BENCHMARKS FOR THE FUTURE: LONG-TERM VEGETATION CHANGE DERIVED FROM PALAEOECOLOGICAL TECHNIQUES IN WEST-COAST RENOSTERVELD, SOUTH AFRICA

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ABSTRACT

This study focuses on long-term vegetation changes in West-Coast Renosterveld in the winter rainfall zone of the Cape Floristic Region (CFR), Western Cape, South Africa. Renosterveld is an evergreen, fire-prone Mediterranean-type shrubland consisting of asteraceous elements, grasses and geophytes. It is restricted to fertile, fine-grained soils and more than 90% of this vegetation type has been transformed by agriculture. High richness of endemic geophytes in particular gives remaining fragments an irreplaceable conservation value. Future climate projections for the region suggest a general warming of 1.5-3.5 °C, a 30-50% decrease in precipitation, an increase in drought periods and shorter rainy seasons with important consequences for the vegetation of the CFR. There is limited information regarding the response of Renosterveld to past climate change and land-use disturbance and there is much debate about the pristine composition of Renosterveld vegetation. The lack of Renosterveld environmental history with appropriate pre-colonial or pre-Iron age benchmarks makes it difficult to build evidence-based arguments for conservation management and restoration. Studying the history of Renosterveld in the late Holocene may provide information on responses to past warmer climates, and the more recent effects of anthropogenic disturbance.

The aim of the present study was to reconstruct vegetation change, fire regime and changes in herbivory over the past ca. 1300 years at a West-Coast Renosterveld site in the Western Cape and to interpret these findings in light of known climate history and land-use change with a specific focus on the effects of disturbance by fire and herbivory. Findings were explored in relation to resilience theory, and the implications for conservation management and restoration. The following research questions were investigated, (1) How has vegetation, fire and herbivory changed over time in West-Coast Renosterveld vegetation? (2) How do changes in vegetation relate to climate and land-use disturbance and what are the main drivers of change? (3) What are the links to theoretical frameworks such as resilience theory? Are recent changes unprecedented and is there evidence of a threshold response to climate and disturbance? (4) What are the implications of these findings for conservation management and restoration such as present day management of fire and herbivores?

The study was carried out on Elandsberg Private Nature Reserve, which is one of the largest West-Coast Renosterveld conservation areas (ca.<1000 ha) in the region. A sediment core was retrieved from Vangkraal Spring wetland which occurs on an ecotone between Swartland Shale Renosterveld and Swartland Alluvium Fynbos. The small wetland is particularly sensitive to changes in local disturbance such as fire and herbivory. The methodology included palaeoecological techniques such as the analysis of fossil pollen, macro- and micro-charcoal, coprophilous spores, AMS radio-carbon and ^{10}Pb dating.

The sediment sequence is ca. 1300 years old ranging from ca. AD 750-2012. Stratigraphy results were not related to pollen, spore and charcoal data. The fossil pollen data show that prior to ca. AD 1943 vegetation remained relatively stable, with asteraceous elements (Asteraceae long-spine type-1 pollen) dominant and *Elytropappus rhinocerotis* and Poaceae less dominant. Over the same time period, macro-charcoal was low in abundance with little fluctuation over time while coprophilous spores were either low in abundance or absent. Micro-charcoal data showed that regional fires were frequent and highly variable from ca. AD 750-1400. Post ca. AD 1943, vegetation changed noticeably with a significant increase in *Elytropappus rhinocerotis* associated with an increase in macro-charcoal abundance and coprophilous spores, suggesting increased local fires and increased herbivory. Micro-charcoal abundance was lower and less variable, suggesting less regional fire.

Comparison with known climate history shows that vegetation composition changed little in response to the warmer and drier conditions of the Medieval Climate Anomaly (ca. AD 900-1400) and cooler and wetter conditions of the Little Ice Age (ca. AD 1400-1800). Land-use by the Khoi-San hunter/herders (ca. AD 750-1650) and early European settlers (ca. AD 1650-1943) appear not to have had a significant effect on the vegetation of the region though changes observed in regional fire frequency and intensity (AD ca.750-1400) were probably due to either climate change or anthropogenic disturbance. Macro-charcoal and coprophilous spore data show that recent land-use, specifically increasing fire and herbivory associated with agricultural intensification, resulted in unprecedented changes in vegetation post ca. AD 1943. There was a notable increase in *Elytropappus rhinocerotis,* an unpalatable shrub, over this period. Statistical analysis of the data suggests that no ecological threshold has been crossed. However, land-use change and recent climate variation interact, and the results cannot rule out a threshold being crossed if further warming and intensive fire and herbivory continues, resulting in a transition to “Degraded Renosterveld” in the future *Elytropappus rhinocerotis*.

The study provides insight into interacting changes in climate and land-use, providing a guide to the restoration and management of West-Coast Renosterveld at Elandsberg Private Nature Reserve. In order to preserve the resilience of the system and prevent an alternative stable state being reached, a pre-AD 1943 benchmark is optimal. Managers are recommended to decrease the abundance of *Elytropappus rhinocerotis* through intermediate levels of fire and herbivory creating patchiness of varying post-fire ages and densities of *Elytropappus rhinocerotis* at the local-landscape level. Climate and land-use impacts (and feedbacks between them) on biodiversity hotspots are of international conservation concern. More high temporal resolution palaeoecological studies are needed to understand the variability of ecosystems over time, in order to design management plans that restore and enhance resilience of highly threatened environments.

February 2014

DECLARATION

I know the meaning of plagiarism and declare that all of the work in ‘Benchmarks for the future: Long-term vegetation change derived from palaeoecological techniques in West-Coast Renosterveld, South Africa’, save for that which is properly acknowledged, is my own and has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

....

Name Date

This thesis is dedicated to my mother, Sharon Ann Peters.

“*I am a rose of Sharon, a lily of the valleys*.” (Song of Solomon 2:1)

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ABBREVIATIONS

BUS	Benguela Upwelling System
cal BP	Calibrated years before present (before 1950)
CFR	Cape Floristic Region
Elandsberg PNR	Elandsberg Private Nature Reserve
HS1	Heinrich Stadial 1
LGIT	Last glacial-interglacial transition
LGM	Last Glacial Maximum
LIA	Little Ice Age
LOI	Loss on Ignition
MCA	Medieval Climate Anomaly
MWP	Medieval Warm Period
Myr/ MYA	Millions of years ago
ODP	Ocean Drilling Program
VANG	Core extracted from Vangkraal Spring wetland on Elandsberg PNR
WRZ	Winter rainfall zone
YD	Younger Dryas

1. GENERAL INTRODUCTION

The Cape Floristic Region (CFR; Figure 1) (traditionally known as the Cape Floristic Kingdom or the more recent term, the Core Cape Subregion; Manning and Goldblatt 2012) is one of 25 biodiversity hotspots in the world (Myers 1990; Mittermeier et al. 1998) and is both the smallest and richest internationally recognized floral kingdom (Low and Rebelo1996; Goldblatt and Manning 2000; Myers et al. 2000). This is largely a result of its floristic diversity and endemism. The CFR contains >9000 plant species, of which 68% are endemic (Manning and Goldblatt 2012). This floristic kingdom is a global priority for conservation since it is vulnerable to processes that threaten its unique biodiversity (Rebelo 1992; Richardson et al. 1996). About 30.3% of its primary vegetation has been lost due to land transformation (Cowling et al. 1997; Fairbanks et al. 2000; Myers et al. 2000) and future climate change also poses a threat.

Much of the work in the CFR has focused on the Fynbos and Succulent Karoo biomes, and to date relatively little attention has been paid to Renosterveld vegetation, a poorly understood component of the Fynbos biome. Over 97% of Renosterveld has already been lost, and there is little long-term information on which to base conservation and restoration targets. The composition of pristine Renosterveld is uncertain and the remaining fragments are scarce. This chapter will discuss the importance and vulnerability of the CFR, and in particular West-Coast Renosterveld (Figure 1), to climate change and land-use. The chapter will explain the necessity of applied palaeoecological research to improve conservation management and restoration. It will also describe the aims and research questions and provide a general outline of the thesis structure.

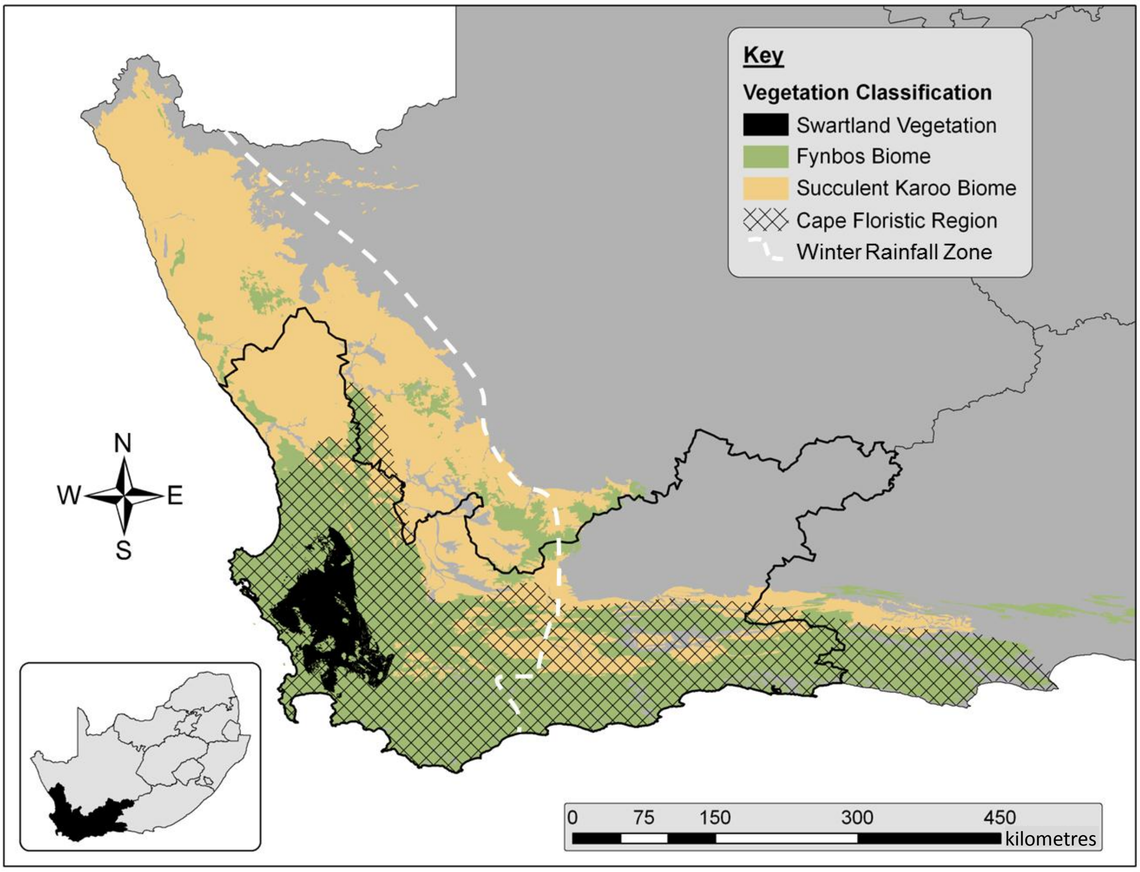


Figure 1: Map showing the Fynbos biome and Succulent Karoo biome in relation to the Winter Rainfall Zone (WRZ) and Cape Floristic Region (CFR). West-Coast Renosterveld (Swartland vegetation) is highlighted in black.

1.1. Background and Rationale

1.1.1. Importance of the Cape Floristic Region (CFR)

The CFR includes four biomes (Rutherford and Westfall 1994; Cowling and Holmes 1992; Mucina and Rutherford 2006), two of which are relevant to this study: (1) the megadiverse Fynbos biome and (2) the most arid biodiversity hotspot, the Succulent Karoo biome which extends northwards (Figure 1) as a part of the Extra Cape Subregion in Greater Cape Floristic Region (Manning and Goldblatt 2012). Two of the main vegetation types of the Fynbos biome are Renosterveld vegetation (covering an area of 24.2% of the CFR and commonly found on granite and shale substrates) and Fynbos vegetation (55% of the CFR and commonly found on sandstone substrates) (Manning and Goldblatt 2012). Approximately 7700 plant species occur in the Fynbos biome, with a very high endemism of over 70% (Lee and Crous 2003). The Succulent Karoo biome only covers an area of 12% in the CFR (Figure 1) (Manning and Goldblatt 2012). Similar to the CFR, it has a unique global status owing to its high plant species richness (Cincotta et al. 2000; Hannah et al. 2002a; Mittermeier et al. 1998) many of which are listed as Red Data Book plant species (Hilton-Taylor 1996; Driver et al.2003).

Renosterveld, which is the vegetation type of focus in the present study, usually occurs on shale and alluvium substrates, often at the ecotone between Fynbos and Succulent Karoo biomes. It is comprised of varying proportions of perennial grasses, geophytes, succulents and reseeding and resprouting evergreen shrubs (Rebelo et al. 2006). Renosterveld is found on fine-grained substrates that are relatively nutrient rich. The substrates may be alluvial in origin but generally they are derived from shale, granite, silcrete or exceptionally, limestone. Both Fynbos and Succulent Karoo are vulnerable to climate change, as will be discussed below (see section 1.1.2), and modelling predictions warn that future contractions will occur in both biomes. In addition, the irreplaceable biodiversity of the CFR is under a great amount of pressure as a result of habitat transformation attributable to agriculture, urban development, unsustainable harvesting and inappropriate land-use planning and the spread of invasive alien species (von Hase et al. 2003).

Out of all the vegetation types within the CFR, Renosterveld has been affected the most by land-use. It is also the least conserved within the CFR, with 91-97% of Renosterveld being transformed mainly for agricultural purposes (Rebelo 1992; von Hase et al. 2003; Rouget et al. 2003a, b; Rebelo et al. 2011). Conservation efforts in the past have concentrated primarily on montane parts of the CFR. However, such areas are less threatened because there is not much competition for land-use and opportunity costs of conservation are low (Pressey 1994; Cowling and Pressey 2003, Rouget et al. 2003a). In 1999, ‘Cape Action Plan for the Environment’ (C.A.P.E), a systematic conservation planning initiative identified Cape Lowlands Renosterveld as a top conservation priority within the CFR (Cowling et al. 1999c; Cowling and Pressey 2003). This priority was due to the greater vulnerability of lowland Renosterveld to agricultural transformation, owing to the higher nutrient status of lowland shales compared with higher elevation Fynbos. Renosterveld is also vulnerable to urbanisation and other development owing to its accessibility compared with montane Fynbos. Restoration of Renosterveld is urgent, but little is known regarding the origin and composition of Renosterveld before impacts by European settlers. Thus, there is debate over restoration targets and best management practices for this vegetation type.

1.1.2. Vulnerability of the CFR to climate change

West-Coast Renosterveld is located in the Winter Rainfall Zone (WRZ) of the CFR. This vegetation type experiences a Mediterranean-type climate which is characterized by summer drought and rainfall being at its maximum during the winter season (Tyson and Preston-Whyte 2000; Midgley et al. 2003; Chase and Meadows 2007; Haensler et al. 2011). Climatic variables such as temperature, wind, rainfall, snow and ocean currents influence environmental conditions and ecological processes through their effect on available moisture (Stenseth et al. 2002; Walther et al. 2002). Climate is therefore one of the key drivers of vegetation change since it has a direct link to plant growth, reproduction and mortality (McDowell 2011; Jamieson et al. 2012). The unique biodiversity of the CFR has the potential to be affected by future climate change. Future climate projections for the WRZ suggest an increase in aridity associated with a poleward drift of the prevailing westerly winds (Boko et al. 2007; Toggweiler and Russell 2008). Haensler et al (2011) provide a series of high-resolution regional climate change simulations until ca. AD 2100 for the region. These simulations suggest a decrease in precipitation (30-50%) in the western and central parts of the southern African region, a general decrease in high intensity events of precipitation, an increase in temperature (of between 1.5 and 3.5 °C) with an increase in drought periods and shorter rainy seasons (Haensler et al. 2011).

Other studies have predicted that the WRZ will experience a decrease of 10-30% in annual runoff by AD 2050 threatening both agricultural production and biodiversity in remaining areas of natural vegetation (Turpie et al. 2002; Meadows 2006). Dramatic contractions of both Fynbos and Succulent Karoo vegetation have been predicted in response to changing climate in the next 50 years (Midgley and Thuiller 2007; Midgley et al 2005; Midgley et al. 2001). In the past two thousand years there have been periods of significant climatic variability. The warm and arid Medieval Climate Anomaly (MCA) occurred in ca. AD 900-1400 (Stager et al. 2012), the cold and wet Little Ice Age (LIA) occurred in ca. AD 1400-1800 (Mayewski et al. 2004) and the 20th century warming has been the most recent change in climate (Cronin et al. 2003; Haensler et al. 2010). If Renosterveld vegetation has changed during the past warm climate of the Medieval Climate Anomaly then it may provide some indication of vegetation response under future climate change.

1.1.3. Land-use in the CFR

Understanding land-use as a key influence on past vegetation change is essential for conservation management and restoration. Changes in land-use include cultivation, urbanization, and manipulation of grazing and fire regimes. Understanding the impacts of land-use helps in determining the historic range of variability of the ecosystem. It therefore enables realistic restoration targets to be identified so that appropriate fire and herbivore management plans can be developed.

Early historical reports suggest that the CFR has a long history of land-use. People have managed fire and herbivory for more than 2000 years. Hunter-gatherers (locally known as San or Bushman) were in the region from 10 000-2000 BP (Deacon 1992) while Khoikhoi pastoralists introduced livestock to the Western Cape approximately 2000 BP (Stow 1905; Cooke1965; Westphal 1963; Elphick 1977; Boonzaier 1996; Henshilwood 1996). It is likely that the Khoikhoi pastoralists used intense fire as a mechanism to improve pastures for better grazing (Botha 1924). From the mid-17th century a new form of land-use was introduced in the Cape region as a result of the arrival and colonization of European settlers. By the 18th century they had established themselves throughout the region (Bergh and Visagie 1985; Hoffman 1997). With the arrival of European settler agriculture came increased grazing pressure and crop cultivation (mostly grain production), and combinations of fire suppression (to protect agriculture and property) in some areas and regular burning in others (Newton 2008). Permanent settlement and agriculture would have intensified the effects on the environment. In the 20th century, agriculture intensification has had an increasingly significant impact as technology and industrialization has allowed further transformation of natural vegetation. Within the Swartland region on the West Coast from the late 20th century to recent times there has been a shift from predominantly grain cultivation towards wine grape cultivation, as well as a general increase in urbanization (Halpern and Meadows 2013).

1.1.4. Effects of climate change and land-use on resilience

Neoecological studies provide important insight for conservation since neoecologists deal with extant species and how they relate to and interact with their current environment. However, neoecology lacks the temporal scale that is necessary to gain a more comprehensive understanding of the effect of environmental fluctuation on ecosystems, specifically the variability in response to past climate change and land-use. There is a need for a palaeoecological perspective in modern ecology and ecological theory and combining these approaches can be beneficial for conservation (Rull 1990; Colles et al. 2009; Rull 2010; Louys et al. 2012). The palaeo-record has the potential to show how resilient Fynbos (Meadows et al. 2010; Quick et al. 2011) and West-Coast Renosterveld vegetation has been to past changes in climate and land-use and could potentially help to disentangle the combination of factors that cause ecosystem re-organization. Given predictions of future climate change and ongoing land-use pressures, it is of conservation relevance that the resilience of these biomes to past climate and land-use change is well understood. This includes the possible changes in distribution, the determination of which environmental thresholds cause a reorganization of vegetation communities, and the interaction between climate and disturbance. If resilience is compromised then there is a possibility that unique biodiversity and ecosystem services could be lost. For example, hot, dry weather together with the increased likelihood of fire ignition during the 21st century could increase fire frequency and intensity (Forsyth et al. 2000). Associated with this is the spread of fire-adapted alien trees and shrubs (e.g. *Acacia saligna*, *Hakea* spp and *Pinus* spp) which in turn influence fire regime characteristics such as frequency, intensity, extent and seasonality (Brooks et al. 2004), and therefore also threaten biodiversity. While conservation managers cannot influence climate, they have the ability to manipulate disturbances like fire and herbivory and thus possible build resilience and buffer against the effects of future climate change.

1.1.5. Motivation for the present study

Given the high value that various human societies have placed on the fertile soils which originally supported West-Coast Renosterveld, urgent conservation and restoration efforts are needed to conserve remaining fragments. In addition, suitable management of fire and herbivory is necessary to build and restore resilience in the face of a changing climate. However, there is limited information regarding the response of West-Coast Renosterveld to past climate change and land-use, and therefore long-term studies are needed. The lack of pre-colonial benchmark conditions of the vegetation makes it difficult to build evidence-based and contextual arguments for conservation, restoration and ecosystem services management. For example, there is little confidence about the original composition of Renosterveld vegetation. Some ecologists argue that it is merely degraded Grassland vegetation (Thom 1952, 1954; Levyns 1956; Cowling et al. 1986) while others believe it is a distinctive vegetation type with overwhelming biodiversity (Curtis 2013). In addition, some classify Renosterveld as a component of ‘karroid’ vegetation (Cowling et al. 1997) while others classify it as a sub-type of Fynbos (Meyer 1875; Marloth 1908; Werger 1978). Similarly, few records show the effects of the Medieval Climate Anomaly and the majority of past palaeoecological studies have focused on longer records at coarser temporal resolution (Meadows 2001; Neumann et al. 2011). Although palaeo-research is relatively scarce in the Fynbos and Succulent Karoo biomes there are sufficient past studies to confirm the feasibility of palaeoecological techniques in the CFR (Chase and Meadows 2007; Chase and Thomas 2007; Meadows et al. 1996; Meadows 2001; Meadows and Baxter 2001). However, there are obvious gaps in knowledge concerning Renosterveld, and this affects the development of realistic restoration plans, and the lack of baseline information makes it difficult to manage for appropriate fire and grazing regimes.

1.1.6. Importance of the study site

The study site is on Elandsberg Private Nature Reserve (Elandsberg PNR) which is situated in the Swartland region of the CFR. The reserve contains one of the largest areas (ca. <1000 ha) of pristine West-Coast Renosterveld that has not been transformed for agriculture (Rebelo 1995; Midoko-Iponga et al. 2005). Used for livestock farming between ca.1705-1970, the Elandsberg PNR was established in 1973 for the purposes of conserving the threatened endemic Geometric Tortoise (*Psammobates geometricus*) (Boycott and Bourquin 1988).

Since then, indigenous wild herbivores such as eland, blue and black wildebeest, zebra, red hartebeest, gemsbok, bontebok and springbok have been reintroduced. The site where a sedimentary sequence was extracted is a small sized wetland called Vangkraal Spring. The site is on an ecotone between Swartland Shale Renosterveld and Swartland Alluvium Fynbos (Mucina and Rutherford 2006). The ecotone between these two vegetation types is useful in the study of vegetation change because at these boundaries species are at their biological and/or environmental limits thus making it possible to identify critical thresholds, or points where one biome collapses and reorganises into a different vegetation assemblage (Gillson and Ekblom 2009). Using a small wetland such as Vangkraal Spring has the added advantage of capturing local vegetation change, and thus making it a sensitive indicator of local land-use disturbance (i.e. the historical use of fire and herbivory by San hunter-gatherers, Khoikhoi pastoralists and European settlers). Local disturbance is of major interest to managers because they are able to manipulate their management practices which is not the case for climate.

1.2. Project aims and objectives

The overall aim of this study was to develop a long-term history of vegetation change at a site within West-Coast Renosterveld, to investigate the drivers of vegetation change with the goal of informing current conservation and management practices in the region. The specific objectives were:

(1) To quantify the extent and nature of vegetation change, fire and herbivory over the past ca. 1300 years within West-Coast Renosterveld vegetation using fossil pollen, charcoal and coprophilous spore analysis.
(2) To interpret the findings in the context of known climate and land-use history.
(3) To explore the links with ecological theory.
(4) To discuss the conservation and management implications of these findings.

1.3. Research questions

The following research questions underpin the project aims and form the foundation for this study:

1) How has vegetation, fire and herbivory changed over time in West-Coast Renosterveld vegetation, at Elandsberg PNR?

2) How do the changes in vegetation at Elandsberg PNR relate to climate and land-use disturbance and therefore what are the main drivers of change?
    a. Climate:
        i. What were the effects of the MCA and LIA?
        ii. What were the effects of 20th century warming?

    b. Fire and herbivory frequency and intensity:
        i. Is there evidence of management of fire and herbivory by San hunter-gatherers and Khoikhoi pastoralists?
        ii. What was the impact of agriculture by early European settlers?
        iii. How have changes in grazing intensity and fire impacted vegetation in the 20th century during the agricultural intensification and conservation periods?

3) What are the links to theoretical frameworks such as resilience theory?
    a. Are recent changes unprecedented or within the historical range of variability?
    b. Is there evidence of threshold behaviour causing a regime shift between vegetation assemblages?

4) What are the implications of this study's findings for conservation management and restoration?
    a. How do the palaeoecological data inform restoration targets?
    b. Are alternative fire and herbivory regimes necessary for biodiversity conservation?
    c. Are there management interventions that might preserve resilience of the vegetation in the face of future climate change?

1.4. Significance of the study

Findings from this study help to establish pre-colonial benchmark conditions of the vegetation and help in assessing whether the vegetation seen in the reserve today is typical of the long-term climate change and land-use history of the site. The interaction between climate and land-use is a topic of international concern and this research can contribute to global debates on these issues. Insights from this analysis also help in the evaluation of the impacts of future climate change scenarios. A pre-colonial benchmark determines suitable levels of fire and herbivory that best promote resilience and biodiversity in this unique and threatened vegetation type. The high temporal resolution study (ca. 1300 years) contributes to palaeoecological (which is often quite a coarse temporal resolution), archaeological and historical literature about the structure, composition and dynamics of pre-colonial, early colonial and 20th century vegetation in the western part of South Africa. The results also provides insight into the resilience of West-Coast Renosterveld to changing climate and land-use and is therefore relevant to the management of fire and grazing.

1.5. Thesis organisation

Chapter 1 General Introduction

This chapter contains the study background and rationale, the aims and objectives of the study and how these translate into research questions. The structure of the thesis is also provided in this section.

Chapter 2 Literature Review

This chapter reviews the literature on palaeoecology, historical ecology and Renosterveld ecology relevant to the present study. The palaeoecological literature review considers past palaeoclimates and vegetation change in southern Africa and in particular the winter rainfall zone (WRZ) of the south-western Cape. The review of long-term ecology considers land-use history and vegetation change from the pre-colonial period up until the present day. Lastly, the review of the ecology of Renosterveld vegetation focuses on the ecology, conservation and dynamics of West-Coast Renosterveld, and explores the theoretical frameworks for understanding changes in this vegetation type.

Chapter 3: Study site

This chapter describes the setting of Elandsberg PNR. It considers topics such as geology, climate, topography and vegetation and land-use history (i.e. fire and herbivory). Site selection is also discussed. The environmental and historical context used to interpret the results of the study is provided.

Chapter 4: Methods

This chapter describes the field and laboratory methods including sediment sampling, vegetation survey, sediment description including physical properties analysis, fossil pollen, spore and charcoal analysis, AMS radio-carbon and Lead-210 (^{210}Pb) dating and statistical analysis.

Chapter 5: Results

This chapter describes the results of the vegetation survey, sediment description and physical proprieties and chronology of the sediment core. The results of the fossil pollen, spores and charcoal analyses are revealed here.

Chapter 6: Discussion

This chapter discusses the changes in vegetation, fire and herbivory with regard to drivers of change such as climate and land-use disturbance. Results are explored in relation to resilience theory, hierarchical patch dynamics and the intermediate disturbance hypothesis. The implications for conservation management and restoration are highlighted. Suggestions for future research are an important part of this chapter.

Chapter 7: General Conclusions

This chapter highlights the conclusions drawn from the study including the impact of past and present climate change, and the effects of land-use change, specifically the effects of changes in fire regime and changes in herbivory including the reintroduction of large indigenous herbivores. Implications for restoration and management of fire and herbivory are summarized

2. LITERATURE REVIEW

2.1. Palaeoecology used as a tool to investigate vegetation history in the winter rainfall zone of South Africa

This synthesis reviews how various palaeoecological techniques have been used to explain the environmental history of the Winter Rainfall Zone (WRZ) of South Africa. The discipline of palaeoecology and fossil pollen as a proxy is introduced and then in order to scrutinize the literature, basic themes (i.e. Palaeoclimates and the response of vegetation; Linking palaeoecology with ecological theory; Applications of palaeoecology in conservation management) are considered. This review deals with environmental history in a chronological order ranging from the onset of the Benguela upwelling ca. 8 MYA up until the present day.

Palaeoecology is described by Birks and Birks (1980) as "…the ecology of the past". It involves the reconstruction and study of past and present ecosystems, including the relations between organisms and their environments (Rull 2010) by the use of proxies (indirect environmental indicators). There is often a disconnection between ecology and palaeoecology but in reality they are merely different approaches with a common objective, which is the ecological understanding of the biosphere (Rull 2010). Palaeoecology is a discipline which provides a longer temporal scale in ecology. Palaeoecological proxies (for example, fossil pollen, charcoal, spores, diatoms and stable isotopes, etc.) can be used as a tool to investigate various themes on a timescales ranging from hundreds of years to the late-Quaternary period.

A few examples of research themes where palaeoecological techniques can be applied are presented by Roberts et al. (2001). These include: (1) Historical biogeography – i.e. how species distributions have changed over time in relation to the history of landforms, ocean basins, and climate, as well as how those changes have contributed to the evolution of biotas. (2) The patterns, magnitude and synchronicity of past climate change between and within different regions. (3) How far modern ecosystems represent their original pristine habitats or instead represent cultural constructs. For instance, palaeoecology can provide insight into the role that humans have played in transforming different landscapes and ecosystems, especially since these roles can often be cryptic.(4) How the ecology of an area has changed in the long-term, specifically the interacting effects of climate, fire, nutrients and in some cases herbivory. (5) The investigation of assumptions around the environmental future of a region, often using resilience theory as a framework for understanding when critical environmental and ecological thresholds are crossed.

Palaeoecological techniques using standard methods are well established and past studies confirm the utility of fossil pollen as a proxy for vegetation change (Meadows et al. 1996; Meadows 2001; Meadows and Baxter 2001; Chase and Thomas 2007; Chase and Meadows 2007). However, there are a few impediments that need to be taken into account.
When analysing pollen records one needs to remember that the taxa identified are probably those that have a high pollen production and are often well dispersed by wind. With this in mind, taxa that are anemophilous (plants that liberate wind-borne pollen) are often over-represented whereas taxa that are entomophilous (plants which rely on insects or other zoological vectors for pollen dispersal) are under-represented in the pollen record.

Many pollen types cannot be identified to species level, and identification to genus or family level is more common. Commonly, taxonomic identification of fossil pollen grains is based on the morphological characteristics visible with an optical microscope (Mullins and Emberlin 1997), but a new technique was proposed to solve the issue of poor taxonomic resolution of pollen. Owing to the advancements made in molecular biology, and since the pollen grain is the male gametophyte in seed plants (thus containing DNA), there is the rare opportunity to analyse ancient DNA in fossil pollen in order to gain better taxonomic resolution (Suyama et al. 1996, Parducci et al. 2005, Zhou et al. 2007). It is the combination of the fossil pollen's sturdy exine and certain characteristics (i.e. low temperatures and anoxic conditions) of wetland, lake or fluvial deposits that increase the chances of DNA preservation. Although the field of palaeogenetic studies is still a relatively new field, it could be quite beneficial to many disciplines (including biodiversity conservation). For this field to grow there needs to be integrated expertise from a number of disciplines such us palaeontology, molecular biology, biochemistry, geology and ecology. Additionally, there needs to be more investment in certain areas such as preparatory work with material, development of specific markers, laboratory equipment and isolation and methodology (Gugerli et al. 2005).

Despite the lack of taxonomic resolution, fossil pollen is still used as a proxy for vegetation change and is an important tool in investigating research themes around past environmental conditions.

2.1.1. Palaeoclimates and vegetation history

Southern African climates reflect a complex range of environmental controls since the region is situated at the interface between tropical, subtropical and temperate climate systems and as a result there has been significant modification of regional climates over time (Chase and Meadows 2007). The region has the potential to be a sensitive indicator of large-scale dynamics of the global climate system (Chase et al. 2011) and is therefore of great importance when studying environmental change. However, because understanding of southern African palaeo-environments is still quite limited, this resource is not fully utilized. Future research needs to focus on more study sites in a range of biomes and geographical areas; studies with greater spatial and temporal resolution; and analytical methods that include independent climate and vegetation proxies. Fossil pollen data have been used to reconstruct Quaternary climates by relying on plants with known climatic affinities (indicator species). However, in order to understand the effect of climate on vegetation, a separate climate proxy is preferable. This section deals with palaeoecological studies that have used fossil pollen data and other proxies including stable isotopes to provide some understanding of palaeoclimates. Figure 2 shows the location of a number of noteworthy palaeoecological study sites and their geographic relation to the present study site at Elandsberg Private Nature Reserve (Elandsberg PNR).

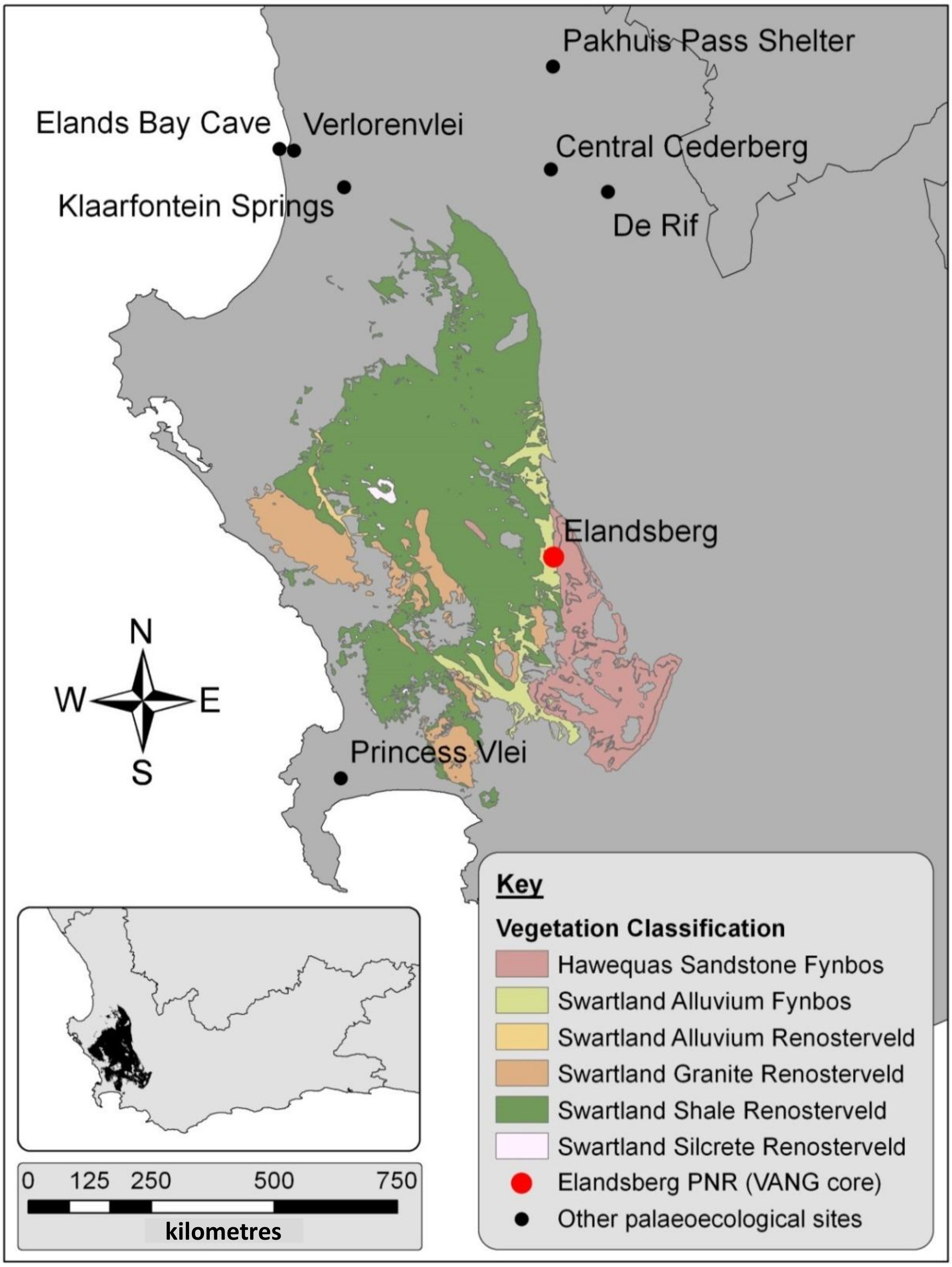


Figure 2: West-Coast Renosterveld vegetation in relation to the study site at Elandsberg PNR and other noteworthy palaeoecological study sites; Princess Vlei (Neumann et al. 2011), Klaarfontein Springs (Meadows and Baxter 2001), Verlorenvlei (Stager et al. 2012), Elands Bay Cave (Cowling et al. 1999a, Parkington et al. 2000), Pakhuis Pass Shelter (Scott and Woodborne 2007a, b), Central Cederberg (Sneeuberg Vlei and Driehoek Vlei (Meadows and Sugden 1991, 1993; Meadows et al. 2010)) and De Rif (Quick et al. 2011).

2.1.1.1. 8 Million Years Ago

The onset of the Benguela upwelling ca. 8 million years ago (MYA) was critical to the development of the WRZ and hence the associated radiation and diversification of the Cape flora. The study conducted by Dupont et al. (2011) was located off the mouth of the Orange River, a site that received both terrestrial input and marine upwelling and thus allowed a direct correlation between changes in terrestrial flora and the marine Benguela Upwelling System (BUS) of the south-east Atlantic Ocean. Pollen was analysed from sediments of the Ocean Drilling Program (ODP) Site 1085 in order to investigate the Middle to Late Miocene and test whether the onset of the Benguela upwelling ca. 8 MYA did play such a facilitating role. Dupont et al. (2011) found that although there were already Fynbos elements present 11 MYA, the development of the BUS indicated a marine-driven climate change of south-western Africa and the changes that occurred in vegetation indicated an increased summer drought typical of the winter rainfall climate (WRZ) evident today. *Podocarpus*-dominated Afromontane forests and tropical grasslands on the coastal plains became less dominant between 10-6 MYA whilst the Cape flora gradually increased (especially within the Aizoaceae family as noted in previous studies by Verboom et al. 2009). The richness of the CFR can be attributed to the combination of climatically induced refugia, by fragmentation and by adaptive radiation. For example, soil type shifts as the most important cause of speciation in *Babiana*, *Moraea*, and *Protea*, shifts in fire-survival strategy as the most important factor for Podalyrieae, and specialized pollination syndromes in other groups (Verboom et al. 2009; Schnitzler et al. 2011).

2.1.1.2. Last Glacial Maximum (LGM)

It appears that the resolution of southern Africa's climate during the Last Glacial Maximum (LGM) is obscure. In southern Africa the LGM occurred between 25 000 and 15 000 BP (Tyson 1999; Tyson et al. 2000). Evidence from Elands Bay Cave (a winter rainfall site – Figure 2) (Cowling et al. 1999a; Parkington et al. 2000) showed that not only was the LGM cooler but also that moisture was in a substantially greater supply. On the other hand, results found at Boomplaas Cave in the southern Cape (a year-round rainfall regime site) (Deacon et al. 1984) revealed evidence for more xeric climates during the LGM in accordance with much of the rest of southern Africa, including the summer rainfall region. Other studies (Deacon and Lancaster 1988; Tyson 1999; Tyson et al. 2000) confirmed drier climatic conditions associated with the cooler temperatures. Given this information, it appears that parts of the WRZ have altered climates out of phase with the rest of the subcontinent (Meadows and Baxter 1999). Owing to the contrasting results found by several studies, Roberts et al. (2001) recognised that the LGM in Africa's south-western Cape region has proved difficult to resolve and whether the winter rainfall was wetter or drier during this period is debatable.

The Last Glacial Maximum (LGM), conventionally defined from sea-level records, is the most recent interval in Earth's climatic history when global ice sheets expanded 20 000 years ago as a result of global cooling associated with Milankovitch forcing of climatic change (Hays et al. 1976). The LGM was the peak of the last glacial stage before the transition to the present interglacial equivalent in time to the Holocene epoch – see below. Parkington et al. (2000) carried out a palaeo-vegetation investigation of the LGM by analysing wood charcoal and pollen evidence from Elands Bay Cave on the west coast (Figure 2). The results suggest a change in assemblage composition with time. According to the wood charcoal data, the most dominant woody species were Afromontane Forest taxa (e.g. *Podocarpus elongatus*, *Grewia occidentalis*, *Myrsine africana*, *Kiggelaria africana*) at the LGM (Parkington et al. 2000). Results obtained by pollen identification during the same time period were consistent with that of the wood charcoal. Scrub forest taxa (which included Afromontane elements) were relatively more abundant during the LGM than at present. This suggests greater moisture availability than the present day since the same area now supports dry asteraceous shrublands (e.g. *Eriocephalus aromatica*, *Aspalathus* spp*, Passerina glomerata, Euryops speciossissimus, Chrysanthemoides* spp*, Hymenolepis parvifolia, Salvia africana-lutea, Phylica* spp) and xeric Thicket vegetation (known as Strandveld and dominated by species such as *Euclea racemosa, Rhus undulata, Ruschia maxima and Zygophyllum morgsana*).

Pollen data can provide good records of vegetation development, but continuous pollen sequences in southern Africa from sources such as wetlands and lakes remain scarce. With this in mind, Scott and Woodborne (2007a,b) analysed a pollen sequence that was preserved in rock hyrax (*Procavia capensis*, locally known as a "dassie") dung middens from a site at Pakhuis Pass Shelter, in the WRZ of the Western Cape (Figure 2). One of the advantages of coring in rock hyrax middens (formed from consolidated faecal material and urine) is that there is good preservation since these deposits are not vulnerable to microbial decay and they may survive for several thousands of years. Although middens can be an excellent resource for palaeoecological data, hyrax diet and other factors (for example, the presence of wind-pollinated types being the most significant component in middens) may bring about a degree of bias, which needs to be taken into account (Scott and Bousman 1990; Scott and Cooremans 1992). The results obtained by Scott and Woodborne (2007a,b) suggest that the vegetation during the LGM was composed primarily of low shrubs (concluded by the presence of low-spine *Stoebe/Elytropappus*-type pollen) and "pure Fynbos" (including Ericaceae, *Passerina*, *Cliffortia* and Proteaceae taxa). The difference in the findings of Scott and Woodborne (2007a) and Parkington et al. (2000) is likely due to different locations. Pakhuis Pass Shelter is further inland, closer to the Cederberg Mountains and therefore could have experienced a variation in climate in comparison with the relatively more moist coastal palaeoecocolgical site at Elands Bay Cave (Figure 2). These different locations and therefore climatic variances could have resulted in the dissimilar vegetation assemblages during the LGM.

2.1.1.3. Last Glacial-interglacial Transition and Heinrich Stadial 1

The first evidence for the last glacial-interglacial transition (LGIT) in the southern African tropics was ca. 18 000-11 500 years ago (Chase et al. 2011). Chase et al. (2011) aimed to identify the timing and extent of past major climate fluctuations in southern Africa with results from stable carbon and nitrogen isotope records obtained from the De Rif middens of rock hyrax (Figure 2). The results from this study found that the Northern Hemisphere exerted a strong influence on nearly all latitudes (with the higher latitudes being an exception) of the Southern Hemisphere after the Heinrich Stadial 1 (HS1; which occurred between 18 000-15 000 years ago). HS1 was a period within the LGIT when there was a coeval poleward shift of the sub-tropical front, where there were sharp reductions in southeast trade winds and upwelling intensity and the peak of this stadial (ca.17 000-16 000 years ago) coincided with one of the most extreme and widespread megadroughts of the past ca. 50 000 years in the Afro-Asian monsoon region (Stager et al. 2011). This resulted in warmer Benguela sea surface temperatures and more humid conditions at the De Rif site. Furthermore, results revealed the first indisputable terrestrial sign of the global event called the Younger Dryas (YD) (ca.13 000-11 500 years ago) and this event was an abrupt return to near-glacial conditions during the LGIT.

The studies by Chase et al. (2011) and Stager et al. (2011) only reveal the climatic conditions during this time, whereas the study conducted by Parkington et al. (2000) at Elands Bay Cave reported on the vegetation conditions towards the end of the LGIT. However, these studies have different locations (Figure 2) and therefore are subject to different climatic and vegetation conditions. Nonetheless, Parkington et al. (2000) found that between 13 600-12 400 years ago proteoid Fynbos elements were most dominant whereas at the Pleistocene-Holocene boundary between about 10 000-8000 years ago, the wood charcoal evidence depicted mesic Thicket vegetation (e.g. *Heeria argentia, Maytenus oleoides, Cassine peragua, Diospyrus glabra, Dodonaea angustifolia*).

