Pinus pinnaster* and *Eucalyptus*- were introduced to the region in the mid-nineteenth century (Scholtz, 1986). Considering these trees spread rapidly, they may have been established in the landscape the mid - late nineteenth century; this seems the likely date at 36cm. The age-depth relationship is however unlikely to be linear through to the base of the core, and age-depth estimates are speculative (Bunting, 2007). Compaction caused by the weight of the column of sediment above is likely to yield a greater age: depth ratio further down the core (Godwin, 1956). Carbon 14 dates from other wetland cores in the region have revealed temporal extension of up to 2570±45 BP for c.90cm in depth (Scholtz, 1986); though it would be presumptuous to assume a base date similar to this for the Wildcliff core. The sedimentary regime at the sample site has likely undergone numerous changes caused by factors such as hydroseral succession (Bunting, 2007), and changes relating to fluvial inputs. Conceivably, the base of the core could date to between 500 and 1000 years BP; this therefore extends into the pre-colonial period.

Pollen Recruitment

The majority of airborne pollen inputs are likely to come from within a c.2km radius of the core sample site (David and Roberts, 1990). This includes significant mountain fynbos cover; afro-montane forest; renostervelt; *Pinus*; *Acacia*; Poaceae meadow and wetland communities. It also includes significant unspecified vegetation cover outside the reserve boundaries, which is largely composed of farmland (Poaceae pasture and degraded CFR vegetation types) (Figures 3-4; Plates 1-2). However, the lithology suggests fluvial sediment inputs to the wetland, and thus pollen recruitment is likely to be heavily influenced by the river catchment vegetation. This is largely mountain fynbos, with some afro-montane forest. Therefore, it can be said that the fossil pollen spectra have likely received significant inputs from mountain fynbos. It is important to note that fluvial inputs may be more significant in the lower strata, where larger clasts are identified, than in the upper strata.

8.4 Pollen Diagram Analysis (Figure 11)

A zonation was undertaken by eye, and this was confirmed as accurate by DCA ordination. Three zones (1a, 1b and 2) can be identified, and are described in Table 7.

High proportions of miscellaneous taxa can often distort the pollen signal from the subject community. However, a pollen diagram was constructed without these taxa included, and the same trends could still be observed as were identified in Figure 11 (see Appendix 3).

Figure 11: Pollen diagram.

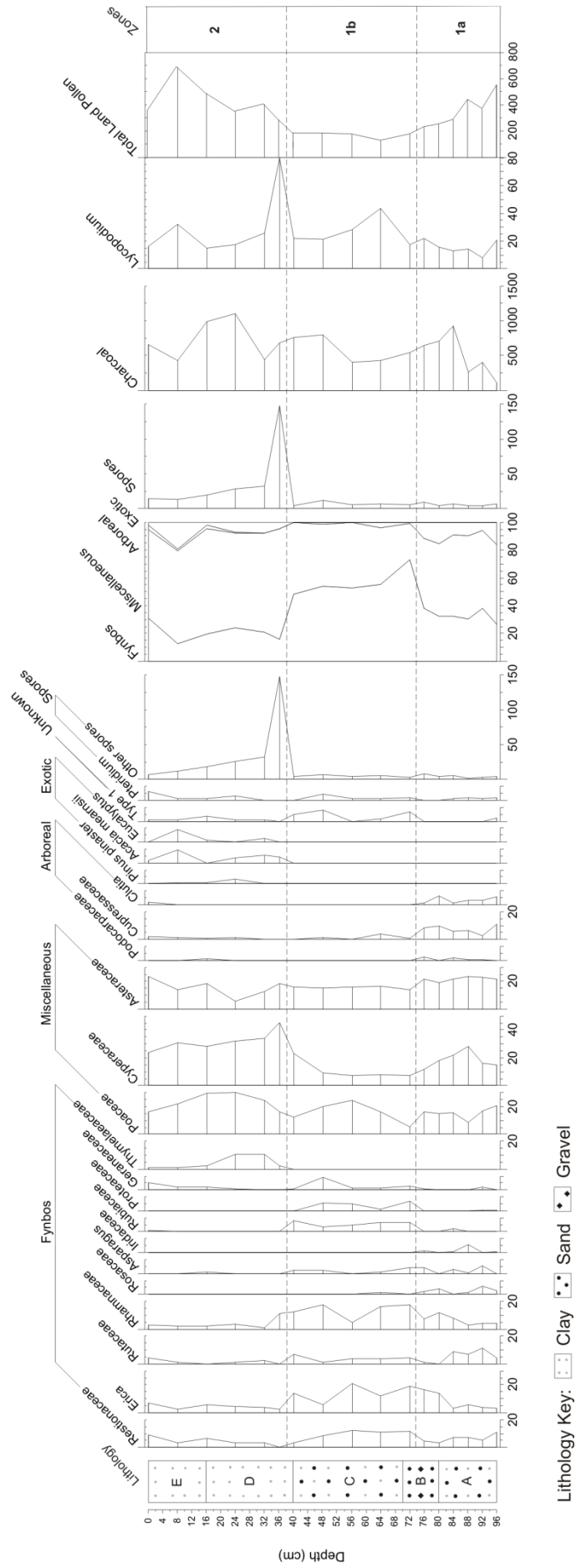


Table 7: Description of pollen zones identified on Figure 15 (and confirmed by DCA).