2.1.1.4. Mid Holocene

Environmental change of the Holocene epoch (from 10 000 BP until the present day) has been recognised as one of the important points of reference by which future valued landscapes and ecosystems can be managed sustainably (Roberts et al. 2001). In particular, reference to warmer times such as the Mid Holocene Altithermal and the Medieval Climate Anomaly (MCA; discussed in section 2.1.1.6.) can offer a baseline for current and future climate change scenarios. The Mid Holocene Altithermal (less usefully known as the Mid Holocene Climatic Optimum) was a postglacial interval centred about 5500 years ago during which temperatures were warmer than at present (Meadows and Baxter 1999; Rosenthal et al. 2013). The Mid Holocene Altithermal could provide the most suitable analogue for the current warmer and drier Western Cape that has most likely been brought about by anthropogenic-induced climate change.

The reconstruction of the Holocene record has remained fragmented until recently owing to discontinuities in the palaeoecological record. Meadows and Baxter (2001) aimed to facilitate a more complete Holocene palaeo-environmental reconstruction and thus investigated a 6 m vibracore sequence at Klaarfontein Springs (at Verlorenvlei in the Western Cape; Figure 2).

This comprehensive evaluation of terrestrial pollen exposed evidence for regional aridity during the early mid-Holocene (ca. 6200-5500 BP) followed by moister conditions during the late mid-Holocene (ca. 3500 BP). The study conducted by Parkington et al. (2000) at Elands Bay Cave confirms the aridity found by Meadows and Baxter (2001) in the late mid-Holocene. Parkington et al. (2000) found that between 4300-3000 years ago the vegetation consisted of asteraceous shrubland elements and the most recent charcoal closely reflected the xeric Thicket found outside the cave today (Parkington et al. 2000). Thus one could infer that the climate experienced between 4300-3000 years ago was dry and similar to that of present times.

Since there is generally a low resolution and limited dating control of pollen sequences in the Cape Peninsula, Neumann et al. (2011) aimed to improve the vegetation history of the late-Holocene by analysing a continuous high resolution (average resolution 1 sample/70 yr) pollen sequence from the Cape Flats region at Princess Vlei, Western Cape (Figure 2). The 4150-year record documents vegetation, climatic and anthropogenic changes in the Fynbos biome. According to the chronology obtained at the Princess Vlei site, it was found that from about 4150-3400 cal BP the natural vegetation experienced a rather dry climate since Asteraceae, *Crassula* and Aizoaceae pollen were common whereas aquatics and sedge pollen percentages were low. Conditions changed from 3400-2600 cal BP when the climate became more humid as evident by the increase in *Morella*, Cyperaceae and *Carpacoce* pollen. Once again, pollen indicators show a shift back to drier environments from 2600-1900 cal BP and then another shift to wetter conditions at about 1850 yr BP. Unfortunately no Renosterveld vegetation elements were captured in the Princess Vlei pollen sequence.

2.1.1.5. Resilience of vegetation changes from the LGM to the Holocene

The pollen sequence analysed by Scott and Woodborne (2007b) at Pakhuis Pass Shelter (Figure 2) indicated that Holocene vegetation consisted of a mosaic of Fynbos and Thicket vegetation (including *Dodonea* and *Olea*) with Aizoaceae-type succulents as well as Asteraceae. The transition of vegetation from the LGM (consisting of asteraceous Fynbos as well as Proteaceae and Ericaceae taxa) to the Holocene could be attributed to a decrease in soil moisture and an increase in ambient temperatures. In contrast, stable isotope and pollen analyses in the Central Cederberg (a site in close proximity to the Pakhuis Pass Shelter; Figure 2) suggest only relatively subtle changes in vegetation and climatic conditions since the last glacial period and over the Holocene (Meadows and Sugden 1991, 1993) and a recent publication confirms these results (Meadows et al. 2010). Roberts et al. (2001) warn that more reliable evidence for mid-Holocene climate change can be found in the aquatic floras in wetlands or around the margins in semi-arid regions. It is at these boundaries (e.g. closer to the coast or ecotonal transitions between vegetation types) that terrestrial vegetation is more sensitive to change and therefore where significant vegetation shifts are likely to occur (Roberts et al. 2001).

Furthermore, Scott and Woodbourne (2007a,b) suggest that differences in results between the studies is due to differences in regional topography. Sites that occur on high peaks in the west of the Cape Fold Mountains (i.e. Swartruggens and Cederberg) experience continuous westerly fronts and therefore, are less affected by climatic changes. The more stable environment provided by a high rainfall at the top of the mountain would result in a more stable pollen record compared to the Pakhuis Pass Shelter in the lower-lying rain shadow of the Cederberg, which was more likely susceptible to climatic changes. It would be useful if the current altitudinal boundary for vegetation stability could be determined and monitored as to whether increased pressure from anthropogenic-induced climate change has altered this boundary. However, past resilience of mountain Fynbos to changes in climate does not necessarily preclude instability under future climate change scenarios.

A recent study conducted in De Rif in the Cederberg (Quick et al. 2011) focused on pollen and stable isotope data derived from two rock hyrax middens in an attempt to understand environmental changes across the LGIT and the Holocene. In general agreement with pollen records found at Sneeuberg Vlei and Driehoek Vlei in Central Cederberg (Figure 2; Meadows and Sugden 1991, 1993; Meadows et al. 2010), Quick et al. (2011) confirmed very subtle vegetation change indicating that the mountain Fynbos communities remained relatively stable during the LGIT and the Holocene. However, the relatively stable environmental conditions differed markedly with the climatic variability displayed by the stable isotope records obtained at the site of the same study. In order to explain this inconsistency, Quick et al. (2011) argued that regardless of the climatic variability, the mountain Fynbos found within the central Cederberg is strongly influenced by geological constraints (in this case oligotrophic sandstone substrates). To support this explanation, a construction of rainfall envelopes for mountain Fynbos taxa in comparison with non-Fynbos taxa illustrated the resilience of mountain Fynbos in response to climate change. The stable isotope signatures displayed by the vegetation in the palaeo-record rightly represent the distinct changes in precipitation and/or fire regime (i.e. the climatic instability), but these changes do not necessarily affect the overall community composition, which remained relatively stable over time. Quick et al. (2011) point out that the resilience of mountain Fynbos suggests that it is less likely to be affected by future climate changes in comparison to other vegetation types within the Fynbos Biome. Furthermore, as Roberts et al. (2001) suggested, other Fynbos vegetation that are near coastal boundaries or vegetation boundaries may be more sensitive to future climate change. This is a fair warning that focus should be placed on the potentially more sensitive lowland Fynbos communities and ecotones, such as the highly threatened Cape Lowlands Renosterveld vegetation type occurring in the Swartland and Overberg regions. It could be argued that the palaeo-record representing the lowland system would reveal a very different vegetation and climatic history in comparison with that of mountain Fynbos. Hence, environmental reconstruction through a study of high temporal resolution will be of great value to conservationists and ecologists in light of future climate change scenarios.

In addition, Quick et al. (2011) explain that the contrasting palynological records found at the study site in the central Cederberg (Meadows and Sugden 1991, 1993, Meadows et al. 2010) and the northern Cederberg site at Pakhuis Pass Shelter (Scott and Woodborne 2007a,b) suggests the possibility that pollen data with low temporal and/or taxonomic resolution may disguise changes in vegetation communities and, therefore, related environmental parameters (Meadows and Sugden 1991, Chase and Meadows 2007). Consequently, it is very important to keep the resolution in mind when analysing the existing palaeoecological literature. Unfortunately, this also means that there is great uncertainty regarding the environmental history of the WRZ during the late Quaternary period in general and thus further research focusing on a high temporal and/or taxonomic resolution needs to be carried out.

2.1.1.6. The Medieval Climate Anomaly and the Little Ice Age

Climatic fluctuations in the last two millennia include the Medieval Climate Anomaly (MCA) which occurred from ca. AD 900-1400 (Stager et al. 2012) and the Little Ice Age (LIA) from ca. AD 1400-1800 (Mayewski et al. 2004). The MCA is a preferred name for the period rather than the Medieval Warm Period (MWP) as MCA emphasizes effects other than temperature alone. The MCA was a controversial subject as its global nature, extent and variation in characteristics of the climate conditions has been questioned (Mann et al. 2009). Its existence was mostly evident in the northern hemisphere and was characterized by abnormally warm, usually wet conditions. However recent studies conducted in the Southern Hemisphere reported evidence for both the MCA and LIA as global events (Orsi et al 2012; Rosenthal et al. 2013). There is increasing emerging evidence from studies in southern Africa which have high enough resolution to detect the MCA. Tyson et al. (2000) present evidence of a warming period derived from oxygen and carbon isotope and colour density data obtained from a stalagmite found in the Makapansgat Valley in Limpopo. The maximum warming at Makapansgat occurred at about AD 1250 and during this time the climate of the interior of South Africa may have been over 3 ˚C warmer than today.

In contrast with the MCA, the LIA is widely accepted to have been global in extent (Bard et al. 1997; Grove 2004; Licciardi et al. 2009; Schaefer et al. 2009). Most studies report that temperatures were cool during the LIA but different regions had varying levels of aridity. Evidence of the LIA in East Africa was found in biogenic silica profiles of varved sediments of Lake Malawi (Johnson et al. 2001). Johnson et al. (2001) found that there was an arid period from about AD 1570 to AD 1850 and during this time the lake level was ±120 m lower than during the past 150 years. Tyson et al. (2000) also found evidence for maximum cooling occurring in AD 1700 with the annual mean daily maximum temperature 1 ˚C cooler compared to the present day. Mayewski et al. (2004) confirmed that southern Africa had a prominent cool, dry episode during the LIA.

A recent study conducted by Stager et al. (2012) presented the first high-resolution, decade-scale rainfall variability over the last 1400 years for the South African WRZ using continuous lacustrine diatom records from Lake Verlorenvlei in the Western Cape (Figure 2). It was found that between ca.1400-1200 cal BP (ca. AD 550-750) there was high precipitation, after which it decreased until ca.950 cal BP (ca. AD 1000). Contrary to other records of the MCA being warm and wet, Stager et al. (2012) noted that the MCA was instead warm and arid. Precipitation increased notably through the LIA with precipitation maxima occurring around ca.600, 530, 470, 330, 200, 90, and 20 cal BP (ca. AD 1350, 1420, 1480, 1620, 1750, 1860 and 1930). Contrary to Johnson et al. (2001) and Mayewski et al. (2004), the diatom record interpreted by Stager et al. (2012) inferred a wet LIA for the WRZ of South Africa. This sort of record, which represents the temperate WRZ of the last millennium, is possibly most relevant to simulations of modern climates and helps in the prediction of future climate scenarios for South Africa.

2.1.2. Linking palaeoecology and ecological theory

Ecological theory can be seen as the conceptual system by which ecologists try to find general rules in an attempt to predict and understand the patterns and processes in a diverse biological world. Despite the importance of ecological theory, there exists a dichotomy between mathematical theory and empiricism in ecology (Fretwell 1972). Theory has a tendency to advance quickly because it is not constrained by place, while empirical ecology usually progresses more gradually and is always constrained by place and time (Krebs 2009). Consequently, palaeoecological data may open doors by providing the necessary detailed temporal information needed to be tested by all the accumulated theory. Palaeoecological techniques are able to bridge the data-gap that most long term (ca. 100 years) observational ecological data-sets cannot, but presently there is still much debate over the nature, extent, causes and rate of environmental change in South Africa and the appropriate theoretical frameworks for interpreting change over time. For example the divergence in theoretical views regarding the equilibrium, disequilibrium or non-equilibrium dynamics of rangelands (Illius and O’Connor 1999; Sullivan and Rohde 2002) illustrates uncertainty in current management priorities. The equilibrium model highlights the importance of biotic feedbacks such as density-dependent regulation of livestock and therefore management is centred around stocking rates and carrying capacity. In contrast, regarding non-equilibrium dynamics, livestock population numbers are less important since abiotic factors such as variations in rainfall regulate population numbers (Vetter 2005). Alternatively, thresholds and resilience theory can be used to interpret and understand the palaeo-record. For example the study conducted by Gillson and Ekblom (2009) in the Kruger National Park of South Africa, showed that an ecological threshold was crossed causing a regime shift from a Grassland phase to a Woodland phase in the Savanna biome.

On a positive note, ecologists are able to investigate hypotheses on larger temporal scales that stretch back for thousands and thousands of years, providing a link to theoretical frameworks that describe change and variability over long time scales. With this restraint lifted, some interesting research questions start to arise in order to fill in the gaps of environmental history knowledge. For example: “How far did Mediterranean- type ecosystems alter their ranges and composition during the climatic variations of the Quaternary? (Roberts et al. 2001) or; “Are today's plant communities simply associations of convenience when viewed on the timescale of glacial-interglacial cycles, which would support a non-equilibrium model for their biogeography?” (Meadows 1999). Or in light of the present study, “How severe are the effects of domestic livestock managed by European settlers compared to large indigenous herbivores which once roamed the land during pre-colonial times?”.

The coarse temporal resolution of most palaeoecological studies (e.g. Meadows and Sugden 1991; Meadows and Baxter 2001; Chase and Meadows 2007) does not facilitate comparison with ecological theory. Hence the current study will provide a high temporal resolution to investigate climate and land-use and the interaction between them under a resilience theory framework (see section 2.3.4.2).

2.1.3. Applications of palaeoecology in conservation management

2.1.3.1. Conservation in a changing climate

Climate change presents a serious challenge to conservation, especially in species-rich regions of the world such as southern Africa. Palaeoecology provides insight about the biotic effects of climate change (Hannah et al. 2002). For example the MCA and LIA described above suggest resilience of Fynbos vegetation has not been exceeded in the past 1000 years, but it is uncertain as to how near the thresholds are, and the interacting effect of climate and land-use change needs to be considered. Long-term vegetation records can be used to evaluate future climate change scenarios in order to inform biodiversity conservation. However, there are uncertainties of the potential trajectory of climate change at the regional level, as well as a lack of scientific understanding of the potential biological responses to climate change, and the possibility of future novel combination of climate parameters (Lovejoy and Hannah 2005; Williams and Jackson 2007; Williams et al. 2007).

2.1.3.2. What are the benchmarks and restoration targets?

There is a lack of high quality pre-colonial (pre-1800s) benchmark data (except for some data by Meadows and Baxter (2001) illustrated in section 2.2.2. below) to describe the vegetation conditions of South Africa and pre-pastoralist benchmarks are even more scarce. This lack of sound environmental history makes it difficult to build evidence-based and contextual arguments for conservation management. According to resilience theory, an ecosystem can persist for a long period of time before shifting from one stable state to another after crossing an environmental threshold (Scheffer et al. 2001; Andersen et al. 2009) (Figure 5, see section 2.3.4.2. for detailed discussion). An example of a driver causing a shift to an alternative stable state is anthropogenic impact (Dearing 2008; Estes et al. 2011) and a shift like this could have been triggered by the colonisation of the Europeans after the 1800s. The likelihood of such shifts occurring increases as human impact decreases the resilience of the system. However, there are many shifts that occur in the absence of humans and for this reason a pre-colonial (as well as a pre-pastoralist) benchmark is essential in determining the natural variability of the ecosystem and the thresholds between alternative stable states.

2.1.4. Conclusions from palaeoclimates review

Palaeoecological studies have shown that environmental change (variability brought about by climatic fluctuations, anthropogenic impact or other agencies) has been the norm rather than the exception over the course of the Holocene. For this reason, planning for the use of land, water and vegetation must aim to take into account the resilience and natural range of environmental variability, and not only seek to optimize resource-use based on steady-state models. A decade ago, Roberts et al. (2001) stated that there was much debate concerning variations in climatic conditions during the Holocene and today this lack of consistency in results from similar regions in the WRZ is still evident (Meadows and Sugden 1991, 1993;

Scott and Woodborne 2007a, b; Quick et al. 2011). It is important to try to use multiple proxy analyses rather than relying purely on palynological investigation, in order to gain insight in to a range of environmental and biological parameters. There are several examples of proxies that can provide a reasonably independent record of climate change and that are supposedly less likely to have been influenced by human action in the way that vegetation is affected. These include palaeolimnological indicators of past regional water balance, geochemical proxies such as stable isotopes and mineralogy and biological proxies such as diatoms, ostracods and phytoliths. Other proxies like charcoal and coprophilous spores can provide indications of changing fire history and herbivory. A multi-proxy approach therefore provides a means of looking at the interacting effects of climate and land-use (i.e. fire and herbivory) on vegetation.

It is not clear how intensively land was used before the arrival of the European settlers and this pre-colonial benchmark still needs to be refined. The next step would be to explore palaeoecological evidence more closely, at an even higher temporal resolution (i.e. over the last 2 millennia), to determine the nature, extent, causes and rate of environmental change. Additionally, combining palaeoecological evidence with knowledge from historical ecology may help determine how large the pre-colonial populations were and therefore how extensive the land-use was. Palaeoecological records can provide important information on the rate that plants and other organisms have responded to climatic and anthropogenic change in the past and it can be a vital tool in the management of South Africa’s high biodiversity. As palaeoecologists make better use of theoretical concepts in ecology, there is a greater chance of integrating past (palaeoecology), present (neoecology) and future (predictive ecology e.g. through future climate change modelling). In addition, if palaeoecologists move towards more high temporal resolution studies there is more opportunity to do applied research that can inform conservation and restoration management. Studies that provide a higher resolution would probably be of more benefit to land-owners (both private farmers and reserve managers). Applied palaeoecology could explore the historical interacting effects of climate and land-use in order to determine the present over-riding drivers of vegetation change and thus inform conservation (future resilience of natural vegetation) and restoration (Gillson and Willis 2004; Dearing 2008; Froyd and Willis 2008; Birks 2012).

2.2. Long-term land-use and vegetation change in the winter rainfall zone (WRZ) of South Africa

This synthesis reviews the findings of various historical, archaeological and palaeoecological records to investigate land-use history of the south western region of South Africa. It considers two basic themes of land-use history. The first explores how the environment influences human activities, while the second investigates the main drivers of land-use change. The analysis follows a chronological sequence ranging from the pre-colonial period up until the 21st century. This time frame reflects transitions from nomadic Hunter-gatherers, Khoikhoi pastoralists, European settler agriculture, and the influence of the industrial and technological revolutions on agricultural intensification followed by conservation interventions. The final part of this review will focus on the Swartland region in more detail, concentrating on the development of agriculture and the level of transformation within the Swartland. This literature review also highlights the importance of historical ecology for environmental conservation and provides some context for the interpretation of palaeoecological data. Combining the findings of palaeoecology, historical ecology and archaeology makes the evidence for the role of humans more robust. Thus the integration of long-term ecology to inform conservation is essential.

In a seminal 1959 lecture, C.P. Snow suggested that the critical intellectual weakness of the later 20th century was the separation of humanities from sciences and this lack of integration has been a concern for decades (Snow 1960; Meine 1999; Szabo and Hedl 2011). Historical ecology (also known as ecological history or environmental history) came into being when it was realised that a historical perspective was essential to understand the origins of the contemporary environmental crisis (Oosthoek and Gills 2005). Historical ecology deals with the impact of humankind on the natural world and the influence that the natural world has on human history. It is important that human societies are recognized as integral parts of ecosystems and societal processes are recognized as driving forces of ecosystem change. Historical ecology investigates the human disturbance history of any given region in order to determine the extent of transformation. Once there is an understanding of the drivers of land-use change and how the environment influences human activities, it will enable the partitioning of climatic and anthropogenic effects and therefore the search for significant feedbacks and interactions that may exist between them.

The vegetation structure and composition of the Fynbos biome has been influenced by humans in a number of ways. Fynbos and Renosterveld have been used for the harvesting of edible plants, grazing by domestic livestock, and for the cultivation of crops (Bulpin and Rennie 1983; Wells et al. 1986; Neumann et al. 2011). Fire has been used to aid better pastures for livestock and vegetation has been cleared for ploughing and settlement (Deacon 1992). Alien plants, some of which are invasive, have been introduced both deliberately and accidentally (Le Maitre et al. 1996; Cowling et al. 1997). However, since the Fynbos biome is topographically and geologically heterogeneous, not all regions within the biome have been used by humans to the same extent (Rouget et al. 2003a, b). Because mountainous areas are less accessible than coastal and lowland regions they have generally been used less intensively. Soil fertility within mountains of the Cape is also lower than on the lowlands and therefore, less than desirable for agriculture. As a result, other Fynbos vegetation types (such as West-Coast Renosterveld) have been affected the most over a centennial to millennial timescale.

2.2.1. Pre-colonial period: Hunter-gatherers and Pastoralists

It is well-known that European colonial impacts mark an obvious discontinuity in human-environment relations, but this by no means represents the first cultural disturbance marked in the South African palaeoecological record. The Stone Age (1.5 Myr BP to historic times) in southern Africa is sometimes considered as a single broad technological stage; however, it is a complex period characterized by technological and behavioural innovation which varied spatially across the subcontinent (Jacobs et al. 2008). A burst of technological innovation occurred 80 000-60 000 years ago where finely-shaped, bifacially-worked, pointed stone tools were used as spears and blunted stone tools were most likely used as composite weapons. Following this period of innovation were the expansions of modern human populations within (Forster 2004) and out of (Macaulay et al. 2005) Africa. It is uncertain whether the emergence of innovative technology was a precursor to population expansion (Mellars 2006), or whether population expansion was the stimulus (Behar et al. 2008; Scholz et al. 2007). The main effect on the vegetation and landscape during the Stone Age was selected harvesting of plants and animals, small-scale burning of vegetation and localized seasonal encampments (Hoffman 1997; Jacobs et al. 2008).

Indigenous Hunter-gatherers (locally referred to as San or Bushmen) occupied the Cape region from 10 000-2000 BP. The lifestyle they had established was thought to have minimal effect on the natural resources of the region as they only used small-scale fires in to order to hunt selective grazers (Deacon 1992). Historically, the Cape region supported a diversity of indigenous animals including mammals such as the lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), wild dog (Lycaon pictus), spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus pardus*). Large herds of herbivores such as the African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), buffalo (*Syncerus caffer*), mountain zebra (*Equus zebra*) and quagga (*Equus quagga quaqqa*) were also present as were small antelope species such as blue buck (*Hippotragus leucophaeus*), red hartebeest (*Alcelaphus buselaphus)*, eland (*Taurotragus oryx*) and bontebok (*Damaliscus dorcas dorcas).*

Historical sources (such as ships' log books and diaries of visitors to the Cape) describe the Khoikhoi people that used to live along the western and southern Cape coasts with livestock such as sheep and cattle. The arrival of Khoikhoi pastoralists in southern Africa (from about 2000 BP to historic times) may have drastically altered both the cultural and ecological effect of the indigenous Hunter-gatherers and the landscape. Interestingly, linguistic and physical anthropological evidence shows that the Khoikhoi pastoralists and San were of the same basic southern African ancestry even though they had physical and cultural differences (Singer and Weiner 1963; Westphal 1963). Given this evidence, it is believed that domestic livestock was introduced into southern Africa by an immigrant population of Hunter-gatherers from Botswana (Elphick 1977). The pastoralist economy was adopted by indigenous people who became herders (i.e. Khoikhoi pastoralists), while some remained Hunter-gatherers (i.e. San). A few authors suggest that there was often switching between the two strategies (Marks 1972; Elphick 1977) and these people can therefore be referred to as "Khoi-San hunter/herders". The term Khoi-San hunter/herders will be in the present study to denote the time period up until the arrival of the European settlers. There are four hypothesised origins and routes (see examples by Stow 1905; Cooke 1965; Westphal 1963; and Elphick 1977) but all theories agree that the herders end up in the southern and western

Cape. The southward movement of the immigrant population with their livestock was influenced by the environment and the need to find and exploit new pastures for stock in addition to a wide range of cultural and agricultural activities such as acquiring stock from their neighbours (Deacon et al. 1978).

Historic records indicate that sheep, cattle and goats are not indigenous to southern Africa. Deacon et al. (1978) used detailed archaeological evidence to verify historic records that explain their existence. They excavated a site at Boomplaas Cave in the southern Cape which represented a sequence of human occupation dating from the Upper Pleistocene (ca. 128 000 BP) to the Holocene (from 10 000 years ago until today). They found remains of pottery and stone artefacts (from ca. 40 000 years ago to the Late Stone Age) in the lower parts of the sequence after which the density and range of stone tools declined. This was explained by the availability of metal tools as a substitute during this time. In the upper part of the sequence (ca. 2000 BP), evidence showed that the cave was used as a kraal (animal enclosure), indicating stock-keeping, as demonstrated by the calcined dung layers and identifiable remains of domestic sheep (Deacon et al. 1978). Here, archaeological evidence adequately confirms that the historic adoption of herding played a significant role in the change in organization and economy in the region. It is important to note that travellers' records by European colonialists and visitors to the Cape mentioned that when they arrived there was already a separation between the Khoikhoi pastoralists and hunter-gatherers, both geographically and culturally (Deacon et al. 1978).

The Khoikhoi pastoralists had established themselves in the more productive lowland environments. As a result of the influx of domestic livestock and since hunting had caused a reduction of large indigenous herbivores in the lowlands, it was inevitable for hunter-gatherers to withdraw to more mountainous areas. This change in land-use probably began during the pre-colonial period over 1 000 years before the Europeans arrived in the southern Cape. This suggests that the introduction of three types of herd animals (sheep, cattle and goats) into a habitat where a diversity of indigenous animals predominated would have had a marked effect on grazing, and could also have led to the local demise of indigenous animals in post-colonial times (Klein 1974; see section 2.2.2 below).

Other archaeological studies also provide evidence of a pastoral economy (namely, sheep and pottery remains from about 2000 BP) in southern Africa with a significant occurrence of sheep in the south western Cape from around 1600 BP (Smith 1992a). Cattle remains only appear later (around 1300 BP in the western Cape) in the archaeological record (Smith 1992b), and this matches up with lack of cattle remains found at the Boomplaas cave. Archaeologists have long been puzzled about the inconsistency between the importance of cattle in the historical records and the absence of cattle bones in archaeological excavations. Two hypotheses have arisen because of this: (1) Herders with large herds of cattle had to move frequently to find sufficient grazing, such that domestic debris was thinly scattered and camp sites are not identifiable today; (2) Sizes of Khoikhoi cattle herds only increased substantially after European sailors visited the Cape regularly, thus providing a new market. If the second hypothesis was true then the historically documented pattern may be too short-lived to be evident in the archaeological record.

A study was conducted by Sealy (2010a,b) in order to investigate these two hypotheses. Stable isotope measurements of radio-carbon dated human skeletons were analysed to track changes in the diet of human populations over time. The study was based on the assumption that cattle strongly prefer eating grass instead of bushes or shrubs, whereas sheep are relatively more flexible in their feeding preferences (Sealy 2010). It is known that grasses (which are consumed preferentially by grazing animals such as cattle) contain more ^{13}C (i.e. higher $^{13}C/^{12}C$ ratios) than trees and bushes (which are more likely consumed by sheep) (Sealy 2010a,b). With this in mind, one could assume the proportions of C_3 (trees) and C_4 (grasses)-based foods consumed by humans at a particular time. Sealy (2010) concluded that cattle pastoralism became important in the second millennium AD before European contact. This was because the skeletons had a higher C_4 grasses signal, indicative of people consuming C_4-based foods such as cattle meat and/or milk. Unfortunately, archaeological sites from the pre-colonial time period are scarce and this is why sites have yielded only a few cattle bones.

The palaeo-record confirms historical and archaeological evidence for Khoikhoi pastoralists in the region and provides further information on the effect they had on the environment. Roberts et al. (2001) suggest that grassy habitats in parts of the WRZ may have been replaced by shrub communities with the arrival of herders. Neumann et al. (2011) speculate that higher charcoal values in the palaeo-record after about 2000 cal BP are a result of the arrival of the Khoikhoi pastoralists at the Cape and this is in general accord with the pollen and charcoal analysis of lake sediments in the Central Cederberg (Figure 2) for 2000 BP (Meadows and Sudgen 1991). The early Khoikhoi pastoralists might have experienced a more humid environment than at present, but whether these conditions prompted their arrival or occurred afterwards is unclear as there are uncertainties in chronology and a lack of accurate data. Neumann et al. (2011) reported that the environment remained damp from about 1900-1000 cal BP.

In the study done at Klaarfontein Springs (Figure 2), Meadows and Baxter (2001) found that by 1900 BP Lowland Sand Plain Fynbos and restioid Strandveld communities had established themselves amongst the low hills to the north of Klaarfontein. In addition there was evidence that sheltered ravines around the sandstone hilltops were occupied by scrub and Afromontane Forest elements (indicated by the presence of *Olea*, *Podocarpus* and Santalaceae in the pollen record). Meadows and Baxter (2001) described the uppermost section of the Klaarfontein Springs core as containing pollen that represents vegetation history of both modern and the pre-colonial period. The pollen spectra indicated a decline in grass (Poaceae) pollen from 1900 BP. Along with the decrease in grass pollen, there was an abundance of microscopic charcoal fragments observed and it may or may not be coincidence that these burnt samples correspond with declining grass values after around 1900 BP. This was denoted as a result of the occupation of the area by the Khoikhoi pastoralists during this pre-colonial phase, although climate change cannot be ruled out as the cause.

2.2.2. European colonial period

With the initial intent of establishing a food supply station for East Indian trade route travellers, European tradesmen and farmers were satisfied to remain close to their point of entry at Cape Town during the mid-17th century (Hoffman 1997). However, this human migration to southern Africa had a greater impact on the indigenous people and land than originally anticipated. By AD 1700, the European settlers had expanded northwards (slightly further than the Berg River) and further eastwards (towards the Hottentots Holland Mountains) (Penn 1987) and by the end of the 18th century, the colonialists claimed the entire region south of the Orange River (Bergh and Visagie 1985). After AD 1835, the discovery of valuable resources (namely, mineral and agricultural wealth) meant that there were no restraints to taking control of the interior of the subcontinent, and consequently the European settlers were able to sustain and expand their growing colonial empires.

Impacts on the vegetation and landscape during the European colonial period include: the harvesting of trees for construction and fuel, burning of natural vegetation, an increase in domestic stock numbers which increased grazing pressure, crop cultivation and mining. There was also an increase in hunting activities which lead to a general decrease in indigenous game between ca. 1700s and 1900s) (Klein 1974). Endemic species such as the blue buck and Quaqqa were hunted to extinction (Krug et al. 2004; Krug and Krug 2007). Furthermore, the colonialists introduced a number of exotic plant species including maize (*Zea mays*), grape vines (V*iti vinivera*), oak (*Quercus* spp), pine (*Pinus* spp), gum (*Eucalyptus*), and *Acacia* spp. Some of these species have become highly invasive in the Fynbos biome today (Le Maitre et al. 1996; Cowling et al. 1997; Higgins et al. 1997; Hoffman et al. 2011a). The land-use activities by the European settlers played a major contribution to the disruption of ecological processes in the ecosystem, which led to further transformation of the region. The European settlers were able to displace the Khoi-San hunter/herders and this was possible owing to various factors such as the dispossession of land, livestock and game, or being outnumbered, assimilated and enslaved (Ross 1983). During AD 1713 a European fleet brought the small pox virus and this decimated the Khoi-San hunter/herders populations since they were not immune to the disease (Elphick and Giliomee 1989).

Meadows and Sugden (1991) provide evidence from the Cederberg site (Figure 2) for the significant phase of agriculture during the Holocene epoch since ca. AD 1700. The pollen spectra was noticeably less diverse, Fynbos elements decreased (e.g. Proteaceae) and there was an increase in succulents and disturbance indicators, “weedy” taxa such as Oxalidaceae, Montiniaceae, Plantaginaceae and *Stoebe*-type (referred to as Asteraceae *Stoebe/Elytropappus*-type in the present study). Meadows and Baxter (2001) confirm that anthropogenic impact was the prevailing cause in the determination of vegetation ecology during the last 170 years as indicated by the exponential increase in asteraceous taxa and the prominent decline in Poaceae (likely associated with increased burning of vegetation) found in the Klaarfontein Springs record.

The pollen sequence at Princess Vlei also marks the distinct impact that the arrival of European settlers had on the vegetation of the Cape region (Neumann et al. 2011). Neumann et al. (2011) showed that there was an introduction of oaks and pines in the 17th century, and later an increase in Australian acacias and *Casuarina*. The Europeans also cultivated the indigenous edible plants from the genus *Aponogeton* (locally known as “waterblommetjies”), and this explains its increase in abundance. Anthropogenic activities seemed to have caused a shift from natural Fynbos vegetation to Grasslands and this can be seen in the prominent decrease in Restionaceae and increase in Poaceae pollen. In the same way that Roberts et al. (2001) questioned the observations in the pollen record being of anthropogenic rather than climatic origin, Neumann et al. (2011) state that it is debatable whether the recent increased occurrence of aridity indicators (Asteraceae and maybe Chenopodiaceae) in the pollen record signifies a drying trend as opposed to human disturbance. After colonisation by the Europeans, there is a period which is characterised by an increase of charcoal which possibly indicates a period of regular burning.

Recent studies conducted in the semi-arid Karoo, Eastern Cape have made the link between livestock and soil erosion (Keay-Bright and Boardman 2007; Mighall et al. 2012). The study by Mighall et al. (2012) showed palaecocological data (fossil pollen and coprophilous spores) coupled with sediment tracing techniques since AD 1930. Their findings were consistent with historical agricultural land-use for the region. With this in mind the following question could be posed: “What irreversible effect has disturbance by domestic livestock had on the vegetative landscapes of the Cape Floristic Region in South Africa?”. Simply de-stocking livestock in the over-exploited rangelands of South Africa will not necessarily reverse the problem, but perhaps considering the effects that indigenous herbivores had on the environment during the Holocene will assist in future management of the land.

2.2.3. Agricultural intensification and conservation period

Regional landscape transformation as a result of the impact of settlements, agriculture practices and transportation networks intensified during the post-colonial period together with a significant growth in human population. Agriculture was the practice with the greatest impact on the vegetation of the Fynbos biome. The agricultural industry first emerged around Stellenbosch and Paarl. However, after transportation networks improved and markets increased in the late 18th century, the industry shifted to the relatively fertile, fine-grained Renosterveld soils of the Swartland (West-Coast Renosterveld) and Overberg (South-Coast Renosterveld) regions. Although transformation of the Swartland and Overberg took place at varying rates the end result is that between 91-97% of Renosterveld has been transformed (Rebelo 1992; von Hase et al. 2003, Rouget et al. 2003a, b; Rebelo et al. 2011). During a period of 77 years (between AD 1911-1988), the area under cultivation in the Swartland region had more than doubled in size (i.e. from 169673.5 ha to 347280 ha) (Figure 3, Appendix 1. Table A1).

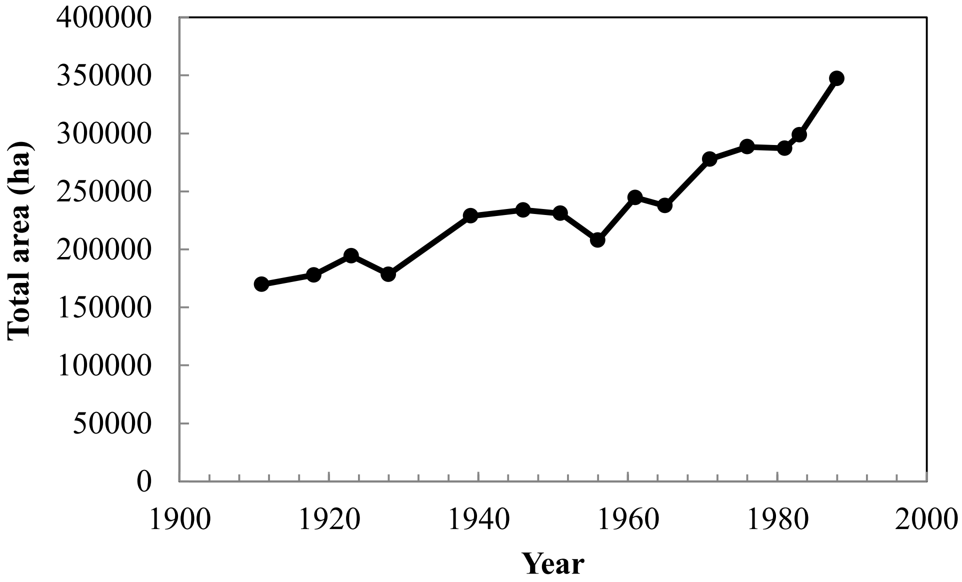


Figure 3: Area (ha) transformed for cereal/grain cultivation (barley, oats, rye, wheat, maize and lucerne) between AD 1911 and 1988 in seven magisterial districts (Hopefield, Malmesbury, Morreesburg, Piketberg, Tulbagh, Vredenburg and Wellington) in the Swartland region (west coast of the Fynbos biome). Data are from Agricultural Censuses.

Crops (such as wheat, oats and vines) which were introduced by European settlers are able to thrive in the Mediterranean-type climate of the region. The cultivation of these crops has thus heavily affected one of the richest vegetation types of the Fynbos biome evident to date.

A study conducted by Meadows (2003) successfully revealed the implications of past and present agricultural policy and practice on the vegetation of the region. For example, a Wheat Importation Restrictions Act was established in South Africa in 1930, which put an end to the importation of wheat or flour. Up until this time, the importation of wheat represented up to 30% of South Africa's requirement. As a result of this Act, there was an increase in production of wheat in the Swartland region by 1934 of up to 40% (Meadows 2003) (see Figure 3). This legislative pressure influenced farmers to transform even more pristine land for agriculture. Although land degradation was recognised in the region after the initial European colonisation in the mid-17th century, it was not until the early 20th century that these concerns were addressed through legislation and policy (Meadows 2003). Over the years intensive land-use has caused a great amount of soil erosion and as a reaction to the devastation, conservation efforts were proposed to aid in the 'recovery' of the Swartland landscape. The Soil Erosion Advisory Council was established in 1930 (Hoffman and Ashwell 2001) and in 1946 the Soil Conservation Act was promulgated. Once again political pressure was the driving force behind the change in land-use and as a result of the active process of policy intervention there was a dramatic reduction in gully densities and in soil erosion overall (Meadows 2003). Land-use change has continued within the Swartland region in the 21st century. Halpern and Meadows (2013) reported the general increase in urbanization and the shift in agricultural practices from primarily grain cultivation towards wine grape cultivation. They warned that this change in land-use type may affect water and soil resources and future climate change poses great implications for land degradation, resource depletion and soil erosion (Halpern and Meadows 2013).

Despite the conservation acts that were set in place, by the time governmental institutions undertook formal conservation practice in Renosterveld vegetation, most of it had already been transformed for agriculture (Newton 2008). However, there have been a number of early studies that have investigated the conservation value (Levyns 1956; Tansley 1982) as well as social and legal factors affecting the conservation of West-Coast Renosterveld by private land owners (MacDowell 1988). A number of formal nature reserves have been formed in order to protect West-Coast Renosterveld. Such reserves include the Darling Nature Reserve (20 ha) established in 1922, Tygerberg Nature Reserve (300 ha) and Elandsberg Private (ca.1000-1600 ha of Renosterveld) both proclaimed in 1973. However, >90% of the land within the Cape Lowlands is privately owned and falls outside of the formal protected area network (von Hase et al. 2010). Farmers are therefore *de facto* custodians of the CFR's most critically endangered vegetation type. For this reason, in addition to the establishment of nature reserves, current conservation efforts need to include informal stewardship agreements with private land owners.

More than a decade ago, the "Fine-Scale Conservation Plan for Cape Lowlands Renosterveld", was produced by von Hase et al. (2003). This report provided the perspective (e.g. fine-scale planning and conservation goals) needed for current and future conservation practice. In order to allocate limited conservation resources judiciously and ensure conservation success, systematic conservation planning is essential (Cowling and Heijnis 2001; Cowling and Pressy 2003; von Hase et al. 2003). von Hase et al. (2010) demonstrated that there has been cohesion between conservation planning and implementation since the Fine-Scale Conservation Plan for Cape Lowlands Renosterveld in 2003 (von Hase et al. 2003), with an increase in vegetation protection through both contractual and informal agreements. If natural vegetation is conserved then the likelihood that supporting and regulating ecosystem services (e.g. soil fertility and pollination) will act as inputs to production on agricultural lands increases (Swift et al. 2004; Zhang et al. 2007). Thus conservation is beneficial to agriculture, because it helps to ensure the ecosystem services upon which agricultural systems depend.

2.2.4. Conclusions for land-use review

Humans are not always considered as an intrinsic ecological factor in current research. Recognising this downfall and making an effort to understand the historical ecology of a region may boost conservation efforts today; both climate change and land-use must be considered when planning conservation strategies (Margules and Pressey 2000; Hannah et al. 2002; Pressey et al. 2007). As will be explored in the interpretation of pollen data (chapter 6), this review demonstrates that various human activities leave their impression on the landscape long after they have occurred and that societal processes can have both a negative and/or positive effect on the natural environment. Although West-Coast Renosterveld has been radically transformed, it has been shown that environmental awareness amongst land users and managers coupled with rigorous legislation and political drive, can change exploitation practices to those that are more sustainable in the long term. An improved understanding of land-use history in the south western region of South Africa will help in the construction of baseline vegetation patterns that may have existed during pre-colonial and pre-pastoralist periods, informing restoration efforts and future conservation management. If the hypothesized 'pristine' conditions of the past are compared with increasing human disturbance over time and the conditions that are seen today, then benchmarks for the future can be established. These benchmarks will support the design of appropriate conservation and management strategies for sustainable environmental land-use in the future.

2.3. West-Coast Renosterveld ecology, conservation and management

2.3.1. Renosterveld ecology and classification

Renosterveld is classified as an evergreen, fire-prone Mediterranean-type shrubland or asteraceous shrubland (Specht and Moll 1983; Rebelo et al. 2006) with mainly tussock (or bunch) grasses and a high diversity of geophytes. The vegetation consists of evergreen asteraceous shrubs with small cupressoid leaves, such as *Eriocephalus, Helichrysum, Oedera, Pteronia* and *Relhania* and is dominated by *Elytropappus rhinocerotis* and *Stoebe plumose*. Other important shrub families (and genera) include Boraginaceae, Fabaceae, Malvaceae, Rosaceae (*Cliffortia*) and Rubiaceae (*Anthospermum*). It also has an understory of grasses (Poaceae) (Goldblatt and Manning 2002). Renosterveld is also known for its high diversity of geophytes which include monocots such as Amaryllidaceae, Asparagaceae, Iridaceae, Hyacinthaceae, Orchidaceae and dicots such as Oxalidaceae and Geraniaceae (Boucher 1980; Moll et al. 1984; McDowell and Moll 1992; Rebelo et al. 2006). Some geophytes species (such as *Freesia, Ixia, Ornithogalum* and *Pelargonium*) are now economically important world cut-flowers (Rebelo et al. 2006).

The origin and application of the word 'Renosterveld', and the current extent of the Renosterveld vegetation is a subject of debate. This is partly due to different authors' perceptions of the vegetation they encountered from the 18th to 21th century (Meyer 1875; Adamson 1938; Talbot 1947; Acocks 1953; Boucher 1980; McDowell 1988; Low and Rebelo

1996; and Cowling and Heijnis 2001; Mucina and Rutherford 2006). Other names and spellings for Renosterveld include ‘Rhenosterveld’, ‘Rhenosterbosveld’ and ‘Rhenoster shrub land’. The literal Afrikaans translation of ‘Renosterveld’ is ‘rhinoceros vegetation’. This could either refer to the historical presence of the black rhinoceros (*Diceros bicornis*) in the landscape or it could be a reference to ‘Renosterbos’ which is the dominant asteraceous shrub *Elytropappus rhinocerotis*. This species is a low shrub with greyish-green shoots and cupressoid leaves (Talbot 1947; Boucher 1980). Ironically, *Elytropappus rhinocerotis* was only fed on by the black rhinoceros whilst other livestock were deterred by the presence of phenolics in the shrub (Rebelo et al. 2006). Additionally, the dark, dull, grey appearance of the vegetation looks similar in colour to rhinoceros hide (Levyns 1972) and also could be the origin for the term ‘Swartland’, which translates into ‘black land’ (Boucher 1980).The word ‘Renosterbos’ has also gone through many variations over the years but it is important to note that it was the word originally used to describe several *Stoebe* species which resemble *Elytropappus rhinocerotis* (Burchell 1822). Furthermore, the name *Elytropappus rhinocerotis* has recently been changed to *Dicerothamnus rhinocerotis* (Koekemoer 2002) however this is not a peer-reviewed publication. For the purpose of this study the terms *Elytropappus rhinocerotis* and Renosterbos will be used because it is commonly used in recent literature (Newton 2008; Vermeulen 2010; Kehinde and Samways 2012; Mills et al. 2013). Additionally, the pollen of *Stoebe* spp and *Elytropappus rhinocerotis* are mostly indistinguishable using a compound light microscope. Previous studies have referred to these two pollen types as “*Stoebe*-type” (Meadows and Baxter 2001; Scott and Woodborne 2007; Neumann et al. 2011; Quick et al. 2011) or “Asteraceae low-spine” (Meadows et al. 2010) and therefore will be referred to as the Asteraceae *Stoebe/Elytropappus*-type pollen in the present study.

Acocks (1953) was the first to describe Renosterveld as a separate vegetative entity to Fynbos, calling it “Coastal Rhenosterbosveld" and “Mountain Rhenosterbosveld”. He also recognized that the coastal Renosterveld found on the west coast was different to the Renosterveld of the south coast and they were separated by the Hottentots-Holland Mountains. Within the context of the present study, West-Coast Renosterveld (Renosterveld vegetation found on shale-derived lowlands of the ‘Swartland’/west coast region of the Western Cape) is the primary focus although there are some instances where West-Coast Renosterveld is compared to South-West Coast Renosterveld (also known as Overberg

Renosterveld). Low and Rebelo (1996) acknowledged that in cases where West-Coast Renosterveld occurred under higher rainfall conditions, Fynbos elements became more prominent and the boundary became more diluted and thus difficult to differentiate. Cowling and Heijnis (2001) used the boundaries set by Low and Rebelo (1996) and came up with a classification system in which Broad Habitat Units (BHU) were identified. The advantage of their study was that they allowed for factors such as geology, topography and climate to play a role in further subdividing Renosterveld. Specific to West-Coast Renosterveld alone, they identified two distinct blocks: Swartland Coastal Renosterveld in the north-west region and Boland Coastal Renosterveld in the south-west region. The most recent vegetation classification (Mucina and Rutherford 2006) focuses on the geological component and what vegetation type it is likely to support. Within the Fynbos biome 14 vegetation units were described of which four Renosterveld units were identified. These are: Shale Renosterveld, Granite and Dolerite Renosterveld, Alluvium Renosterveld and Silcrete and Limestone Renosterveld (Mucina and Rutherford 2006).

The classification of Renosterveld vegetation is based on the few fragments (ca. 3-5%; see section 2.3.5.) that remain after centuries of cultivation and grazing. Therefore, it is debatable what pristine Renosterveld should consist of but it has been speculated that it is greatly influenced by previous land-use disturbance (see section 2.3.3.4. below for further discussion). Early reports have suggested that Renosterveld was predominantly grassy (Thom 1952, 1954) before the European agricultural period. This hypothesis has been supported by other authors (Levyns 1956; Cowling et al. 1986; Newton 2008). Newton (2008) proposed that prior to the arrival of Khoikhoi pastoralists 2000 BP, West-Coast Renosterveld consisted of a shrubland-grassland mosaic with a dominance of shrubs. The land-use impacts by the Khoikhoi pastoralists and their animals converted these shrub-dominated areas it to grasslands. However, when European colonialists arrived they transformed the “grassy shrubland” to a “shrubby grassland” through agricultural practices (Newton 2008). Therefore it could be argued that the current state of Renosterveld is “degraded Grassland”. An alternative argument could be that Renosterveld is merely “degraded Fynbos”. Before the classification by Acocks (1953), many early classifications (AD 1872-1936) of Renosterveld did not recognize it as a separate entity to Fynbos (Newton 2008). A recent study conducted by Curtis (2013) using stable isotope analysis in Overberg Renosterveld suggests that Renosterveld was previously comprised of C_3 shrubs and grasses as opposed to C_4 grasses being the dominant component. Instead the original compositional state was most likely a combination of C_4 and C_3 grasses and shrubs. This suggests that Renosterveld was never purely a C_4 Grassland as previously speculated (Thom 1952, 1954; Cowling et al. 1986) but rather a grassy-shrubland (Newton 2008; Curtis 2013) and there may be variation between West-Coast and South-Coast Renosterveld with more C_4 grassy components in the south (Curtis 2013). Further investigation of the composition of pristine West-Coast Renosterveld is essential to corroborate these findings for conservation management and restoration if the structural integrity and diversity of the system is to be preserved.

2.3.2. Geology, soils, and climate of West-Coast Renosterveld

West-Coast Renosterveld occupies an area of 6 141 km² (Boucher 1980; Moll *et al.* 1984; Low and Jones 1995) in the coastal foreland between Piketberg and Somerset West. The topography of West-Coast Renosterveld is relatively flat with a few notable hills. South-Coast Renosterveld in the Overberg region, however, has greater topographic variation with the average difference between hilltop and valley bottom being more than twice that typical of the West-Coast Renosterveld region (von Hase et al. 2003). This vegetation occurs on fine-grained clay and silt soils that are generally nutrient-rich. They are derived from Devonian-Ordovician sediments (Bokkeveld Group) and underlying Precambrian sediments of the Malmesbury Group (Deacon et al. 1992). During the breakup of Gondwanaland, these ancient sediments were exposed and then folded in the 50 million years which followed, after which the geology has remained relatively stable (Cowling 2001). The majority of the undulating plains that underlie West-Coast Renosterveld is made up of Malmesbury shales (86%) with granite (6%) and silcrete (3%) soils found to a lesser extent (Deacon et al. 1992; Rebelo et al. 2006). The type of West-Coast Renosterveld that falls within the scope of this study is Swartland Shale Renosterveld (Figure 7; refer to study site chapter 3 section 3.1.3.). For more details regarding the other Renosterveld types see Rebelo et al. (2006) in Mucina and Rutherford (2006).

West-Coast Renosterveld is located in a region that experiences a typical Mediterranean climate with summer drought and winter rainfall. During the summer months (October-March) temperatures can reach up to 40 °C, but are likely to remain between 15-27 °C. Winter months (April-September) are usually frost free with the exception of some low-lying areas where temperatures may fall below 2 °C. The cold Benguela current carries dense polar water up the southern African west coast and is responsible for relatively stable climatic conditions in the region. It is also a source of fog which provides an important additional input of moisture. The prevailing trade winds from the south-east generate high wind speeds during summer months (Deacon et al. 1992) whilst during winter months the winds come from the north-west (Taylor 1996). About 80% of the rainfall occurs from April to September. The altitude of West-Coast Renosterveld ranges between 10 and 450 m above sea level and rainfall variation is significantly related to altitude. Low altitudinal areas receive approximately 350 mm per year where as higher altitudes receive approximately 700 mm per year (Lambrechts 1998). This rainfall regime is suitable for rainfed crop production. Previous palaeoecological studies in the Western Cape area suggest that the climate has remained remarkably constant over the last 14 000 years (Meadows and Sugden 1991a) whereas others suggest more variability in rainfall and climate (Scott and Woodborne 2007a, b). For a more in depth discussion on the palaeoclimate of the Western Cape, see previous section discussed above.

2.3.3. Renosterveld dynamics and relation to other vegetation types

2.3.3.1. The Fynbos-Renosterveld transition

Both Fynbos and Renosterveld vegetation types are characterized by very high species diversity although Fynbos may be slightly higher in endemism (von Hase et al. 2003). Many families and genera (apart from geophytes) are shared between Renosterveld and Fynbos but Fynbos families such as Ericaceae and Proteaceae are relatively uncommon in Renosterveld. Very few species are shared except for instances where boundaries are often diffuse such as in the shale and granite Fynbos types (Rebelo et al. 2006). Renosterveld is reported to have faster growing rates and finer fuel grasses, thus is required to burn more frequently (3-5 years, especially in higher rainfall areas) than Fynbos (10-25 years) (Rebelo et al. 2006).

Since both Fynbos and Renosterveld are dominated by fire, the Fynbos-Renosterveld boundary is not controlled by fire and therefore cannot be used as a differentiating component. Therefore other habitat components such as annual rainfall and geology (i.e. substrate type and leaching) are used when separating Renosterveld and Fynbos vegetation (Rebelo et al. 2006). In areas where relatively higher rainfall is received (usually over 500 - 800 mm), Renosterveld is replaced by Fynbos and typically Renosterveld occurs on clay and silt and not on sandstone and quartzite. It is the combination of the increase in fire frequency, soil fertility and aridity, which results in the increased frequency and diversity of geophytes (Kruger 1979).

2.3.3.2. The Renosterveld-Succulent Karoo transition

Rebelo et al. (2006) found that Renosterveld formed the ecotone between Fynbos and Succulent Karroo on shale and alluvium substrates but that the transition between Renosterveld and Succulent Karroo had never been studied fully. It is suggested that the boundary is controlled by levels of succulence and aridity so that in areas where less rainfall is received (usually below 250-300 mm) Renosterveld is replaced by Succulent Karoo shrublands. The boundary is also determined by levels of flammability of the vegetation so unlike the Fynbos-Renosterveld boundary it is controlled by fire. In contrast to the Fynbos-Renosterveld transition, Succulent Karoo vegetation is too sparse to carry fire and plants are not fire adapted. While most authors classify Renosterveld as a sub-type of the Fynbos biome, some classify Renosterveld as a component of ‘karroid’ vegetation (Cowling et al. 1997). Evidently Renosterveld forms transitions with both Fynbos and Succulent Karoo but whether it is a degraded form of vegetation or a distinctive form with overwhelming diversity is still uncertain, and thus requires additional research.

2.3.3.3. Climate as a driver of Renosterveld vegetation dynamics

Although climate influences plant growth, reproduction and mortality and is one of the key drivers of vegetation change (Stenseth et al. 2002; Walther et al. 2002; McDowell 2011; Jamieson et al. 2012), its role as a regional driver in Renosterveld vegetation dynamics has not been widely addressed in the literature. Generally, Renosterveld occurs along a rainfall gradient between more mesic Fynbos elements and arid Karoo or thicket elements (as discussed above). Given that anthropogenic-induced climate change could cause an increase in temperatures and drought periods (Boko et al. 2007; Toggweiler and Russell 2008; Haensler et al. 2011), it would be expected (given the correct substrates) that Renosterveld elements would invade Fynbos vegetation and karroid or thicket elements would invade existing Rensoterveld remnants wherever existing transitions occurred.

A few studies have addressed historic climate change in the Cape Floristic Region (CFR) (Kruger and Shongwe 2004; Midgley et al. 2005; Power and Mills 2005; Haensler et al. 2010; Hoffman et al. 2011b) but only the study conducted by Haensler et al. (2010) covers a long enough time series (from AD 1901-2006) meaningful to the present study. Long-term weather station data are scarce for the southern African region, hence Haensler et al. (2010) used the global CRU3 dataset available at a horizontal resolution of 0.25-0.5 degrees from the Climate Research Unit for southwest Africa. Haensler et al. (2010) reported an increase in average temperature of 0.1 to 0.2 °C per decade. It was found that the western region of South Africa was one of the regions that experienced the most rapid warming and that more warming occurred during the second half of the study period (ca. AD 1953-2006) (Haensler et al. 2010). This finding was supported by Warburton et al. (2005) who noted that temperatures were higher in AD 1980-2000 compared to AD 1950-1970. Contrary to the temperature data, historic rainfall data show no uniform pattern for southwest Africa and no significant trends emerge. However, a study conducted by Midgley et al. (2005) reported rainfall trends for the Western Cape from AD 1950-1999. They found that lowland areas had become more arid while mountainous areas had received more rainfall over the period that they examined. A recent study conducted by Hoffman et al. (2011) reported on climatic variable recorded at 20 weather stations within the WRZ of the CFR from 1974-2005. They found that there was a significant increase in temperature while there was little change in rainfall; however, Hoffman et al. (2011b) noted that other variables such as pan evaporation and wind-run need to be considered when assessing the effect of climate change on vegetation in the future. They noted that during this study period pan evaporation and wind-run decreased significantly. However, even though the evaporative demand had declined over time, the combination of these with increasing temperatures could increase heat stress of plants during the summer droughts of the Mediterranean -type climate.

Long-term vegetation records obtained through palaeoecological studies can be used to track vegetation dynamics in relation to past climates and thereafter used as a modelling tool to predict vegetation patterns for future climate change scenarios. However, there have been few studies in Renosterveld (Figure 2). This tool is not only compromised by the circularity of using fossil pollen as a climate proxy but there is also uncertainty in future climatic predictions. Anthropogenic-induced climate change presents a serious challenge to conservation owing to the uncertainties of the potential trajectory of climate change at the regional level and the many unknown biological responses to climate change. Despite the uncertainty, the most recent future climate predictions for the CFR include a decrease in precipitation (30-50%), a general decrease in high intensity events of precipitation, an increase in temperature (up to 1.5 and 3.5 °C) with an increase in drought periods and shorter rainy seasons (Haensler et al. 2011).

2.3.3.4. Land-use disturbance and the role of fire and herbivory

Fire and herbivory are important disturbance factors. The types of disturbance in question are described as endogenous disturbance (factors arising due to biological interactions such as herbivory) and exogenous disturbance (factors usually arising outside the area such as fluctuations in physical factors and catastrophes such as fire). Although disturbance disrupts community structure there are also beneficial effects such as ecological succession which occurs after disturbance. The most current and major land-use pressures for Renosterveld vegetation (Cowling et al. 1999b; Heijnis et al. 1999; Kemper et al. 1999) include (1) Agricultural expansion, usually by ploughing for new crops or high intensity grazing of stock. The main crops that are grown in Renosterveld include wheat, barley, oats, rye, deciduous fruit, forage (e.g. Lucerne), olives and vineyards. For more than the last decade some farmers have used minimum tillage (also known as conservation tillage) (Fowler 1999), which has reduced the effect of ploughing and burning. Overgrazing by sheep and cattle can also be problematic in some areas but more so in the Overberg than in West-Coast Renosterveld. Another widespread, but less obvious, negative effect of agriculture includes the indiscriminate spraying of herbicides and pesticides. (2) The spread of invasive alien plants (e.g. *Eucalyptus* spp, *Acacia* spp, *Pinus*) mostly a result of the leaching of fertilizer from fields used for agriculture. Invasive annual grasses are a major threat to the rich bulb flora found in West-Coast Renosterveld (Vlok 1988). (3) Urban development and associated infrastructure (e.g. pipelines and roads) also pose a threat to Renosterveld vegetation.

The nature of disturbance differs in diverse environments and what is considered disadvantageous disturbance for one species may have little or no effect on the next species. For example, thicket taxa are fire-sensitive while Renosterveld and Fynbos taxa are fire-prone (van Wilgen et al. 2012). Owing to the inherent resilience and dominant species having short maturation times, Renosterveld is thought to be adapted to a fairly frequent fire regime in comparison to Fynbos (Boucher 1980). It seems that a shorter fire frequency is tolerated by vegetation in wetter areas, and Renosterveld can generally persist for longer without fire than a similar area of Fynbos (von Hase et al. 2003). Current recommended fire frequency is 3-5 years, but there is still debate over optimal fire frequency (Rebelo et al. 2006; Curtis 2013) and there is no evidence that the current vegetation assemblage is not an artifact of too frequent burning. Similarly, there is debate over the optimal stocking levels of herbivores. Today West-Coast Renosterveld is ecologically important for the Geometric Tortoise (*Psammobates geometricus*) since it is endemic to the region, and is one of the rarest tortoise species in the world (Baard 1993). Historically, however, the fertile soils of West-Coast Renosterveld supported mammals, large herds of herbivores and antelope species which became locally extinct due to hunting during the post-colonial period (i.e. between ca. 1700s and 1900s) (Klein 1974). Land-use changes (with transitions from nomadic herding to permanent settlement) that have occurred in West-Coast Renosterveld over time have also affected some key processes such as herbivory and fire.

Although fire and herbivory are two separate forms of disturbance, fire can also be indirectly linked to herbivory because post-fire environments attract grazers to new plant growth (Bond and van Wilgen 1996). Historically, fire was coupled with grazing and different groups of people living in the south-western part of South Africa used fire in different ways. The San (Hunter-gatherers) used fire-stick farming as a means to stimulate grass growth in order to capture selective grazers. This practice was speculated to have probably been with small groups of herbivores and within infertile environments in the Fynbos biome (Deacon 1983). The fires were regarded as small scale (Deacon 1992), implying that the land-use impact of the San was probably not detrimental to the structure of the vegetation. During this time, the main form of disturbance was probably as a result of indigenous herbivores. Their grazing, browsing and trampling promoted plant diversity as they created gaps in the landscape. Recent studies have found that one of the main dispersal syndromes for Renosterveld (apart from wind-dispersal) is endozoochory, whereby grasses and some geophytes were dispersed by animals (Shiponeni 2003; Shiponeni and Milton 2006). During the period when San were common in the region it is thought that West-Coast Renosterveld consisted of a shrubland-grassland mosaic (Newton 2008).

In contrast to the lifestyle of the San people, hunting pressure by the Khoikhoi pastoralists is thought to have been relatively low (Klein 1974; Krug and Krug 2007). However, pastoralists applied pressure on the fertile coastal lowlands through the use of fire on a larger scale. They utilized a short fire cycle by burning areas to stimulate plant growth before returning to the same area 1-4 years later for intensive grazing by their livestock (cattle, sheep and goats). This form of land-use is thought to have created a regime of seasonal disturbance (Thom 1952, 1954; Deacon 1983). The resting period after burning implies that grasses were not grazed immediately after fire and therefore grasses were not heavily utilized in the immediate post-fire environment. Therefore, the impact on the vegetation due to seasonal burning and grazing by the Khoikhoi pastoralists was assumed to have caused a shift from Renosterveld shrublands to grasslands and the landscape became more homogenous (Thom 1952, 1954; Cowling et al. 1986; Newton 2008).

Unlike the land-use disturbance brought about by the Khoikhoi pastoralists, the European settlers were sedentary which meant that livestock was mostly held stationary. In this case even shorter fire cycles were applied to promote sufficient pastures for grazing. When European colonialists first arrived in the region there was an increase in human population numbers and hence an increased use of fire and its impact on the environment (Botha 1924). During the colonial period hunting pressure on indigenous game also increased significantly. During the 1700s, endemic species such as the blue buck were hunted to extinction (Krug et al. 2004; Krug and Krug 2007) and the Quaqqa became extinct in the early 1900s (Newton 2008). The Mountain zebra and the leopard were the only two types of large mammals that survived as they were able to survive in the mountains. Consequently the large indigenous herbivores which played a major role in the former disturbance regime were taken out of the system. Studies have shown that they have the ability to aid seed dispersal (Shiponeni 2003; Shiponeni and Milton 2006) as well as influence competition between plant species (Adamson 1938). Thus herbivory is an important driving force behind succession of vegetation and significantly influences the structure and function of ecosystems.

2.3.4. Theoretical frameworks for understanding vegetation dynamics

2.3.4.1. Disturbance, patch dynamics and scale

A disturbance is any isolated event that disrupts community structure by changing available resources, substrate availability or the physical environment. Since disturbance disrupts community structure it therefore prevents equilibrium in a system. There has been much debate around theoretical views regarding the equilibrium, disequilibrium or non-equilibrium systems of rangelands (Illius and O'Connor 1999; Sullivan and Rohde 2002). According to the equilibrium view, when a community is disturbed it will develop through a series of predictable stages, known as succession (Clements 1916; Connell and Slatyer 1977; Drake 1990). According to successional theory, the transformation is usually time-ordered, organized changes in composition, structure and function. It may reach a relatively stable state whereby climax characteristics are obtained. For example, *Elytropappus rhinocerotis* is considered a typical climax species in Renosterveld for as long as there is no disturbance. However, sometimes it undergoes continual succession as one species is replaced by a new species (Kruger 1984; Kraaij et al. 2013) or cyclic succession where each species alternated with one or two others (Walker and Moral 2003). In the disequilibrium view, a stable climax community is unlikely to be reached, or will be transitory, because extrinsic disturbance will constantly send the system away from equilibrium. In the non-equilibrium view, systems may tend towards and equilibrium, but the equilibrium will not persist because of intrinsic or extrinsic factors (Gillson and Hoffman 2007).

Varying levels of disturbance (whether it is frequency or intensity) affect systems differently, such that if there is too much disturbance it could lead to the extinction of some species (Tilman 1982). This is because species that are able to cope in high disturbance areas (like ruderal plants or animals) outcompete them. On the other hand, when disturbances are low the system can go into a state of competitive equilibrium (Alley 1982; Hirzel and Le Lay 2008) and this causes species with a low competitive ability to be lost from the system. An intermediate level of disturbance is thought to be optimal for biodiversity (Connell 1975), but defining intermediate levels is difficult without long-term and/or experimental data. The effect of disturbance on diversity seems to be dependent on the trade-off between dispersal and competitive abilities (Connell 1975). Boucher (1980) suggested that the intermediate disturbance hypothesis best applies to Renosterveld vegetation. Biodiversity tends to be greatest when vegetation is subjected to intermediate frequencies or spatial scales of fire, herbivory and the period of time without disturbance (Milton 2007). The Renosterveld system in which the study has been conducted is fire and herbivory driven, anthropogenically disturbed and this disturbance is likely to prevent equilibrium in the system. If disturbances occur at small spatial scales, then the system may remain meta-stable at the landscape level despite the instability or non-equilibrium of individual patches. For example, in Renosterveld, individual patches might contain different proportions of grass, shrub and thicket elements under intermediate fire and grazing pressure (Figure 4; Cowling et al. 1986; Rebelo 1995; Ludwig et al. 1997; Milton 2007).

Figure 4 shows the influence that different frequencies and intensities of fire and herbivory can have on compositional structure and hence biodiversity within a Renosterveld landscape (Cowling et al. 1986; Rebelo 1995; Milton 2007). The timing of fires (i.e. burn season in autumn versus spring; Levyns 1935; Cowling et al. 1986) and grazing (i.e. immediately after a burn or not; Rebelo 1995) are also important factors that will effect biodiversity and patch structure (as discussed below). Specifically, it is the combination of a spring fire with grazing that prevents the grasses from setting seed and propagating, therefore benefiting *Elytropappus rhinocerotis* (Renosterbos) and other winter-seeding shrubs (e.g. *Athanasia* and *Relhania)* that are unpalatable and often ignored by livestock (Figure 4). Alternatively, the combination of an autumn fire with grazing prevents the shrubs from setting seed and therefore grass recruitment is favoured. “Sweet Grassland” (e.g. *Themeda triandra*) becomes more dominant, and as a result is ideal for livestock management. Generally, an increased fire frequency in conjunction with overgrazing (removing of fuel load) immediately after burning tends to give the opposite outcome desired by livestock farmers since grassy Renosterveld (also known as “Grassy Shrubland”; (Figure 4) becomes dominated by unpalatable shrubs (Rebelo 1995) and perhaps even promoting Succulent Karoo elements in Renosterveld (Mucina and Rutherford 2006). If the initial state is “Grassy Shrubland” that is not exposed to fire or grazing, with time it will tend towards “Thicket” and perhaps favour browsers more than grazers.

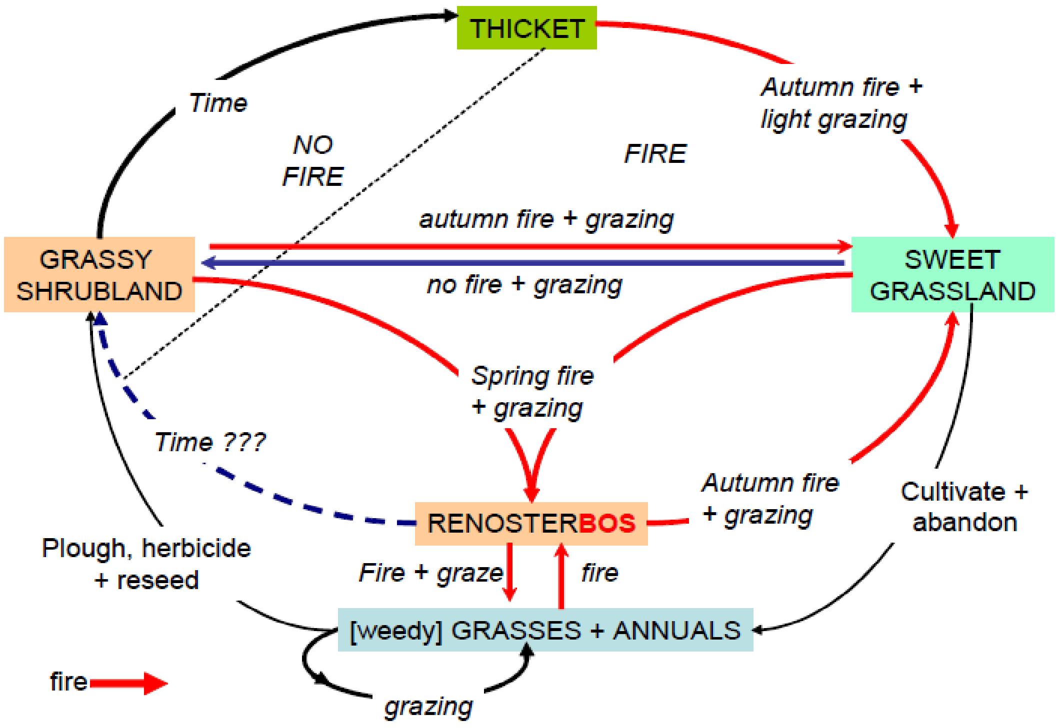


Figure 4: Conceptual model (adapted by Milton 2007 from Rebelo (1995) and Cowling et al. (1986)) showing how fire and grazing interact to result in different compositional states of Renosterveld.

Figure 4 also considers the vegetation dynamics that occur after ploughing. For example, old abandoned fields that were previously comprised of Renosterveld vegetation are initially colonised by annual forbs and grasses. If these old fields are open to grazers and fire is excluded then they are maintained and classified as “Weedy Grasses and Annuals” since they are abundant in lawn grass (*Cynodon dactylon)* and weedy winter-growing annuals (McDowell 1995; Walton 2005). Unfortunately, this has the potential to decrease biodiversity as the weeds exclude indigenous perennial grass and also prevent shrubs from establishing (Midoko-Iponga et al. 2005). Although with the correct restoration efforts such as ploughing, burning, the use of herbicide to clear weeds and subsequent reseeding, can promote a more species-rich state of Renosterveld. An example of a more species-rich state would be Renosterveld comprised of residual indigenous geophytes (Musil et al. 2005), wind-dispersed indigenous Asteraceae and indigenous grasses and geophytes dispersed by animals

(Shiponeni 2003; Shiponeni and Milton 2006). In contrast, it is possible that an alternative stable, degraded state could be reached at the landscape level (as discussed below) if intense grazing and fire are at spatial scales that disturb the patch structure which is maintained over time. In this case intense grazing and fire pressure might homogenise patch structure leading to overall dominance of *Elytropappus rhinocerotis* (Renosterbos).

It has been identified that an intermediate disturbance is desired to maintain Renosterveld biodiversity and patch structure, but it is difficult to define the term “intermediate” when a baseline condition does not exist. Regardless of the findings about the importance of animal-dispersal in Renosterveld (Shiponeni and Milton 2006) and the advancement in conceptual models (e.g. Figure 4; Milton 2007), still very little is known about the role of large herbivores and fires in the dynamics of West-Coast Renosterveld vegetation (Cowling et al. 1986, Rebelo 1992b; Newton and Knight 2004; Radloff 2008). Pre-colonial levels of fire and herbivory disturbance are still not known and this is why a historical or long-term perspective is necessary in order to compare with the current state of remaining West-Coast Renosterveld vegetation.

In addition to this temporal perspective, the consideration of scale is also important. The consequences of disturbance at the patch scale need to be considered at the landscape level. Landscape ecology is the study of the relationship between spatial patterns and ecological processes over a series of scales. A landscape scale perspective is important in West-Coast Renosterveld vegetation dynamics, since it encompasses the understanding of the origin, extent and ecological consequences of spatial heterogeneity across multiple spatial scales. It also considers human influences on landscapes and thus involves the restoration of degraded landscapes. A landscape can be described as a heterogeneous area consisting of distinctive ecosystems or patches and these patches are organized into a mosaic-like pattern (Molles 2008). Landscape structure (patchiness) consists of the size, shape, composition, number and position of patches in a landscape. These patches are a result of landscape processes and change at a range of spatial and temporal scales. Some processes include geological processes (e.g. sedimentation and erosion), climate change, various activities of organisms such as herbivores (ecosystem engineers) and fire frequency and intensity. Spatial patchiness can promote community resilience and persistence at landscape scales (Krebs 2009; Molles 2008). In other words, a local patch or patches can be unstable but the metapopulation remains stable and patches provide space for recolonization by dispersal between patches. If species ever go extinct in local patches, as long as these local populations are out of phase with one another, the species will persist in the landscape (Watt 1947; Levins 1969; Hanski 1991).

The theory called Hierarchical Patch Dynamics, proposed by Wu and Loucks (1995), provides a framework for conceptualising landscape heterogeneity and scale as it links patterns with processes and scale. The mosaic-like patterns (vegetation assemblages or patches) are described as undergoing different processes (different stages of succession) at various ecological scales (hierarchical levels or systems with sub-systems) (Wu and Loucks 1995). Different patterns exist at different scales. Wiens (1989) highlights how at broader scales, physical processes may dominate or dissipate biological effects. For example, the relationship between climate and vegetation at broader scales could be overridden by biological effects such as competition at finer scales (Greig-Smith 1979; Woodward and Williams 1987). Scale needs to be taken into consideration when it comes to vegetation structure in Renosterveld. As mentioned above, Renosterveld occurs between Fynbos and Succulent Karroo in a rainfall gradient, given suitable geological substrates. Therefore at regional scales, rainfall gradients and underlying geology determine distribution of Renosterveld. Within Renosterveld, which is the focus of the present study, fires in Renosterveld occur at both patch scale and landscape scale, contributing to the overall heterogeneity (Walton 2006). The spatial patterns that emerge as a result of fire history in a given area will in turn influence herbivory since herbivores will select the most desirable vegetation depending on whether they are grazers, browsers or mixed-feeders. Consequently, herbivores may reinforce the patterns of the landscape created by fires. For example, grazers may maintain grassy patches that have been burnt more recently whereas browsers could maintain thicket patches that have not burnt in many years. Alternatively, overgrazing would result in the domination of undesirable *Elytropappus rhinocerotis*. Undoubtedly feedbacks exist between fire and herbivory making landscapes complex ecological entities, as they are spatially and temporally heterogeneous and consist of a range of interacting components at different hierarchical levels. Large-scale over-grazing or intense wild fires could disrupt patch structure and homogenise landscapes, leading to loss of resilience, as will be discussed below.

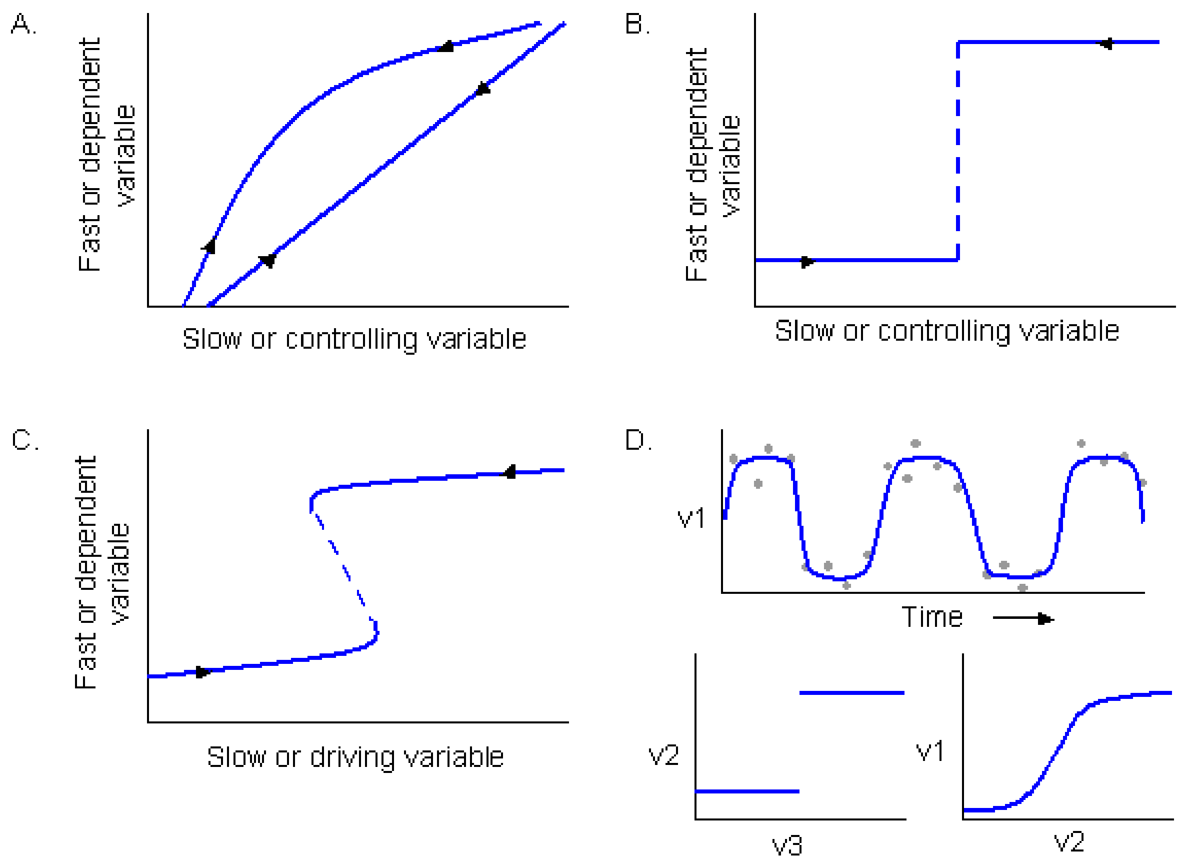


Figure 5: Schematic showing four possible changes in systems: (A) no regime shift; (B) regime shift, but there are no alternate stable states; (C) regime shift with alternate stable states; (D) a class of regime shift involving three variables (for example, v1 = salmon stocks, v2 = temperature, and v3 = ocean currents), with no feedback from the dependent (v1) to the slow variable (v3) (Walker and Meyers 2004).

2.3.4.2. Resilience theory and alternative stable states

Resilience is defined as the ability of an ecosystem to absorb disturbance, be changed and then re-organise but retains the same basic structure and functioning (Walker and Meyers 2004). There are conceptual models that describe resilience and thresholds in both ecological (e.g. climate, fire, herbivory) and socio-ecological (e.g. societies with varying land-use practices) systems. The conceptual model by Walker and Meyers (2004) (Figure 5) shows the four broad possible changes that can occur in a system. The first example Figure 5A shows no regime shift but changes are continuous and smoothly reversible. Secondly, Figure 5B shows that there is a regime shift but there are no alternate attractors (e.g. the changes between ice and water in response to temperature). Figure 5C shows a regime shift with alternate attractors indicating that alternative stable states are reached. Lastly, Figure 5D shows that a regime shift can occur which involves three variables. In this case there is no feedback from the dependent to the slow variable (examples can be seen in Walker and Meyer 2004). The present study will consider resilience theory with regards to alternative stable sates.

Disturbance can cause an ecosystem to undergo a regime shift from one stable state to another after crossing an ecolological threshold (Scheffer et al. 2001; Andersen et al. 2009). As the resilience of the system declines, the amount of disturbance needed to cross the threshold also declines (Walker and Meyers 2004). An alternative stable state is reached when a threshold level that controls the system (e.g. land-use disturbance) is passed. This causes the nature and extent of feedbacks to change and therefore the system experiences a change in direction (Walker and Meyer 2004). The shift occurs when internal processes of the system (e.g. mortality, growth, decomposition) changes and the state of the system (e.g. state variables such as vegetation, fire, herbivory) shifts in a different direction. A regime shift can either be sudden and dramatic or it can be gradual. The study conducted by Ludwig et al. (1997) is an example pertaining to rangelands where a change from a grass-dominated to a shrub-dominated rangeland was reported. The regime shift was gradual but once the threshold was crossed the dynamics of the system shifted from one stable state to another. At the shrub density threshold, the feedback from shrubs to grass changed to a point where there was insufficient grass to enable fire to spread and burn the shrub layer. Similarly, Figure 4 above shows how the dominance of shrub, grass and thicket components responds to changing fire and grazing pressure. However, Figure 4 shows different compositional states of Renosterveld that could lie within natural variability and are not necessarily the same as alternative stable states that would occur at the landscape level.

Understanding the resilience and thresholds is increasingly important in the context of the possible impact that future climate change may have on biodiversity. Neoecology is limited in investigating the true resilient response of ecosystems as it lacks a long enough temporal scale to determine natural variability. A system may vary naturally without a threshold being crossed, or could alternate between stable states as a result of natural drivers or anthropogenic disturbances. Establishing natural variability is important as a benchmark against which current environmental conditions and alternatives in the future can be evaluated. The present study deals with one study site of a high temporal resolution and therefore this sort of application of ecological theory is well-suited.

2.3.5. Renosterveld conservation status

Despite the global biodiversity importance (Cowling et al. 1999b) and regional conservation priority of Renosterveld (Rebelo 1997), West-Coast Renosterveld is not well conserved and is considered critically endangered (Rebelo et al. 2006). The natural vegetation has been largely (91-97%) transformed mainly due to agriculture (Rebelo 1992; von Hase et al. 2003, Rouget et al. 2003a, b; Rebelo et al. 2011) which has resulted in severe fragmentation of the natural vegetation. A number of authors have commented on the percentage of West-Coast Renosterveld that remains. Figures vary considerably between different studies and include 5.76% (Boucher and Moll 1981); 3% (McDowell 1988); 9% (Reyers et al. 2001); 6.5% (Newton and Knight 2005). Von Hase et al. (2003) suggest further that only 5% of West-Coast Renosterveld remains in 1200 isolated fragments, with only 660 fragments larger than 1 ha. von Hase et al. (2003) also reported that only 2% of West-Coast Renosterveld had been formally protected. Remnants of the natural vegetation can be found on soils that are too poor for cultivation or steep slopes that are unsuitable for planting, but even these remnants are occasionally used for grazing of livestock (sheep, cattle, goats and ostrich) (Lambrechts 1998) and/or large herbivores (e.g. eland, gemsbok, springbok, grey rhebok, zebra, red hartebeest, ostrich, black wildebeest and bontebok) (Cowling et al. 1986; Scott 1986; Low and Jones 1995; Cupido 2005; Raitt 2006). Consequently, these vulnerable remnants accommodate most of the biodiversity and are therefore important for conservation efforts. In contrast, the transformed parts (urbanized, cultivated or areas containing high alien plant densities) of the landscape are of little or no conservation value. Many Renosterveld species are endemic, rare or threatened and many are geophytes. For example, Iridaceae is a family of geophytes that occur in Renosterveld (von Hase et al. 2003) and about 48% of these known species are listed as rare or threatened and about 76% are endemic to Renosterveld.

There is no definite record of the original extent of natural Renosterveld vegetation before the European colonial period but rather a hypothetical total extent as per the National Biodiversity Spatial Assessment (NSBA) (Rouget et al. 2004). Unfortunately, in cases of exceptionally high transformation there is often no remaining vegetation to verify original vegetation patterns. In situations like these the most advantageous variable used to detect vegetation patterns and boundaries is the underlying geology. A strong correlation exists between soil or geology type (shale and some granite), the level of transformation (very high) and original vegetation type (Renosterveld) because the soil is more fertile and better for crop cultivation and therefore likely to be transformed. As a result transformation itself serves as a relatively accurate substitute for original vegetation patterns (von Hase et al. 2003). When focusing on the remaining Renosterveld fragments for conservation purposes, a major component to consider is the ability of the area to persist and retain ecological and evolutionary processes in the future (von Hase et al. 2003). This is important because not all remaining natural fragments are large enough or allow for relatively good habitat connectivity.

2.3.6. Conservation, restoration and management uncertainties

Given the degree of transformation of Renosterveld vegetation, good management of remaining fragments is essential. Management has both temporal and spatial aspects. A temporal perspective is needed since there is a lack of Renosterveld environmental history, such as the effect that past climate change and land-use change (such as fire and herbivory) has had on vegetation. If a temporal perspective is able to provide a baseline of pristine West-Coast Renosterveld composition then there are possibilities to inform management on restoration targets as well as future resilience to climate change and land-use.

While temporal aspects can be explored via palaeoecology, neoecological studies have shown that identifying spatial components (i.e. physical landscape features) is beneficial for conservation planning. These spatial components are important for ecological and evolutionary processes especially in a landscape as threatened and transformed as West-Coast Renosterveld (Cowling et al 1999c; Rouget et al. 2003a). Spatial components can either be spatially fixed landscape features or they can be spatially flexible. The fine scale technical report produced by von Hase et al. (2003) identified three spatially fixed components of ecological and evolutionary processes for Renosterveld. They include the following: (1) edaphic interfaces between very different substrates, (2) upland-lowland Renosterveld vegetation interfaces and (3) river corridors. For the purpose of this study less emphasis will be placed on the spatially fixed components and more emphasis will be placed on the most important spatially flexible component which they identified as habitat connectivity. Spatial flexibility within fragments has been discussed in the context of the effects of fire and herbivory on patch dynamics (as discussed above in section 2.3.4.1.)

Habitat connectivity in Cape Lowlands Renosterveld can be defined as at least 500 m connectivity distance between fragments (von Hase et al. 2003). In other words, if the distance between two fragments was <500 m then the fragments would be classified as connected; however, this may vary for different species. Habitat connectivity is generally a precondition for maintaining natural systems whereas fragmentation (resulting from transformation) is believed to have unfavourable effects on biodiversity. For example, Renosterveld connectivity is critical for key processes such as plant and animal dispersal, pollination and genetic exchange (Donaldson et al. 2002; Pauw 2004). Therefore, even the active agricultural lands (which make up more than 80% of the cape lowlands and thus cause the fragmentation) are highly dependent on the ecosystem services such as pollination, water provision and soil formation that Renosterveld biodiversity provides. Maintaining habitat connectivity is thus important in ensuring the continued provision of these services. Significantly more remnants are relatively well-connected in the Overberg (74.6%) compared to West-Coast Renosterveld (20.3%) (von Hase et al. 2003), where much less Renosterveld remains and thus fewer options are available for conserving ecological and evolutionary processes.

2.3.6.1. Importance of palaeoecological data and long-term data on climate change and land-use in the conservation and management of Elandsberg Private Nature Reserve

Informed management and conservation decisions need to incorporate the dynamics of long-term evolutionary and ecological processes, and therefore there is a growing recognition of the application of palaeoecology in conservation (Gillson and Willis 2004; Willis and Birks 2006; Dearing 2008; Gil-Romera et al. 2010; Birks 2012). These studies include the use of

multi-proxy data to determine vegetation responses to climate change and human disturbance and interactions between them. Applied palaeoecology demonstrates its effectiveness in establishing benchmarks that inform conservation management and restoration targets within thresholds of natural variability.
There is very little information about the history and origin of Renosterveld, and therefore the current palaeoecological study at Elandsberg Private Nature Reserve (Elandsberg PNR) is of significance. Elandsberg PNR (see chapter 3 for a more detailed discussion) is a Stewardship Contract Nature Reserve which has been identified as one of the most important areas for West-Coast Renosterveld conservation (Low and Rebelo 1996). The reserve is situated between two extreme types of land-use impact (Figure 6). To the west of the reserve there are hectares of transformed, highly fragmented land mostly used for livestock farming and crop cultivation. To the east of the reserve is the less accessible mountainous area (i.e. Elandskloof Mountains) which are not desirable for agriculture and therefore less affected (Figure 6). The reserve has the potential to provide ecosystem services (e.g. biodiversity, water purification, nutrient cycling, pollination, invasion resistance, erosion regulation) to the active agricultural lands adjacent to it. Since there is no permanent barrier between the reserve and Elandskloof Mountains, there is connectivity between Renosterveld and mountain Fynbos, of significance to fauna that inhabit both vegetation types. The importance of the reserve is even more significant owing to the presence of the threatened Geometric Tortoise and the large indigenous herbivores that were reintroduced when the reserve was established.

When generating palaeoecological information for use in conservation management, it is important to integrate it with ecological frameworks so that it too can be used to understand ecological process and predict future change (see section 2.3.4.). However, detailed studies that have been conducted over a long period of time and can therefore give insight into community and ecosystem stability and resilience are very rare. In addition, the disturbance magnitude, its influence, as well as origin and history of West-Coast Renosterveld are still subject to discussion and there is uncertainty about how the current landscape at Elandsberg PNR compares with pre-colonial and pre-pastoralist times.

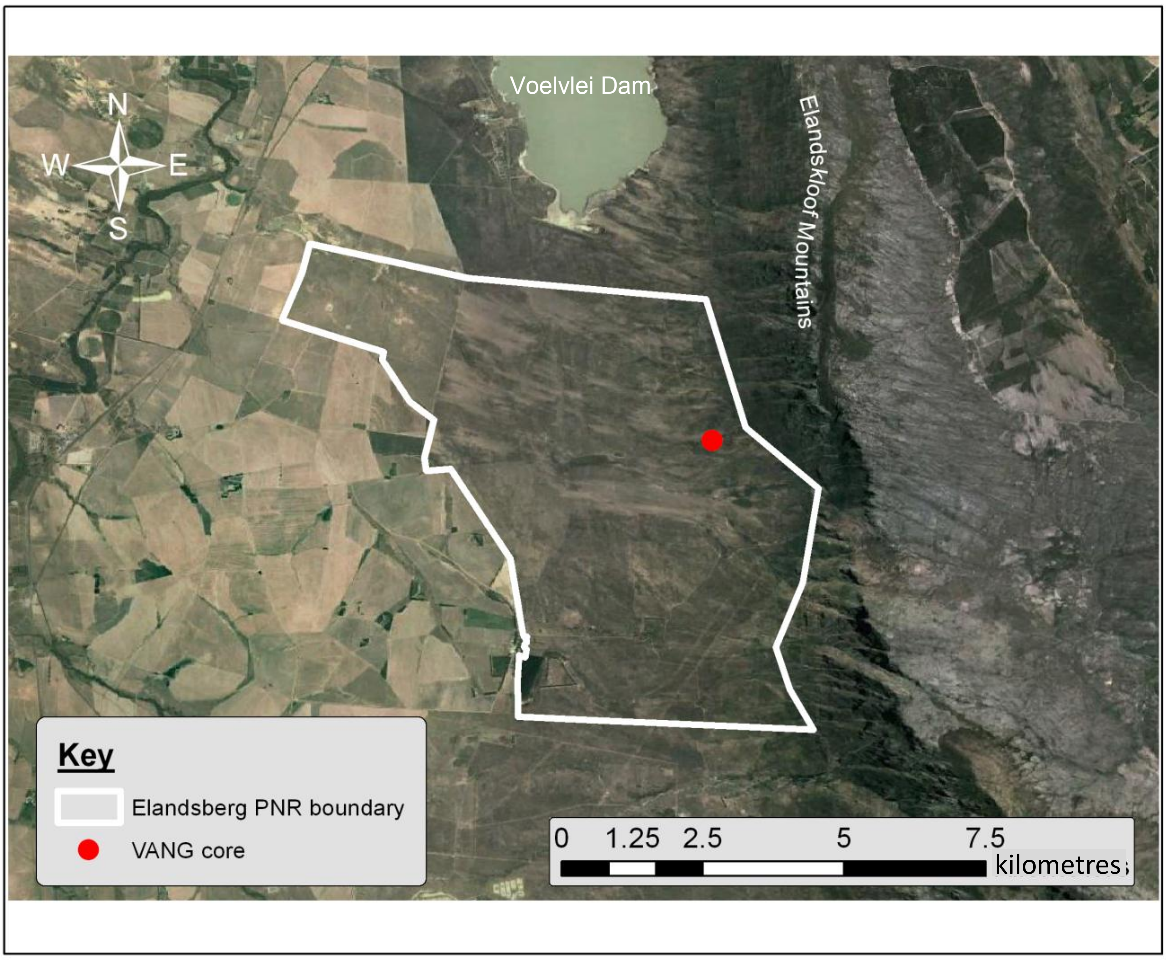


Figure 6: Google earth image showing the location of Elandsberg PNR situated between highly transformed lowlands to the west and the generally more protected area of Elandskloof Mountains to the east of the reserve. Note the pine plantation called Suurvlak to the north-east of Elandsberg PNR on the eastern side of the mountain. The coring site is marked by a red dot.