Pollen Zone:	Description:
<p>Zone 1a (96-74 cm):</p>	<ul style="list-style-type: none"> - Fynbos taxa, including Restionaceae, <i>Erica</i>, Rutaceae, Rhamnaceae, Rosaceae, Asparagus and Rosaceae are well represented, constituting ~25-40% of Total Land Pollen (TLP). <i>Erica</i> and Rubiaceae proliferate in the latter part of this zone, while Rhamnaceae, Rutaceae and Rosaceae begin to decline. - Poaceae, Cyperaceae and Asteraceae are abundant in zone 1a (~50-60% of TLP). Cyperaceae peaks and declines, while Asteraceae and Poaceae are fairly stable. - Arboreal taxa are present, particularly Cupressaceae, contributing ~5-15% of TLP. - Charcoal content fluctuates, and no trend is discernible.
<p>Zone 1b (74-38 cm):</p>	<ul style="list-style-type: none"> - Fynbos taxa proliferate in zone 1b (50-70% of TLP). Restionaceae is more abundant than in zone 1a (by almost 5%) and fairly stable, declining in the latter part of the zone. <i>Erica</i>, Rutaceae, Rhamnaceae, Rubiaceae, Proteaceae and Geraneaeceae are all abundant, but fluctuate. - Miscellaneous taxa are abundant again (30-50% of TLP), but slightly less so than in zone 1a (giving way to increased Fynbos pollen). These taxa appear fairly stable; however Cyperaceae begins to increase towards the zone boundary. - Arboreal representation (0-5% of TLP) is significantly reduced, and only Cupressaceae is recorded. - 'Type 1' increases in this zone, appearing to be linked to the fynbos proliferation, although in absence of a taxonomic identification no interpretation can be made. - Charcoal was again very abundant, but showed less dramatic variation than in zone 1a.
<p>Zone 2 (38-0cm):</p>	<ul style="list-style-type: none"> - Fynbos taxa decline sharply at the zone 1a-2 boundary, and are less well represented (~10-30% of TLP). The previously abundant elements Restionaceae, <i>Erica</i>, Rutaceae and Rhamnaceae are poorly represented. Other fynbos elements are almost undetected, apart for Thymelaeaceae and Geraneaeceae which show an anomalous minor proliferation. Towards the end of zone 2 there is a slight resurgence in some of the fynbos taxa, however the trend is too short to determine whether or not it is a longer-term dynamical change. - Miscellaneous taxa are dominant in zone 2 (~65-75% of TLP). Cyperaceae increases rapidly at the zone 1b-2 boundary, followed by a sharp decrease and gradual decline

	<p>towards the surface.</p> <ul style="list-style-type: none">- Arboreal taxa are rare (~0-2% of TLP).- Exotic arboreal taxa appear in the pollen spectra in zone 2, and are well represented (~2-20% of TPS) (suggesting significant colonization of the landscape).- A dramatic increase in the spore count also occurs at the beginning of this zone, and decreases shortly thereafter. A notable majority of these are fungal spores, although a more specific identification was not possible. This is indicative of a land use change.- Charcoal is significantly more abundant in zone 2 than the previous zones. A marked increase occurs, however this does not correspond to the timing of the decline in fynbos and proliferation of miscellaneous group taxa.
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DCA

DCA is a multivariate ordination method. The results are presented on charts, where the distance between each symbol (representing a sample/ taxon) represents the degree of variance between them (Kent and Coker, 1992; McCune and Grace, 2002). For the models run (Figures 12-19), axis 1 explains ~33% of the variation, and axis 2 explains ~15% (eigen values 0.34 and 0.15, respectively). Axis 3 represented ~12% of the variance. Plots of axis 1 versus axis 3 are presented in Appendix 4, and broadly support the trends identified by axis 1 versus 2. Axis 4 and 5 were excluded, as they represented very low proportions of the total variance.

Figure 12 shows the DCA samples plot for the fossil pollen spectra. Three main groupings emerged from this analysis, which corresponded almost exactly to groups 1a, 1b and 2 identified on the pollen diagram (Figure 11):

- Group 1a includes samples from depths of 96-76 cm;
- Group 1b includes samples from 72-40 cm;
- Group 2 contains samples from 36-8 cm.

The sample at 0cm, however, showed greatest similarity to the samples of group 1a, suggesting a return to conditions analogous with those recorded towards the base of the core. While groups 1a and 1b appear to be very dissimilar owing to their dislocation in Figure 12, it should be emphasised that the majority of this variation occurs along axis two. Along the most significant axis (1) there is much less variation. Group 2 however is considerably dislocated from groups 1a and 1b along axis one, representing a significant change in composition within the samples.

Figure 13 shows the DCA taxa plot; an ordination of all taxa in all samples. Five groups are highlighted, and are described in Table 8.

Figure 12: DCA samples plot.