There is currently no information on how far Elandsberg PNR differs from a "pristine" state and baseline restoration targets are therefore lacking. The present study aims to address questions of long-term change and interpret the findings in terms of key conservation and management issues for the reserve. For example, comparing the present state of the ecosystem with pre-colonial times. Levels of disturbance over time need to be interpreted in the effect on biodiversity, and major transitions between alternate stable states need to be distinguished from reversible structural changes of Renosterveld within a landscape (e.g. increases in Grassland, Shrubland or Thicket elements; Figure 4). This information can help in assessing whether current levels of fire and herbivory are appropriate or outside the historical range of variability. Further information on the conservation and management of the Elandsberg PNR is provided in chapter 3.

3. STUDY SITE

This chapter provides context for the present study, including the geology, climate, topography, vegetation and land-use history (i.e. fire regimes and herbivory) of the Elandsberg Private Nature Reserve (Elandsberg PNR). This description also considers the coring site selection.

3.1. The Elandsberg Private Nature Reserve (Elandsberg PNR) study site

3.1.1. The setting of Elandsberg PNR

The Elandsberg Private Nature Reserve (Elandsberg PNR) is a privately owned reserve situated on the Farm Bartholomeus Klip (33.45000 S and 19.05000 E). It is located in the Wellington District of the Western Cape approximately 15 km east of Hermon and 25 km north of Wellington. The reserve is found at the foot of the Elandskloof Mountains, south of Voelvlei dam (Figure 6). Voelvlei Nature Reserve, which borders the northern part of Elandsberg PNR, is managed by Cape Nature and belongs to the City of Cape Town. Along the eastern border of Elandsberg PNR lies Liemietberg Nature Reserve, owned and managed by Cape Nature (Wooding 2011). This state-owned land supports mountain Fynbos vegetation, which grows on the characteristic nutrient poor sandstone soils in this area (Boucher and Moll 1981). The southern-most section of Elandsberg PNR borders the privately owned land called Kranskop which is the site of a munitions factory. The land surrounding the factory is leased out to farmers for wheat production or for game/hunting on the natural veld.

Until the proclamation of Elandsberg PNR in 1973 (Anon. 1977; Becker 1996), it was used for the grazing of cattle and sheep (Stander 1988). The primary function for the reserve was for the conservation of the Geometric Tortoise, *Psammobates geometricus*, which is endemic to this region and one of the rarest tortoises in the world (Boycott and Bourquin 1988). The initial size of the reserve was 2600 ha (Jarman 1986) but it was extended in 2001. Currently the official area of Elandsberg PNR is given as 3400 ha (Newton and Knight 2005), although other reports of 3900 ha (Midoko-Iponga et al. 2005) and 3606.ha (Shiponeni and Milton

2006) exist in the literature. To date Elandsberg PNR contains one of the largest areas (ca. >1000 ha) of West Coast Renosterveld (Rebelo 1995) (Figure 7).

3.1.2. The geology, climate and topography of Elandsberg PNR

Elandsberg PNR is situated along the edge of an erosion resistant ridge of sandstone, which forms the Elandskloof Mountains (Figure 6 and 7). This Cape Granite suite overlies the Malmesbury geology group, which consists mainly of sedimentary rocks. Together with granites they form a base-rich substrate (Wooding 2011). Thus the geology of Elandsberg PNR is predominantly composed of Terrace Gravel and alluvial debris, with patchy areas of Malmesbury shales in the centre (Anon. 1997, cited by Newton and Knight 2005). The reserve is generally quite stony (Wooding pers. comm. 2013) and this is probably the reason why this land was not used intensively for agricultural purposes before proclamation. Elandsberg PNR supported only small areas of ploughed land and livestock grazing (discussed below in section 3.1.4). This stands in contrast to neighbouring farms further west which have been extensively transformed by crop cultivation and grazing (Figure 6).

Elandsberg PNR has an altitude ranging from 68 m to 400 m above sea level with the mountains bordering the eastern side of the reserve reaching heights up to 1378 m above sea level. The reserve experiences an annual average temperature of 18.4 ºC (range from 1.3-45.6 ºC) with the coldest month in winter being July (mean 12.2 ºC) and the hottest month being January (mean 24.2 ºC). The average rainfall is approximately 600 mm per year with the highest average in June (98.8 mm) and the lowest in January (14.5 mm) (Wooding 2011). To the east of Elandsberg PNR, at the top of the Elandskloof Mountains, rainfall levels are high ranging from 1000 mm in the north to 1400.mm in the south (Schulze and Maharaj 1997). Newton (2008) noted that the soil moisture levels in the reserve are above that which would be expected from local rainfall alone and a likely explanation would be the run-off that is received from the mountain. Heavy fog events are a frequent occurrence during the winter months (Wooding 2011).

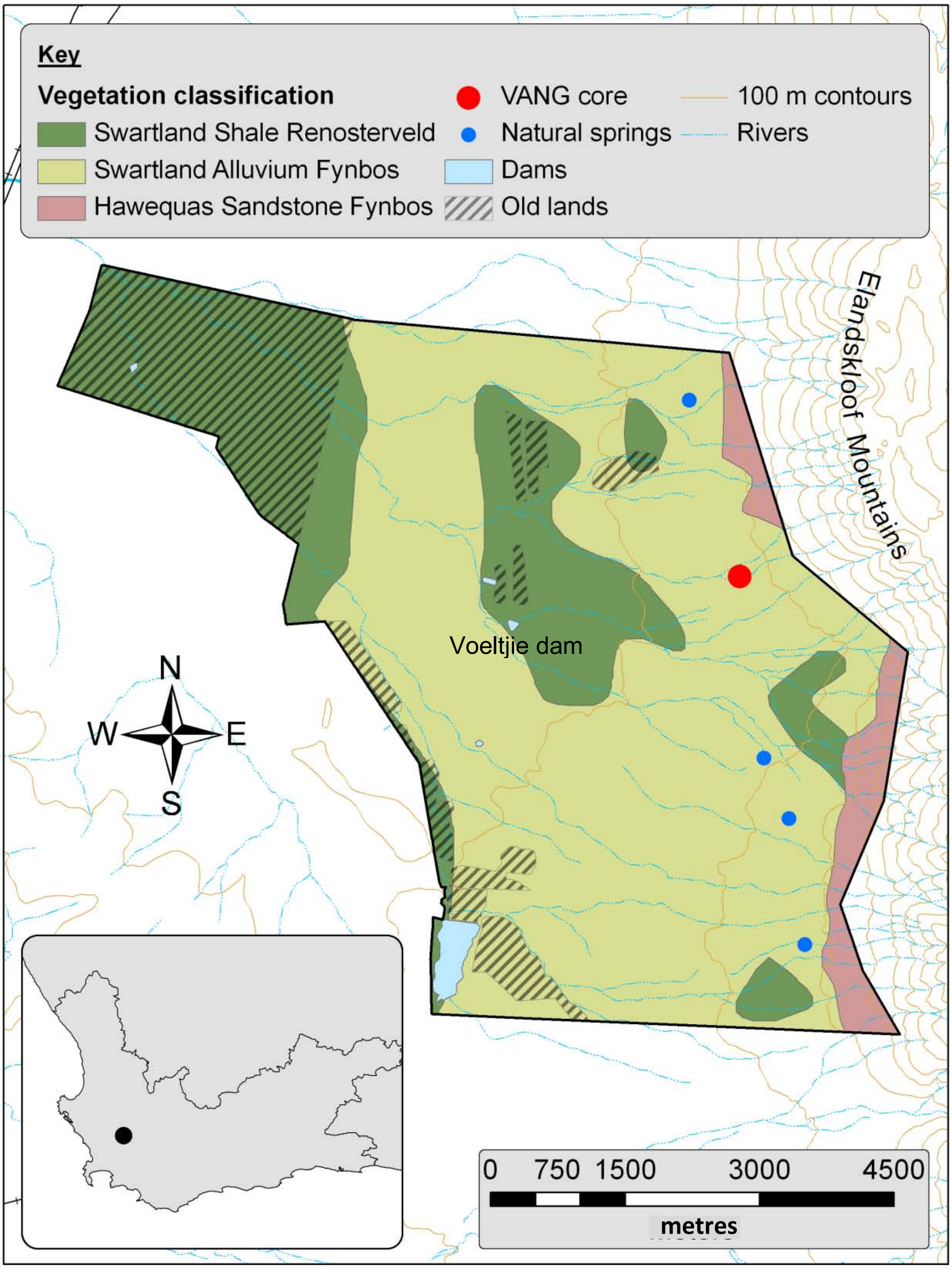


Figure 7: Map of Elandsberg PNR study site showing location of Vangkraal Spring wetland where the VANG core was retrieved (red dot). Blue dots represent other springs occurring in Elandsberg PNR. Diagonally crossed areas represent old lands that were previously cultivated.

The topography can be described as a gentle slope (0.02° – 20.50°) from north-west to south-east (Newton and Knight 2005). However, the gradient increases steeply at the eastern border of the reserve where it meets the Elandskloof Mountains which have a west-facing aspect. Generally the soils are poorly developed across the reserve and are derived from the adjoining mountains. They are characterized by sandy lithosols and coarse sand (Schloms et al. 1983). On the eastern part of the reserve where the slope is steep, the soils are more nutrient poor with low levels of N and P. This low nutrient content is due to the infertile parent rock (Ordovician sandstones of the Table Mountain Group) from which they are derived (Mucina and Rutherford 2006) as well as the percolating action of water on these steep slopes which leaches nutrients from the soil. The soil is acidic, whitish in colour and has many rocks and stones. However, the amount and size of the rocks decreases further from the mountain. The lower slopes and flat areas have sandy clay soils which are more fertile than the steeper slopes. The most western part of the reserve is more fertile and was consequently used for the planting of crops in the past (Figure 7) since its parent rock material (Malmesbury shales) allows for deeper loamy soils and fewer rocks (Wooding 2011).

3.1.3. The vegetation of Elandsberg PNR

There are three identifiable vegetation types classified by Mucina and Rutherford (2006) that occur on Elandsberg PNR, namely: Swartland Shale Renosterveld (FRs), Swartland Alluvium Fynbos (FFa 3) and Hawequas Sandstone Fynbos (FFs 10) (Figure 7). Swartland Shale Renosterveld is characterized by a low to moderately tall leptophyllous shrubland of varying canopy cover as well as low open shrubland dominated by *Elytropappus rhinocerotis*. While large termite mounds (known locally as heuweltjies (Afrikaans) or little hills) (Booi 2011) are prominent in this vegetation unit and are usually associated with stunted trees and thicket taxa, no heuweltjies were observed at the Elandsberg PNR site. Disturbed areas are commonly dominated by *Athanasia trifurcata* and *Otholobium hirtum* and patches of natural ‘grazing lawn’ (*Cynodon dactylon*) are often abundant. Mucina and Rutherford (2006) describe Swartland Alluvium Fynbos as a matrix of low, evergreen shrubland with emergent sparse moderately tall shrubs and a noticeable graminoid layer. Proteaceae, Restionaceae and Asteraceae taxa are dominant. Scrub fynbos can be found along the river courses and Ericaceae and Restionaceae taxa are found in seeps. Lastly, Hawequas Sandstone Fynbos (occurring on the steep eastern slopes of Elandsberg PNR) comprises plant communities distinguished by a low closed shrubland dotted with emergent tall proteoid, restioid and asteraceous shrubs. Patches of Cape Thicket are found along the cliffs, ravines and rocky slopes (Mucina and Rutherford 2006). The Thicket patches are dominated by trees such as milkwoods (*Sideroxylon inerme* - Sapotaceae), wild almond (*Brabejum stellatifolium* - Proteaceae) and willow (*Salix* spp - Salicaceae) although these species were not common in the Thicket vegetation unit close to the Vangkraal Spring wetland (see Figure 11 and 12). Short restioid shrubs can be found along the foothills and lower mountain slopes (Wooding 2011). A few old abandoned cultivated areas, including scattered fields in the north of Elandsberg PNR as well as old lands along the western border of the reserve, previously supported wheat and other grain crops (Figure 7). The old lands along the western border forms a buffer strip and although a few pioneer shrubs occur along the edges bordering the natural vegetation these areas are dominated by grasses, notably *Cynodon dactylon* (Wooding 2011).

There has been much debate over the actual amount of West-Coast Renosterveld conserved on Elandsberg PNR. Reported figures vary between 1000 ha (Rebelo 1995; Midoko-Iponga et al. 2005) and 1600 ha (Krug 2004). Mucina and Rutherford (2006) noted that Swartland Alluvium Fynbos was incorrectly classified as West-Coast Renosterveld by previous authors (Moll and Bossi 1984; Low and Rebelo 1996). At its lower extremity this vegetation unit often forms a complex mosaic with Swartland Shale Renosterveld. This mosaic has ecotonal characteristics especially when soils consist largely of clay-rich silts.

Despite the efforts by Mucina and Rutherford (2006) in reallocating a large proportion of the original reserve to rightful areas of Swartland Alluvium Fynbos, the 2001 extension of the reserve was incorrectly mapped as Swartland Shale Renosterveld even though it is of alluvial origin (Anon. 1997). The reserve is currently being ground-truthed by John Manning in order to obtain a more accurate understanding of the contribution (in terms of ha) Elandsberg PNR is making in conserving West-Coast Renosterveld (Wooding pers. comm. 2013). According to the most recent ground-truthing, the Vangkraal Spring wetland occurs on the ecotone and this is not seen in the latest classification by Mucina and Rutherford (2006) (see Figure 7).

3.1.4. The land-use (fire and herbivory) history of Elandsberg PNR

Important information that provides environmental and historical context is summarized in Table 1. It includes general climatic and land-use information for the region (from the literature reviews, see chapter 2) as well as specifically for Elandsberg PNR. Up until the 17th century the main land-use in the region included light burning by the San and more intense fire usage and livestock grazing by the Khoikhoi pastoralists. Before the 18th century (i.e. before Elandsberg PNR was established) the land was used for hunting wild game (i.e. all types of antelope, for example blue buck, red hartebeest, eland and bontebok) and was considered a hobby farm (Wooding pers. com. 2013). The wetland cored in the present study is called Vangkraal Spring. The co-ordinates of the VANG core extracted from Vangkraal Spring wetland are 33.438317 S and 19.068967 E (Figure 7). Vangkraal Spring is in close proximity to a capture enclosure or known as "vangkraal".

The first recorded farmer, Frans Youster, kept cattle on the land from 1705 to 1759 (Becker 1996). Sheep were introduced on the farm around the time of the second Anglo-Boer War (1899-1902). In 1900 the state owned the land and it was used as a horse remount (where horses were rested and fed) for the British army based in Cape Town (Becker 1996). In the 1900s there was an ostrich camp consisting of grass fields about 1ha in size located at the "vangkraal", close to Voeltjie dam (Figure 7) but according to anecdotal evidence this burnt down in the 1920s (Wooding pers. com. 2013). Cattle and sheep were reintroduced on the farm in 1958 and until 1983 it was used for the grazing of livestock (Stander 1988). However, stock numbers were low as the veld was not of good quality. During 1963 the veld was fenced off into paddocks and a more intensive management system introduced (Stander 1988; Becker 1996). During this time, the farm owners also had major problems with predators such as caracal and leopard (Wooding pers. com. 2013). By 1967 all cattle were removed and some sheep were kept until 1970 (Wooding pers. com. 2013). However, the fences of the south paddock were only removed in 1984 while those of the north paddock were removed two years later in 1986 (Stander 1988). The land is too rocky and pebbly for cultivation but there are areas on the reserve (now patches of old Renosterveld) which would have been nutrient-rich shale substrate suitable for wheat and vineyards (Wooding pers. com. 2013) (Figure 7).

Table 1: Timeline describing long-term climatic, vegetation and land-use change during the study period (ca. 1300 years) documented by the VANG core. Dates with an asterisk (*) are converted to AD. Inserts highlighted in bold are specific to Elandsberg PNR.

Climate	Land-use	Date	Description	Reference
20th century warming	**Conservation**	**AD 2012**	**Fire on Elandsberg PNR**	**Wooding pers. comm. 2013**
		AD 2004	**Minimum tillage (reduction in fire usage) on Elandsberg farms adjacent to Elandsberg PNR**	**Wooding pers. comm. 2013**
		AD 1999	**Extensive wind-driven fire on Elandsberg PNR**	**Wooding pers. comm. 2013**
		AD 1988	**Fire on Elandsberg PNR**	**Wooding pers. comm. 2013**
		AD 1985	Maize (*Zea mays*) and grape vines (*Viti vinivera*) common in the region	Deacon 1986 (from Neumann et al. 2010)
		AD 1983	Conservation of Agricultural Resources Act (Act No. 43 of 1983)	Vester et al. 1992
		AD 1982	**Extensive fire on Elandsberg PNR**	**Wooding pers. comm. 2013**
		AD 1973	**Elandsberg PNR established (reintroduction of eland, blue and black wildebeest, zebra, red hartebeest, gemsbok, bontebok, springbok)**	**Becker 1996**
	Agricultural intensification	AD 1969	Soil Conservation Act (Act No. 76 of 1969)	Vester et al. 1992
		AD 1966	**Elandsberg Farm (Pty) Ltd established**	**Becker 1996**
		AD 1963	**Veld fenced into livestock camps on Elandsberg land**	**Becker 1996**
		AD 1958	**Both cattle and sheep were kept on Elandsberg land**	**Stander 1988**
		AD 1946	Soil Conservation Act (Act No. 54 of 1964)	Vester et al. 1992
		AD 1930	Wheat Importation Restrictions Act (Act No. 10 of 1930); Soil Erosion Adversary Council was established	Meadows 2003; Hoffman and Ashwell 2001
		AD 1920	**Ostrich camp and anecdotal evidence of fire on Elandsberg land**	**Wooding pers. comm. 2013**
		AD 1900s	Quaqqa (*Equus quagga quaqqa*) became extinct	Krug et al. 2004; Krug and Krug 2007; Newton 2008
		AD 1900	**Sheep on Elandsberg land**	**Becker 1996**
		AD 1900	**Elandsberg land used as a horse remount for British Army**	**Becker 1996**

Table 1: Timeline (continued).

Climate	Land-use	Date	Description	Reference
	European settler agriculture	AD 1853	Gum (*Eucalyptus*) seeds sold	Wells et al. 1986
		AD 1827 and AD 1835	Introduction of Acacia spp by European colonialists	Neumann et al. 2011
LIA - cold and wet (ca. AD 1400-1800)		170 BP (*AD 1780)	Exponential increase in asteraceous taxa, decline in Poaceae continuing to present (Klaarfontein Springs study)	Meadows and Baxter 2001
		AD 1705-1759	Dutch settler had cattle on Elandsberg farm	Becker 1996
		AD 1700s	Endemic species such as the Blue buck (*Hippotragus leucophaeus*) were hunted to extinction	Krug et al. 2004; Krug and Krug 2007; Newton 2008
		ca. AD 1700	Expansion of European colonial agriculture	Meadows and Sugden 1991
		AD 1700	Little Ice Age: maximum cooling	Tyson et al. 2000
		AD 1656	Dutch planted maize (*Zea mays*)	Wells et al. 1986
		AD 1652-1662	Dutch planted grape vine (*Viti vinivera*)	Bulpin and Rennie 1983
		17th century	Introduction of oaks (*Quercus* spp) and pines (*Pinus* spp)	Neumann et al. 2011
		17th century	European colonialists cultivated indigenous edible plants commonly known as "waterblommetjies" (*Aponogeton* spp)	Neumann et al. 2011
	Khoi-San hunter/ herders	Last 500 years (*AD 1507)	Wetter conditions from ca.1500 and continuing to the present (Pakhuis Pass Shelter study)	Scott and Woodborne 2007 a,b
MCA - warm and arid (ca. AD 900-1400)		Since 1900 BP (*since ca. AD 50)	Decline in Poaceae pollen and increase in micro-charcoal from 1900 BP attributed to Khoikhoi pastoralists and/or climate change.	Meadows and Baxter 2001
		2000 BP- AD 1650 (*50 BC- AD 1650)	Khoikhoi pastoralists occupied the region	Stow 1905; Westphal 1963; Cooke 1965; Marks 1972; Elphick 1977, 1983

In the 1960s and 1970s there were areas where oats were hand-sown (small areas of old lands in Figure 7; Newton and Knight 2005) and this was used to supplement the grazing (Fish 1988). In 1973 the farm was declared a nature reserve and indigenous herbivores were reintroduced (Table 2). Some species (e.g. bontebok and black wildebeest) that historically were not found in the area (Skead 1980) have been introduced in order to breed a population of these vulnerable animals.

Table 2: Large indigenous herbivores currently occurring in Elandsberg PNR. Feeding type specific to each herbivore is shown in the column on the right.

Herbivore common name	Herbivore species name	Feeding type
Eland	*Taurotragus oryx*	Mixed
Gemsbok	*Oryx gazelle*	Mixed
Springbok	*Antidorcas marsupialis*	Mixed
Grey rhebok	*Pelea capreolus*	Mixed
Zebra	*Equus* spp	Grazer
Red Hartebeest	*Alcelaphus buselaphus*	Grazer
Ostrich	*Struthio camelus*	Grazer
Black Wildebeest	*Connochaetes gnou*	Grazer
Bontebok	*Damaliscus dorcas dorcas*	Grazer

There is no written record of fires pre-1980s and people living in the area say that there was a fire in the 1920s. There were no fires between AD 1960 and AD 1980 (Wooding pers. com. 2013) as this would have been a period when fire breaks were being made to keep fires out of the lowlands. It is uncertain whether the firebreaks protected the Vangkraal Spring (where the VANG core was extracted) from being burnt because it is situated on the slope of the Elandskloof Mountains. It is possible that the Vangkraal Spring could have been in the area where fire was allowed. On average one to three fires have occurred every decade since 1980. Local records suggest that a fire occurred in 1980; a relatively extensive fire in 1982 and 1988; a widespread wind-driven fire in 1999; less extensive fires in 2008 and 2010; and the most recent fire in 2012 (Figure 8; Wooding pers. com. 2013). These were wild fires that were most likely caused by humans. Fires always started in the Bainskloof area (east of Elandsberg PNR) and with the prevailing south-easterly wind during summer months, the fire comes off the mountain and into the lowlands. These fires often take place during the festive season (December-January) as this is when many people go up the mountain (Wooding pers. com. 2013). Visual inspection of burnt skeletons of Proteaceae and *Elytropappus rhinocerotis* confirmed that the site had burnt recently (pers. obs. 2012). According to recent management plans drawn up for Elandsberg PNR (Wooding 2011) the vegetation on the reserve needs to burn approximately every 8-14 years depending on the veld type. A burning regime has been put in place involving block burns to prevent vegetation from becoming old and senescent and areas of young vegetation are preserved. Figure 8A) shows how fires have created a patchy landscape in the reserve with various areas having different post-fire ages. The most recent fire (Figure 8B) was extensive and has potentially impacted the patchiness that existed before 2012.

Farm Bartholomeus Klip on the western border of Elandsberg PNR stopped using ploughs from ca.1996 and began to use rippers to reduce tillage until 2004, after which the farm used "planters" as they changed to a minimum tillage system, and this is still practiced today (Wooding pers. com. 2013). The goal of this practice is minimum soil manipulation unlike intensive tillage which changes the soil structure when using a plough. As a result of the change in agricultural practice, the amount of fire used has been reduced since the early 2000s (Wooding pers. com. 2013).

3.2. Site selection at Elandsberg PNR

As described in detail in the methods chapter (section 4.1.1), a sediment core was retrieved from a wetland situated on an ecotone of Swartland Shale Renosterveld and Swartland Alluvium Fynbos. Ecotones are by definition transitions from one type of ecosystem to another. Associated with this transition is a change in the relative densities of species that are usually associated with different vegetation types. Such an abrupt change in species composition and density often points to a shift in environmental or biological conditions which underpin the transition from one vegetation type to another. Milne et al. (1996) suggested that when there is a sharp change in vegetation type, there is most likely a steep environmental gradient causing it. Similarly, when there is a gradual change in vegetation type at the ecotone there is a gradual environmental gradient.

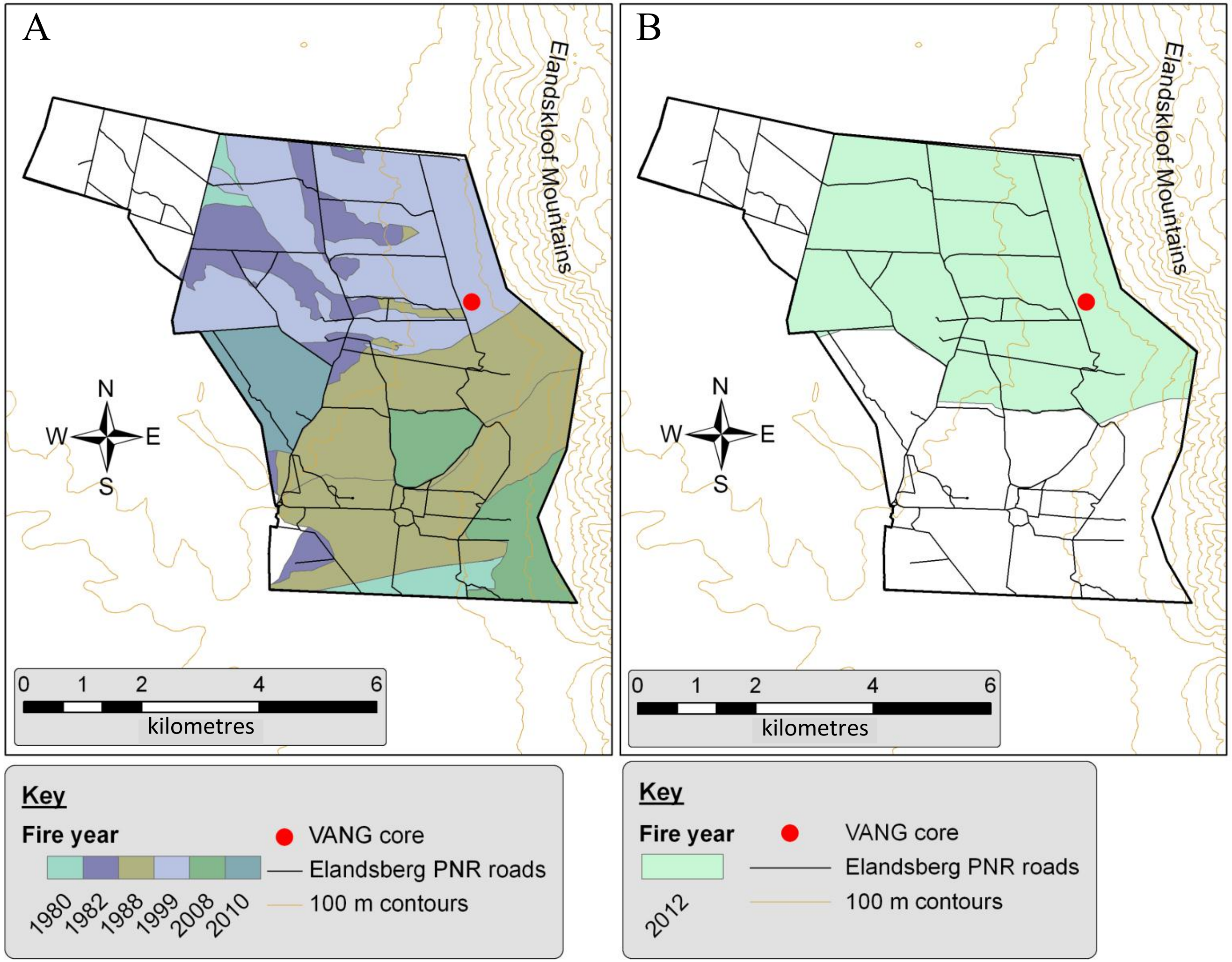


Figure 8: Map of Elandsberg PNR showing fire history from (A) 1980-2010 and (B) the most recent fire in 2012. Roads are included since they often act as fire breaks. The site the VANG core was retrieved is marked by a red dot.

These gradual environmental gradients are useful areas for studying biological and ecological responses to environmental change. Ecotones can also occur as a result of biological factors and feedbacks with disturbance such as the Forest-Savanna ecotone in Hluhluwe, South Africa (Bond 2010; Bond and Parr 2010).

A sediment core from an ecotone is more likely to detect sporadic shifts between vegetation types brought about by changes in environmental variables at a local to landscape scale. In this way vegetation changes at Elandsberg PNR can be detected at both a spatial scale (via the ecotone) and temporal scale (via the sediment core). The fossil pollen grains as a proxy for vegetation changes, can be compared alongside other proxies such as charcoal and coprophilous spores to investigate the effects of fire and herbivory, as well as response to past climate change either from an independent climate proxy or from known palaeoclimate history.

3.3. Theoretical and practical considerations in selecting a coring site

Generally, South Africa is a semi-arid country which receives about 450 mm of rain per year and this value is less than half the world's average rainfall. Low rainfall and the lack of lakes means that palaeoecological research to date is relatively scarce. However, alternative bodies of water such as wetlands and pans are yielding interesting results (Gillson and Ekblom 2009; Ekblom et al. 2011; 2012). In order to obtain a sediment core that has continuously accumulated sediment and has an intact chronological sequence, a few criteria are essential. To ensure good pollen preservation and stratigraphical integrity, the objective is to find a wetland that has not been degraded for example by dredging, receives minimal disturbance, is permanently wet (i.e. does not dry out seasonally). In the West-Coast Renosterveld regional rainfall is strongly seasonal (winter) and as a result the wetlands that occur in the region are often ephemeral. Since the wetland in the present study is a spring, it remains wet throughout the year. According to Bennett and Willis (2001) good preservation of pollen is obtained when conditions are anoxic, preferably acidic and waterlogged.

Depending on the research questions being answered, basin size of the wetland plays a big role as it determines the relevant source area of pollen. The source area increases as basin size increases (Jacobson and Bradshaw 1981; McQueen and MacPhail 1983; Sugita 1994; Figure 9; Table 3). The present study is focused on reconstructing vegetation dynamics at the local level and therefore a small basin size was appropriate, in order to study the effects of local level land-use changes over time (as discussed below).

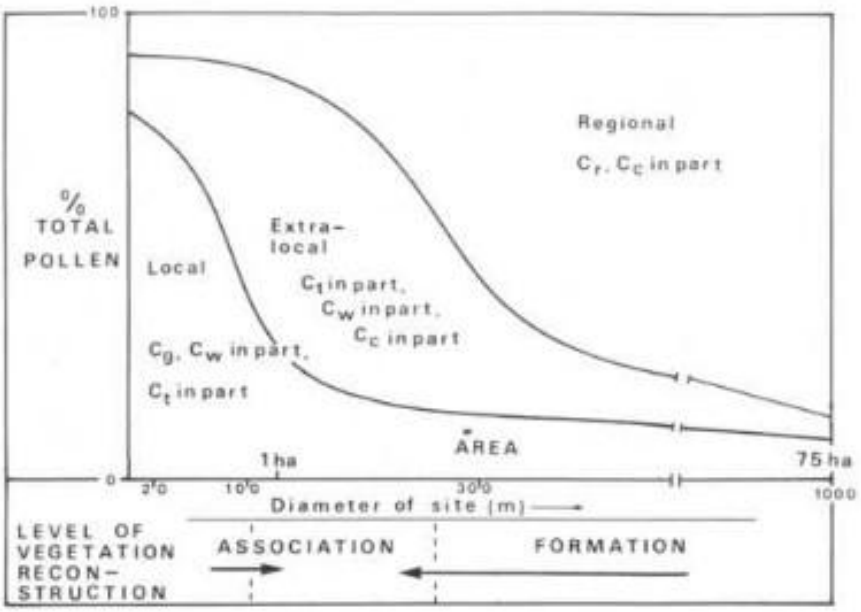


Figure 9: The generalized relationship between the size of a coring site that has no inflowing stream, the relative proportions of pollen originating from different areas around the site and level of vegetation reconstruction (Jacobson and Bradshaw 1981).

A small wetland that has no inflow or outflow of water will contain micro-fossils found in the sediment from aerial and overland deposition, thus emphasizing local scale rather than regional scale vegetation dynamics. This scale is of interest to land managers as it is more site specific and palaeoecological evidence obtained will relate to local land-use disturbance. Figure 9 shows the generalized relationship between the size of basin (wetland coring site) that has no inflowing stream and the relative proportions of pollen originating from different areas around the site. A local pollen representation would be from plants growing within 20 m of the basin edge; extralocal would be from plants growing between ca. 20-300 m from the basin edge; and regional would be plants growing at distances greater than *ca.* 300 m. Sugita (1994) predicted that in patchy landscapes where sediment basins are small (radius = 50 m or less) approximately 50% of the pollen would come from the 300-400 m immediately surrounding the basin. Furthermore, studies by Sugita (1994) and others (Calcote 1995; Gaillard et al. 1999; Davis 2000) demonstrated that the relevant source area for pollen in small forest hollows (radius of hollow radius = 2 m) was within 50-100 m from the lake edge (Sugita 1994). Three potential sites around the Shale Renosterveld-Alluvium Fynbos ecotone were identified for coring (two springs and one wetland). Initial subsampling and pollen analysis (as described in section 4.2.3.) of each of these cores revealed that only one site (Vangkraal Spring) was suitable for further analysis because it had the best pollen preservation and site location.

Table 3: Relationship between the size of the site cored and the pollen source area.

Reference	**Diameter (m)**	**Area (m^2)**	**Pollen source (m)**
Jacobson and Bradshaw 1981 cited by McQueen and MacPhail 1983	<100	7854	20 (local)
	100-300	7854-70 686	20 to several 100 (extra-local)
	>300	>70 686	regional
Sugita 1994	<4	12.6	50-100
	100	7854	300-400
	500	196 350	600-800

4. METHODS

The present study reconstructs vegetation change, fire and herbivory in West-Coast Renosterveld using a number of palaeoecological techniques, specifically the analysis of fossil pollen, charcoal and coprophilous spores. This chapter provides a description of field methods including core retrieval, surface sample collection, modern vegetation survey, and a detailed description of laboratory procedures and statistical analysis. The present study aims to reconstruct vegetation changes over the past ca.1300 years, describing West-Coast Renosterveld dynamics during pre-colonial, early colonial, and 20th and early 21st century period. This study period includes a number of important changes in land-use such as the transition from hunter-gatherer lifestyles of the San to the arrival of domestic animals by the Khoikhoi pastoralists (2000 BP to historic times; Singer and Weiner 1963; Westphal 1963; Elphick 1977), the local extinction of large herbivores (post-1800s; Hoffman 1997), as well as the effect of European settler agriculture (AD 1700 to mid-1900s; Hoffman 1997) and conservation period (1973-present; Becker 1996). The study period also includes climatic changes such as the MCA (between ca. AD 900-1400), the LIA (from ca. AD 1400-1800; Mayewski et al. 2004; Stager et al. 2012) and 20th century warming (Haensler et al. 2010).

4.1. Field methods

4.1.1. Sediment core retrieval and collection of sediment surface sample

An undisturbed sedimentary sequence from a small, closed basin was required. This would provide a continuous chronology at a high temporal resolution and the small sized basin would capture a pollen source area suitable for detecting local vegetation dynamics. Accordingly, a wetland area in the Swartland region was chosen. This site was situated within Elandsberg Private Nature Reserve (Elandsberg PNR) at the ecotone between West-Coast Renosterveld (Swartland Shale Renosterveld) and Fynbos (Swartland Alluvium Fynbos) (see chapter 3). The sediment core (VANG core) was extracted from a wetland basin of 22.5 m diameter, ($\pi(11.5\text{ m})^2 = 397.6\text{ m}^2$) called Vangkraal Spring located at 33.4383167 S and 19.068967 E and 151 m above sea level (Figure 7). To core the wetland, an aluminium pipe of 7.62 cm in diameter, 1.6 mm thickness, and 3 m in length was used. A handle attached to the aluminium pipe enabled it to be pushed down into the sediment with minimal disturbance (Smith 1987; Miller et al. 1991). A coarse sandy layer with gravel-like pieces (assumed to be bedrock) at 87 cm prevented further coring and probably marked the depth of the accumulated sediment at this site.

To retrieve the core a rubber bung was inserted into the top of the pipe creating a vacuum that kept the sample sediments in place while the core was removed from the sediment. Once the core was horizontal, excess piping was cut off using a hand-held saw and the ends of the core were packed with plastic bags and sealed with tape. The core was labelled and measured and was kept horizontal and transported to Cape Town. A surface sample was collected in addition to the sediment core by scooping a trowel-sized amount of surface sediment from the top 2-3 cm close to where the core was retrieved. This sample was taken in order to assess modern pollen “rain”, and to establish the relationship between modern vegetation type and pollen spectra (see section 4.1.2. below for vegetation survey methodology).

At the University of Cape Town the pipe was split in half using an electric jig saw, with little or no displacement of the sediment. It was also noted that approximately 15 cm compression of the sediment had occurred within the pipe as a result of the coring procedure used. One half of the core was wrapped in plastic cling wrap, placed in a black plastic bag and stored as an archive. Both halves were stored in a 4 °C fridge to inhibit the growth of micro-organisms. The VANG core comprised a total length of 87 cm but only 54 cm was used for pollen preparation because deeper layers were sandy and had poor pollen preservation. In addition to an analysis of the fossil pollen, the VANG core was used for the analysis of spore, and charcoal (macro- and micro-fossil charcoal) abundance, organic carbon abundance (Loss on Ignition), inorganic carbonate content, Lead-210 (^{210}Pb) dating and AMS radio-carbon dating. Sediment was described using a modified Troels-Smith protocol (1955).

4.1.2. Vegetation survey

A survey of the vegetation surrounding the Vangkraal Spring wetland was carried out, structured by distance from the wetland and by patches of different vegetation types. Eight vegetation type units were recognized: Shale Renosterveld, Alluvium Fynbos, Renosterveld-Fynbos Ecotone, Grassland, Grassland-Renosterveld matrix, Olive stand, Thicket and a wetland vegetation unit that incorporated the vegetation immediately surrounding the Vangkraal Spring itself (Figure 11 and 12; Table 5). The vegetation survey consisted of assessing the vegetation within 5x10 m plots in each vegetation unit around the Vangkraal Spring wetland. The dominant species present in each plot were identified, and their respective percentage abundance was recorded with species less abundant being classified as 'other'. Data from the vegetation survey were to be used to evaluate the relationship between modern vegetation type and modern pollen rain (see chapter 5, section 5.1 for results).

The underlying assumption in this approach is that the pollen profile from the VANG core represents changes in vegetation and the effects of climate and land-use over time at a local scale. A relationship exists between coring site (wetland) size and the predicted pollen source area. Large wetlands collect pollen from a wider area where as small wetlands reflect a more local pollen signature (Figure 9; Table 3). Since the Vangkraal Spring wetland is small (diameter is ca. 22.5 m), it was assumed that most of the pollen in the VANG core would have originated locally. Based on previous work in patchy landscapes it was estimated that most pollen would originate from within 300 m, with a smaller component of regional pollen originating further away (Jacobson and Bradshaw 1981; McQueen and MacPhail 1983; Sugita 1994).

4.2. Laboratory methods

4.2.1. Sediment description

Sediment composition was described using a modification of the scheme devised by Troels-Smith (1955). The composition of the sediment core was described in terms of the abundance of four main components of sediment particles namely: *Turfa*, *Detritus*, *Limus* and Minerals (*Argilla* and *Grana*) (Table 4). The sediment was also described by colour changes using the Munsell (1954) colour chart. The core sediments were divided into units of similar lithology and points of change in lithology stratification were recorded. The results of sediment description were plotted using Psimpoll (Bennett 1996) so that sediment description could be plotted alongside the pollen diagram.

Table 4: Troels-Smith (1955) classes available to describe the composition of sediment from the Vangkraal Spring, at Elandsberg PNR.

Class	Element	Description
***Turfa* (peat)**		Consists of macroscopic plant remains which are visible to the naked eye, and includes a term describing the humicity component. This is described using a five-point scale with 0 representing the absence of humic matter and 4 representing the complete dominance of humic matter.
	T. Bryophitica (Tb)	Consists of mosses.
	T. Lignosa (Tl)	Consists of stump, roots, intertwined rootlets, trunks, stems, branches, etc., all of lignified plant tissue.
	T.herbacea (Th)	Consists of roots, intertwined rootlets, rhizomes, stems, leaves, etc., all of herbaceous plants.
Detritus		Consists of above ground parts of plants.
	D. Lignosus (Dl)	Consists of fragments of ligneous plants greater than 2 mm in size.
	D. herbosus (Dh)	Consists of fragments of herbaceous plants greater than 2 rnm in size.
	D. Granosis (Dg)	Consists of smaller fragments of ligneous and sometimes animal fossils, ranging from less than 2 mm to 0,1 mm in size.
Limus		Consist of aquatic mud made up from <0.1 mm fragments of plants and animals and also includes a humicity component using the five point scale described above. The small size of the *Limus* particles makes the subdivision of this class difficult.
	L. detrituosus (Ld)	Plants and animals or fragments of these; particles <ca.0.1 mm ± humous substance (i.e. peaty).
	L. ferrugineus (Lf)	Has iron oxide present resulting in its red coloration and making it distinguishable from other *Limus*.
Argilla		Describes the mineral components of the sediments.
	Clay (As)	<0.002 mm in size
	Silt (Ag)	0.002 - 0.06 mm in size
Grana		Describes the mineral components of the sediments.
	Fine sand (Ga)	0.06 - 0.5 mm in size
	Coarse sand (Gs)	0.5 – 2 mm in size
	Gravel (Gg)	>2 mm in size

4.2.2. Physical properties analysis (Loss on ignition)

Loss on ignition (LoI) is a commonly used method to estimate the organic carbon content and carbonate content of sediments but can also be used to determine the water content (Bennett and Willis 2001). For the analysis of LoI the protocol of Heiri et al (2001) was followed unless otherwise stated. Samples were removed from the core at between 1-2.5 cm intervals (the same as for pollen analysis) from the top of the core to the base using a 3 ml syringe with the tip removed. The LoI determination required sequential heating of samples in a muffle furnace (Dean 1974; Bengtsson and Enell 1986), five sets of weights (designated here as A-E) followed by a series of calculations.

A: A labelled set of dry crucibles was weighed and recorded.

B: A known volume of sediment was transferred to each crucible and a new weight (wet sample + crucible) was recorded.

C: Samples were dried overnight for 16 hours to constant weight at a temperature of around 100°C and the dry weight recorded.

D: Samples were exposed to a temperature of 550 °C (LoI_{550} or the carbon content) for five hours, in order to remove organic carbon (organic matter oxidised into carbon dioxide and ash). Samples were put into the muffle furnace cold, the timer was only set (in this case 40 minutes after the sample had been put in) once the furnace had reached the desired temperature. Samples were allowed five hours to cool whilst in the furnace. Crucibles were placed in a desiccator when they were removed from the oven and between weighing to prevent absorption of moisture from the air, which would affect weights.

E: In the final step samples were heated at 1000 °C (LoI_{1000} or the carbonate content) for two and a half hours, re-weighed, carbon dioxide escapes from the sediment, thus enabling carbonate content to be calculated from the final weight of the sample (Dean 1974). The oven was then switched off and the samples left to cool overnight (12 hours) to be reweighed in the morning.

The following equations adapted from Heiri et al (2001) and Gillson (2002) were used where the symbols A-E refer to the steps outlined above:

$$Percentage\ water\ (\%) = \frac{(B - A) - (C - A)}{B - A}$$

$$Dry\ Weight\ (DW) = C - A$$

$$Percentage\ organic\ carbon\ (\%\ \mathrm{LoI}_{550}) = \left(\frac{(C - A) - (D - A)}{C - A}\right) * 100$$

$$Percentage\ carbonate\ content(\%\ \mathrm{LoI}_{1000}) = \left(\frac{(D - A) - (E - A)}{C - A}\right) * 100$$

4.2.3. Pollen analysis

Sub-samples of 1 cm^3 of sediment for pollen analysis were collected from the sediment core using a plastic medical syringe with the tip removed. Sub-samples were initially taken at 14 cm intervals down the length of the core. After range finder radio-carbon dates had been obtained (see section 4.2.6 below), sampling resolution was increased to 2-3 cm for the first 54 cm of the core and thereafter 0.5-1 cm in areas of the core that showed significant changes.