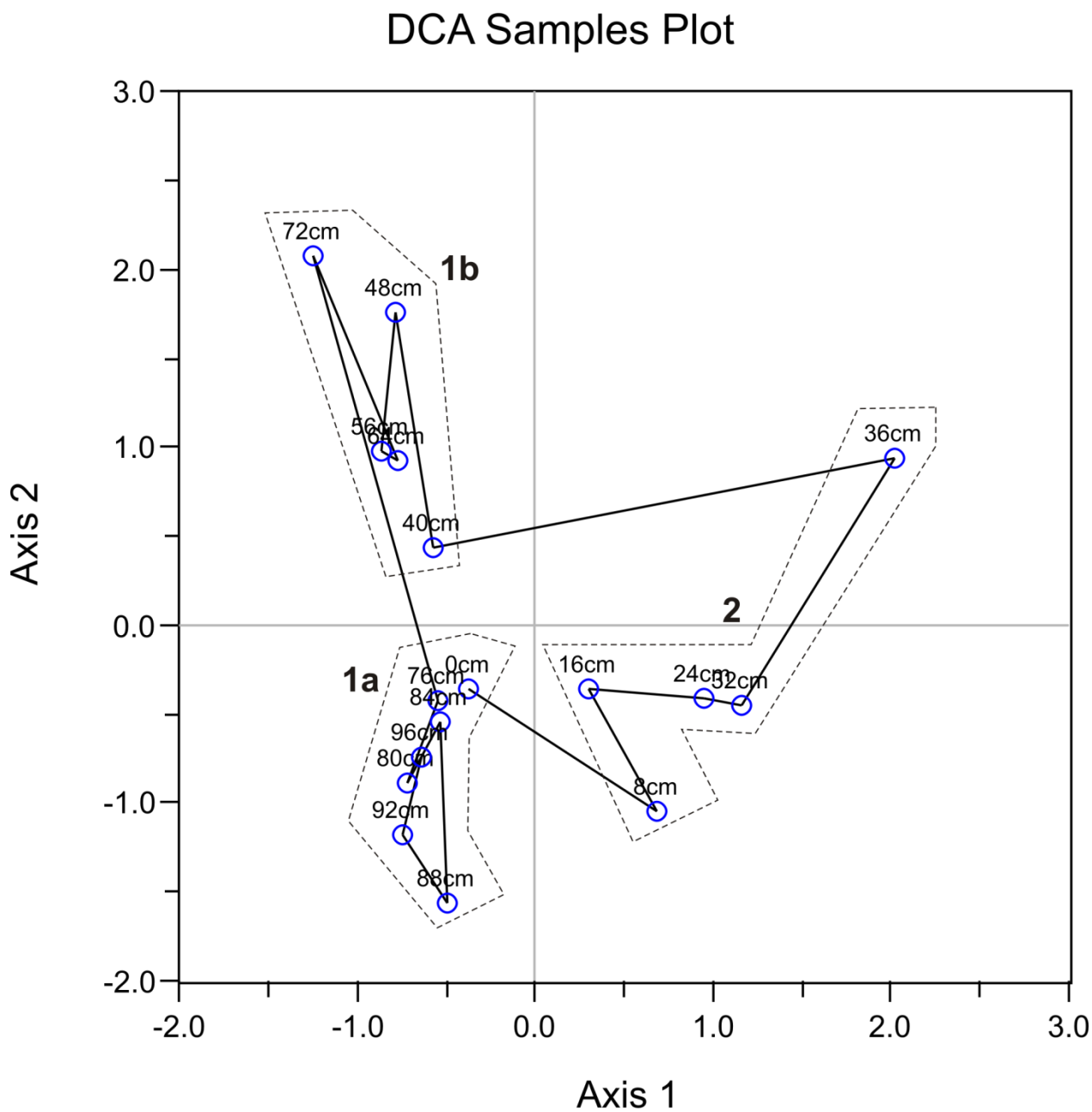


Figure 13: DCA Taxa plot.

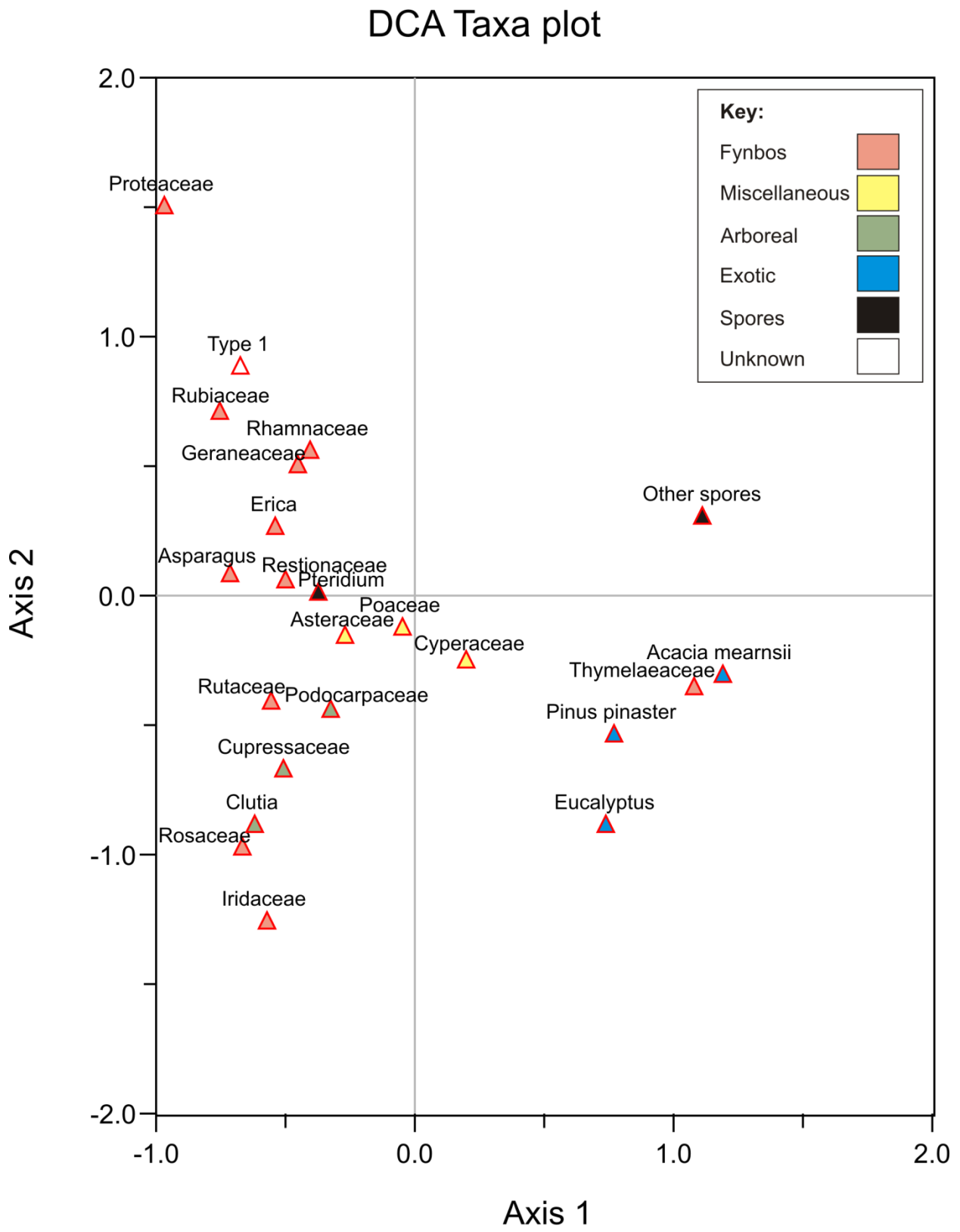


Table 8: Description of groups highlighted by the DCA taxa plot (Figure 13)

Group :	Description:
<i>Fynbos taxa:</i>	Most taxa are dispersed widely along axis 2, but within a fairly narrow band along axis 1. This confirms that most fynbos taxa have proliferated and declined as a unit. Type 1 shows similarity to this group. Thymelaeaceae is anomalous, and its increase in zone 2 may be linked to the introduction of exotic arboreal taxa.
<i>Miscellaneous taxa:</i>	Asteraceae, Poaceae and Cyperaceae appear to be closely associated. However, Cyperaceae is the most removed along axis 1, suggesting that it may have fluctuated under independent controls, such as hydroseral succession.
<i>Arboreal taxa:</i>	Podocarpaceae, Cupressaceae and <i>Clusia</i> appear closely related. This group, however, does not show significant dissimilarity from the fynbos taxa, which disagrees with the trend observable in the pollen diagram (Figure 15). This may be a result of 'dilution' (Bunting, 2007) of the data by higher percentages of other groups (e.g. miscellaneous taxa).
<i>Exotic taxa:</i>	The invasives <i>P. pinaster</i> , <i>A. mearnsii</i> and <i>Eucalyptus</i> are significantly removed from native flora, except for Thymelaeaceae which appears to be associated. This highlights their disequilibrium with natural ecology.
<i>Spores:</i>	While <i>Pteridium</i> shows association with the other native groups (indicating its equilibrium with natural ecology), 'other spores' are highly anomalous from all other taxa. This indicates an anomalous event.

The Figures 14 to 19 show the abundances of selected key taxa within each of the ordinated fossil pollen samples. Abundance of a taxon within each sample is represented by the size of the respective circle. The sample points are plotted in terms of their overall content, and thus show the three groups identified in Figure 12. A number of characteristics can be observed:

- The distribution of abundance of Restionaceae and *Erica* are similar. Groups 1a and 1b contain the highest proportions of these taxa, while their abundance dramatically declines in group 2 samples (particularly for *Erica*). Restionaceae seems to make a recovery in the uppermost core sample, but this is not notable for *Erica* (Figures 14, 15).
- Rhamnaceae is present in low abundance in group 1a. The taxon then proliferates in group 1b. This is followed by a sharp decline in group 2 samples, and no recovery is made at the top of the core (Figure 16).

- Rutaceae is most abundant in group 1a. This is followed by a decline in group 1b, and low abundance of the taxon is maintained through to a depth of 0cm, where a slight proliferation is notable (Figure 17).
- Cyperaceae shows a different trend than that observed for the four fynbos taxa. It is fairly abundant in group 1a samples. This is followed by a decline in group 1b, then proliferation in group 2 (notably at 36cm). This follows an almost opposite sequence to the fynbos taxa, which proliferated in group 1b, then declined in group 2 (Figure 18).
- Asteraceae is most abundant in group 1a, and then declines in group 1b. Abundance remains low in group 2 samples, but increases again at 0cm (Figure 19).

Figure 14: DCA plot for Restionaceae

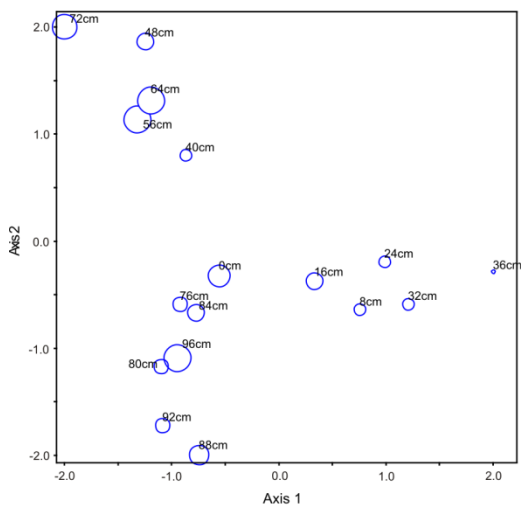


Figure 15: DCA plot for Erica

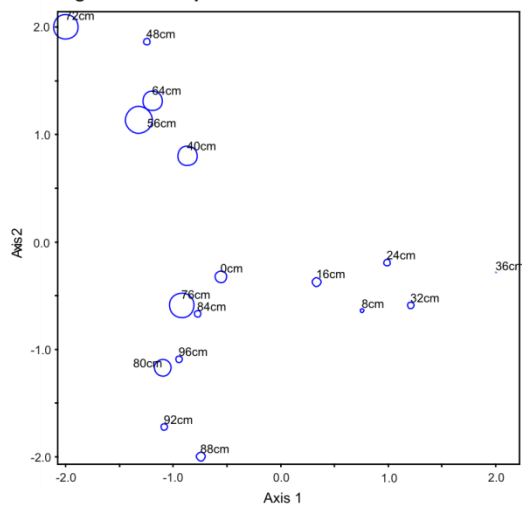


Figure 16: DCA plot for Rhamnaceae

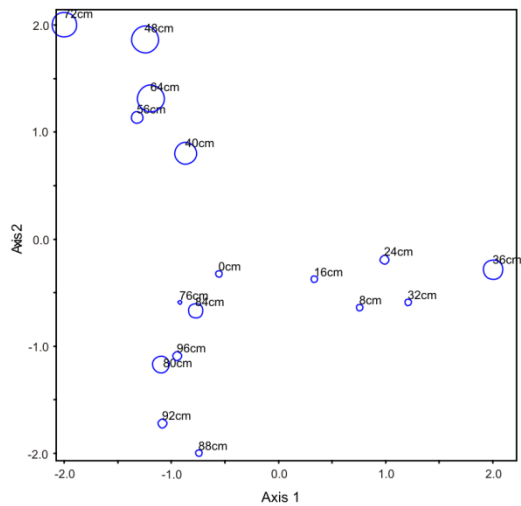


Figure 17: DCA plot for Rutaceae

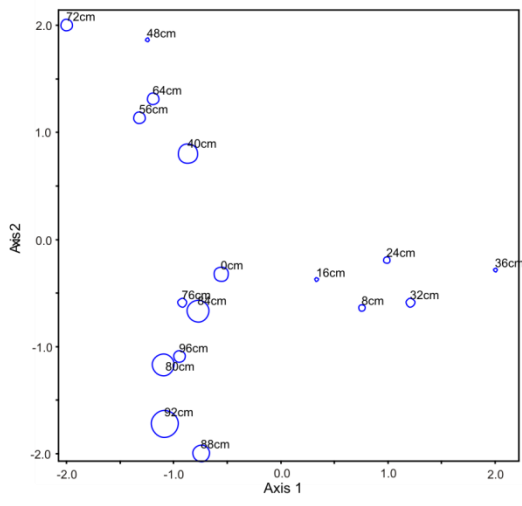


Figure 18: DCA plot for Cyperaceae.