The sample together with distilled water was transferred into 50 ml Nalgene® Centrifuge tubes with sealable caps and stored in a refrigerator. Pollen was extracted from the sediment samples using standard procedures outlined in Bennett and Willis (2001). Samples were mixed using a 'vortex mixer' during each step (see Figure 10). Two exotic spore (*Lycopodium*) tablets were added to each 1 cm^3 of sediment (Step 1, Figure 10). The use of *Lycopodium* tablets allows for pollen concentration to be calculated as well as changes in sedimentation rate (Stockmar 1971; Bennett and Willis 2001) (Appendix 2.1.). The *Lycopodium* tablets (batch number 483216; concentration = 18583 for one tablet) were produced and distributed by the Department of Quaternary Geology at the University of Lund. Pollen concentration was then calculated by using the following equation modified from Bennett and Willis (2001):

$$Fossilpollen\ concentration = \frac{Lycopodium\ added \times fossil\ pollen\ counted}{Lycopodium\ counted}$$

To remove carbonates from the sediments and break up the *Lycopodium* tablets, 7% Hydrochloric acid (HC1) was added to the samples (Step 2, Figure 10). They were then heated at 90 °C for 30 minutes, washed with distilled water, centrifuged at 3500 RPM for 5 minutes, after which the supernatant was decanted. To remove humic acids (Step 3, Figure 10), samples were treated with 10% Sodium hydroxide (NaOH) solution and then heated at 90 °C for 20 minutes. For highly organic and peaty samples, this process was repeated 3-4 times and more clayey samples were only heated once for 4 minutes. A deflocculant, 10% Sodium pyrophosphate ($Na_4P_2O_7$), was used to deflocculate clay (Step 4, Figure 10), samples were heated at 90 °C for 30 minutes. This step was stopped with the addition of distilled water and the samples were sieved at 150 microns into another set of test tubes in order to separate out macrofossils and large sand and gravel particles (Step 4, Figure 10). Samples were then rinsed (at least 5 but up to 15 times) until the supernatant was clear, centrifuging and decanting between washes. In order to acidify the sediments for the next step, samples were washed with 7% HCl. Concentrated (71-75%) Hydrofluoric acid (HF) was used in order to dissolve silica and silicates from the sediments. HF was added (Step 5, Figure 10) and the test tubes were placed in a water bath at 90 °C for 60 minutes. Sometimes a second treatment of HF was required in order to remove all silica.

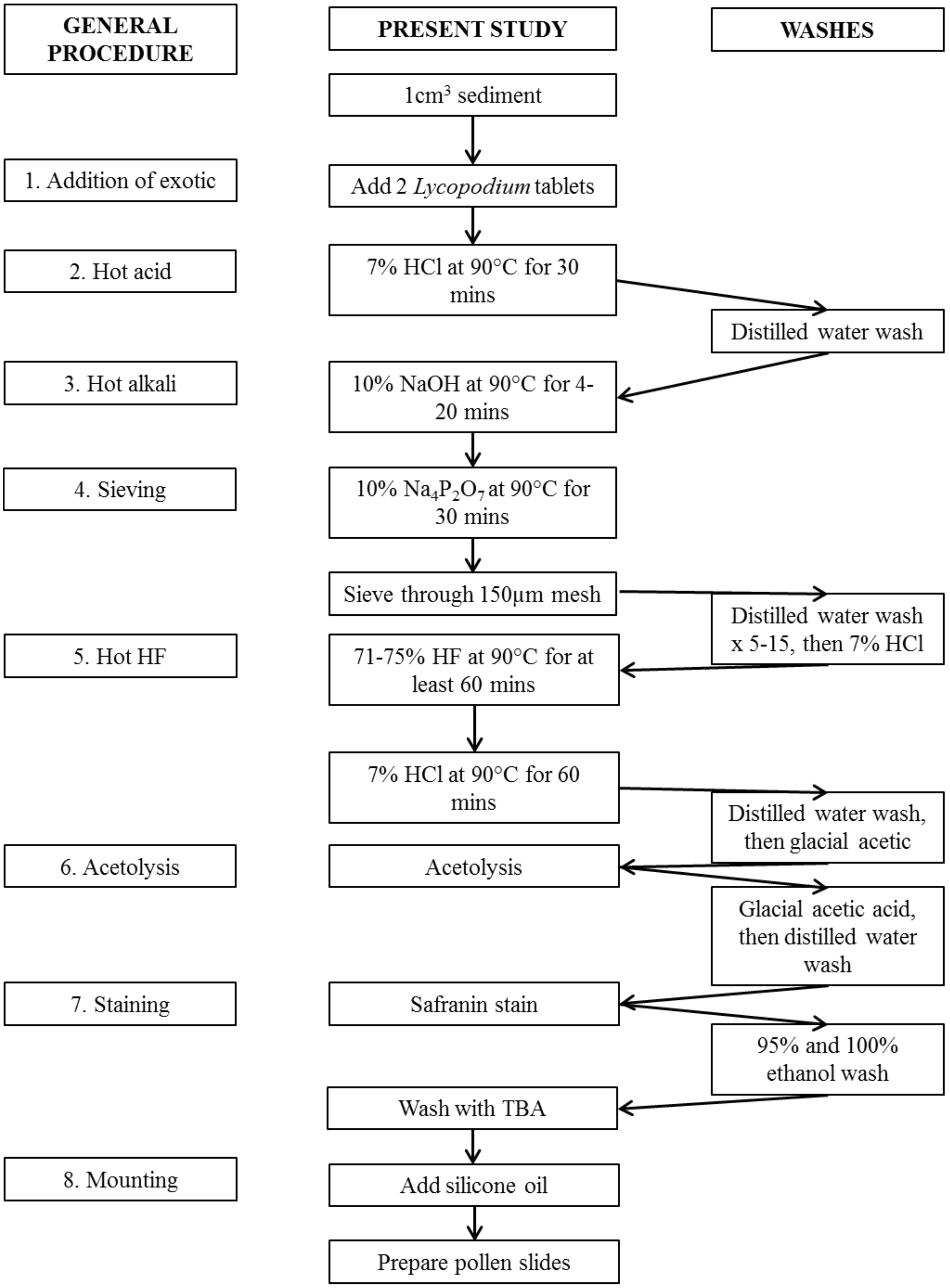


Figure 10: Pollen preparation process adapted from Bennett and Willis (2001).

Immediately after HF, 7% HC1 was added in order to remove colloidal silica and silicofluorides created during the HF step (Bennett and Willis 2001). Samples are heated at 90 °C for 60 minutes (Step 5, Figure 10). Samples were washed with distilled water and transferred to 15 ml test tubes. They were then washed with glacial acetic acid (Step 6, Figure 10) as a way of dehydrating the sample in preparation for the next step, acetolysis.

In a process called acetylation (or acetolysis; Step 6, Figure 10) a mixture of acetic anhydride and concentrated sulphuric acid was made and added to the samples in order to hydrolyse cellulose. In this process polysaccharides are digested which may otherwise obscure the pollen grains (Bennett and Willis 2001). After the acetolysis mixture was added the samples were placed in a water bath at 90 °C for 4 minutes. Samples were removed from the water bath and glacial acetic acid was used to stop the reaction (Step 6, Figure 10). The samples were washed again with glacial acetic acid, then with distilled water for several washes (2-6 times) until the pH of the samples tested neutral. The samples were then stained using 3 drops of undiluted Safranin solution (Step 7, Figure 10) which increases the contrast of sculptural elements on the pollen grains and spores (Bennett and Willis 2001) after which they were washed with distilled water. In order to dehydrate the samples, 95% and 100% ethanol was added (Step 7, Figure 10). This was done in order to remove all of the water. If the sample is not properly dehydrated, then irreversible clumping would occur and the sample would have to be discarded. Samples were transferred into 5 m1 plastic vials using tertiary butyl alcohol (TBA) (Step 7, Figure 10). Silicone oil was then mixed into the samples and the tubes left uncovered in order for the TBA to evaporate (Step 7, Figure 10). Silicone oil was chosen as the mounting medium because it is miscible with TBA, and silicone oil does not set, making it possible to move and rotate pollen grains by applying gentle pressure on the cover slip during the process of pollen identification (Step 8, Figure 10). At this stage of the pollen preparation procedure, the remaining mixture consisted of silicone oil, charcoal pieces and stained pollen and spores. This mixture was stirred well before slides were prepared to ensure that the pollen grains were equally distributed throughout the mixture. Prepared pollen samples were mounted (Step 8, Figure 10) on glass slides using square glass cover slips and then sealed with clear nail polish.

Slides were analysed using a Leica DM750 microscope with 4x, 10x, 40x and 100x objectives. Most identification took place at 400x magnification, though in order to view the sculpting on pollen grains, 1000x total magnification was used in conjunction with an immersion oil. The calibrated stage of the microscope was used to traverse the slide systematically at 1 mm intervals. For each level (depth in the sediment core) a minimum of 250 pollen grains (Gil-Romera et al. 2006; Scott and Woodborne 2007a,b; Quick et al 2011) (excluding aquatics Cyperaceae and *Polygonum*) were counted to allow for statistical significance and the calculation of 95% confidence intervals (Maher 1972). The number of slides needed to attain this level varied between one and four. Images were captured using a Leica ICC50 HD camera and Leica LAS EZ (V 2.1.0) software and digitally stored. Pollen was identified using a reference slide collection (kept in the Department of Biological Sciences, UCT), general pollen reference books (Bonnefille and Riollet 1980; Moore et al. 1991) and the African Pollen Database (http://medias3.mediasfrance.org/pollen/). Using the most recent vegetation classification of vegetation types (Mucina and Rutherford 2006) as well as species lists specific to Elandsberg PNR, a plant species list was drawn up to help identify pollen grains. When pollen was not identifiable it was classified as either ‘unknown’, ‘concealed’ or ‘degraded’. Concealed and degraded grains were not included in the pollen sum. Whilst systematically traversing the slide, pollen grains were counted and tallied in a workbook. Later the data were entered into Excel spread sheets for further analysis. Unknown grains were sketched or photographed and also tallied and later identified using pollen reference collections and databases.

4.2.4. Spore analysis

Coprophilous spores are those that are associated with fungi that grow on animal dung (Davis and Shafer 2006; Graf and Chmura 2006), decaying wood (Massee and Salmon 1901; Lundqvist 1972) and/or associated with human dwelling sites (van Geel et al. 2003). Using previous work completed worldwide (Gelorini et al. 2011; van Geel and Aptroot 2006; Jarzen and Elsik 1986; van Geel et al. 1986, 2003; Graf and Chmura 2006; Prager et al. 2006), a list of coprophilous spores (i.e. *Sporormiella*, Sordariaceae, *Gelasinospora* and *Coniochaeta*) was drawn up to help identification. The same slides as for pollen identification were used. Spores which were not coprophilous (i.e. Trilete, Monolete and Other non- coprophilous spores) were also counted and were grouped together as ‘non- coprophilous spores’ and therefore included in the total spore sum. In a similar way to the pollen counts, the calibrated stage of the microscope was used to traverse the slide systematically at 1 mm intervals to count spores. For each level a minimum of 100 coprophilous spores (Ekblom pers. comm. 2013) and 100 *Lycopodium* exotic spores were counted. For levels when coprophilous spores were scarce (although there was still a number of non-coprophilous spores present) and a coprophilous spore sum of 100 could not be reached, methods by Gelorini et al. (2012) were adapted so that counting of coprophilous spores continued until 100 terrestrial pollen grains were encountered, to ensure statistical robustness of the results.

4.2.5. Charcoal analysis

Micro-charcoal abundance was estimated using a slight adaptation of the point count estimation proposed by Clark (1982) and the same slides that were used for pollen analysis were used for the assessment of micro-charcoal abundance. The procedure proposed by Clark (1982) is relatively quick and accurate as it allows the calculation of the surface area of charcoal per unit volume of sediment expressed in crn^2 cm^{-3} (see equation below). A sampling grid was created as a means to traverse the slide and sample all areas of the slide equally. The eyepiece graticule was used to sample the field of view (f.o.v.). The points form the ends of the 11 lines (major units) of the eyepiece graticule units resulting in a total of 22 sampling points. Charcoal concentration was then calculated by using the following equation modified from Bennett and Willis (2001):

$$Charcoal\ concentration\ = \frac{f.o.v.\ \times no.charcoal\ hits}{no.points} \times \frac{\frac{Lycopodium\ added}{Lycopodium\ counted}}{sediment\ volume}$$

Where f.o.v. is the area of the field of view in microns, no. of charcoal hits is the total number of points that coincided with a charcoal fragment, for the entire level (i.e. depth in the sediment core) and no. points is the largest number of possible points that can coincided with a charcoal fragment . *Lycopodium* added is the number of *Lycopodium* spores contained in the tablets added to the 1cm^3 sample taken at each depth (i.e. 18583 x 2). *Lycopodium* counted is the number of *Lycopodium* spores counted at each depth and sediment volume is the volume of sediment analysed in the laboratory for each depth (i.e. 1cm^3).

At each 1 mm point on the sampling grid the f.o.v. of the microscope was examined. Charcoal abundance was assessed by recording when the points (the end of the line of the eyepiece graticule) touched a piece of charcoal. The total number of *Lycopodium* spores in each f.o.v. was also recorded. Assessment was done at 400x total magnification and a minimum of 200 items (sum of charcoal hits and *Lycopodium* spores) were counted (Finsinger and Tinner 2005), and at least 100 charcoal particles were counted in each sample (Duffin et al. 2008). Compared to pieces of organic material, charcoal was identified by its dark colour and its characteristic sharp angular edges. Only charcoal pieces greater than 10 µm in length were recorded and any ambiguous fragments were excluded (Mooney and Tinner 2010).The point count estimation method used in this study allowed for standardization between levels and charcoal concentrations could therefore be compared at different levels.

Macroscopic charcoal was counted using a Leica ZOOM 2000 microscope at 10x magnification. Macro-charcoal (>150 µm) was recovered during the pollen preparation (see section 4.2.3.). Macro-charcoal that had been stored in distilled water were re-suspended in very dilute Hydrogen peroxide (6% H_2O_2) and left overnight. The H_2O_2 bleaches the organic material excluding the charcoal and pyrite, leaving them black and making macro-charcoal easy to identify. The solution is poured into a petri dish that is examined under a binocular dissecting microscope (at 10x total magnification). The angular black (opaque) particles were counted. When there were few charcoal particles, all were counted. Alternatively, when there were many, a sub-sampling exercise was performed where only a proportion of randomly selected ‘pie slices’ were counted and multiplied to obtain the total charcoal fragments. The final result was expressed as exact particle counts for each level (Duffin et al. 2008).

Macro- and micro-charcoal abundance was measured for each of the 36 depths where pollen abundance was measured. However, an additional 11 samples in the lower depths (i.e. 35-53 cm) of the VANG core were analysed for micro-charcoal abundance only since the initial subsampling of 36 was insufficient to determine the patterns that emerged.

4.2.6. Chronology

A combination of dating techniques was used to establish a chronology for the VANG core. Initially accelerator mass spectrometry (AMS) radio-carbon dating was used to determine the age of the bottom part of the core. After an initial pollen analysis was completed it was suspected that the top part of the core contained sediments from the last 100 years and hence was sampled for Lead-210 (^{210}Pb) dating (Appleby et al. 1979). Two further samples were radio-carbon dated and then an age depth model was constructed. The dates for the introduction of various crops and alien plants in South Africa were also used for calibration and provided relative age horizons (Becker 1996; Wooding pers. com. 2013).

4.2.6.1. Accelerator mass spectrometry radio-carbon dating

AMS radio-carbon dating is one of the earliest and most widely used of the radiometric techniques. Carbon-14 (^{14}C) is a radioactive isotope of carbon which eventually decays (via the emission of beta (β) particles) to form the stable element Nitrogen-14 (^{14}N). ^{14}C atoms are oxidised by carbon-dioxide (CO_2) and become mixed throughout the atmosphere and absorbed by oceans and living organisms. It is accepted in general terms that all living organisms absorb CO_2 (during tissue-building) in a ratio that is roughly in equilibrium (i.e. will be in similar isotopic ratio) with atmospheric CO_2. When the living matter dies, the ^{14}C within the organic tissues continue to decay but no replacement takes place and thus if the rate of decay of ^{14}C is known then the date of death can be calculated from the measured residual ^{14}C activity (with a half life of 5570 + 30 years) (Lowe and Walker 1997).

Accelerator mass spectrometry (AMS) carbon-14 dating is used to measure the residual ^{14}C activity in a sample. To do this the actual numbers of ^{14}C atoms in a sample of material are counted by using particle accelerators as mass spectrometers, which differs from conventional radio-carbon dating, which measures the radioactivity of a sample as it decays over time. Conventional mass spectrometry involves the deflection (by a factor that is proportionate to atomic weight) of charged particles moving in a magnetic field such that the lighter the particle, the greater the amount of deflection. A disadvantage of conventional mass spectrometry is that there is no discrimination between ^{14}C and other elements with similar weights. Thus the principle behind AMS is that if particles travel at very high speeds (because they are subjected to large voltage differences) even the very small number of ^{14}C atoms in a sample can be detected. A much smaller sample is required for AMS dating, enabling higher chronological resolution making it an ideal technique for high resolution palynology, such as the present study.

A sample was taken from VANG core at a depth of 54 cm using a parallel pair of razor blades in order to remove a 1cm stratigraphic slice of sediment. Caution was taken to avoid contaminating the samples with sources of carbon. The sample was wrapped in aluminium foil before being packaged and sent to the Beta Analytic Inc. Laboratory in Florida at the North American Facility Headquarters. The sample dated was the bulk organic fraction that remained after sieving the sediment to <150 µm to remove any roots or macro-fossils. After this a pre-treatment was applied to remove possible contamination from bicarbonate in the water, humic acids from decaying plants, dissolved carbon dioxide from the atmosphere, and carbon from humus leaching or adsorbing down the sediment profile. The chemical pre-treatment is known as the acid-alkali-acid (AAA) method. The AAA pre-treatment involved washing the sample with hot HCl followed by a NaOH wash. A final HCl acid wash was done before the sample was dried.

AMS dating was carried out using a Tandem Accelerator which is a large nuclear particle accelerator operating at 0.2 to many million volts with two stages operating in tandem to accelerate the particles. Samples were converted to graphite (or a CO_2 source) and mounted on a metal disc after which caesium ions are fired at the target and the negatively ionised carbon atoms (C^-) produced were accelerated towards the positive terminal. Since ^{14}N does not produce negative ions there is discrimination between it and ^{14}C, and the ^{14}N is eliminated. At the connecting point between the two stages, the ions change charge from negative to positive (four electrons lost from C^- and changed to triple positive charge C^{3+}) by passing through a thin layer of matter (‘stripping’). Molecules are broken apart in this stripping stage and other molecules are also lost. The second stage is brought on by the repulsion by the positive terminal, where the acceleration of the carbon ions occur due to the focusing of magnets where deflection occurs according to mass and thus the concentration of the ^{14}C and stable isotopes ^{13}C and ^{12}C can be measured. A radio-carbon age of the sample is calculated in years before present (BP, i.e. uncalibrated dates where "present" is defined as

AD 1950) by comparing the $^{14}C/^{12}C$ ratio measured to the modern reference standard (known ^{14}C activity in oxalic acid). Once various corrections are made, the sample/modern ratio allows for an age to be calculated. A plus or minus sign accompanies the calculated age and this reveals the statistical uncertainties associated with determining activity. Two more samples (at 46 cm and 31.5 cm) were AMS radio-carbon dated following the same procedure as above.

Since the level of atmospheric ^{14}C has not been constant for the duration of time that can be radio-carbon dated, a BP date cannot be used as a direct calendar date and thus calibration needs to take place. Reservoirs of carbon also exist in organic matter, the ocean, ocean sediments and sedimentary rocks and changes in the Earth's climate can affect the carbon flows between these reservoirs and the atmosphere, leading to changes in the atmospheric ^{14}C. In addition to the changes caused by natural processes, the level of atmospheric ^{14}C has also been affected by human activities. The fractional level of ^{14}C decreased during the industrial revolution (1800s to 1950s), because of the large quantities of CO_2 released into the atmosphere as a result of excavated oil reserves and combustion production of fossil fuel. This decline in atmospheric ^{14}C is known as the Suess effect. However, atmospheric ^{14}C nearly doubled during the 1950s and 1960s as a result of atmospheric atomic bomb tests. Thus, the time range covered by radio-carbon dating is >50 000 years and with the exception of using the ‘bomb peak’ it is generally unreliable when dating anything with relatively new carbon (i.e. younger than the 18th century) because of the release of ancient carbon from fossil fuels. The ages of the three samples from the VANG core were calibrated to give dates in calendar years using a standard calibration programme called BCal (see section 4.3) (Buck et al. 1999).

4.2.6.2. Lead-210 dating

Lead-210 (^{210}Pb) (an unstable isotope) forms one of the daughter nuclides in a series of nuclides that form part of the Uranium-series decay chain involved in the decay of inert Radon gas (^{222}Rn). ^{210}Pb is removed from the atmosphere as it accumulates in marine sediments, soils, peats and glacial ice and consequently decays over a period of about 150 years to form the stable isotope ^{206}Pb. As this half-life is relatively short, this technique is used to date soils that are younger than150 years old (Bennion and Appleby 1999). Assuming that the atmospheric flux of ^{210}Pb has remained constant, the time that has passed since the lead has been deposited can be determined by measuring the ratio of ^{210}Pb to ^{206}Pb in a column of sediment in relation to depth. In this manner, the rate of sedimentation can be ascertained. The main setback of this method is what is termed 'supported' ^{210}Pb and this is due to most sediment containing small amounts of ^{210}Pb derived from the decay of uranium or its daughters. It is important to determine the 'supported' ^{210}Pb and subtract it from the 'unsupported' ^{210}Pb produced in the atmosphere. The constant rate of supply (CRS) model (Appleby and Oldfield 1978; Appleby 2001) is used to calculate the inputs of supported and unsupported ^{210}Pb to the sediment. This model assumes that unsupported ^{210}Pb is being supplied to the sediments at a constant rate. This model is convenient, as the rate of sediment accumulation does not have to be constant over time in order to calculate the age of the sediment accurately. This is useful as recent sediments often have an increasing rate of accumulation owing to erosion caused by modern land-use. The data were analysed using a second statistical model known as the Slope Regression model in order to compare results and to be confident that the sedimentation accumulation rates and ages were accurate estimates for the VANG core.

The analysis of ^{210}Pb requires a continuum of sediment to be sampled with each section of sediment amounting to a minimum of 2 g of wet weight. The continuum of sediment should be 150 years old or younger. Where the depth of the age horizon was not known, samples were systematically taken from the top of the core downwards at predetermined intervals. For the VANG core, an AMS date for sediment taken at 54 cm had an age of 1350±30yr BP (Cal AD 751) therefore sediments considered for ^{210}Pb dating were taken above 54 cm. By looking at the pollen spectrum of the VANG core, *Pinus* spp pollen first appeared at 20 cm and according to historical records, a pine plantation near the study site at Elandsberg PNR was established about 100 years ago (Wooding pers. com. 2013). Therefore, the core was subsampled until 37 cm was reached, with thinner sections of 2-3 cm at the top of core and thicker sections of 5-7 cm lower down the core. The subsampling sections were as follows: 0-2cm, 2-5cm, 5-8cm, 8-11cm, 11-15cm, 15-20cm, 20-25cm, 25-30cm, 30-37cm. This resulted in 9 sections in total. This sampling strategy was adopted with the aim of including several levels of sediments that have no measurable quantities of unsupported ^{210}Pb left (e.g. 25-30cm, 30-37cm), as required by the CRS model described above. Samples were removed from the core using blades and an isotope spatula after carefully cleaning the surface in order to remove any contaminating sediments.

Samples were placed in ziplock plastic bags and sent to Core Scientific International in Canada. Here they were allowed to equilibrate for three weeks before being measured using an OrtecOctect Alpha spectrometer. This method determines ^{210}Pb in sediment (dry weights 0.05-0.5g) via the granddaughter (the third chain of the decay chain) Polonium-210 (^{210}Po). Using a simple distillation apparatus, the ^{210}Po is distilled and converted to chloride (Cl-) at 500°C. The ^{210}Po distillate is digested in a nitric acid (HNO_3) medium, converted back to the Cl- salt, plated out onto silver (Ag), and then counted by alpha spectroscopy using the OrtecOctect Alpha spectrometer. The recovery is monitored by concurrently measuring the activity of a ^{209}Po spike which was added at the beginning of the sample processing (Eakins and Morrison 1978; Appleby et al. 1979; Cornett et al. 1984).

4.3. Statistical software and analysis

Pollen, spore, charcoal and LoI data was prepared and descriptive statistical analyses performed in Microsoft® Office Excel 2010 edition. Excel was also used for constructing bar charts and scatter plots for LoI data. Flowcharts and timelines were created in Microsoft® Office PowerPoint 2010 edition. Maps throughout this study were constructed using ArcMap™ (version 10), ArcGIS® software by Esri. They are the intellectual property of Esri and are used herein under license. Copyright © Esri and for more information see www.esri.com.

The use of pollen percentages in palaeoecology is common (Webb et al. 1981; Sugita 1994; Meadows and Baxter 2001; Meadows et al. 2010; Neumann et al. 2011; Quick et al. 2011). There is no linear relationship between variables transformed to proportions, because changes in the abundance of one variable will affect all of the others. This is known in as the "Fagerlind effect" (Fagerlind 1952; Prentice 1988). For this reason an alternative data representation was used (i.e. absolute concentration data measured as grains/cm^3) alongside the percentage data in order to make comparisons and determine trends within the results. Pollen, spore and charcoal data were plotted and analysed using the Psimpoll programme version 4.27 found at http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html. An online manual was used for guidance, see http://www.chrono.qub.ac.uk/psimpoll/psimpoll_manual/4.27/psimpoll.htm. Zonation of pollen data was carried out using Psimpoll and the ‘optimal splitting by information content’ (Bennett 1996). The data (both percentage and concentration data analysed separately) were normalised by applying the square root transformation.

Further statistical analysis was performed using Primer 6 (Version 6.1.5, Primer-E Ltd, Plymouth, United Kingdom). A non-metric multi-dimensional scaling (NMDS) Ordination (McCune & Grace, 2002) was run on the pollen percentage data (i.e. excluding spores, macro- and micro-charcoal) using Primer 6. Before the data were transformed, factors were added to the original dataset such that each depth was labelled according to the two zones (zone V-1 and V-2) that were identified by the zonation analysis in Psimpoll (described above). The original dataset was transformed using a square root transformation after which a Similarity Matrix was calculated using the transformed data. A Bray-Curtis Similarity was used to analyse similarity between samples that reflected the different depths of the VANG core based on pollen taxa composition. A NMDS Ordination was run with the default number of restarts set at 25 and a minimum stress of 0.0 after which a two-dimensional graph was plotted. Stress values can vary from 0 (minimum) to 1 (maximum) indicating how easily the data can be arranged on two and three-dimensional graphs respectively but the lower the stress value the more appropriate the graph. A CLUSTER analysis was also carried out on the similarity matrix and a dendrogram was plotted. The clusters were overlaid on the NMDS plot with 70% and 80% resemblance levels chosen such that a contour line is drawn around each of the clusters it defines. Following this a SIMPER analysis (Clarke and Warwick 1994) was conducted on the transformed data to determine the role of individual species contributing to the separation of the depths into zones V-1 and V-2. This is implemented in the ‘similarity percentages’ (SIMPER) routine by: using a one-way design, the Bray-Curtis similarity measure and listing only higher-contributing pollen taxa with a cut-off percentage of 90%. A principal components analysis (PCA) was performed on the percentage data using the Vegan package in R (http://www.R-project.org/). Data were set to a minimum of 2% inclusion before the PCA analysis in order to account for the bias of less abundant taxa. No transformation was used, the PCA was constrained and distance plot based on PCA scores. The data was presented as a distance biplot. In order to test the significance, a scree plot was plotted using the broken-stick model (MacArthur 1957). See Appendix 2.1 for PCA script.

Radio-carbon dates were calibrated online using the Bayesian radio-carbon calibration tool called BCal, see http://bcal.shef.ac.uk/ (Buck et al. 1999) and the calibration curve for the southern hemisphere was used (Hogg et al. 2013). The ^{210}Pb and AMS radio-carbon dating results were combined in an Age-depth model using a cubic spline interpolation in Psimpoll (Bennett 1994).

5. RESULTS

5.1. Vegetation survey and modern pollen of Elandsberg PNR site

The eight vegetation type units in the vicinity of the Vangkraal Spring wetland at Elandsberg Private Nature Reserve (Elandsberg PNR) site are shown in Figure 11 and 12 and are described in Table 5. Table 6 shows the most abundant taxa in each vegetation unit determined during the vegetation survey. The most dominant species in each vegetation unit are *Protea* spp in Alluvium Fynbos, *Themeda* spp in the Renosterveld-Fynbos Ecotone and Grassland, *Elytropappus rhinocerotis* in Shale Renosterveld and Grassland-Renosterveld matrix, *Olea europea africana* in Olive stand, *Olea europea africana* and three *Rhus* (*Searsia*) spp in Thicket, and Cyperaceae in Vangkraal Spring wetland. Of the 31 species that were identified during the modern vegetation survey, many of them come from families that are indistinguishable in the pollen record below family level (Proteaceae, Restionaceae, Poaceae, Cyperaceae, and Anacardiaceae). When this is taken into consideration 20 types would be identifiable in the pollen subsampled from the surface sample. This would include 18 families and 2 genera (Asteraceae *Stoebe/Elytropappus*-type and *Cliffortia*).

5.1.1. Modern pollen in the Elandsberg PNR site

Fourteen pollen types were identified in the surface sample of the VANG core. Nine of these pollen types overlapped with those recorded in the vegetation survey including seven families (Asteraceae, Cyperaceae, Poaceae, Proteaceae, Restionaceae, Rhamnaceae, and Scrophulariaceae) and two genera (Asteraceae *Stoebe/Elytropappus*-type and *Cliffortia*). There were variations in the way the most abundant modern vegetation related to the most abundant pollen taxa in the surface sample. The following taxa were the most abundant in the vegetation units but their abundance was relatively lower in the surface sample: Proteaceae, Poaceae, Oleaceae and *Rhus/Searsia* spp. In contrast *Elytropappus rhinocerotis* was the most abundant in both the vegetation survey and the surface sample. Cyperaceae (classified as an aquatic taxon) was the dominant vegetation type in the Vangkraal Spring wetland and its abundance was relatively high in the surface sample but it had reached higher levels deeper in the VANG core (see section 5.4.1 below). Five of the pollen types identified in the surface sample were not recorded by the vegetation survey (Table 6). These were: Chenopodiaceae/Amaranthaceae, Ericaceae, Euphorbiaceae (*Clutia*), Pinus and Rubiaceae

(*Anthospermum*). Meanwhile, 10 of the taxa recorded in the vegetation survey were not found in the surface sample pollen assemblage of which five were not recorded in the pollen spectrum of the VANG core at all, namely: *Asparagus* spp (Asparagaceae), *Diospyros* spp (Ebenaceae), *Chasmanthe* spp (Iridaceae), *Salvia* spp (Lamiaceae) and *Juncus* (Juncaceae) (Table 6). Although Juncaceae was recorded in the vegetation survey, it may have been detected in the surface sample and the rest of the VANG core but incorrectly assigned to 'crumpled Poaceae/Restionaceae' pollen which was not included in the pollen sum. Additionally, Juncaceae is an aquatic taxa and was not included in the terrestrial pollen sum thus the missing Juncaceae data in the pollen record did not affect the pollen results.

Table 5: Vegetation units at Vangkraal Spring wetland, Elandsberg PNR study site.

Vegetation Unit	Description
Alluvium Fynbos	Ring of Alluvium Fynbos on the ridge north and east of the spring.
Renosterveld-Fynbos Ecotone	A transitional Fynbos-Renosterveld matrix. This is where the spring is located. There is an erosion gully on the margins of the ecotone.
Grassland	South of the spring there is a depression in the landscape. This area is dominated by grasses and is probably seasonally waterlogged.
Shale Renosterveld	West of the wetland is an area dominated by Renosterveld which has not been burnt recently.
Grassland-Renosterveld matrix	Further to the south of the Renosterveld vegetation unit there occurs a Grassland-Renosterveld matrix. The area has burnt recently as evidenced by the presence of burnt *Elytropappus rhinocerotis* skeletons.
Olive stand	A large stand of mature olives trees (*Olea europaea africana*) occurs with individuals clustered in the erosion gulley where the stream flows.
Thicket	North-east of the spring, situated on the mountain slopes lies a small patch comprised of Thicket and forest edge Afro-montane species.
Vangkraal Spring wetland	The VANG core was retrieved from this wetland which remains waterlogged throughout the year due to the spring. The diameter of the wetland is 22.5 m.

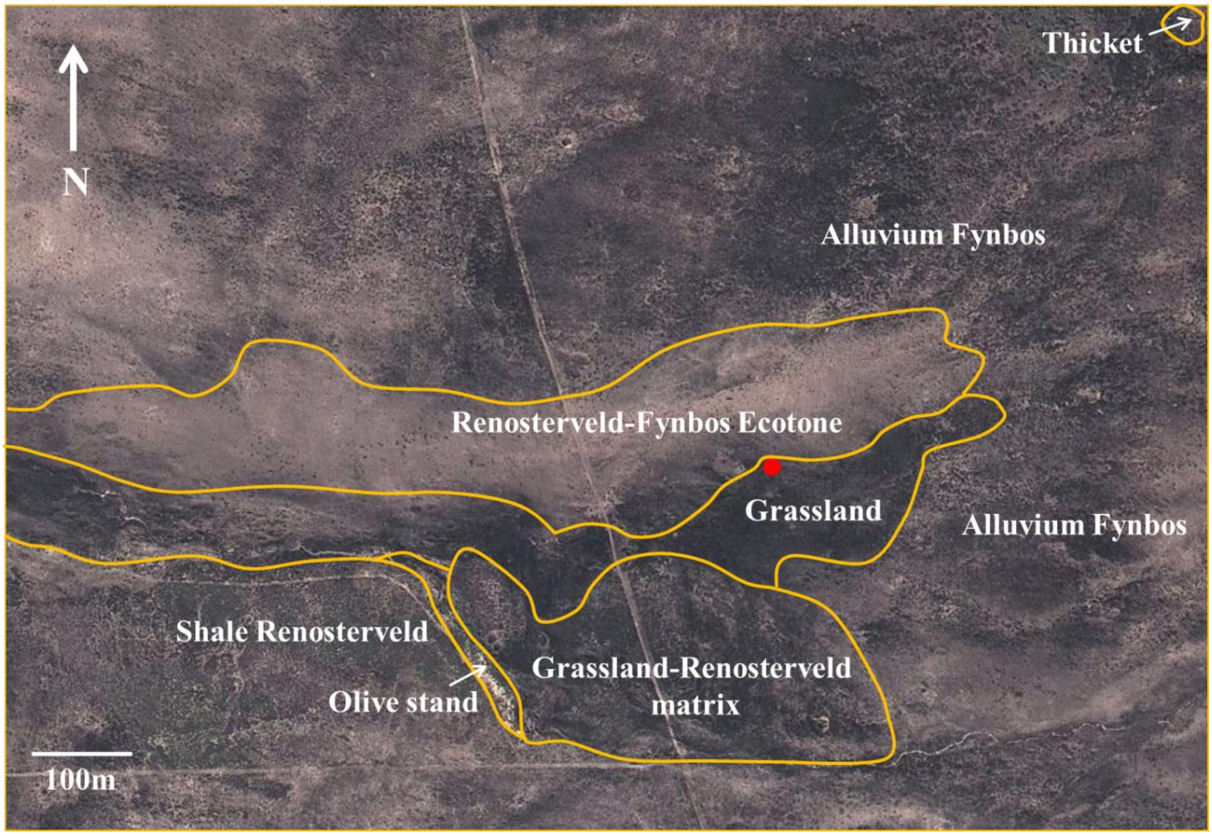


Figure 11: Map of the study site at Elandsberg PNR where the VANG core was retrieved. Demarcated areas (in orange) represent vegetation units that were chosen according to the most dominant vegetation type present in the vegetation survey. See Table 5 for description. The VANG core was retrieved from Vangkraal Spring wetland which is marked by the red dot.

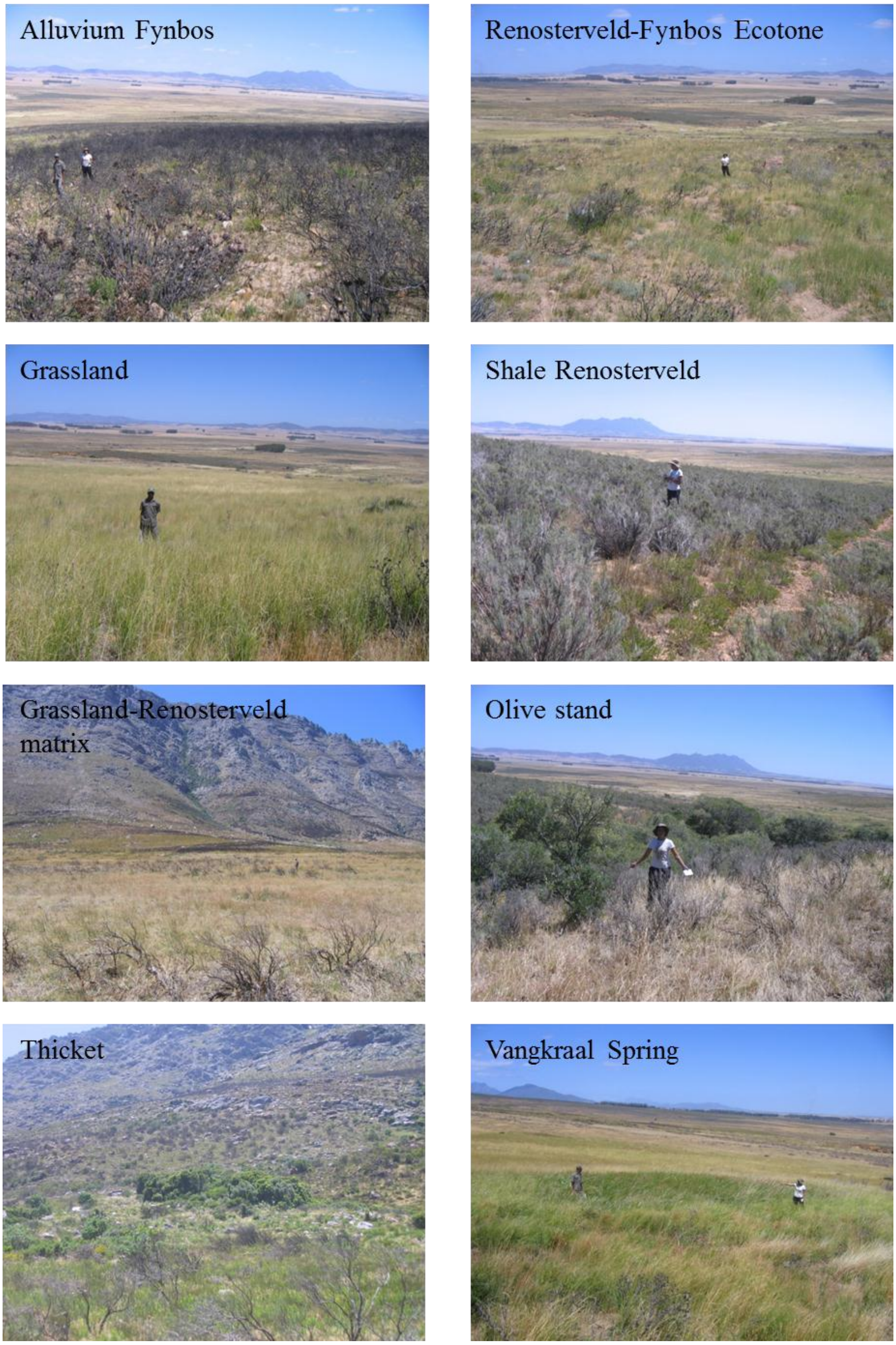


Figure 12: Photographs of vegetation units which were chosen according to the most dominant vegetation type present at the Elandsberg PNR study site where the VANG core was retrieved. See Table 5 for description.

***Table 6: Modern vegetation survey**, showing the relative contribution of each taxon within 8 vegetation units at Elandsberg PNR study site. Taxa highlighted in bold were the most dominant at present while taxa marked with an asterisk (*) were not recorded in the pollen spectrum throughout the VANG core.*

Vegetation Unit	**Taxa**	**%**
Shale Renosterveld	***Elytropappus rhinocerotis* (Asteraceae)**	70
	Themeda spp (Poaceae)	10
	Aspalathus spp (Fabaceae)	10
	Other	7
	Restio spp (Restionaceae)	2
	Corymbium spp (Asteraceae)	1
Alluvium fynbos	***Protea* spp (Proteaceae)**	78
	Leucadendron adults (Proteaceae)	9
	Leucadendron juveniles (Proteaceae)	5
	Ischyrolepis spp (Restionaceae)	5
	Cyperaceae	1
	Corymbium spp (Asteraceae)	1
	**Salvia* spp (Laminaceae)	0.5
	Other	0.5
Renosterveld-Fynbos Ecotone	***Themeda* spp (Poaceae)**	68
	Restio spp (Restionaceae)	9
	Leucadendron adults (Proteaceae)	7
	Rhus spp (Anacardiaceae)	4
	Lebostemon spp (Boraginaceae)	4
	**Diospyros* spp (Ebenaceae)	4
	Stoebe spp (Asteraceae)	1
	Senecio spp (Asteraceae high spine)	1
	Lampranthus spp (Aizoaceae)	1
	Cliffortia spp (Rubiaceae)	1
Grassland-Renosterveld matrix	***Elytropappus rhinocerotis* (Asteraceae)**	52
	Other	22
	Themeda spp (Poaceae)	11
	**Aspalathus* spp (Fabaceae)	7
	Restio spp (Restionaceae)	2
	Lebostemon spp (Boraginaceae)	2
	Asteraceae spp (Asteraceae)	2
	Lampranthus spp (Aizoaceae)	1
	Hermonia	1
Grassland	***Themeda* spp (Poaceae)**	70
	Cyperaceae	10
	Leucadendron adults (Proteaceae)	5
	Other	4
	Maytenus oleoides (Celastraceae)	4
	Rhus spp (Anacardiaceae)	3
	Stoebe spp (Asteraceae)	2
	Cullumia spp (Asteraceae)	1
	Aspalathus spp (Fabaceae)	1
Thicket	***Olea europea africana* (Oleaceae)**	35
	***Searsia tomentosa* (Anacardiaceae)**	15
	***Rhus* spp (Anacardiaceae)**	15
	Other	13
	Searsia laevigata (Anacardiaceae)	5
	Maytenus oleoides (Celastraceae)	5
	Phylica buxifolia (Rhamnaceae)	3
	Maytenus schinoides (Celastraceae)	3
	Helleria elliptica (Scrophulariaceae)	2
	Diospyros spp (Ebenaceae)	2
	**Chasmanthe* spp (Iridaceae)	1
	Asparagus spp (Asparagaceae)	1

Table 6: Modern vegetation survey (continued).

Vegetation Unit	**Taxa**	**%**
Olive stand	***Olea europea africana* (Oleaceae)** Other	90 10
Vangkraal Spring wetland	***Cyperaceae*** *Themeda* spp (Poaceae) **Juncus* (Juncaceae)	90 5 5

5.2. Sediment description and physical properties analysis (Loss on Ignition)

An 87 cm sediment core was recovered from Vangkraal Spring but only the top 54 cm included preserved pollen and therefore results from the bottom 34 cm of the core are not presented. Results for sediment composition (Troels-Smith 1955) and Loss on Ignition (LOI) (Dean 1974; Bengtsson and Enell 1986; Heiri et al. 2001) can be found in Figure 13 and 14 respectively. Water content of the sediments increased from deeper to shallower depths, with the lowest percentage water content at 51 cm (16.2%) and the highest at 2 cm (58.3%) (Figure 14B). The lower percentage of water found deeper in the core is due to the high proportion of sand found in these layers (see sediment description below) which is more porous than the rest of the sediments making up the core owing to larger particle size. The percentage water content closely followed the trend for percentage organic carbon (described below) found in the sediment.

The deepest section of sediment where fossil pollen was recovered (41-54 cm) consisted of a majority of coarse sand with some fine sand and silt. Here no vegetative matter was found Figure 13). The two sections below 54 cm had poor pollen preservation and are described below. Sediments from 54-72 cm consisted of very dark grey fine sand, coarse sand and silt that was dark grey in colour and the upper contact was gradational to the section above it. The lowest section of the core from 72-88 cm consisted only of coarse sand which was light grey in colour and the upper contact was sharp. The bottom of the core was deformed when the corer struck the base of the sediments indicating that the wetland probably had a rocky base and thus the maximum length of the sediment core was recovered. The majority (12-41cm) of the sediment which made up the VANG core consisted of a black brown matrix of fine sand, silt and clay with occasional small rootlets and stems from herbaceous plants (Figure 13). The top 12 cm of the core was very black in colour, consisted of mostly fine sand

and clay and of highly humified organic matter and a considerably densely packed amount of rootlets and stems of herbaceous plants (Figure 13).