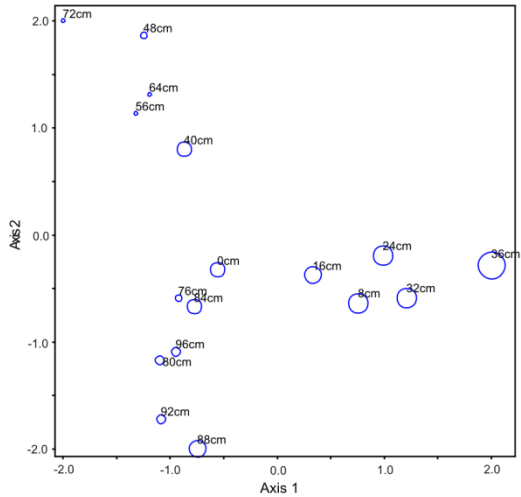
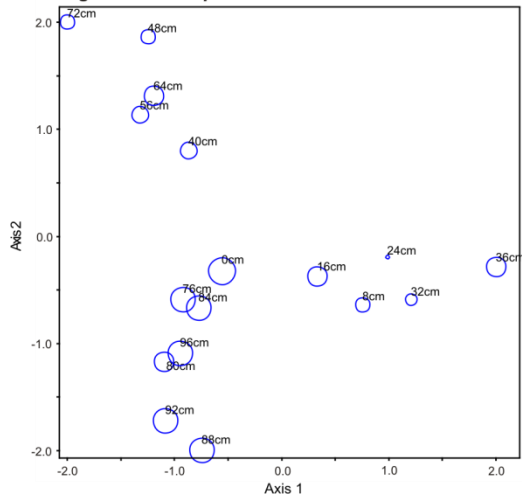


Figure 19: DCA plot for Asteraceae.



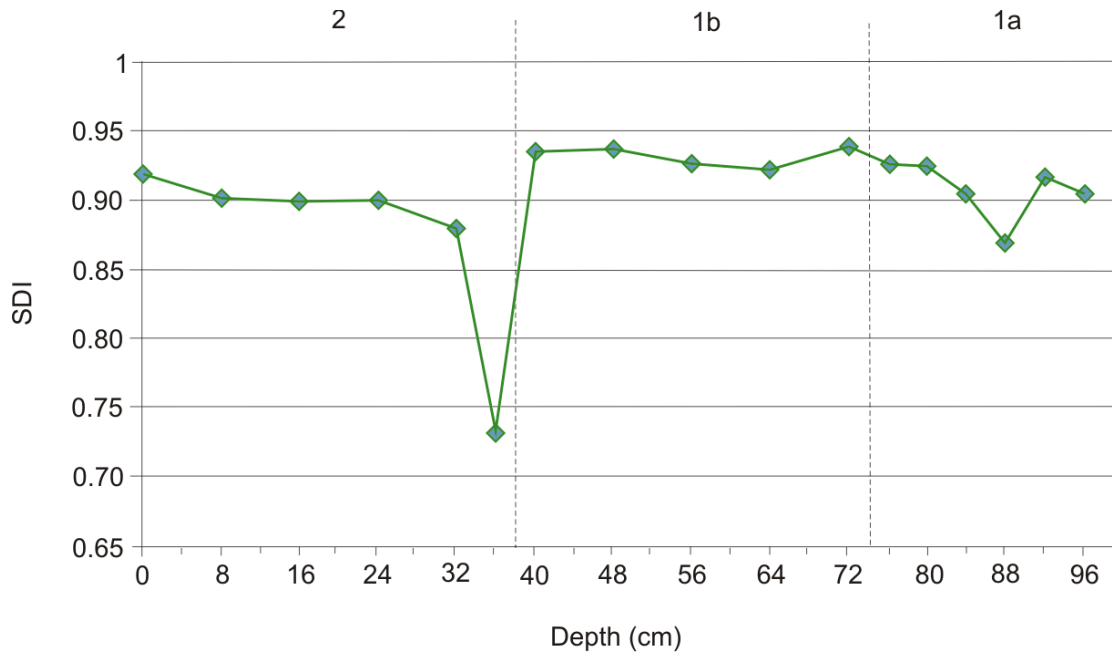
Pollen Diversity

Figure 24 shows the results of the pollen diversity analysis (using SDI) through the core. Similarly to the results of the pollen diagram and DCA, zones 1a, 1b and 2 can be identified. These zones are described in Table 9.

Table 9: Description of diversity zones through the core.

Zone:	Description:
Zone 1a: (96-74 cm)	Some fluctuation in diversity occurs (note fall at 88cm), indicating either instability or dynamic equilibrium; however diversity is generally high.
Zone 1b: (74-38 cm)	Diversity is generally higher through this stage, and no major declines are recorded. There appears to be greater stability, however it should be noted that the increased sample interval could have caused falls in diversity, such as at 88cm, to go undetected.
Zone 2: (38-0 cm)	A dramatic fall in diversity occurs at the beginning of this zone. A drop in SDI of ~0.2 occurs (approximately a 20% fall in diversity). Some recovery is made (to levels recorded in zone 1a), although the level of diversity recorded in zone 1b is not matched. The trend in the latter part of the zone appears stable, and a slight increase is recorded in the uppermost sample.

Figure 20: Simpson's diversity index scores through the core.



Discussion

Palaeoecological reconstruction

In pollen zone 1a, fynbos taxa are fairly well represented, constituting ~25-40% of total land pollen (TLP) (~85-135% of present cover). Miscellaneous elements dominate however. Considering the general under/ over-representation of the respective taxa, it is conceivable that fynbos was well established in the pollen recruitment area. Afromontane arboreal elements show the greatest proliferation recorded through the strata in zone 1a, while fynbos elements are less well represented compared to later observed trends (Figure 11). This supports Scholtz's (1986) research, which recorded the proliferation of afromontane forest while fynbos declined, and vice-versa. Scholtz attributes this pattern to Late Holocene climate oscillation, with mesic conditions favouring fynbos decline, and afromontane proliferation. Conditions observed in zone 1a could be evidence of the Medieval Warm Period (MWP), an interstadial oscillation that occurred around AD 1000- 1400, in which climate was warm and mesic (Mann, 2007). Current climate can also be considered mesic (Scholtz, 1986), and therefore zone 1a could represent suitable reference conditions for ecosystem state (Froyd and Willis, 2007; Millar and Wolfenden, 1999). Fynbos cover may have been between 85 and 135% of present cover in the pollen recruitment area. Knysna-Amatole afromontane forest might have propagated across the presently moist, relatively sheltered meadow in Wildcliff South, and surrounding areas where invasive *P. pinaster* and *A. mearnsii* now persist (Figures 3-8). This would be characteristic of the biome's contemporary biogeography and ecology (Cowling, 1995; Mucina and Rutherford, 2006). However, it should be noted that arboreal pollen could potentially have a more distal source, outside of Wildcliff.

Pollen zone 1b saw a marked change in the proportional vegetation sums, which DCA confirmed to be statistically significant (Figure 11, 12). Almost all fynbos taxa increase (Figures 11, 14-16). This fynbos proliferation (50-70% of TLP; 135-225% of present cover) coincides with a decline in all identified afromontane elements (0-5% of TLP) (Figure 11). Cyperaceae also declines in zone 1b (Figures 15; 22), which is assumed to be a result of wetland recession (Scott and Woodbourne, 2007), although a terrestrial 'confusion' signal (Bunting, 2007) cannot be ruled out. More xeric conditions may be linked to a cool, dry stadial period - known as the Little Ice Age (LIA) - that occurred between ~AD1400-1800, and is well evidenced regionally and globally (although chronology varies) (Mann, 2007; Jones, et al. 1999; Repinski, 1999; Wanner, et al. 2008). Asteraceae, a common element in fynbos and renostervelt (both of which are presently distributed within the pollen recruitment area (Figures 2-4)) does not appear to be linked to fynbos proliferation (Figures 11, 14-19), as it fluctuates fairly independently. However, the taxon also declines in zone 1b, suggesting it is not a signal from the characteristically more xeric renostervelt. Determining interplay between fynbos and renostervelt will necessitate a deeper understanding of the respective communities' pollen rain from modern analogues, and more detailed taxonomy, in order to disentangle the pollen signals. This evidence indicates that more arid conditions than present may have caused fynbos to proliferate, while afromontane forest contracts, and vice-versa for mesic climatic conditions.

However, without a firm chronology through the core, it would be over-presumptuous to assume the observed trends are contemporaneous with the aforementioned

climatic events. Moreover, other palaeoecological scenarios could account for the record. The 'Intermediate Disturbance Hypothesis' (Huston, 1979) proposes that disturbance of moderate frequency (and intensity) will enhance diversity (D'Odorico, et al. 2008; Roxburgh, et al. 2004). This is based in the principal that heterogeneous disturbance patterns create mosaics of differential habitat (Warren, et al. 2007). In the early 1700s, European farmers began to advance north and east from Cape Colony. Preceding this, European settlement had largely been confined to the Cape Colony outpost (Cowling, 1995; Meredith, 2007) (see Appendix 1). Increased grazing, for example, in the Wildcliff region could constitute 'intermediate disturbance', and thus have caused the increased diversity in zone 1b (Naveh, 1974). Growing human population in the area and associated demand for timber resources could also account for the decrease in arboreal taxa. Assuming a linear age-depth relationship, this chronology could fit the trends observed.

The intermediate disturbance hypothesis as an explanation for the observed sequence, however, has a number of weaknesses. Firstly, features commonly identifiable in other palaeoecological records following the increased anthropogenic operation in the landscape, such as increased burning (Burnley, 1987; Roberts, 1998) and spore influxes (van Geel, 2006), are not evidenced (although deforestation could be indicated). The use of higher technology and intensity agriculture practiced by European farmers (Crosby, 2004) would likely have strongly manifested impacts. Thus, any European agricultural practice in the region at this time must not have impacted across the whole landscape. Secondly, other pollen records in the Cape have noted falls in biodiversity following the arrival of Europeans in the landscape (e.g. Meadows and Baxter, 2001). Thirdly, the proposed hypothesis only attempts to explain the observed increase in diversity (and, in turn, arboreal decline), rather than accounting for the increase in fynbos taxa over other vegetation (e.g. Cyperaceae). Moreover, increased landscape diversity may be a feature of the proliferation of fynbos associated with the LIA. Thus, the assertion of climate as the zone 1b fynbos proliferation driver seems more plausible.

At the onset of zone 2, a large and abrupt change is recorded, which is highlighted by DCA (Figures 11-12, 14-19). All fynbos taxa decline considerably (~15-30% of TLP; ~50-100% of present cover), most showing their lowest recorded proportional representation (Figures 11; 14-19). The core lithology suggests that differential sedimentation regimes for the lower and upper zones, respectively, could have altered the dominant taphonomic process, thus causing the observed 'fynbos decline' feature in the data. Lager clasts in the basal units (A-C) suggest fluvial sedimentation occurred for a period corresponding to pollen zones 1a and 1b (Table 6; Appendix 2; Figure 12). The fluvial pollen load is largely determined by catchment vegetation (Brown, et al. 2007), and in the contemporary environment this is predominantly ericaceous mountain fynbos (and some afro-montane forest). Significant contributions to the pollen spectra in units A-C are also likely to have come from airborne inputs, sourced from a ~2km radius surrounding the site (David and Roberts, 1990). However, the upper units (D and E) (corresponding to zone 2) contained no larger clasts. This indicates that fluvial pollen transport became less significant in pollen zone 2, and airborne transport became more dominant. Because the fluvial pollen recruitment area has, at present, more dominant fynbos cover than the airborne recruitment area (Figures 2-4; Plates 1-4), confusion arises in determining if the fynbos decline at the zone 1b-2 boundary is a 'true' feature of ecological change, or a result of changes in taphonomy.