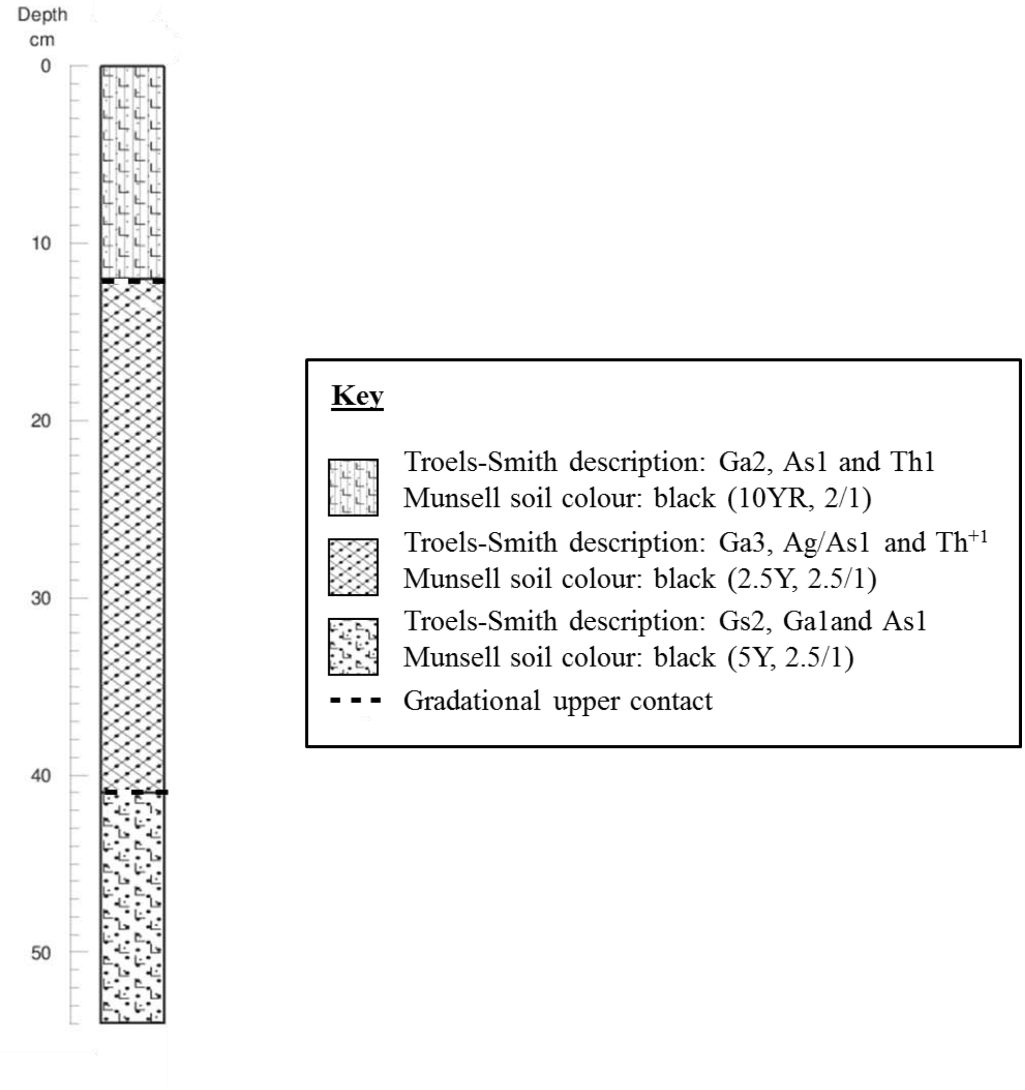


Figure 13: Schematic of the VANG core showing Troels-Smith (1995) and Munsell soil colour sediment description. For explanation of Troels-Smith sediment description see Table 4.

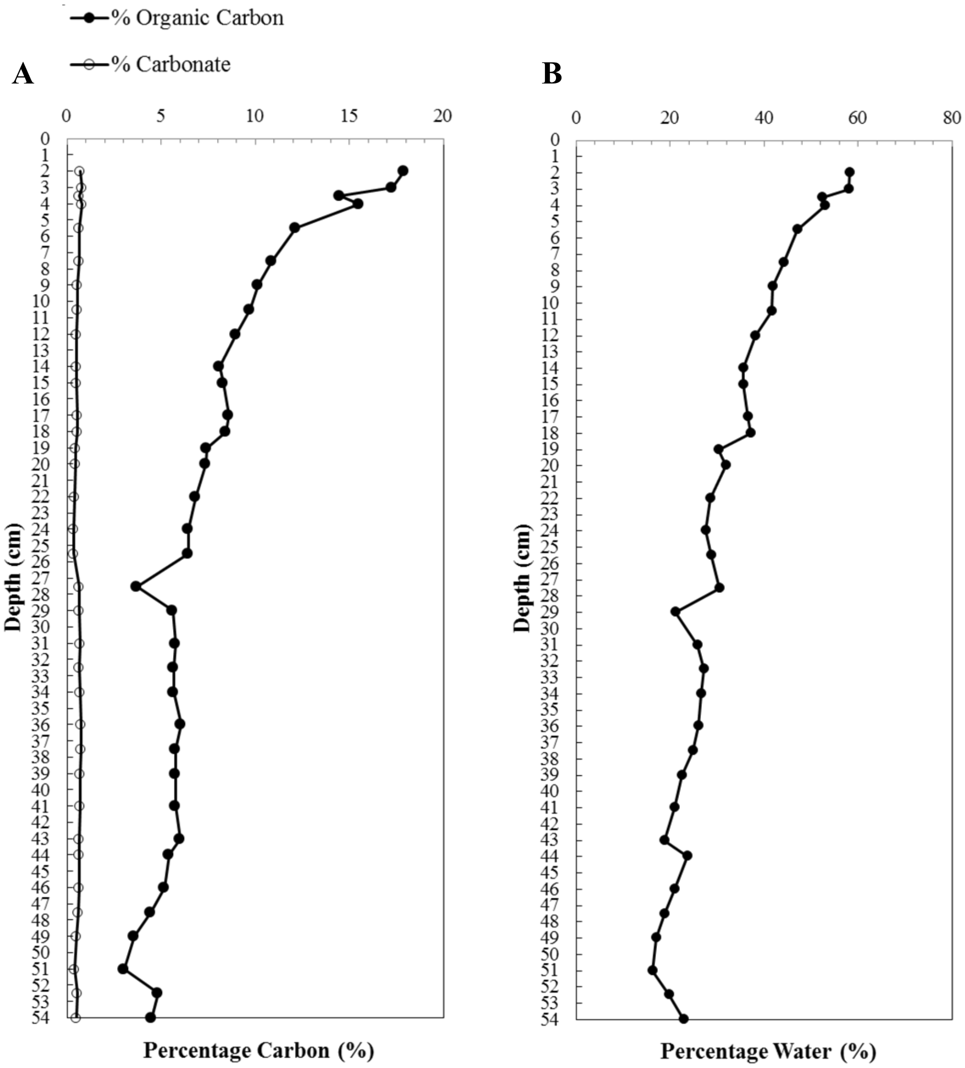


Figure 14: (A) Graph depicting the percentage of organic carbon (LoI$_{550}$) and carbonate (inorganic carbon, CO$_3$) content per dry weight of sample for the VANG core, Elandsberg PNR. (B) The percentage water content per wet weight of the sediments is shown on the right of this figure.

The sediments found in the VANG core largely contained high amounts of organic carbon (ranging from 3-17.9%, with a mean of 7.6%) and low amounts of inorganic carbon, in the form of carbonate, (ranging from 0.4-0.8%, with a mean of 0.6%) (Figure 14A). There was a general trend of increasing organic carbon whilst moving up the core. The highest organic carbon content (17.9%) found at 2 cm corresponds with sediment composed of fine sand, clay and highly humified organic matter consisting predominantly of small rootlets and stems of herbaceous plants (Figure 13). The lowest amount of organic carbon (3%) was at a depth of

51 cm where the sediment consisted of predominantly fine and coarse sand. The amount of carbonate was lowest at 24 and 25.5 cm (Figure 14A). A shift from relatively higher (0.7%) to lower (0.4%) carbonate percentages occurred between 27.5 cm and 25.5 cm. This shift coincided with an unexpected change in organic carbon which decreased from 5.6% to 3.7% between 29 cm and 27.5 cm and then increased again to 6.4% at 25.5 cm (Figure 14A).

5.3. Chronology

AMS radio-carbon dating at 54 cm showed a calibrated age of ca. AD 750 (Table 7). The date for a sample at a depth of 46 cm was ca. AD 1220 while the age for the sample taken at a depth of 31.5 cm was ca. AD 1450 (Table 7). The radio-carbon dates suggest slow sediment accumulation (0.17 mm per year) between 54 cm and 46 cm, followed by higher sediment accumulation (0.63 mm per year) from 46 to 31.5 cm (Figure 15).

Table 7: Results obtained from AMS radio-carbon dating for three samples from the VANG core.

Sample name	Sample depth (cm)	Radio-carbon date (yr BP)	BCal Calibrated date (cal yr BP)	Probability (Standard deviation and %)	Calendar years (AD)
VANG31.5cm CJF2	31.5	470±30	524-451 and 355-388	2 SD (95%)	1452
VANG46cm CJF3	46	850±30	769-677	2 SD (95%)	1223
VANG54cm CJF1	54	1350±30	1199	2 SD (95%)	751

Measurable quantities of ^{210}Pb were found in the VANG core between 0-25 cm, below which no measurable ^{210}Pb was found suggesting that sediments below 25 cm were older than 150 years. Ages for sediments that were ^{210}Pb dated can be found in Table 8. Separate sediment accumulation results were found for the CRS model and the Slope Regression model applied to the ^{210}Pb data; and these are described below. Compared to most depths (below 25 cm) of the VANG core, samples that were ^{210}Pb dated had a generally higher or faster sediment accumulation rate (mean 0.788 g/cm^2/yr) (Table 8 and Figure 16 and 17).

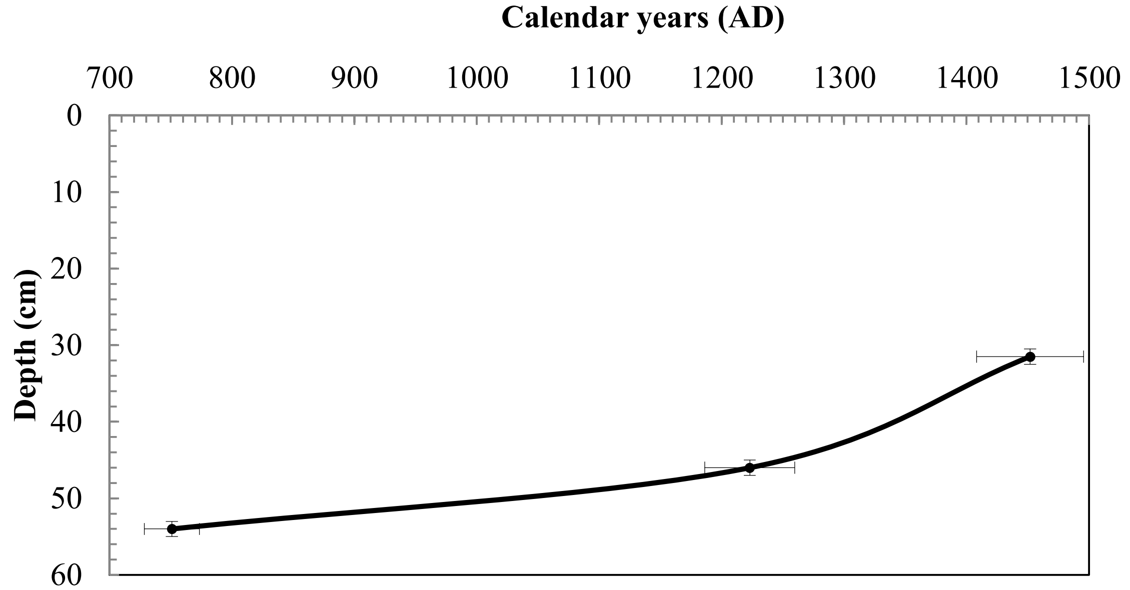


Figure 15: Age-depth model for the VANG core including three AMS radio-carbon dates with ±SD error bars.

Table 8: Results obtained from ^{210}Pb dating for nine samples from the VANG core.

Sedi-ment section no.	Depth of bottom edge of sediment section (cm)	Age at Bottom of Extrapolated Section (CRS Model Estimate) (yr)	Age in Calendar years (AD)	CRS Sediment Accumulation Rate (g/cm^2/yr)	^{210}Pb Total Activity (DPM/g)	^{210}Pb Unsupported Activity (DPM/g)
1	2	3.239	2008	0.934	13.222	11.482
2	5	9.520	2002	0.881	12.584	10.844
3	8	16.296	1996	0.851	11.089	9.349
4	11	24.420	1988	0.809	10.014	8.274
5	15	35.260	1977	0.791	7.709	5.969
6	20	53.695	1958	0.719	6.684	4.944
7	25	97.070	1915	0.530	5.682	3.942
8	30	-	-	-	3.023	1.283
9	37	-	-	-	1.741	-
				Mean 0.788		

5.3.1. Constant Rate of Supply model for Lead-210 dating

The Constant Rate of Supply (CRS) model included sediment sections 1- 9. Similarly to the Slope Regression model described later, the CRS model assumed a constant input of ^{210}Pb and a core that is long enough to include the entire measurable atmospheric source ^{210}Pb. The advantage of the CRS model over the Slope Regression model is that the rate of sediment accumulation does not have to be constant over time in order to calculate the age of the sediment accurately. It was assumed that the lowest observed activity (1.74 DPM/g) of the core at section 30-37 cm was the true background ^{210}Pb level, and thus the CRS model could be applied. The average sediment accumulation rate of the VANG core using the CRS model was 0.7880 g/cm^2/year. The sediment accumulation rate, from the surface of the core to the extrapolated bottom depth of any section, was calculated by dividing the cumulative dry mass at the bottom of the extrapolated section by the calculated age at that depth. For example, the average sediment accumulation rate at the bottom of section 4 (extrapolated depth 8-11cm) was calculated as: 19.766 / 24.4 = 0.81008 g/cm^2/year. Generally, sediments at lower depths experienced a slower accumulation rate compared to sediments in the top of the core (Figure 16).

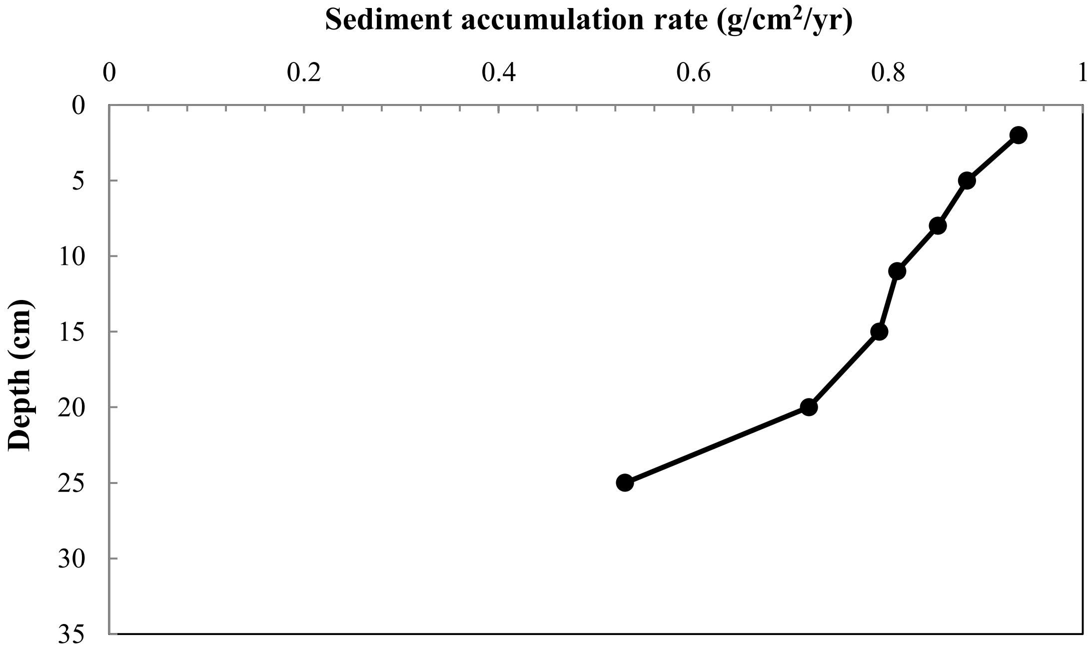


Figure 16: Constant Rate of Supply (CRS) model showing sediment accumulation rate vs. depth at the bottom of each section. Note that the CRS model includes sediment sections 1-9 but there were no sediment accumulation rates for sections 8 and 9 (see Table 8).

5.3.2. Slope Regression model for Lead-210 dating

The Slope Regression model assumed constant sediment accumulation and ^{210}Pb input. An associated R^2 table was used to determine the sediment accumulation rate where the R^2 values provide a suitable fit as a function of the background level of ^{210}Pb which was subtracted (see Appendix 1. Table A1). R^2 values showed equally good fits for a large range of background ^{210}Pb values in the VANG core. It was assumed that the lowest observed activity (1.74 DPM/g; where DPM is the abbreviation for disintegration per minute) of the core at section 30-37 cm was the true background ^{210}Pb level. Hence the closest corresponding sediment accumulation rate in the R^2 table (for $R^2 = 0.9298$) was 0.8259 g/cm^2/yr. The unsupported ^{210}Pb activities in the VANG core exhibited a decay profile with increasing depth (Figure 17) thus there was a logarithmic increase in ^{210}Pb activity through time. The surface activity of ^{210}Pb (i.e. 13.22 DPM/g) was 7.6 times greater than the observed background activity (i.e. 1.74 DPM/g; the lowest observed activity of the VANG core).

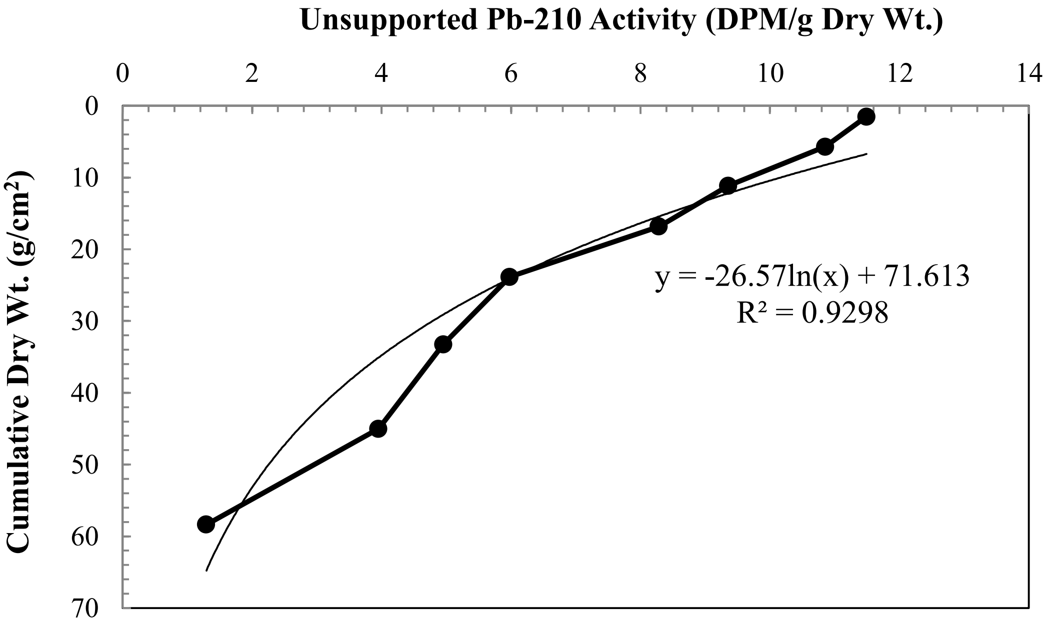


Figure 17: Slope Regression model of Unsupported ^{210}Pb Activity vs. Cumulative Dry Weight (g/cm^2). Unsupported ^{210}Pb Activity = Total ^{210}Pb Activity - Background Observed ^{210}Pb Activity (i.e. 1.7295 DPM/g). Note that the Regression Plot includes sediment sections 1-8 (see Table 8).

The average sediment accumulation rate determined by the Slope Regression model (mean 0.8259 g/cm^2/yr) was in close agreement with that of the CRS model (mean 0.788 g/cm^2/yr). Therefore, the sediment accumulation rates are reasonable estimates for the part of the VANG core that was ^{210}Pb dated. However, the CRS model was a more appropriate model to determine the mass accumulation rate since the VANG core was not constant (Table 8).

5.4. Pollen, spore and charcoal results

Selected pollen, spore and charcoal results are presented in two pollen diagrams showing pollen percentage (expressed as a proportion of the total pollen sum) (Figure 18) and the absolute pollen concentrations per 1 cm^3 of sediment (Figure 19) found in different levels of the VANG core. The results of the zonation analysis determined by the Psimpoll programme are presented in section 5.4.1. Statistical significance was found when the data were split into two zones. Each zone represents a section of the core that was similar in terms of the terrestrial pollen data only. The number and position of the zones were the same in the percentage and concentration data suggesting that the zonation was robust and there is confidence that there are true ecologically meaningful zones. Terrestrial pollen taxa are also grouped into species characteristic of various vegetation types which can be seen in the summary diagram at the end of the percentage diagram (Figure 18). The structure for the results presented below are as follows. Section 5.4.1. describes general zonation results determined by pollen percentage and concentration data but also described in relation to the spore, aquatics and charcoal abundance. Thereafter, changes in individual pollen and spore taxa are described in more detail for the VANG core. It is important to note that results may vary between the percentage and concentration data. For percentage data, there is no dependence of the results on sediment accumulation rate, but a change in the abundance of one pollen type affects the percentage of all pollen taxa in the pollen sum (the Fagerlind effect) (Fagerlind 1952; Prentice 1988). For concentration data, the data are presented as absolute values in grains per cm^3 of sediment; the abundance of taxa are therefore not affected by one another, but they are affected by changes in sediment accumulation rate. For this reason percentage and concentration data are described alongside one another to facilitate comparisons and identify patterns that are robust across both data types.

Figure 18 (see overleaf): Percentage diagram for selected pollen taxa, spore and charcoal abundance from the VANG core. The pollen sum included terrestrial and unknown pollen. Black dots represent taxa with 5% threshold, which would otherwise not be visible in this figure. Pollen zones are calculated by Psimpoll using a 2% threshold and are indicated by the dashed line and boxes V-1 and V-2 to the far right of the diagram. Troels-Smith (1955) stratigraphy shown on the left. This diagram includes aquatics and degraded pollen which were not included in the pollen sum. It also includes a vegetation summary.

Figure 19 (see page 112): Concentration pollen diagram for selected taxa from the VANG core. The pollen sum included terrestrial and unknown pollen. x10 exaggeration is shown since concentration values are often low for most taxa. Pollen zones are calculated by Psimpoll using a 2% threshold and are indicated by the dashed line and boxes V-1 and V-2 to the far right of the diagram. Troels-Smith (1955) stratigraphy shown on the left.

Taxa that were low in abundance and showed no trends are not included in Figure 18 and 19. These results can be found in the full pollen percentage and concentration diagrams in Appendix 4. Figure A1 and Appendix 5. Figure A2 respectively.

Figure 18: Percentage diagram.

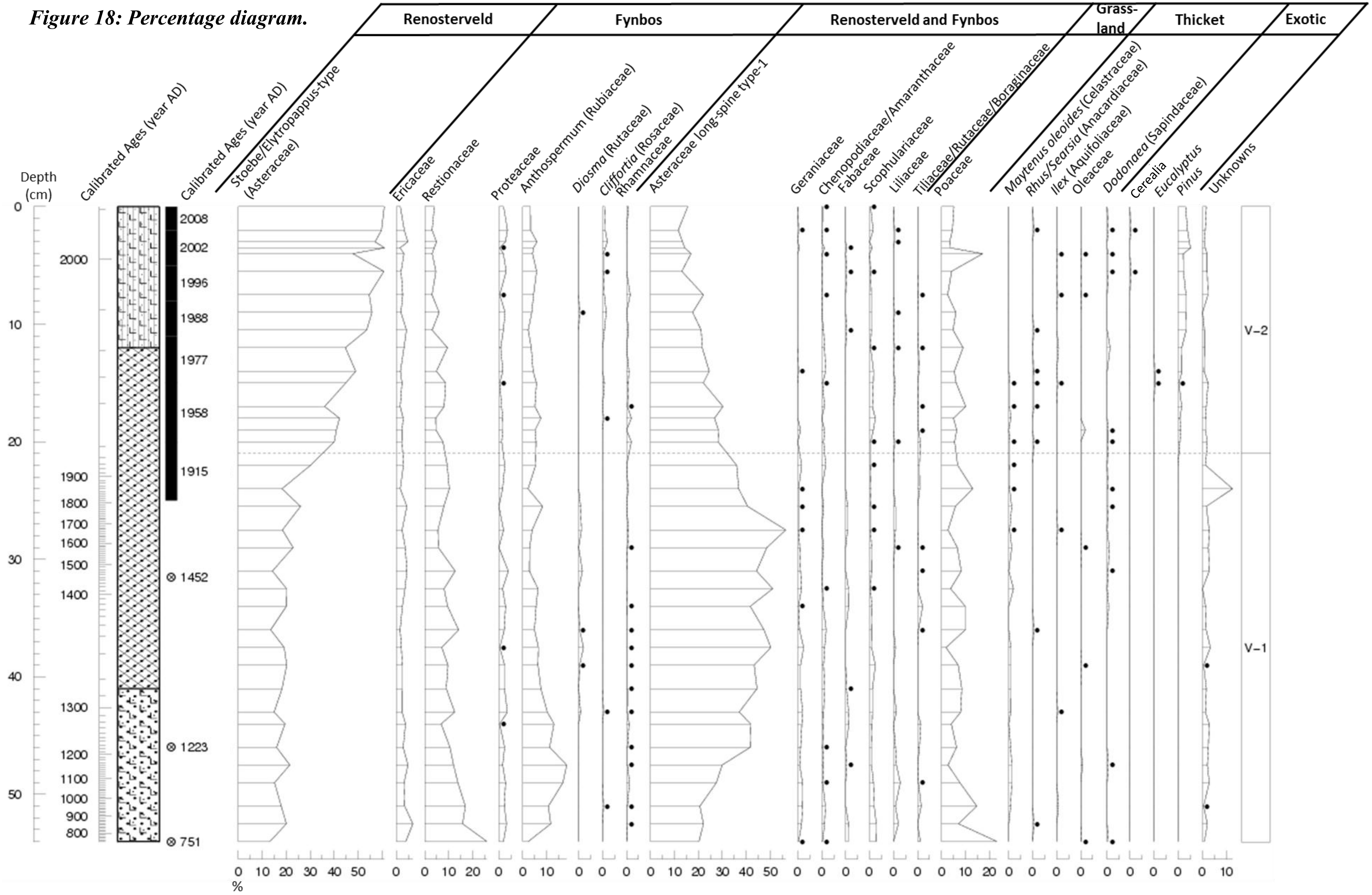


Figure 18: Percentage diagram (continued).

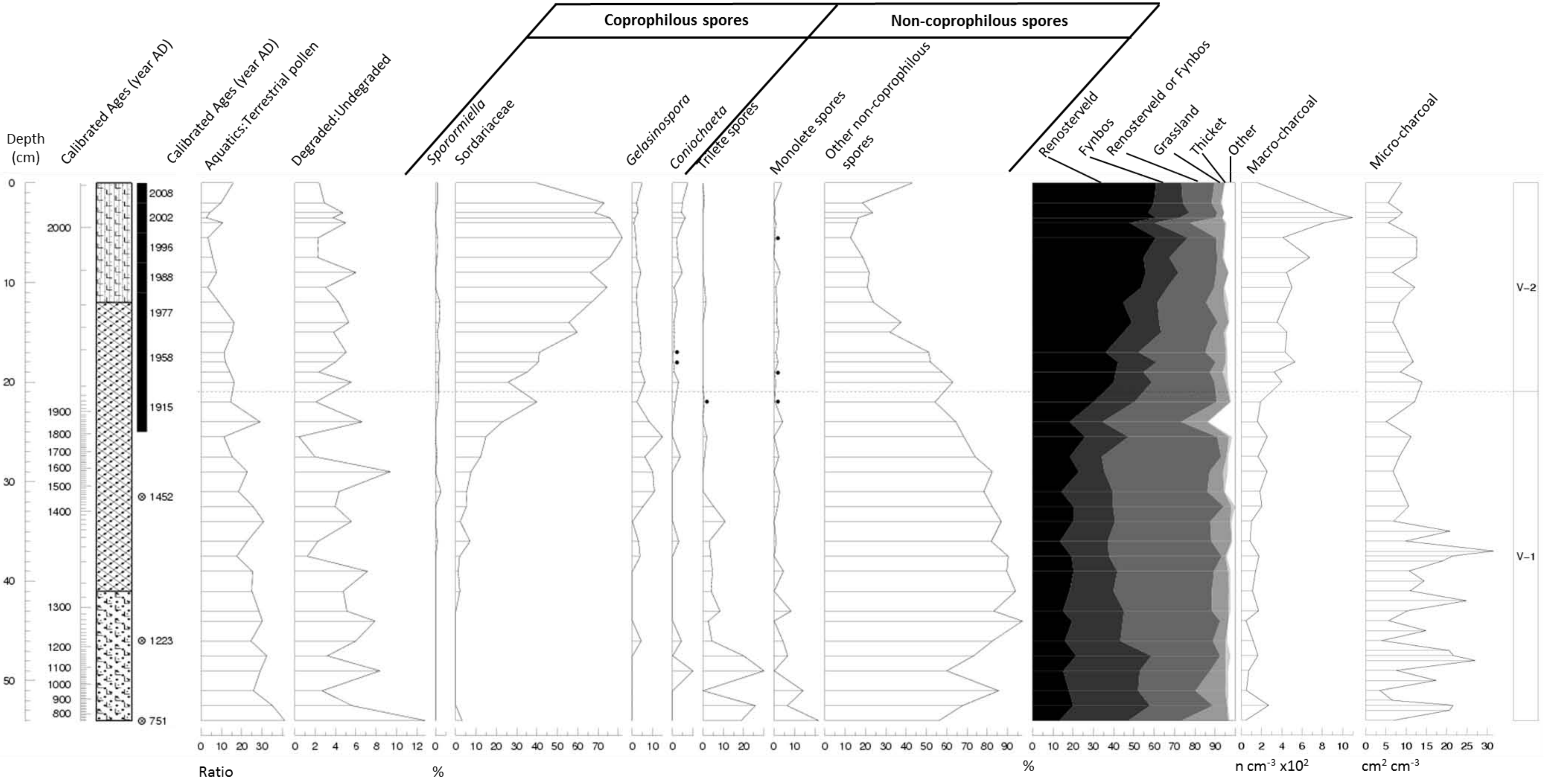
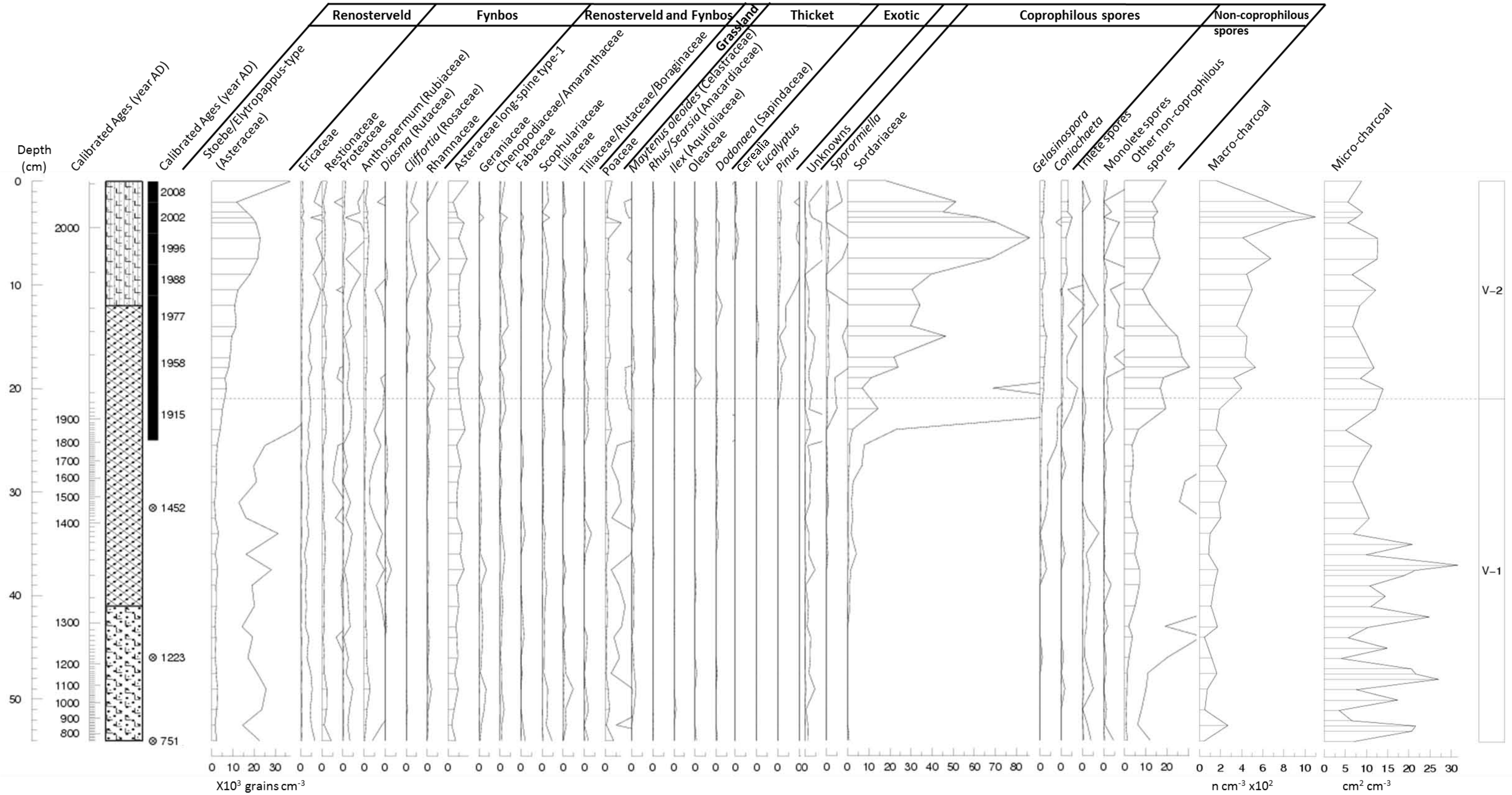


Figure 19: Concentration diagram.



5.4.1. Pollen percentage and concentration zonation

Two statistically significant pollen zones were identified. The first zone (zone V-1) ranged from 54 cm to 21 cm and the second zone (zone V-2) ranged from 21 cm to 0 cm. For the pollen percentage data, 38.6% of the variance was explained by the two zones. However, for the concentration data, only 21.3% variance was explained between the two zones The boundary between zones at 21 cm for both the percentage and concentration data coincided with the calibrated calendar date of ca. AD 1943 (date obtained via the age-depth model). Below, the zones determined for the percentage and concentration data are described in terms of their average pollen (terrestrial, aquatics, degraded and where relevant, pollen grains of interest such as exotic pollen), spore, macro- and micro-charcoal composition.

5.4.1.1. General results for Zone V-1 (20 levels; 54-21 cm)

Percentage data: Zone V-1consisted of 18 levels ranging from ca. AD 750-1943 (54 cm to 21 cm) which was characterized by a high abundance of Asteraceae long-spine type-1. This pollen type made up 31% of the pollen sum. Asteraceae long-spine type-1 reached its highest value of 56.5% in ca. AD 1670 (27.5 cm). The following taxa were also at their highest during this zone: *Anthospermum* (Rubiaceae) (18%), Ericaceae (7%), Proteaceae (4%), Restionaceae (26%) and Poaceae (23%). Asteraceae *Stoebe/Elytropappus*-type pollen was at its lowest in this zone, with 13%. Unknown grains had a high peak (mean 13%) in ca. AD 1860 (24 cm). Coprophilous spores (*Sporormiella*, Sordariaceae, *Gelasinospora* and *Coniochaeta*) were low in abundance and mostly absent in this zone while non-coprophilous spores (Trilete, Monolete and Other non-coprophilous spores) made up the bulk of the total spore sum.

Concentration data: Out of all the pollen taxa present in zone V-1, Asteraceae long-spine type-1 was the most abundant and it made up an average of 4632 grain/cm^3 of the pollen found in this zone. However, its highest level was not reached in this zone (as it did so with the percentage data) on the contrary its lowest level (1602 grains/cm^3) was reached. Asteraceae *Stoebe/Elytropappus*-type pollen was the next abundant pollen type in this zone but it was low on average (mean 2295 grains/cm^3) and reached its lowest of 1284 grains/cm^3 in zone V-1. The following taxa reached their highest during this zone: *Anthospermum* (Rubiaceae) (2843 grain/cm^3) and Restionaceae (4437 grains/cm^3). Concentration data for coprophilous spores were similar to percentage data and they were mostly absent in this zone. However, non-coprophilous spores were also low (especially Trilete and Monolete spores)

Charcoal, aquatics and degraded pollen data: On average macro-fossil charcoal was low (mean 147.5 n/cm^3) and reached its lowest concentration in this zone with 44 n/cm^3. Conversely, micro-fossil charcoal was generally high (mean 13.6cm^2/cm^3) and more variable in this zone and reached its highest value of 31.6 cm^2/cm^3 in ca. AD 1340 (37 cm). Other very high charcoal peak events occurred in ca. AD 858 (52.5 cm), ca. AD 1140 (48 cm), ca. AD 1310 (42 cm) and ca. AD 1360 (35 cm). Despite the variability in fire during the first ca.650 years of the VANG core, there seemed to be no big changes in vegetation as the pollen data only fluctuated slightly for some and not at all for most taxa. For example, some taxa which showed similar, although only slight, increasing trends during low regional fire events (ca. AD 960 (51 cm) and ca. AD 1080 (49 cm)) and decreasing trends during high fire peaks (ca. AD 860 (52.5 cm) and ca. AD 1160 (47.5 cm)) include: Asteraceae long-spine type-1, Asteraceae Stoebe/Elytropappus-type, *Anthospermum* spp, Poaceae and Restionaceae. Total aquatics (Cyperaceae, *Polygonum* and *Myriophyllum*) which were calculated as proportion of total aquatics/(terrestrial pollen + aquatics) were higher in zone V-1 with a mean of 25%. The ratio of degraded pollen to undegraded (terrestrial pollen) was only slightly higher in this zone (mean ratio of 0.05).

5.4.1.2. General results for Zone V-2 (16 levels; 21-0 cm)

Percentage data: Zone V-2 consisted of 16 levels ranging from ca. AD 1943-2012 (21 cm to 0 cm). This zone was strikingly different when compared to the underlying zone, as there was a notable increase in Asteraceae *Stoebe/Elytropappus*-type pollen which made up on average 33% of the pollen sum and reached its highest value of 61% in ca. AD 2003 (3.5 cm). Asteraceae long-spine type-1 decreased noticeably making it less abundant (mean 20%) in this zone together with *Anthospermum* (Rubiaceae) (mean 5%) and Restionaceae (mean 5%). Although generally low in abundance in the VANG core, *Rhus/Searsia* occurred more often in this zone than in V-1. Exotic taxa such as Cereal crop grains (also known as Cerealia), *Eucalyptus* and *Pinus* occurred in the pollen spectrum for the first time in this zone. Coprophilous spores (*Sporormiella*, Sordariaceae, *Gelasinospora* and *Conichaeta*) made up the bulk of the total spore sum in this zone and non-coprophilous spores were relatively low.

Concentration data: For the concentration data this zone was also dominated by Asteraceae *Stoebe/ Elytropappus*-type pollen which made up on average 15132 grains/cm^3 of the total pollen in zone V-2. It reached its highest of 37166 grains/cm^3 in AD 2012 (0cm). Asteraceae long-spine type-1 pollen was the next most abundant (mean 5552 grains/cm^3) taxa during zone V-2 and here it reached its maximum abundance (9474 grains/cm^3). On average, the following pollen taxa were more abundant during this zone: *Anthospermum* (Rubiaceae) (mean 1289grains/cm^3), Fynbos taxa (Ericaceae (mean 716 grains/cm^3), Proteaceae (mean 496 grains/cm^3) and Restionaceae (mean 1419 grains/cm^3), Poaceae (mean 1836 grains/cm^3) and *Cliffortia* (Rosaceae) (mean 194 grains/cm^3). Exotic taxa such as Cereal crop (Cerealia) grains (mean 13 grains/cm^3) and *Eucalyptus* (mean 10 grains/cm^3) are almost undetectable in the concentration pollen diagram because their concentrations are so low. *Pinus* is the dominant exotic with an average of 780 grains/cm^3. Coprophilous spores made up the bulk of the total spore sum with Sordariaceae (mean 40327grains/cm^3) being the dominant spore type in this zone.

Charcoal, aquatics and degraded pollen data: On average macro-fossil charcoal was higher (mean 537.4 n/cm^3) in this zone and reached its highest (1100 n/cm^3) in AD 2003 (3.5 cm). On the other hand, micro-fossil charcoal was generally low (mean 9.3 cm^2/cm^3) and less variable in this zone. Total aquatics were lower in zone V-2 with a mean of 10%. There was a steady decline over time from 41% in ca. AD 750 (54 cm) to its lowest of 3% in AD 2003 (3.5 cm).The ratio of degraded pollen to undegraded (terrestrial pollen) was slightly lower in this zone V-2 (mean ratio of 0.04) compared to zone V-1.

5.4.1.3. Detailed description of selected pollen and spore taxa in the VANG core; comparing percentage and concentration data

Taxa characteristic of Renosterveld vegetation

Asteraceae *Stoebe/Elytropappus*-type: The abundance of Asteraceae *Stoebe/Elytropappus*-type in the pollen spectrum fluctuated stably at a low level in zone V-1 (mean 19% and 2295 grains/cm^3) from ca. AD 750-1790 (54-25.5 cm). It was the second most abundant pollen type in zone V-1and was at its lowest (13%) in ca. AD 750 (54 cm) for the percentage data and for the concentration data it was its lowest (1284 grains/cm^3) in ca. AD 1470 (31 cm).

Asteraceae *Stoebe/Elytropappus*-type pollen was the most abundant pollen type in the VANG core during V-2. During zone V-2, Asteraceae *Stoebe/Elytropappus*-type percentage data had a mean of 51% and for the concentration data the mean of zone V-2 (15132 grains/cm^3) was 6.6 times higher than that of zone V-1 (2295 grains/cm^3). The past century showed a very large increase in Asteraceae *Stoebe/Elytropappus*-type pollen to its highest level (61%) in AD 2003 (3.5 cm) for the percentage data and for the concentration data it reached its highest level (37166 grains/cm^3) in AD 2012 (0 cm). The percentage and concentration data show the same general trend for Asteraceae *Stoebe/Elytropappus*-type pollen. However, the prominent decrease that takes place after from ca. AD 1997-2008 is only detected in the concentration data.

Taxa characteristic of Fynbos vegetation

Ericaceae: Generally the percentage and concentration data show the same trend for Ericaceae pollen such that abundance was low (mean 2.3% and 524 grains/cm^3) throughout the VANG core and it remained relatively stable. However, for the percentage data zone V-1 had a slightly higher abundance (mean 3.2%) compared to zone V-2 (mean 2.6%). Whereas for the concentration data its abundance was higher during zone V-2 (mean 4632 grains/cm^3). It reached its highest (1385 grains/cm^3) in ca. AD 2004 (3cm) for percentage data and for the concentration data its highest (6.8%) was in zone V-1in ca. AD 860 (52.5cm).

Restionaceae: Although there were no significant changes in Restionaceae abundance, the percentage data suggest a declining trend over time whereas the concentration does not. For the percentage data, the average abundance of Restionaceae pollen in zone V-1 (mean 11%) was just over double the amount in zone V-2 (mean 5%). From ca. AD 750 (54 cm) to AD 2008 (2 cm) Restionaceae pollen abundance decreased steadily from its highest in zone V-1 (26%) to its lowest in zone V-2 (3%). In contrast to the percentage data, the average abundance of Restionaceae pollen was relatively stable over time for the concentration data. Zone V-1 was only slightly less abundant (mean 1397 grains/cm^3) than zone V-2 (mean 1419 grains/cm^3). Its lowest occurrence (524 grains/cm^3) was during zone V-1 in ca. AD 1580 (29 cm) and the highest occurrence (4437 grains/cm^3) was in ca. AD 750 (54 cm).

Proteaceae: Generally the percentage and concentration data for Proteaceae pollen show stability over time. Out of the three prominent Fynbos taxa (i.e. Ericaceae, Proteaceae and Restionaceae), Proteaceae pollen was the lowest in average abundance (mean 1.85% and 355 grains/cm^3). For percentage data, the average abundance of Proteaceae was slightly higher in zone V-1 (mean 2%) compared to zone V-2 (mean 1.7%). Contrary to this, concentration data showed that the average abundance of Proteaceae pollen was lower in zone V-1 (mean 242 grains/cm^3) compared to zone V-2 (mean 496 grains/cm^3) and in zone V-2 it reached its maximum abundance of 1215 grains/cm^3 in AD 2012 (0 cm). No Proteaceae pollen was recorded at two instances in zone V-1, namely in ca. AD 1580 and ca. AD 1790 (29 cm and 25.5 cm respectively).

***Anthospermum* (Rubiaceae):** Generally both the percentage and concentration data show that there were no significant changes in *Anthospermum* abundance; however, the percentage data in particular suggest that there was more *Anthospermum* in the lower depths. *Anthospermum* pollen made up an average of 6% and 1080 grains/cm^3 of the pollen sum for the VANG core. For the percentage data, the abundance of *Anthospermum* pollen was higher in zone V-1 (mean 7.8%) compared to zone V-2 (mean 4.6%) where it was more stable over time. In zone V-1 from ca. AD 750, *Anthospermum* pollen increased from 2.3% until it reached a maximum of 18% in ca. AD 1160 (47.5 cm) after which it decreased again to 6.3% in ca. AD 1330 (39 cm) where it remained relatively stable until the present day. Unlike the percentage data, the concentration data showed that it reached its highest abundance (2843 grains/cm^3) during zone V-1 in ca. AD 1080 (49 cm). Its abundance was lower in zone V-1 (mean 113 grains/cm^3) than in zone V-2 (mean 1289 grains/cm^3). During V-1 it reached its lowest (250 grains/cm^3) in ca. AD 1470 (31 cm). The abundance during ca. AD 1080 (2843 grains/cm^3) was similar to that in ca. AD 1997 (2169 grains/cm^3).

***Diosma* (Rutaceae)**: The results for percentage and concentration data were similar. *Diosma* pollen abundance was low in the VANG core but it was more abundant during zone V-1 (mean 0.4% and 40 grains/cm^3) compared to zone V-2 (mean 0.02% and 8 grains/cm^3).

***Cliffortia* (Rosaceae):** The results for percentage and concentration data were similar. The abundance of *Cliffortia* was low (mean 0.29% and 89 grains/cm^3) in the VANG core pollen spectrum, and occurrence was more prominent in zone V-2 (mean 0.6% and 194 grains/cm^3) compared to zone V-1 (mean 0.04% and 4 grains/cm^3).

Rhamnaceae: The percentage and concentration data show the same trend for Rhamnaceae pollen. It was generally low in abundance in the VANG core (mean 0.5% and 96 grains/cm^3). It was lower in zone V-1 (mean 0.4% and 50 grains/cm^3) and more prominent in zone V-2 (mean 0.6% and 153 grains/cm^3) where it reached its highest level (mean 595 grains/cm^3) in ca. AD 1993 (7.5 cm).

Taxa characteristic of both Renosterveld and Fynbos vegetation

Asteraceae long-spine type-1: For the percentage data, Asteraceae long-spine type-1 pollen was higher in zone V-1 (39%) than zone V-2 (20%). Between ca. AD 750 and ca. AD 1080 (54-49 cm, mean 23%) the abundance of Asteraceae long-spine type-1 was similar to what was in the last 45 years (ca. AD 1967-2012, 15-0 cm, mean 18%). After ca. AD 1080 (49 cm) the abundance increased until it reached its highest (57%) in ca. AD 1670 (27.5 cm), after which it declined drastically until the present day. The lowest abundance was 12% in ca. AD 2008 (2 cm). In contrast, the concentration data showed that its abundance stayed fairly stable over time and it was lower in zone V-1 (mean 4632 grains/cm^3) than zone V-2 (mean 5552 grains/cm^3). Its lowest level (mean 1602 grains/cm^3) was reached in ca. AD 860 (52.5 cm) and its highest level (9474 grains/cm^3) was reached during zone V-2 in AD 2012 (0 cm).

Geraniaceae: The average Geraniaceae abundance was relatively low throughout the VANG core but it was more abundant (mean 1.2% and 141 grains/cm^3) and always present in zone V-1 compared to zone V-2 (mean 0.2% and 35 grains/cm^3) where it often disappeared from the pollen record.

Chenopodiaceae or Amaranthaceae: Chenopodiaceae/Amaranthaceae pollen was generally low in abundance (mean 0.7% and 120 grains/cm^3) throughout the VANG core and there were differences between percentage and concentration data. For the percentage data, it was slightly higher in V-1 (mean 0.7%) than V-2 (mean 0.6%) whereas for the concentration data is was higher during zone V-2 (mean 115 grains/cm^3) than V-1 (mean 93 grains/cm^3).

Fabaceae: Although Fabaceae pollen was low (mean 0.3% and 39 grains/cm^3) in abundance throughout the VANG core, it was more abundant in zone V-1 (mean 0.5% and 53 grains/cm^3) than in zone V-2 (mean 0.1% and 22 grains/cm^3) where it was absent for most of the time.

Scrophulariaceae: Percentage and concentration data for Scrophulariaceae pollen was low throughout the VANG core. However, percentage data showed that its abundance was slightly higher (mean 1.1%) in zone V-1 compared to zone V-2 (mean 0.9%), whereas the concentration data showed that V-1 had a lower abundance (137 grains/cm^3) than zone V-2 (mean 0.9% and 224 grains/cm^3).

Liliaceae: Liliaceae pollen was low in abundance throughout the VANG core and it decreased in abundance over time. Zone V-1 (mean 0.6% and 68 grains/cm^3) had a higher average than zone V-2 (mean 0.2% and 39 grains/cm^3).

Tiliaceae/Rutaceae/Boraginaceae: The pollen abundance of this type was also low throughout the VANG core and its abundance was higher in zone V-1 (mean 0.5% and 74 grains/cm^3) than in zone V-2 (mean 0.2% and 47 grains/cm^3).

Taxa characteristic of Grassland vegetation

Poaceae: There were slight discrepancies between Poaceae percentage and concentration data but as a whole the results were similar. Poaceae abundance was slightly variable throughout time and was not very high in abundance (mean 7% and 1397 grains/cm^3). For the percentage data there were a few increases in abundance at changeable times. In zone V-1 it reached its highest (23%) in ca. AD 750 (54 cm) and 15% in ca. AD 960 (51 cm). In zone V-2 there was a peak of 13% in ca. AD 1860 (24 cm) and 17% in ca. AD 2001 (4 cm). Poaceae pollen abundance was only slightly higher in zone V-1 (mean 8%) in comparison to zone V-2 (mean 6%). In contrast, the concentration showed that zone V-1 experienced a lower average concentration (mean 1046 grains/cm^3) and here Poaceae pollen was at its lowest (274 grains/cm^3) in ca. AD 1160 (47.5 cm). The average abundance was higher in zone V-2 (mean 1836 grains/cm^3) and the highest peak (7530 grains/cm^3) was during V-2 in AD 2001 (4 cm), not in ca. AD 750 like the percentage data showed.

Taxa characteristic of Thicket vegetation

***Maytenus oleoides* (Celastraceae):** The percentage and concentration data were the same for this pollen type. It was more abundant in the V-1 zone (mean 0.6% and 72 grains/cm^3) than the V-2 zone (mean 0.1% and 24 grains/cm^3) and did not appear in the pollen spectrum again from ca. AD 1972 until present (14-0 cm).

***Rhus/Searsia* (Anacardiaceae):** *Rhus/Searsia* pollen was generally low in abundance for both percentage and concentration data (mean 0.08% and 15 grains/cm^3). It occurred more in zone V-2 (0.14% and 30 grains/cm^3) than in V-1 (0.04% and 4 grains/cm^3).

***Ilex* (Aquifoliaceae)**: *Ilex* pollen was generally low in abundance for both percentage and concentration data and it occurred more in zone V-2 (0.1% and 35 grains/cm^3) than in V-1 (0.07% and 9 grains/cm^3).

Oleaceae: For both the percentage and concentration data, Oleaceae pollen was low in abundance (mean 0.13% and 23 grains/cm^3) in the VANG core. It occurred more in zone V-2 (0.7% and 37 grains/cm^3) than in V-1 (0.09% and 11 grains/cm^3).

***Dodenaea* (Sapindaceae)**: For both the percentage and concentration data, *Dodenaea* pollen was very low (mean 0.2% and 33 grains/cm^3) in abundance throughout the VANG core and it appeared more often during ca. AD 1380 to ca. AD 1954 (34-19 cm).

Exotic taxa

Cereal crop pollen (Cerealia): The percentage and concentration results were the same for Cereal crop pollen. It was very low (mean 0.02% and 6 grains/cm^3) in abundance in the VANG core and it only occurred in zone V-2. Its first and highest (0.4% and 145 grains/cm^3) occurrence was in ca. AD 1997 (5.5 cm).

Eucalyptus: *Eucalyptus* pollen was also very low in abundance (mean 0.02% and 4 grains/cm^3) and only occurred in zone V-2. Its first and highest (0.4% and 80 grains/cm^3) occurrence was in ca. AD 1967 (15 cm).

Pinus: *Pinus* pollen was more abundant (mean 1% and 347 grains/cm^3) in the VANG core than the other exotic taxa. It also only occurred in zone V-2 (mean 3% and 780 grains/cm^3)

with its first occurrence in ca. AD 1951 (20 cm). The only difference was that its highest occurrence was 5% in ca. AD 2003 (3.5 cm) for the percentage data whereas its highest was 1943 grains/cm^3 in 2012 (0 cm) for the concentration data.

Unknowns: Most pollen grains in the VANG core were identified so that the abundance of Unknown pollen grains was generally low (mean 1.6%). Unknown pollen was more common in the zone V-1 (mean 2.6% and 313 grains/cm^3) than in zone V-2 (mean 1% and 296 grains/cm^3). The unusual high peak during zone V-1 in ca. AD 1860 (24cm) was largely due to two out of 34 unknown taxa.

Coprophilous spores

***Sporormiella*:** Compared to the other coprophilous spores, *Sporormiella* was relatively low in abundance (mean 0.6% and 268 grains/cm^3) throughout the VANG core. Its abundance was markedly lower in zone V-1 (mean 0.3% and 34 grains/cm^3) compared to zone V-2 (mean 1% and 550 grains/cm^3). The difference in the percentage data was that *Sporormiella* experienced its highest occurrence during V-1 with 3% in ca. AD 1470 (31 cm). Whereas in the concentration data, its highest was in V-2 (1115 grains/cm^3) in ca. AD 1981 and ca. AD 1997 (12 cm and 5.5 cm). *Sporormiella* first occurred in ca. AD 1435 (36 cm) after which it disappeared and reappeared a few times during zone V-1. It persisted at a consistently low level for a few decades (ca. AD 1929-1981, 22-12 cm) during zone V-2.

Sordariaceae: The trends for Sordariaceae percentage and concentration data were very similar. Sordariaceae spores were the most abundant coprophilous spores in the VANG core (mean 18471 grains/cm^3). They were almost absent in zone V-1 (mean 6% and 986 grains/cm^3) and first appeared in the record in ca. AD 750 (54 cm) after which it disappeared for a long while before reappearing centuries later in ca. AD 1310 (41 cm). There was a large increase in zone V-2 which started gradually about 152 years ago (ca. AD 1860, 24 cm). For the percentage data Sordariaceae abundance was 10 times greater in zone V-2 (mean 60%) and for the concentration data it was ca.40 times greater (mean 40327 grains/cm^3). After reaching its maximum abundance (82% and 86225 grains/cm^3) in ca. AD 1997 (5.5 cm), there was a noticeable decline until ca. AD 2012. The abundance at ca. AD 2012 was similar to what it was in ca. AD 1929 and ca. AD 1956 (22 cm and 18 cm respectively).

Gelasinospora**:** There were noticeable differences between the percentage and concentration data of *Gelasinospora*. It first occurred in ca. AD 1220 (46 cm), then disappeared and reappeared again in ca. AD 1330 (37.5 cm). It disappeared again in ca. AD 1380 (34 cm) and appeared in ca. AD 1420 (32.5 cm). Although the abundance of these spores were lower in zone V-1 for both percentage and concentration data (mean 3.4% and 214 grains/cm^3), *Gelasinospora* spores increased to its maximum (15%) in ca. AD 1785 (25.5 cm) for the percentage data. Unlike the percentage data where the maximum occurrence appeared in zone V-1, the maximum occurrence of *Gelasinospora* for the concentration data (2973 grains/cm^3) was during V-2 in ca. AD 1967 (15 cm).

Coniochaeta**:** *Coniochaeta* was generally low in abundance and the trends for percentage and concentration data were very similar. *Coniochaeta* first occurred in the record in ca. AD 1080 (49 cm). It disappeared and reappeared in the record for the rest of zone V-1 where it was lower (mean 1% and 57 grains/cm^3) compared to zone V-2 (mean 3% and 1975 grains/cm^3). Despite being low in abundance it persisted until the present day. Different from the percentage data where its maximum abundance was 10% in ca. AD 1080, the concentration data showed it reached its maximum (5101 grains/cm^3) during zone V-2 in ca. AD 2003 (3.5 cm) thereafter it declined slightly until the present day.

Non-coprophilous spores

Trilete spores: There were a few differences between percentage and concentration results for Trilete spores. For both percentage and concentration data, Trilete spores were most abundant during zone V-1 (mean 7% and 209 grains/cm^3) than V-2 (mean 0.2% and 90 grains/cm^3). However the maximum of 30% reached in ca. AD 1080 (49 cm) was only evident for the percentage data. They reappeared and disappeared intermittently in zone V-2 until the present day but remained at a low abundance.

Monolete spores: Monolete spores were present intermittently (at a low level) throughout the VANG core for both percentage and concentration data. However, zone V-1 had a higher average (mean 3.9%) than zone V-2 (mean 1.1%) for percentage data, whereas for the concentration data V-1 had a lower average (mean 117 grains/cm^3) than V-2 (mean 653 grains/cm^3). The abundance of Monolete spores was at its maximum (22%) in ca. AD 750 (54 cm) but this was not evident in the concentration data.

Other non-coprophilous spores: There were marked difference between percentage and concentration data for these spores and this is likely due to the Fagerlind effect. For the percentage data Other non-coprophilous spores made up majority of the total spore sum during zone V-1 (mean 78%) and reached a maximum of 97% in ca. AD 1280 (44 cm). In zone V-2 (mean 32%) it began to decline rapidly until 13% (the lowest abundance) in ca. AD 1997 (5.5 cm). It increased slightly after this until the present AD 2012. In contrast, the concentration data showed that Other non-coprophilous spores were lower during zone V-1 (mean 4246 grains/cm^3) than V-2 (mean 17374 grains/cm^3). Unlike the coprophilous spores (*Sporormiella*, Sordariaceae, *Gelasinospora* and *Coniochaeta*), Other non-coprophilous spores were always present throughout the VANG core (mean 10081 grains/cm^3).

5.4.2. Ordination, SIMPER and BEST results for percentage data only

The results of the NMDS Ordination are shown in Figure 20. The stress value was 0.14 (i.e. less than 0.3), consequently the graph produced is of satisfactory quality and the similarity relationships between the depths were represented accurately in the NMDS. Based on the 70% minimum resemblance levels of the CLUSTER analysis, two distinct groups were determined. These distinct groups were consistent with the zonation analysis performed using the Psimpoll programme (Figures 18 and 19). The group on the right consisted of depths classified as zone V-1 (shown in blue). Within this group depths with 80% minimum resemblance were also identified: 41 cm, 39 cm, 32.5 cm, 22 cm, 36 cm, 34 cm, 44 cm, 29 cm and 25.5 cm were grouped together; 37.5 cm and 27.5 cm were grouped together; and 49 cm, 46 cm, 43 cm, 47.5 cm, 52.5 cm and 51 cm were grouped together (Figure 20 and 21). The group on the right was made up of depths that were classified as zone V-2 only (shown in green). Within zone V-2 the following depths were grouped together based on the 80% minimum resemblance: 19 cm and 12 cm were grouped together; 14 cm, 15 cm 17 cm, 18 cm and 20 cm and were grouped together; and 0 cm, 2 cm, 3 cm, 3.5 cm, 5.5 cm, 7.5 cm, 9 cm and 10.5 cm and were grouped together (Figure 20 and 21).

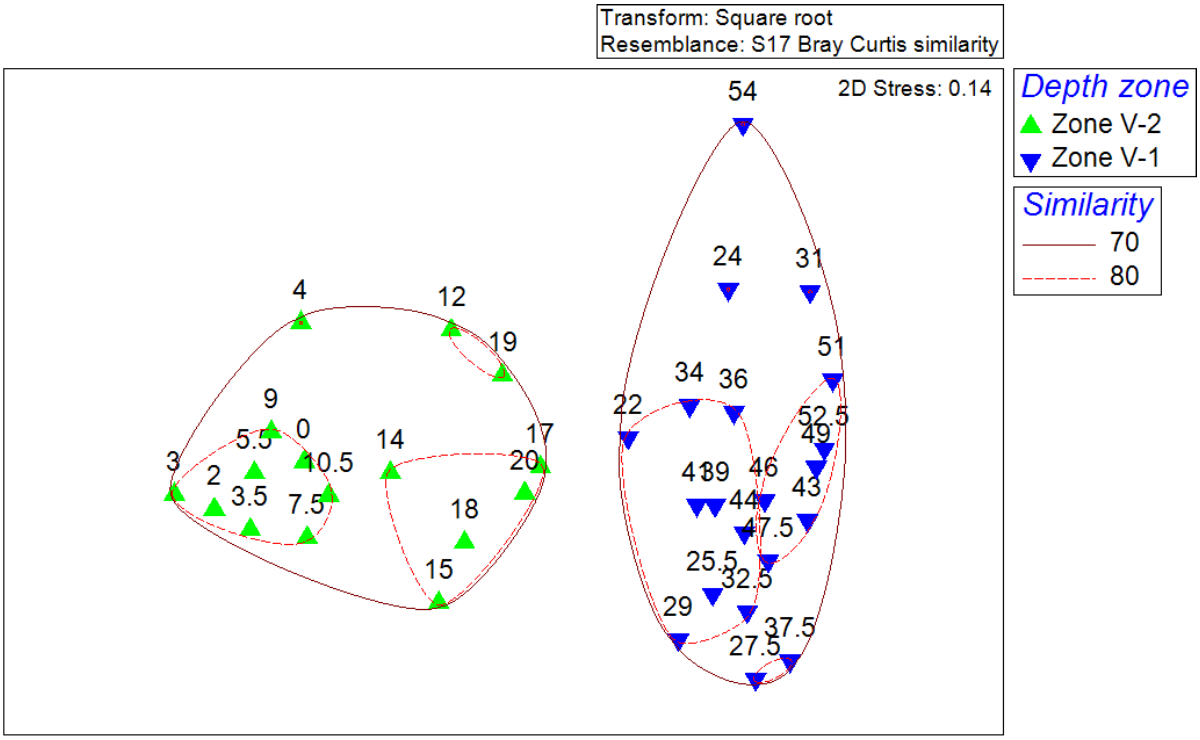


Figure 20: NMDS ordination showing distribution of pollen taxa based on depth for the VANG core from Elandsberg PNR. The depth factor was classified into two different zones: V-1 (shown in blue) and V-2 (shown in green). Ordination based on square root transformed and Bray-Curtis similarity data with a stress factor of 0.14.

Regarding the SIMPER analysis, the average of the Bray-Curtis dissimilarity between zone V-1 and V-2 was 31.59%. Taxa contributing to this made up at least 60% of the cumulative percentage and they include Asteraceae *Stoebe/Elytropappus*-type (4.53 i.e. 14.33% of 31.59%), Asteraceae long spine Type-1 (2.98 i.e. 9.43%), *Pinus* (2.48 i.e.7.85%), Restionaceae (1.76 i.e. 5.56%), Geraniaceae (1.44 i.e. 4.54%), *Anthospermum* spp (1.31i.e.4.16%), Poaceae (1.30 i.e. 4.13%), Unknowns (1.11i.e. 3.51 %), *Cliffortia* spp (1.01i.e. 3.19%), *Maytenus oleoides* (Celastraceae) (0.96 i.e. 3.05%), Rhamnaceae (0.88 i.e. 2.77%).

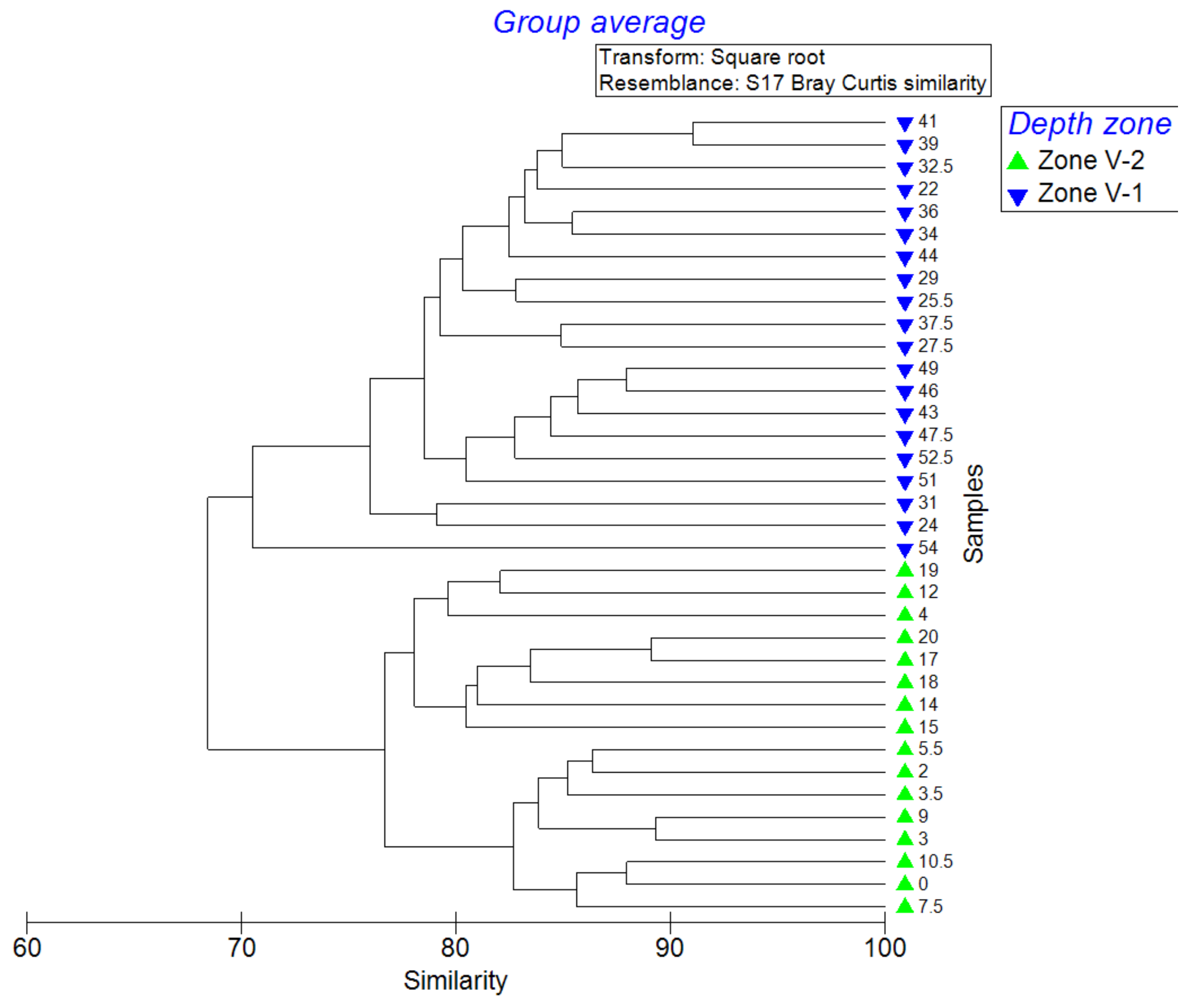


Figure 21: Dendrogram determined by a CLUSTER analysis showing distribution of pollen taxa based on depth for the VANG core from Elandsberg PNR. The depth factor was classified into two different zones: V-1 (shown in blue) and V-2 (shown in green). CLUSTER analysis based on square root transformed and Bray-Curtis similarity data.

The average Bray-Curtis similarity between all species within zone V-1 was 78.43%. This was made up mainly of contributions from 4 pollen taxa (making up at least 60% of the cumulative percentage): Asteraceae long spine type-1 (18.15 i.e. 23.14% of 78.43%), Asteraceae Stoebe/Elytropappus-type (12.93 i.e. 16.49%), Restionaceae (9.21 i.e. 11.74%) and Poaceae (7.13 i.e. 9.10%). These taxa can be described as typical of zone V-1 since they were most common in all levels within this zone. The average Bray-Curtis similarity between all species within zone V-2 was 79.05%. It was made up mainly of contributions from four pollen taxa (making up at least 60% of the cumulative percentage): Asteraceae

Stoebe/Elytropappus-type (22.88 i.e. 28.94% of 79.05%), Asteraceae long spine Type-1 (13.78 i.e.17.43%), Poaceae (7.11 i.e. 8.99%) and Restionaceae (6.74 i.e. 8.52%). These taxa can be described as typical of zone V-2 since they were most common in all levels within this zone.

From the BEST analysis, ρ is optimized (at 0.72) for 3 variables, namely: macro-charcoal, the proportion of aquatics:terrestrial pollen and Sordariaceaea. This means that macro-charcoal, aquatics and Sordariaceae were the three sets of proxy data that 'explain' the patterns seen in the VANG core pollen record since they had the best match. These results were statistically significant since the 999 permutations (999 values of ρ) was presented in a histogram and the real ρ (0.72) was larger than any of those in the histogram. The null hypothesis was rejected at $p<0.001$.

5.4.3. Histograms to test for bimodality

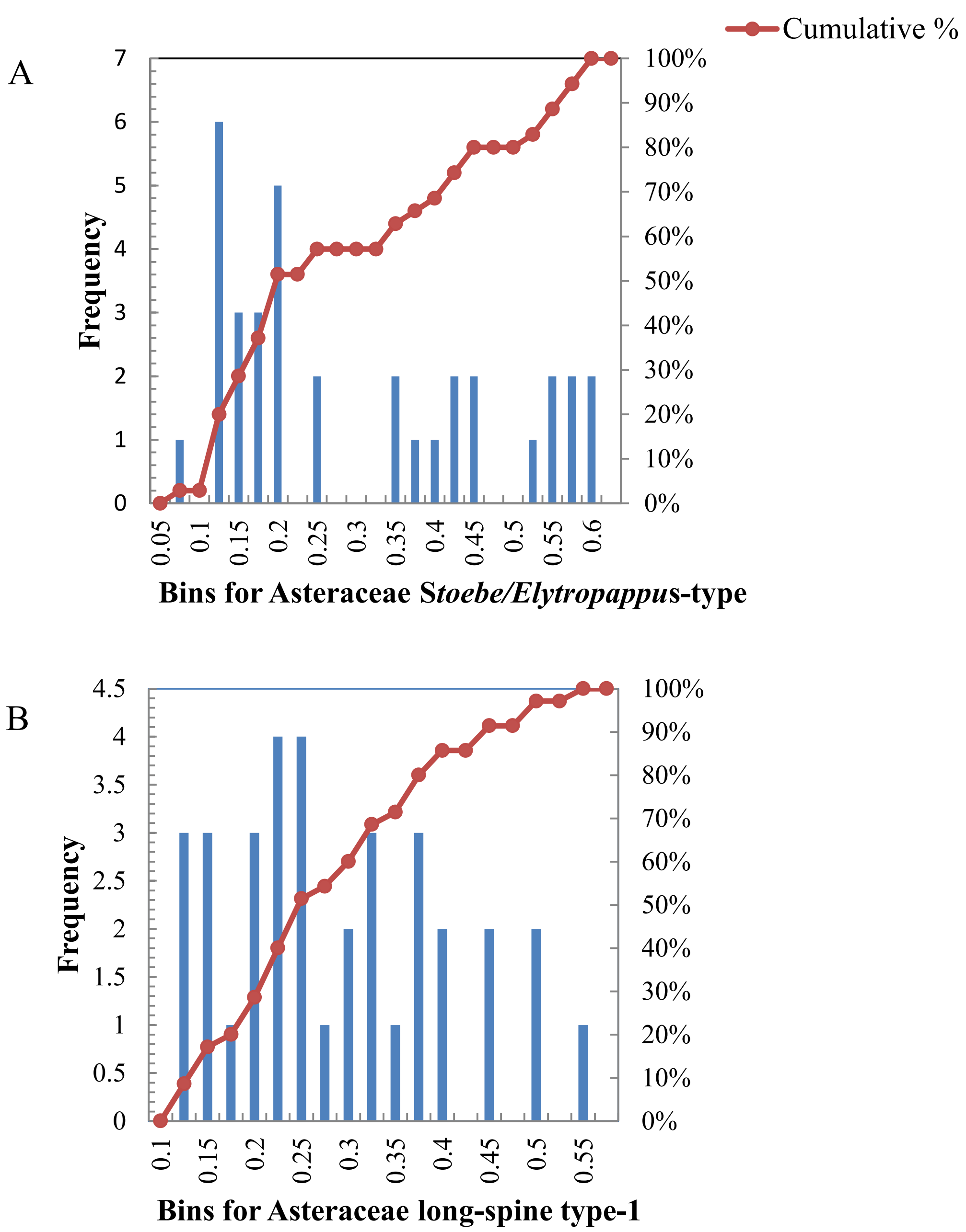


Figure 22: Histogram of the frequency distribution for (A) Asteraceae Stoebe/Elytropappus-type and (B) Asteraceae long-spine type-1 pollen abundance.

Figure 22 shows the frequency distribution for Asteraceae *Stoebe/Elytropappus*-type and Asteraceae long-spine type-1 pollen abundance. In both cases the histogram was skewed to the right and therefore the data had a unimodal distribution.

5.4.4. Principal Components Analysis for percentage data

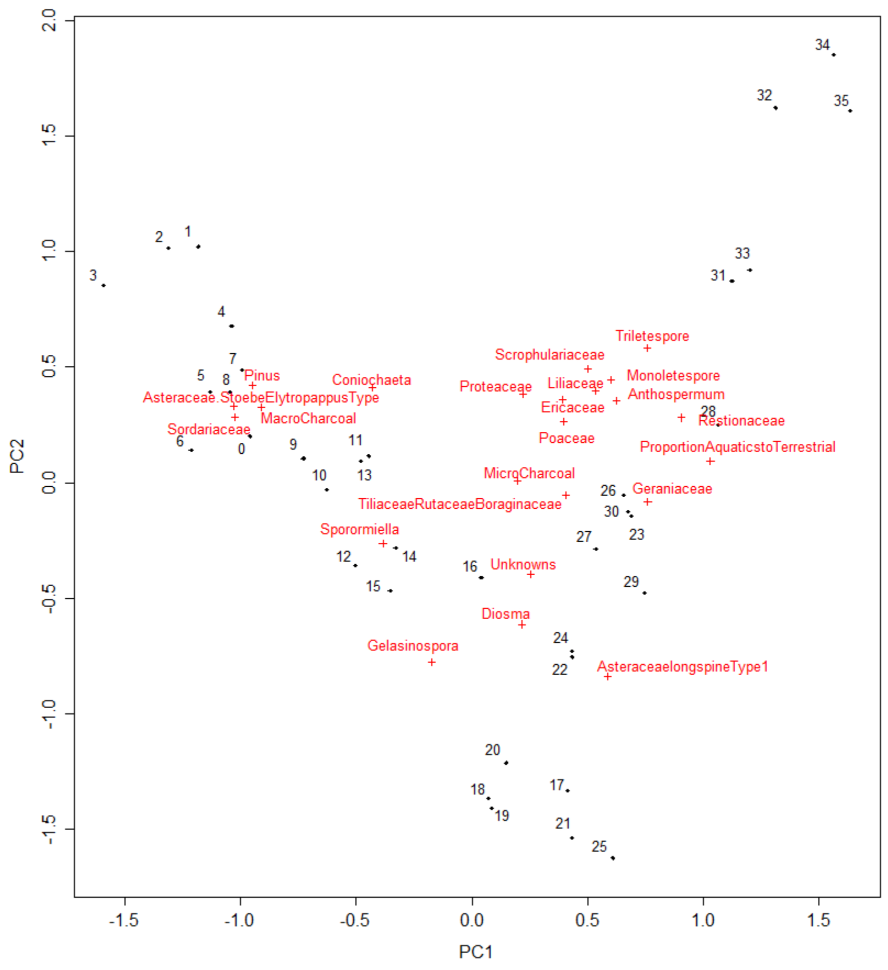


Figure 23: PCA distance biplot of pollen, spore taxa and macro- and micro-charcoal data. Analysis set to minimum of 2% inclusion. PC1 (principal component 1) is the primary axis and PC2 (principal component 2) is the secondary axis. Numbers represent sample analysed in the VANG core, with 1 being the surface sample and 35 being the basal sample.

Figure 24 shows that the first three components were significant for the PCA (Figure 23). Eigenvalues reported that PC1 and PC2 explained 47.9% of the variance. The distance biplot shows that Asteraceae *Stoebe/Elytropappus*-type, macro-charcoal, Sordariaceae, *Coniochaeta* and *Pinus* were grouped together and show strong positive relationship with PC1 and PC2. Taxa are not clustered according to vegetation type units (e.g. Renosterveld, Fynbos, Thicket, Grassland) as the cluster in the top right includes taxa such as Ericaceae, Proteaceae, Restionaceae, *Anthospermum* spp Poaceae, Scrophulariaceae, Liliaceae, Monolete and Trilete spores and Aquatics (i.e. the proportion of Aquatics to terrestrial pollen). Asteraceae long-spine type-1 pollen is associated with *Diosma* spp and partially associated with to the coprophilous spore, *Gelasinospora*. Coprophilous spores, *Gelasinospora* and *Sporormiella*, are in the same quadrant. Micro-charcoal is on close to the origin on the PCA.

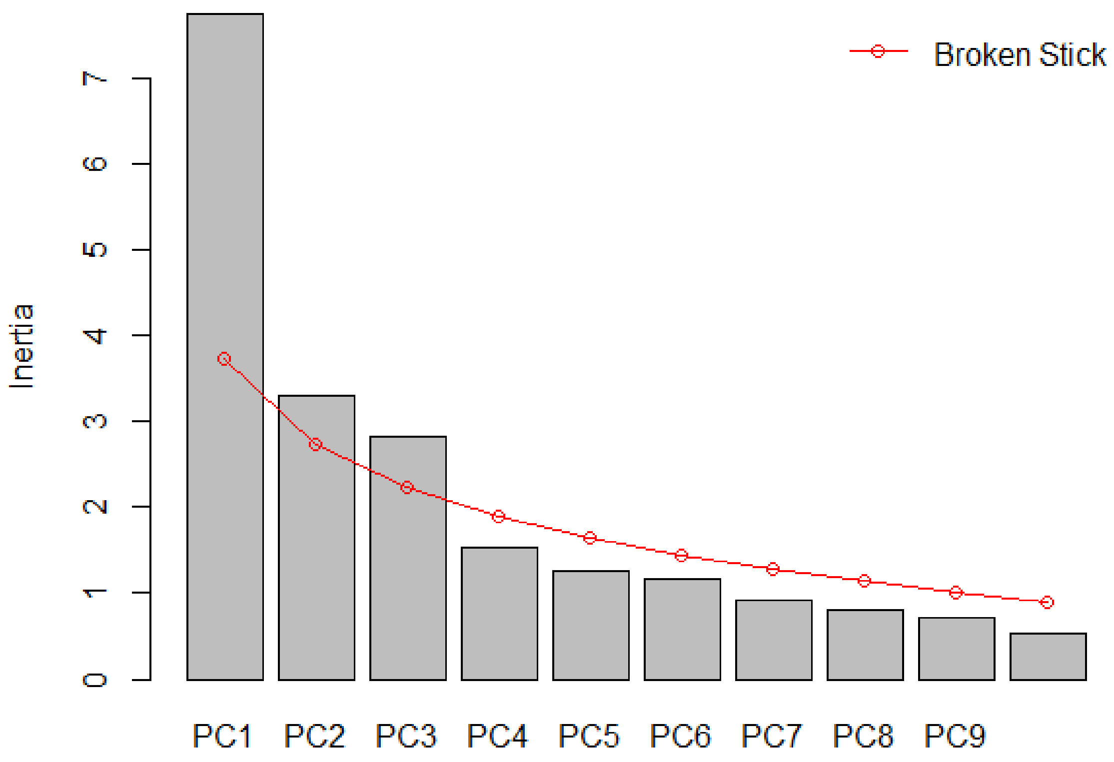


Figure 24: Scree plot showing the significance of the PCA for the pollen, spore taxa and macro- and micro-charcoal data set to 2% threshold of inclusion.

6. DISCUSSION

6.1. Introduction

Despite West-Coast Renosterveld occurring in the globally recognized biodiversity hotspot of the Cape Floristic Region (CFR) (Figure 1), it is the most transformed of all vegetation types within the region. The few remaining fragments of natural Renosterveld are of high conservation value, but even the protection of these fragments is compromised since they are often subject to land-use disturbance (fire, herbivory, ploughing and urbanization) and future climate change also poses a threat. Applied palaeoecological research in West-Coast Renosterveld is useful since the origin and history of Renosterveld is poorly understood. It is debatable as to what the vegetation was originally comprised of and this could have major implications for current management and restoration activities.

The objectives of the present study were to quantify the extent and nature of vegetation change, fire and herbivory history over the past ca. 1300 years within West-Coast Renosterveld vegetation. An analysis of fossil pollen, charcoal and coprophilous spores was used to reconstruct pre-colonial benchmark conditions. The study site, Vangkraal Spring wetland, is located on the ecotone between Swartland Shale Renosterveld and Swartland Alluvium Fynbos on Elandsberg Private Nature Reserve (Elandsberg PNR). The small wetland reflects local changes in vegetation and therefore is a good disturbance indicator, especially of local land-use change such as fire and herbivory. This discussion interprets the findings in the context of known climate and land-use history and explores the links with ecological theory. Palaeoecological investigations of benchmark conditions have the potential to inform conservation management and restoration of the highly threatened West-Coast Renosterveld vegetation.

6.2. How has vegetation, charcoal and coprophilous spores at Elandsberg PNR changed over time?

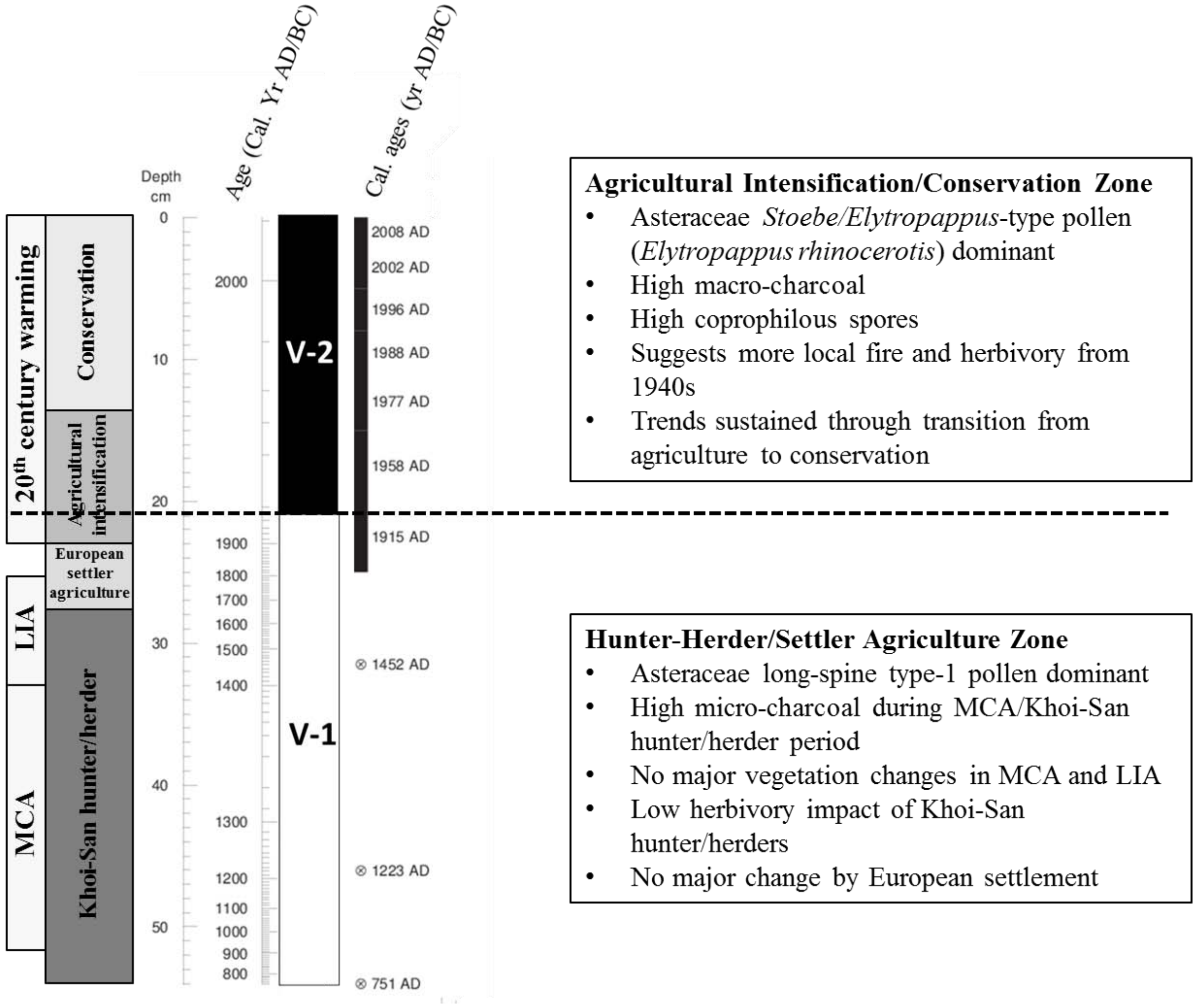
The fossil pollen data suggest a major change in vegetation composition around the mid-20th century, which is characterized by an increase in Asteraceae *Stoebe/Elytropappus*-type pollen. It is likely that the increase in Asteraceae *Stoebe/Elytropappus*-type pollen is due to increased *Elytropappus rhinocerotis* (Renosterbos), because *Stoebe* spp occurs infrequently in the landscape today whereas *Elytropappus rhinocerotis* is common. This change is associated with increased levels of herbivory and a greater incidence of local fires, as evidence by increasing coprophilous fungal spores and macro-charcoal. Before this, vegetation showed only subtle changes and was relatively stable over time. Also, evidence for herbivory and local fires was also low during this period although micro-charcoal data suggest higher regional fire frequency.

The main change in vegetation assemblage over time is defined by a change in dominance from Asteraceae long-spine type-1 pollen to Asteraceae *Stoebe/Elytropappus*-type pollen. However, there are major discrepancies between the percentage and concentration data for Asteraceae long-spine type-1 (Figure 18 and 19) pollen and this is likely due to the Fagerlind effect (Fagerlind 1952; Prentice 1988; see section 4.3.). Therefore the notable decrease in Asteraceae long-spine type-1 over time in the percentage diagram (Figure 18) is not a true reflection of vegetation change; however, it was the most abundant pollen type during the Hunter-Herder/Settler Agriculture Zone (Figure 19). The vegetation survey conducted at Elandsberg PNR study site showed that the largest recorded abundance of *Stoebe* spp was only 2%, providing confidence that the change in composition was due to *Elytropappus rhinocerotis* and not *Stoebe* spp. The Psimpoll zonation analysis carried out on the fossil pollen shows that the vegetation assemblages before and after the increase in *Elytropappus rhinocerotis* are statistically distinct. AMS radio-carbon dating, ^{210}Pb dating and exotic pollen markers reveal the time periods covered by the two vegetation zones. The first zone (V-1) occurred from ca. AD 750-1940 (depths 54-21 cm) and this time period is classified as the 'Hunter-Herder/Settler Agriculture Zone'. The second zone (V-2) occurred from ca. AD 1943-2012 (depths 21-0 cm) and this time period is classified as the 'Agricultural Intensification/Conservation Zone'. The consistent presence of Cerealia pollen and exotic tree pollen (*Eucalyptus* and *Pinus*) in the Agricultural Intensification/Conservation Zone (Figure 18 and 19) supports this interpretation of the chronology. The number and position of the zones are the same in the percentage and concentration pollen data giving confidence that the zones are ecologically meaningful (Figure 18 and 19) Furthermore, the NMDS ordination with a cluster analysis of 70% minimum resemblance confirms the Psimpoll zonation by displaying the two periods graphically (Figure 20 and 21).

The observed changes in pollen, charcoal and spores are not related to stratigraphy within Vangkraal Spring wetland, which consists mostly of clay and fine sand throughout, with coarser sand and less humified vegetation matter in the deeper layers (Figure 13). Similarly, the changes were not related to the organic, inorganic or water content of the VANG core (Figure 14). There is consistent presence of organic carbon in top 54 cm associated with good pollen preservation and there was generally good correspondence between pollen surface samples and the modern vegetation survey. Taxa such as Proteaceae, Poaceae, *Elytropappus rhinocerotis* and Cyperaceae were also abundant in the pollen spectrum and there were a number of taxa recorded in both the current vegetation and the VANG core (Table 6). Therefore there is confidence that changes in pollen abundance represent real vegetation changes not taphonomic processes. Despite increased impact of herbivores and local fires, there is no evidence from Troels-Smith sediment description and Loss on Ignition (LoI) of intense erosion events. This suggests that no degradation/erosion threshold has been crossed over ca. 1300 years.