In addition to the lithological changes at the zone 1b-2 boundary, a number of other contemporaneous features occur. Pollen diversity is impacted heavily, and falls to a level unprecedented in the record obtained (Figure 20). This coincides with three strong indicators of European colonial settlement. Firstly, a rapid influx in the spore content at 36 cm suggests increased intensity of human land use in the area. The majority of these were fungal spores, which are likely to have been released from topsoil stores as a result of disturbance from increased intensity agricultural practice (Coates, 1998; Crosby, 2004; Smith, 1999; van Geel, 2006). Second, the proposed land use change could have resulted in a differential sedimentary regime, causing the change in lithology at 40 cm (Table 6; Appendix 2; Figure 11). Therefore, it is likely that the change in sediment composition in the upper strata is associated with human activity, rather than reduced fluvial inputs. Thirdly, the emergence of exotic pollen (*P. pinnaster*, *A. mearnsii*, and *Eucalyptus*) in the record dates these changes to c. mid - late nineteenth century; around the time historical records date the founding of settlements in the area (Appendix 1). Although European populations had spread to the eastern extent of the Western Cape region by c.1750 (Cowling, 1995), it is conceivable that their impact on the landscape was sporadic (particularly in mountainous areas), and the Wildcliff catchment may have avoided large scale impact up until the mid - late nineteenth century.

Conversely, the 36cm spore influx could have resulted from a number of natural occurrences. For example, a localised event such as a landslide may have released spores held in topsoil. However, the general scarcity of pollen in the 36cm sample (indicated by a high *Lycopodium* counts; see Figure 11) suggests drought conditions have increased microbial activity, causing poor pollen preservation (Godwin, 1981; Holden, 2005), resulting in a higher proportional representation of spores. This could have been induced by a climax in the LIG stadial period. However, this event has been dated to between c.1750 and 1790 for the region (Scott and Lee-Thorp, 2004; Jones, et al. 1999), and thus would not correlate with the date obtained by exotic pollen indicators. Although it seems a natural event could have caused the dramatic changes at the zone 1b-2 boundary, the combination of evidence of exotic plant introduction, sedimentation change, spore influx, biodiversity decline and historical records points to European anthropogenic change as the driver (see Meadows and Baxter, 2001; Meadows, et al. 1996; Scholtz, 1986). Thus, the fynbos decline is likely to be a 'true' palaeoecological feature, rather than a result of changed taphonomic processes.

At the top of zone 2 however, a noteworthy change occurs. The key fynbos taxa (excluding Rhamnaceae) increase, while Cyperaceae and Poaceae decline (Figures 11; 14-19). Landscape biodiversity also makes a slight resurgence to a level only marginally below that recorded before the colonial arrival (Figure 20). DCA highlights this surface sample as analogous with zone 1a, at the base of the core (Figure 12). This suggests that vegetation at, or close to present, is statistically analogous with that which persisted in pre-colonial ecology. The proxy record therefore confirms that recent conservation efforts have moved in the right direction, where restoration of the site to pre-colonial conditions is the target. However, a prominent difference between the pollen spectra of zone 1a and Wildcliff's contemporary biogeography (Figures 2-4; Plates 1-4) is the representation of afro-montane taxa, which have not made resurgence. Moreover, considering fynbos cover at present is analogous with pre-colonial conditions (zone 1a), and afro-montane cover may only have propagated across low, sheltered and moist areas, a significant proportion of the pollen

recruitment area's 'natural' vegetation is unaccounted for. Conceivably, wetland vegetation and renostervelt were well established, and grassy fynbos may also have persisted on the surrounding foothills (Figures 2-4; Plates 1-2) (Mucina and Rutherford, 2006). However, modern pollen analogues from the respective communities would be necessary to determine this.

In general, changes in fire appear to have had little impact on fynbos proliferation or decline. This disagrees with the predominant view of fire's role in fynbos ecology (e.g. Bond, 1997; Cowling, 1995; DeBano, 1999; MacDonald and Cowling, 1993). Zone 1a contained the lowest abundance of micro-charcoal deposits. This is possibly due to the more mesic MWP climate, which may have favoured the propagation of afro-montane forest over fynbos. Drier LIA climate that arguably occurred in zone 1b could have caused fynbos proliferation and increased burning, accounting for the marginal increase in abundance of charcoal deposits. A significant increase in charcoal abundance in zone 2 suggests more burning associated with human activity. However, this increase occurs after the fynbos decline, indicating the two events are not directly linked. Conversely, the apparent lag-time in burning increase could be due to nineteenth/ twentieth century efforts to suppress burning, and subsequent increases following realisation of futility (Cowling, 1995). While this appears to be conclusive upon the basis of the data obtained, it is important to consider that the sites fire regimes may have been perturbed by human activity through, and beyond, the extension of the record (Appendix 1). Thus, the observed trends may be part of a plagioclimax disequilibrium. Furthermore, the detrimental effects of the post-colonial arrival burning increase may take longer to emerge in the pollen record, or be totally ignored by it altogether.

'Thresholds of Potential Concern' and the 'Range of Natural Variability'

This research aimed to not only establish a proxy record for ecosystems state, but to apply that information to conservation in the form of ecologically sound management objectives. Two quantitative approaches can be taken. Firstly, TPCs (Froyd and Willis, 2007; Gillson and Duffin, 2007) can be applied. These are measurable relative to present-day fynbos cover in the pollen recruitment area (a 2km radius surrounding the core site, and the river catchment) (Figures 2-4). Considering an anthropogenic disturbance explanation for zone 1b cannot be ruled out, only zone 1a seems conclusively suitable as a pre-colonial reference condition. Thus, a lower TPC can be set at 85%, and an upper at 135%. This indicates fynbos should not fall below 85% or above 135% of present cover (zone 1a fynbos remained between these parameters). Should deviation beyond these TPCs occur, a change out of sync with pre-colonial ecology might be underway.

The IPCC Fourth Assessment Report (Meehl, et al. 2007) predicts warming for the Wildcliff region of between ~2-2.5°C by 2046-2065, and ~2-4°C by the end of the century (on 1980-1999 levels). This may be in-line with temperatures of the MWP (Mann, 2007). However, precipitation and soil moisture availability are both predicted to fall significantly (Meehl, et al. 2007; Midgley, et al, 2005). Moisture is the more important climatic parameter for the region due to its general aridity (Scott and Lee-Thorp, 2004), therefore it is questionable whether zone 1a (possibly the MWP) would provide suitable reference conditions for future climate. Should zone 1b be identified conclusively as the LIA, this might provide more suitable reference conditions for future moisture availability levels. Under such a scenario, fynbos cover should remain between an RNV of 85-225% of present cover over the coming centuries.

However, it should be emphasised the stated climate predictions and palaeoclimate reconstructions are characterised by uncertainty.

Figure 21 provides a summary of the key palaeoecological changes that have been identified in the Wildcliff fossil pollen record, and the application of TPCs and the RNV.

Aim attainment and hypothesis testing

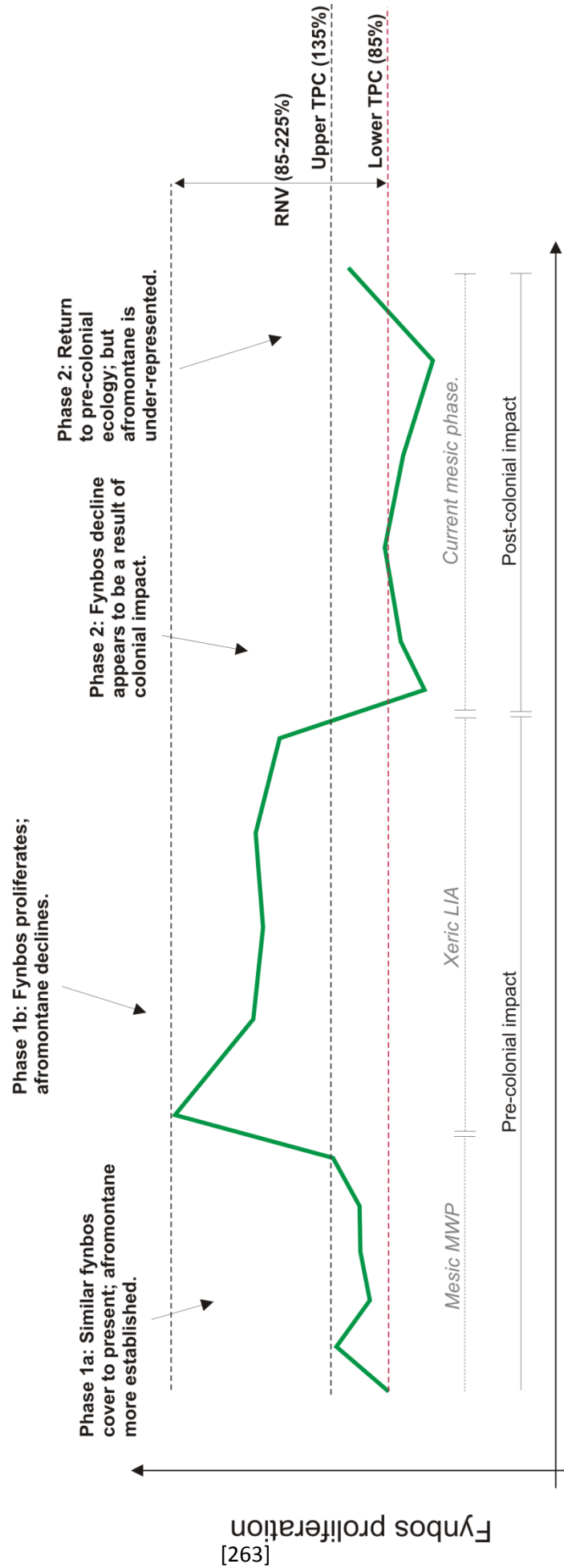
A proxy record for ecosystem state has been established, and this has been applied to provide clear conservation objectives (in the form of TPCs); therefore this investigation's initial aim has been met. In terms of the hypotheses tested, H_1 , H_2 and H_3 can be rejected, as fynbos vegetation has both declined and proliferated periodically over time. H_4 cannot be falsified, and is therefore accepted as likely to be true. It must be noted, however, that H_4 is a modified form of H_1 and H_2 .

Conclusions

Fynbos vegetation at Wildcliff has both proliferated and declined over time. This may have occurred due to interstadial and stadial climatic fluctuation of the MWP and LIA, respectively. However, the role of anthropogenic disturbance in the trends observed cannot be ruled out. Interplay between fynbos and afro-montane vegetation cover has transpired, although ericaceous fynbos has been more dominant. It can be deduced that other vegetation types have persisted substantially at, and close to, the Wildcliff site; however determination of their palaeoecology will require modern analogues for the respective communities. Abrupt and dramatic environmental degradation seems to have occurred at the colonial arrival, probably due to more intense and technologically potent agriculture. In the following period, fynbos persistence fell to an unprecedented low, outside the RNV. Recent efforts, however, appear to be encouraging a return to pre-colonial conditions, which may be suitable reference conditions given current climate. Afro-montane cover is significantly reduced at present, more so than perhaps should occur in the contemporary mesic climate.

Determining if past conditions evidenced in the record are suitable climatic analogues for future conservation management will necessitate further investigation to test the MWP, LIA and intermediate disturbance hypotheses, and is also dependent on future precipitation trends. Fire has not shown to be linked strongly to the vegetation trends observed, possibly as a result of human perturbation. Due to possible human perturbation and more xeric climate in zone 1b, only zone 1a is decisively suitable as a reference for current ecology.

Figure 21: Summary diagram.



Upper and lower TPSs can conclusively be set at 85 and 135%, respectively, (as evidence for zone 1a being pre-colonial seems convincing), although the relevance of these thresholds over the medium and long term is unknown. Thus, for the future a RNV of 85-225% might provide more suitable conservation parameters.

The use of modern pollen analogues has increased the reliability and accuracy of the fossil pollen investigation. Fynbos taxa were largely underrepresented in the pollen rain. However, a sufficient signal was obtained for a palaeoecological analysis to take place, as disentanglement of noise in the data and indicator species has been possible. However, future studies should take a more comprehensive approach to this, and establish modern analogues for all major vegetation communities in the area (e.g. wetlands, afro-montane, renostervelt, and grassy fynbos). The investigation of pollen recruitment has also proved to be fundamental; particularly as applied palaeoecologists may be forced to use sample sites that are dislocated from the subject community.

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Appendices

The appendices to this report can be viewed in the folder 'Supplementary Files' located in the Reading Tools menu list.