The co-occurrence of increasing charcoal, coprophilous spores and Asteraceae *Stoebe/Elytropappus*-type pollen since ca. AD 1943 suggests that fire and herbivory (which are associated with land-use disturbance) may play a role in the vegetation dynamics of Elandsberg PNR. The Hunter-Herder/Settler Agriculture Zone was characterised by high regional fire frequency and intensity, evidenced by micro-charcoal abundance, low herbivory, suggested by low abundance of coprophilous spores, and relatively stable vegetation conditions. On the other hand, the Agricultural Intensification/Conservation Zone experienced no high peak in micro-charcoal events but local fires, evidence by macro-charcoal and herbivory were the highest they had ever been in the past ca.1300 years. The vegetation was dominated by *Elytropappus rhinocerotis*. The intensification of agricultural practices in the 20th century was the main change in land-use at Elandsberg PNR which co-occurred during the transition from Hunter-Herder/Settler Agriculture Zone to the Agricultural Intensification/Conservation Zone.

Known climate changes such as the Medieval Climate Anomaly (MCA, ca. AD 900-1400) and Little Ice Age (LIA, ca. AD 1400-1800) are not associated with vegetation change, nor is early 20th century warming. However, warming during the mid-20th century could be interacting with land-use, thus creating vegetation changes that occurred from ca. AD 1943. Figure 25 shows how the dates from the VANG core relate to the general land-use and climatic conditions over the past ca.1300 years, and in relation to the two vegetation zones. Climate change, land-use or the combination of the two are possible drivers for vegetation change experienced during the mid-20th century.



Agricultural Intensification/Conservation Zone

- Asteraceae *Stoebe/Elytropappus*-type pollen (*Elytropappus rhinocerotis*) dominant
- High macro-charcoal
- High coprophilous spores
- Suggests more local fire and herbivory from 1940s
- Trends sustained through transition from agriculture to conservation

Hunter-Herder/Settler Agriculture Zone

- Asteraceae long-spine type-1 pollen dominant
- High micro-charcoal during MCA/Khoi-San hunter/herder period
- No major vegetation changes in MCA and LIA
- Low herbivory impact of Khoi-San hunter/herders
- No major change by European settlement

Figure 25: Schematic showing how the main findings of the VANG core relate to long-term climate change (i.e. Medieval Climate Anomaly (MCA, ca. AD 900-1400) and Little Ice Age (LIA, ca. AD 1400-1800)) and land-use (i.e. Khoi-San hunter/herders, European settlers, agricultural intensification and conservation period); shown on the far left of the diagram. Pollen zonation is shown on the far right: zone V-1 is the 'Hunter-Herder/Settler Agriculture Zone' and zone V-2 is the 'Agricultural Intensification/Conservation Zone'.

6.3. Drivers of vegetation dynamics at Elandsberg PNR

6.3.1. Climate as a driver of vegetation change at Elandsberg PNR

The time period under study covers three main periods of known climate change, namely the MCA, LIA and the 20th century warming. The MCA occurred from ca. AD 900-1400 (Stager et al. 2012). During this time the winter rainfall zone (WRZ) of South Africa was warm and arid (Stager et al. 2012). The LIA occurred from ca. AD 1400-1800 (Mayewski et al. 2004) and was characterized by cool and wet conditions in the WRZ of South Africa (Stager et al. 2012). From the early 20th century up until the present the climate for the WRZ has been characterised by a regional increase in temperature (Haensler et al. 2010). A recent report by the Intergovernmental Panel on Climate Change (IPCC) shows that global temperature of the 20th century is anomalous (Change 2007). Cronin et al. (2003) conducted a study in Chesapeake Bay, in the northern hemisphere, and reported that the 20th century onwards has been described globally as anomalous since the extremes in high temperature have never been experienced any other time within the last 2200 years. On the other hand rainfall does not seem to follow a trend and is more variable in the WRZ for this time period (Kruger and Shongwe 2004; Midgley et al. 2005; Power and Mills 2005; Haensler et al. 2010; Hoffman et al. 2011b). The variation in vegetation described in section 6.2. shows only subtle changes in response to the climate changes of the MCA and LIA, suggesting resilience to known climate change within the study period. Significant vegetation changes in the 20th century only occur from ca. AD 1943 suggesting that either a climate threshold was crossed or an over-riding influence of land-use caused this change. The possibility of recent climate change being a driver of vegetation change will be discussed below.

Considering the pollen record for the three common Fynbos taxa found in the VANG core (Ericaceae, Restionaceae and Proteaceae), slight but insignificant changes occurred in the sequence. These taxa remain relatively stable over time in spite of the change in climate during the MCA and LIA. Other relatively abundant pollen taxa such as Asteraceae long spine type-1, Asteraceae Stoebe/Elytropappus-type, Poaceae, *Anthospermum* spp also remained unchanged and therefore confirm the stability of vegetation during the MCA (Figure 18 and 19). However, the micro-charcoal data suggests higher fire frequency and intensity between ca. AD 750-1380, which could be attributed to the warm arid conditions of the MCA. Although fires can occur under a wide range of weather conditions, large fires are often restricted to periods of high fire danger (Forsyth and van Wilgen 2008). Data used to calculate the fire danger index include daily maximum temperature and minimum relative humidity, wind speed, time since the last rain fell and moisture deficit (Noble et al. 1980). Warm arid conditions during the MCA may be classified as having the potential for high fire danger and therefore may have increased the likelihood of large wildfires. However, this period of higher fire frequency and intensity could also be associated with land-use impacts by Khoi-San hunter/herders (see section 6.3.2. below).

Similarly during the LIA, slight but noticeable changes occurred in various pollen taxa, spore taxa and micro-charcoal deposits. The following four taxa increased in abundance: Asteraceae long-spine type-1, Ericaceae and *Gelasinospora* for the percentage data; and Rutaceae for both the percentage and concentration data. In contrast, the following nine taxa decreased in abundance: Trilete spores for the percentage data; Chenopodiaceae, Scrophulariaceae, Poaceae, Restionaceae, Proteaceae and Other non-coprophilous spores for the concentration data; and *Anthospermum* spp and Asteraceae long-spine type-1 for both the percentage and concentration data. Interestingly, for the concentration data, Asteraceae *Stoebe/Elytropappus*-type pollen was at its lowest abundance in ca. AD 1470. However, the initial increase in Asteraceae *Stoebe/Elytropappus*-type occurred after ca. AD 1790, but it was only able to dominate in the pollen record ca. 143 years after the LIA had ended. In general, micro-charcoal abundance was low during the LIA compared to previous periods and no high peak events were evident during the LIA or even until the present day (Figure 18 and 19).

Future climate change scenarios predict warmer temperatures which will affect plant water availability. The MCA may be an analogue for current warming and future climate change. Cronin et al. (2003) suggest that the mean temperatures during the early MCA ca. AD 450-900 (13.52°C), are comparable with those of the 20th century (13.37°C). If this is true then it would be expected that vegetation patterns during the 20th and early 21st century would mimic those of the early MCA. The present study revealed subtle changes and similarities in abundances of pollen taxa during periods characterized by warmer conditions (i.e. during the MCA and the 20th century warming). For the percentage data, the abundance of Asteraceae long-spine type-1 during ca. AD 750-1080 is similar to what it was in the last ca. 45 years (ca. AD 1967-2012) (Figure 18). For the concentration data, the abundance of Ericaceae in ca. AD 955 is similar to the abundance in ca. AD 1997 and ca. AD 2008. Lastly, the abundance *Anthospermum* spp for the concentration data was similar in ca. AD 1080 and ca. AD 1997 (Figure 19).

Previous water potential studies have focused on the effects that drought may have on a range of Fynbos species (West et al. 2012; Skelton et al. 2013). West et al. (2012) found that Erica species are highly drought sensitive and more vulnerable to desiccation during periods of low rainfall compared to species in the Proteaceae and Restionaceae. Deep-rooted, species in the Proteaceae coped best during drought periods. Although species within the Restionaceae were more variable under drought conditions, they were mostly able to cope and suffered low mortality (West et al. 2012). If the slight changes in the common Fynbos taxa of the VANG core are considered then the present study is consistent with the findings of West et al. (2012). Fossil pollen data show that after enduring the drought-like conditions in the arid environment of the MCA, Ericaceae pollen experienced a slight increase during the LIA and this may be attributed to the increase in water availability. Restionaceae pollen was slightly more abundant during the warm and arid MCA which suggests that it was better at coping with the lower rainfall conditions at the time. However, during the wet conditions of the LIA it did not increase in abundance but rather decreased slightly until reaching its lowest abundance in ca. AD 1580 (Figure 19). Proteaceae showed little variation throughout the MCA and the LIA and therefore appeared to be the most resilient to climate change.

However, the changes described in pollen abundance were subtle and the pollen record suggests that Ericaceae, Restionaceae and Proteaceae remained resilient to past climate variations. The apparent resilience to climate change is consistent with previous work showing that mountain Fynbos in the central Cederberg (Figure 2) remained unchanged despite climate instability (Quick et al. 2011). It has been suggested that mountain Fynbos, such as the vegetation surrounding the Elandsberg PNR site, is more resilient to climate change than lowland Fynbos (Meadows et al. 2010; Quick et al. 2011). The general vegetation stability of Elandsberg PNR during the MCA and LIA could be a result of the present study site occurring quite close to the Elandskloof mountains and reflecting montane rather than lowland fynbos. The general stability of all abundant pollen taxa during the MCA also suggests that this vegetation is more resilient than modelling predictions for future climate change would suggest. The Fynbos and Succulent Karoo biomes have been predicted to contract dramatically in response to changing climate in the next 50 years (Midgley and Thuiller 2007; Midgley et al. 2005; Midgley et al. 2008). However, no significant decreases in vegetation were seen in response to the warm and arid conditions of the MCA and no decreases appear to have happened over the course of the warmer 20th century either. Even if Fynbos vegetation types are more resilient than predicted, anthropogenic pressures have increased during the past century possibly exacerbating the changes in vegetation after the cold wet conditions during the LIA and 19th century, especially for Asteraceae *Stoebe/Elytropappus*-type.

An alternative explanation for the apparent stability during the Hunter-Herder/Settler Agriculture Zone is that some taxa in the pollen record (e.g. Ericaceae, Proteaceae and Restionaceae) are only resolved to family level. This lack of taxonomic resolution of pollen means that there is a possibility that Proteaceae and Restionaceae are responding to climate change through species turnover, but that such changes would not be apparent in the pollen record. The remaining natural vegetation fragments within the Fynbos biome that contain this species diversity are of top conservation priority (von Hase et al. 2003). Though stable at the family level, sensitive species may be lost and replaced by more resilient ones. One of the main reasons why the CFR is an internationally recognized biodiversity hotspot is due to its floristic species diversity and endemism, and therefore loss of less resilient species would be of conservation concern (Goldblatt and Manning 2000; Myers et al. 2000). From a biodiversity point of view, resilience at family level may not be suitable to inform biodiversity conservation. Therefore it is extremely important for future research to improve on the taxonomic resolution of pollen to species level and to monitor the effects of changing climate on species composition.

Though no resilience threshold has been crossed for Fynbos and Renosterveld vegetation, nevertheless changes in disturbance/land-use might cause variation in community composition. For example, the abundance of *Diosma* (typical of Fynbos) and Geraniaceae, Fabaceae, Liliaceae, Tiliaceae/Rutaceae/Boraginaceae pollen (typical of both Fynbos and Renosterveld) is higher in the Hunter-Herder/Settler Agriculture Zone, possibly suggesting sensitivity to changing land-use, though this interpretation is tentative owing to low pollen abundance throughout the VANG core (Figure 18 and 19). *Cliffortia* and Rhamnaceae (characteristic of Fynbos), on the other hand, become more abundant during the Agricultural Intensification/Conservation Zone, possibly suggesting greater tolerance to disturbance. Therefore, although the common Fynbos taxa (Ericaceae, Proteaceae and Restionaceae) appear resilient, there may be reshuffling within the Fynbos community over time.

Considering recent anthropogenic warming of the 20th century and the concern over its effects on biodiversity (Thomas et al. 2004; Midgley et al. 2005; Midgley and Thuiller, 2007), changes in vegetation might be expected to have occurred since the early 20th century. There is evidence of increasing temperatures in the WRZ since AD 1901 (Haensler et al. 2010) but the pollen data do not show a synchronous response since the significant change in vegetation only took place in ca. AD 1943. The increase in temperature in the CFR region began at least 40 years before the noticeable change in vegetation towards *Elytropappus rhinocerotis* dominance (Figure 18 and 19). In fact, warming is likely to have started earlier than weather station records began, probably at the end of the LIA in ca. AD 1800 (Mayewski et al. 2004; Stager et al. 2012). The pollen data indicate that Asteraceae *Stoebe/Elytropappus*-type, Proteaceae, Ericaceae, Restionaceae, Poaceae and *Anthospermum* spp showed slight increases in abundance after ca. AD 1790 (post LIA) suggesting that post LIA warming may be playing a role in vegetation dynamics. However, the main change in vegetation occurred in ca. AD 1943, which does not coincide with the climatic boundary at the start of the 20th century. This suggests a role for disturbance (i.e. fire and herbivory) brought about through land-use (see section 6.3.2. below) but the present study does not completely exclude the influence that climate change has on contributing to vegetation change in conjunction with these disturbance indicators.

Another consideration is the size of the wetland from which the VANG core was retrieved. This small basin would capture ca. >80% of a local to extra-local pollen signal (Figure 9; Table 3). Consequently it is likely to be very sensitive to local disturbance factors rather than regional climate change. One of the reasons why this study site was chosen is because of its sensitivity to local disturbance and the insight it would provide into the role played by large indigenous herbivores and domestic livestock both before and after the European colonial period. One of the concerns of a smaller sized wetland is that the relationship between climate and vegetation at larger scales could be overridden by biological effects such as fire and disturbance at smaller scales (Greig-Smith 1979; Woodward and Williams 1987; Wiens 1989).

Although the noticeable change in vegetation at ca. AD 1943 occurred after regional temperatures began to increase, it has been reported that more rapid warming occurred in the latter part of the 20th century. Haensler et al. (2010) reported that temperatures were higher during ca. AD 1953-2006. Furthermore, Warburton et al. (2005) reported that temperatures were higher in AD 1980-2000 compared to AD 1950-1970. There is a possibility that the increased warming may have compounded the effects brought on by increased local fire and herbivory during the Agricultural Intensification/Conservation Zone. Likewise, greater variation in rainfall (e.g. drought periods, heavy rainfall periods) over the past ca. 69 years could have also played a role in compounding the effects of fire and herbivory. Drought events could have increased the likelihood of fires spreading through Elandsberg PNR as there would be a dry fuel load to carry fires. Heavy rainfall events could allow for the growth of better pasture for herbivores as well as allow shrubs such as the flammable *Elytropappus rhinocerotis* to increase in abundance and size thus promoting more local fires.

6.3.2. The effect of land-use (fire and herbivory) on the vegetation at Elandsberg PNR

The results from fossil pollen, macro-charcoal and coprophilous spores show that the major change in vegetation composition, which is characterized by an increase in the shrub, *Elytropappus rhinocerotis* in ca. AD 1943 (Figure 18 and 19), is associated with an increase in fire and herbivory. This suggests that the main driver of vegetation change at Elandsberg PNR is land-use disturbance, in the form of fire and herbivory. This is clearly associated with the period of agricultural intensification until AD 1973 and then with conservation management including the reintroduction of large indigenous herbivores. Previous land-use changes such as the nomadic herding of domestic livestock by Khoikhoi pastoralists and the permanent settlement and intensification of agriculture by the settlers during the European colonial period did not seem to affect vegetation, fire and herbivory to the same extent. The evidence for disturbance as a major driver of vegetation change is strengthened by changes in some of the other, less abundant taxa shown in Figure 18 and 19. For example, thicket vegetation is known to be sensitive to disturbance such as fire and *Maytenus oleoides*, a characteristic thicket taxon, is higher in abundance during the Hunter-Herder/Settler Agriculture Zone than in the Agricultural Intensification/Conservation Zone.

The time period under study captures changes in land-use brought about by San hunter-gatherers, Khoikhoi pastoralists, early European settlers and more recent intensive agricultural practices of commercial farmers as well as the rise of conservation management since 1973 at Elandsberg PNR (Figure 25). The Khoikhoi pastoralists occupied the land from 2000 yr BP until the mid-17th century. The dominant form of land-use by Khoikhoi pastoralists was large-scale burning of areas to promote pasture for livestock (such as sheep, goats and cattle). They would return to previously burnt areas 1-4 years later (Thom 1952, 1954; Deacon 1983) and it is speculated that their land-use practices caused Renosterveld to be dominated by grasses rather than shrubs (Thom 1952, 1954; Cowling et al. 1986; Newton 2008). The micro-charcoal data suggest that regional fire was more frequent, intense and variable from ca. AD 750-1400 than for the rest of the sedimentary sequence and this was before Europeans colonized the region.

The micro-charcoal data suggests high variability in fire during the first ca.650 years documented in the present study, but there appears to have been no significant change in vegetation as the pollen data only fluctuated slightly for some (e.g. *Anthospermum* spp, Poaceae and Restionaceae) and not at all for most taxa (Figure 18 and 19). These findings are partly consistent with those of Meadows and Baxter (2001) who described the pre-colonial period as being abundant in micro-charcoal fragments. There is no pre-pastoralist baseline in this record with which to compare the high micro-charcoal and vegetation stability, so it is uncertain whether the results are due to Khoikhoi pastoralists or climate variability, specifically the warmer conditions of the MCA. In addition, coprophilous spores (such as *Sporormiella*, Sordariaceae, *Gelasinospora* and *Coniochaeta*) are present during this time but they are low in abundance (Figure 18 and 19). The level of herbivory was not high and so the effect of the Khoi-San hunter/herders is not large at this particular site within the Swartland region.

After the European colonialists arrived in the Cape during the mid-17th century (Hoffman 1997), regional land-use changed significantly. By the mid-19th century the reach and impact of the early colonial settlers had increased considerably. Natural vegetation was either used for construction, fuel or cleared for agriculture (livestock farming and/or crop cultivation). One of the main differences in livestock management between European colonialists and Khoikhoi pastoralists was that European colonialists settled permanently with their livestock, rather than moving between seasonal grazing areas in the mountains and at the coast (Deacon 1992). Fire intervals were thus even shorter than those used by Khoikhoi pastoralists to increase grazing availability throughout the year. Neumann et al. (2011) reported that after colonization by European settlers, there was a period characterized by uncontrolled burning as evidenced by an increase of charcoal. Given the increased use of fire to stimulate pasture for intense grazing, it would be expected that macro- and micro-charcoal abundance would increase dramatically. However, this is not evident in the record from Elandsberg PNR (Figure 18 and 19). Instead, results indicate that local fires at Elandsberg PNR were low and regional fires were less intense and less variable than during the time when San hunter-gatherers and Khoikhoi pastoralists occupied the region. Perhaps this increase in charcoal is not evident because only light livestock grazing occurred at Elandsberg PNR and perhaps it reflects fire suppression in some areas within the region. It was noted that some European settlers practiced fire suppression from ca. AD 1678 onwards to protect certain agricultural areas and properties (Newton 2008). In addition, the cooler conditions of the LIA may have been less conducive to fire.

Another land-use activity to consider during the European colonial period is the increase in hunting which led to a decline in populations of large indigenous herbivores and other wild game. Their removal during the ca. 1700s-1900s (Klein 1974) probably disrupted some of the ecological processes that govern West-Coast Renosterveld. However, European settlers also increased domestic stock numbers which made grazing pressure more intense. This also means that the necessary processes could have been partially compensated for by the replacement of wild herbivores by domestic livestock. There is evidence of increasing abundances of coprophilous spores (Sordariaceae, *Gelasinospora* and *Coniochaeta*) from ca. AD 1790 (Figure 18 and 19) indicating that herbivory had increased. This increase in coprophilous spores was likely due to an increase in domestic livestock. Interestingly, *Sporormiella*, another coprophilous spore that has previously been used to detect both Quaternary megafaunal extinctions (Davis and Shafer 2006; Gill et al. 2009; Wood and Wilmshurst 2013) and the introduction of domestic livestock such as cattle (Burney et al. 2003; Raper and Bush 2009) did not follow the same pattern as the other spores. This highlights the need to use a range of spore types to track herbivory over time, rather than relying solely on Sporormiella (Graf and Chmura 2006; van Geel and Aptroot 2006; Gelorini et al. 2011). Despite this increased land-use pressure by European settlers the vegetation remained unchanged.

Pre-colonial vegetation conditions were only marginally different from the vegetation state during the time that early European settlers occupied the land. However, it is the range of land-use activities that were initiated by European colonialists during the 17th to19th century that intensified and influenced regional land-use change from about the 20th century onwards. This demonstrates that human activities can affect the landscape long after they have occurred and also that they may become more intensive over time. During the 20th century there was an increase in transformation of natural vegetation for agricultural expansion (Figure 3) and urbanization through increased technology and industrialization. Although a number of exotic taxa were introduced into the region from the late 17th century by the European settlers (Table 1), they were only detected later in the VANG core in the Agricultural Intensification/Conservation Zone. Exotic taxa that were found in the pollen record of the present study include pine (*Pinus* spp), gum (*Eucalyptus* spp) and cereal crop pollen such as barley (*Hordeum vulgare*), oats (*Avena sativa*), rye (*Secale cereal*) and wheat (*Triticum* spp). A pine plantation near Elandsberg PNR was established about 100 years ago (Wooding pers. com. 2013) but the first time *Pinus* appeared in the pollen record was only in ca. AD 1951.

During the Hunter-Herder/Settler Agriculture Zone the vegetation community was dominated by Asteraceae long-spine type-1pollen. However, after ca. AD 1943, during the Agricultural Intensification/Conservation Zone it changed to one dominated by Asteraceae *Stoebe/Elytropappus*-type pollen (i.e. *Elytropappus rhinocerotis*). The macro-charcoal and coprophilous spore data suggest that land-use disturbance such as local fire and herbivory were the main drivers for this general change in the composition of Renosterveld vegetation and these results accord well with the known history of land-use at Elandsberg PNR (Table 1). The land was used as a horse remount by the British Army and some sheep were kept on the land during 1900 (Becker 1996). From 1958-1983 it was used for both cattle and sheep farming (Stander 1988; Becker 1996) and during this time a few areas were used to grow oats to supplement grazing for the livestock (Fish 1988). In 1973 the Elandsberg PNR was established, livestock were no longer kept on the land and large indigenous herbivores were reintroduced (Table 1 and 2). The significant change in vegetation had taken place 30 years before the reintroduction of indigenous herbivores suggesting that the change in vegetation composition was brought about by land-use impacts of permanent settlement and livestock farming.

Macro-charcoal reflects the incidence of local fires which is closely linked to land-use management at Elandsberg PNR. Before the present study, little was known about the long-term fire history of the Elandsberg Reserve. There is anecdotal evidence of a fire in the 1920s, but no written record of fires before 1980 (Table 1). It would seem that there is a lag of about 5 years (Duffin et al. 2008) in the macro-charcoal record but reported fires are noticeable in the VANG core. For example, there are peaks in macro-charcoal coinciding relatively well with known fires. Since ca. AD 1943, the increase in unpalatable *Elytropappus rhinocerotis* together with that of macro-charcoal and the coprophilous spore-type, Sordariaceae, continued rather steadily until AD 1973, after which a noticeable increase in all three indicators occurred. Even though the change in vegetation composition had occurred before the reserve was established in AD 1973, the added herbivory pressure due to the reintroduction of large indigenous herbivores and increasing local fires seemed to encourage the increase in *Elytropappus rhinocerotis*. This result is probably contrary to what most conservation managers would expect given the reintroduction of indigenous herbivores at Elandsberg PNR which would best reflect perceived “pristine” conditions.

The results suggest that the re-stocking of indigenous herbivores has occurred at levels that are much higher than would have occurred historically during pre-colonial times. However, the vegetation was also affected decades before by the replacement of a range of indigenous herbivores which varied in size and grazing behaviour, by a large number of highly selected grazers such as cattle and sheep (Becker 1996). This resulted in the change in Renosterveld composition from ca. AD 1943 which was not reversed after the removal of domestic stock and reintroduction of indigenous herbivores.

Figure 23 confirms the results that indicate disturbance as a driver of vegetation dynamics. The PCA showed that disturbance indicators were grouped together in the upper layers of the VANG core and confirm the change in vegetation, fire and herbivory after ca. AD 1943. These indicators included Asteraceae *Stoebe/Elytropappus*-type, macro-charcoal, Sordariaceae, *Coniochaeta* and *Pinus*. Asteraceae long-spine type-1 pollen is indicative of a more pristine vegetation state and as a result was furthest away from the disturbance indicators and partly associated with the coprophilous spore, *Gelasinospora* (Figure 23) which could be associated with pastoralism during the Hunter-Herder/Settler Agriculture Zone. The cluster that showed a strong positive relationship with PC1 and PC2 is probably indicative of moisture availability as it included Trilete and Monolete spores and Aquatics (Neumann et al. 2011). This quadrat includes taxa such as Proteaceae (less positive on the PC1) which are drought tolerant and Ericaceae (more positive on the PC1) which are drought sensitive (West et al. 2012). Similarly, the results determined by the BEST analysis indicate that macro-charcoal, aquatics and Sordariaceae were the three sets of proxy data that best explain the patterns seen in the pollen record (section 5.4.2.). Furthermore, micro-charcoal does not appear to be associated with the other variables (Figure 23). This may be because the pollen and spore results are more indicative of local disturbance, whereas micro-charcoal shows a regional signal in the incidence of fire.

The vegetation composition in the Agricultural Intensification/Conservation Zone is to some extent consistent with conceptual models that have shown that fire and herbivory have a great influence in driving the compositional state of Renosterveld (see section 6.4. below for further discussion; Cowling et al. 1986; Rebelo 1995; Milton 2007). Rebelo (1995) stated that increased fire frequency in conjunction with overgrazing immediately after burning tends to convert grassy Renosterveld to a shrubland strongly dominated by *Elytropappus rhinocerotis* (Figure 4). Contrary to findings by Rebelo (1995), no decline in Poaceae was seen with the increase in Asteraceae *Stoebe/Elytropappus*-type in the VANG core record. There is, however, one exception where the relationship between *Elytropappus rhinocerotis*, grass, fire and herbivory is evident (Figure 19; Table 1). In ca. AD 1997, Asteraceae *Stoebe/Elytropappus*-type pollen and coprophilous spore-type Sordariaceae reached their highest abundance compared to the ca. 1247 years before then. In AD 1999 a wind-driven fire occurred on Elandsberg PNR, after which Asteraceae *Stoebe/Elytropappus*-type pollen began to decline and Poaceae increased to its highest abundance in ca. AD 2001.

6.4. Links to theoretical frameworks/resilience theory

The significant increase in abundance of Asteraceae *Stoebe/Elytropappus*-type pollen, as well as abundant macro-charcoal and coprophilous spores post ca. AD 1943 was not evident at any other time in the study period. Thus, the changes seen after ca. AD 1943 are unprecedented within the past ca. 1300 years. The palaeoecological record clearly shows two different vegetation assemblages and disturbance regimes, linked to changes in land-use. It is not clear, however, whether these two zones are alternate stable states (Figure 5) which are separated by an ecological or disturbance threshold, or whether different types and frequencies of disturbance have resulted in different compositional states of Renosterveld comprising a continuum from low to high *Elytropappus rhinocerotis* abundance (Figure 4).

To test the idea of alternate stable states, a frequency histogram of Asteraceae *Stoebe/Elytropappus*-type and Asteraceae long-spine type-1 pollen was plotted. This approach has been used to distinguish Woodland and Grassland phases in the pollen record of the Savanna biome. For example, a study conducted by Gillson and Ekblom (2009) in the Kruger National Park, South Africa found a bimodal distribution for Poaceae pollen abundance, suggesting alternate grassland and woodland states rather than a continuum of woody plant abundance, which would have produced a unimodal frequency distribution in the pollen record. The bimodal distribution was evidence that a threshold controlled by fire and nitrogen was crossed and there was a shift from Grassland to Savanna (Gillson and

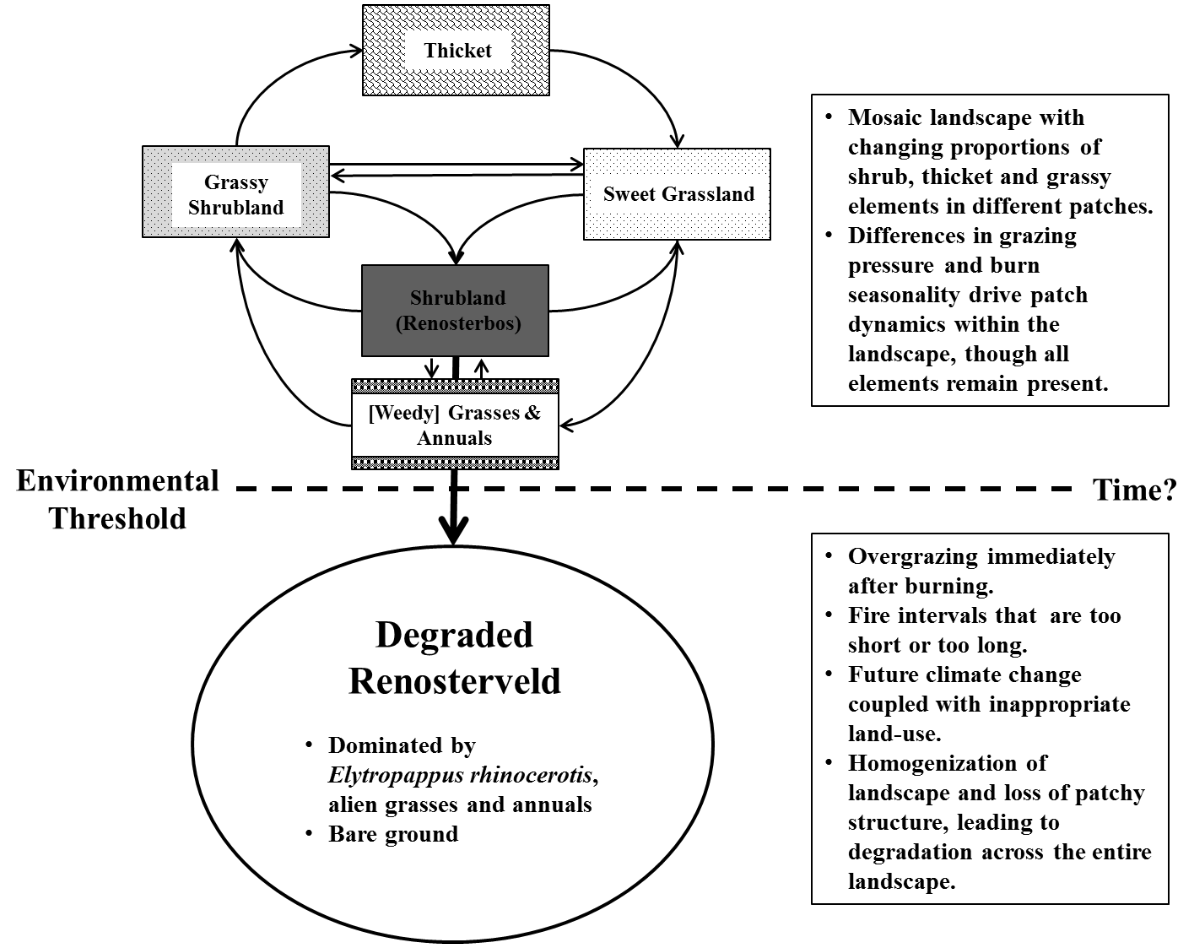
Ekblom 2009). In contrast, there was no evidence of bimodality in *Elytropappus rhinocerotis* and Asteraceae long-spine type-1 pollen abundance (Figure 22). This suggests a continuum of *Elytropappus rhinocerotis* abundance rather than two distinct vegetation assemblages. If the two zones were to be considered as representing alternative stable states then there would be a shift from the Hunter-Herder/Settler Agriculture Zone dominated by Asteraceae long-spine type-1pollen with low Asteraceae *Stoebe/Elytropappus*-type pollen to the Agricultural Intensification/Conservation Zone dominated by high Asteraceae *Stoebe/Elytropappus*-type pollen abundance. Instead, there is a re-shuffling of dominance in the vegetation community with one taxa (i.e. Asteraceae *Stoebe/Elytropappus*-type) becoming more dominant gradually over time and showing a unimodal frequency distribution. This finding is confirmed by the SIMPER analysis which shows that zones V-1 (Hunter-Herder/Settler Agriculture Zone) and V-2 (Agricultural Intensification/Conservation Zone) are significantly different (Figure 20 and 21) but that the average dissimilarity of 31.59% is not very high statistically despite the change in vegetation.

These analyses suggest that no threshold has been crossed between the low and high abundance of Asteraceae *Stoebe/Elytropappus*-type pollen during the Hunter-Herder/Settler Agriculture Zone and Agricultural Intensification/Conservation Zone respectively and that there is, therefore, no regime shift between vegetation assemblages. This argument is strengthened by some fire-sensitive Thicket taxa such as *Rhus*/*Searsia*, *Ilex* and Oleaceae which are found in higher abundance during the Agricultural Intensification/Conservation Zone (Figure 18 and 19). If a landscape scale change to “Degraded Renosterveld” (as discussed below) has occurred, thicket patches and associated taxa would most likely disappear, since they are sensitive to fire and over-grazing (Figure 4). The continued presence of thicket taxa in the pollen record, alongside increasing *Elytropappus rhinocerotis* suggests that despite the increase in disturbance (altered fire regime and increased herbivory) over time, the landscape is still heterogeneous with patches that act as fire refugia, and thereby contribute to the maintenance of biodiversity.

The results suggest that the change in the ecological system is continuous and more likely to be reversible. This type of change in Renosterveld vegetation is known as an alternative compositional state which is not the same as an alternative stable state (see Walker and Meyers 2004). A different compositional state is described in conceptual models that combine general principles of vegetation dynamics within Renosterveld (Figure 4; Cowling et al. 1986; Rebelo 1995; Milton 2007).

Depending on the type of disturbance (grazing, browsing or fire), Renosterveld can have three compositional states namely Grassland, Thicket and Shrubland. Renosterveld dominated by grass would benefit grazers, thicket would benefit browsers and dense shrubland dominated by *Elytropappus rhinocerotis* would promote fire (Figure 4). According to Milton (2007), the vegetation of the Agricultural Intensification/Conservation Zone is classified as a Shrubland, since the landscape is dominated by *Elytropappus rhinocerotis*. However, if disturbance increases further, an ecological or disturbance threshold could be crossed and the vegetation structure could shift to an alternative stable state (Walker and Meyers 2004) at the landscape level known as “Degraded Renosterveld”.

Patches of vegetation with high *Elytropappus rhinocerotis* abundance have been observed in the reserve. These patches are characterized by low biodiversity, with 60% bare ground consisting mainly of stones and with the remaining 40% being vegetation consisting predominantly of *Elytropappus rhinocerotis* (see “Shale Renosterveld” vegetation unit in Figure 12). Fortunately for Elandsberg PNR, this extreme case of disturbance has not yet been reached at a landscape scale, and the patches of *Elytropappus rhinocerotis* dominated shrubland are considered to have conservation value because they can act as refugia for other plant species (Walton 2006) (see section 6.5.2. below). The conceptual model which the present study proposes (Figure 26 and 27) adds to the already existing model of different compositional states (Milton 2007) but it includes an alternative stable state that would exist if a regime shift occurred at the landscape scale as a result of an ecological threshold being crossed. The intermediate disturbance that would benefit Renosterveld biodiversity would be compromised and no patch level heterogeneity would be visible. Instead, “Degraded Renosterveld” would consist of ca.60% bare ground, ca.40% vegetation consisting of a landscape level homogenous patch dominated by *Elytropappus rhinocerotis* and some alien grasses and annuals. Such a degraded landscape may occur if disturbance is too low or too high. Too frequent disturbance would include short fire cycles characterized by spring fires coupled with overgrazing immediately after burning. Alternatively, loss of diversity may also occur if disturbance is too low. Under such circumstances for example, a longer fire return interval coupled with overgrazing may also lead to degradation. Experimental work is needed to determine the required level of intermediate disturbance brought about by fire and herbivores.

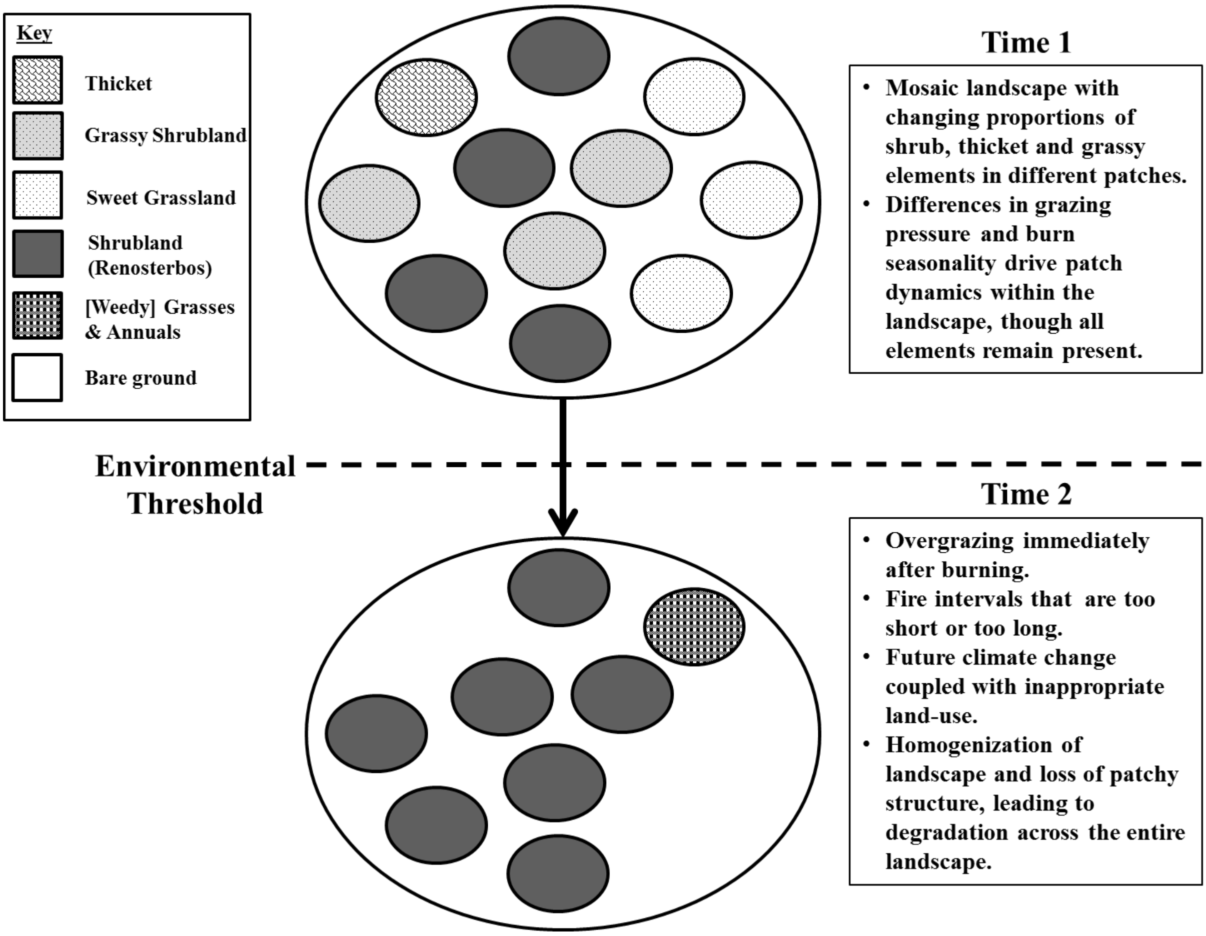


- Dominated by *Elytropappus rhinocerotis*, alien grasses and annuals
- Bare ground

- Mosaic landscape with changing proportions of shrub, thicket and grassy elements in different patches.
- Differences in grazing pressure and burn seasonality drive patch dynamics within the landscape, though all elements remain present.

- Overgrazing immediately after burning.
- Fire intervals that are too short or too long.
- Future climate change coupled with inappropriate land-use.
- Homogenization of landscape and loss of patchy structure, leading to degradation across the entire landscape.

Figure 26: Conceptual model (adapted from Milton 2007) showing how fire and overgrazing may interact to alter the composition of Renosterveld. For example, thicket elements are likely to increase if fire is reduced, whereas shrub and grassy elements will increase if fire and grazing increased. If all elements are present in a patchy landscape, a dynamic, metastable mosaic can persist. However, a regime shift can take place if an environmental threshold is crossed. The landscape will be characterized by an alternative, degraded, stable Renosterveld state.



Time 1

- Mosaic landscape with changing proportions of shrub, thicket and grassy elements in different patches.
- Differences in grazing pressure and burn seasonality drive patch dynamics within the landscape, though all elements remain present.

Time 2

- Overgrazing immediately after burning.
- Fire intervals that are too short or too long.
- Future climate change coupled with inappropriate land-use.
- Homogenization of landscape and loss of patchy structure, leading to degradation across the entire landscape.

Figure 27: Conceptual model showing a regime shift from (Time 1) a stable patchy landscape to (Time 2) an alternative stable state, Degraded Renosterveld, once an environmental threshold is crossed. Degraded Renosterveld would consist of >60% bare ground, is homogenous at the landscape level and would be dominated by Elytropappus rhinocerotis and alien species. The time taken for this shift is uncertain and the shift could be due to incorrect levels of land-use disturbance (fire and overgrazing) and/or climate change.

The resilience of the Elandsberg PNR system to climate change and disturbance may depend on landscape heterogeneity or patchiness. The current vegetation that is in close proximity (Figure 11) to Vangkraal Spring wetland comprises a patch-mosaic landscape of vegetation units. These include Alluvium Fynbos dominated by Proteaceae, a Renosterveld-Fynbos Ecotone and Grassland dominated by Poaceae (*Themeda* spp), a Shale Renosterveld and

Grassland-Renosterveld matrix dominated by *Elytropappus rhinocerotis*, an Olive stand dominated by *Olea europea africana* and Thicket dominated by *Olea europea africana* and *Rhus* (*Searsia*) spp (Table 6). The dynamism that is evident at local scales does not preclude metastability since a patch dynamic landscape can remain stable at large scales. Spatial patchiness promotes community stability for species at the landscape level so that if a local patch is unstable, recolonization by dispersal between other patches ensures that the metapopulation remains stable (Ingegnoli 1991; Berryman 2003). Patches of different post-fire ages and fire frequency may harbour different vegetation assemblages, promoting biodiversity. Individual patches might be highly variable, experiencing burning then post-fire succession.

Hierarchical Patch Dynamics considers vegetation change within and between patches, as well as at wider landscape scales, thereby creating the link between heterogeneity and scale (Wu and Loucks1995). Different patterns and processes exist at different scale. For example, rainfall gradients and underlying geology determine the distribution of West-Coast Renosterveld at a regional scale and regional processes such as climate change have an impact on its resilience. At smaller scales Renosterveld is controlled by other processes such as local disturbance which can influence the growth, mortality and decomposition of species both within and between patches at the landscape level. Within the context of the present study the mosaic-like vegetation patterns at the local to landscape scale are affected by fire and herbivory which contribute to the overall heterogeneity of the area. Intensification or loss of disturbance may lead to the homogenisation of vegetation and loss of the resilience conferred by a patch dynamic structure.

Despite the increase in Asteraceae *Stoebe/Elytropappus*-type pollen over time, it appears that no threshold has yet been crossed and there is still heterogeneity within the landscape. Local patches can be unstable but the resilience of the system is conserved through the patchiness that is evident today. For example, it could be proposed that the Shale Renosterveld vegetation unit identified in the vegetation survey (Figure 11 and 12) about 500 m away from the wetland is an unstable patch. It is made up of approximately 60% bare ground and 40% vegetation. Of the vegetation, 70% is *Elytropappus rhinocerotis* which was approximately 80 cm tall and was not burnt during the 2012 fire. The Shale Renosterveld unit is out of phase (e.g. different post-fire ages, encouraging different large herbivores with varying feeding preferences including grazers, browsers or mixed-feeders) with local patches suggesting that there is still stability in the metapopulation as species can persist in the landscape.

In summary, there is unprecedented change within the last ca. 69 years but the data suggest that no threshold has been crossed. Though the vegetation has changed in composition, it is not in an alternative stable state, but an altered compositional state dominated by an increasing frequency of patches with high cover of *Elytropappus rhinocerotis*, which promotes fire. This increase in *Elytropappus rhinocerotis* may be reversible by varying the season of burning and by herbivory. The vegetation has been resilient to past changes in climate and land-use and the dynamism of patches maintains the heterogeneity and thus resilience of the system. An intermediate disturbance needs to be applied in order to maintain resilience. This is evident through the patchiness created by having vegetation of different post-fire ages present in the landscape.

6.5. Conservation and management implications

6.5.1. Can the palaeoecological record inform restoration targets?

The palaeoecological data show unprecedented levels of *Elytropappus rhinocerotis* since ca. AD 1943, compared with the past ca.1300 years, a change associated with unusually high levels of burning and herbivory. Results obtained from the present study could provide insight into what West-Coast Renosterveld would have looked like in the past century had it not been transformed but rather conserved. This needs to be taken into consideration for future conservation planning.

The present study does not support early reports (Thom 1952, 1954; Cowling et al. 1986) that have suggested that pristine Renosterveld was comprised predominantly of grasses before European settlers occupied the land. However, there is evidence that pre-AD 1943 Renosterveld vegetation at Elandsberg PNR was a grassy-shrubland (Newton 2008; Curtis

2013). The dominant asteraceous component was an average of 19% for Asteraceae *Stoebe/Elytropappus*-type pollen and 39% for Asteraceae long-spine type-1 pollen (Figure 18). However the grass component (mean 8%) was not as high as one would expect before ca. AD 1943. The VANG core only comprises the last ca. 1300 years therefore there is no pre-pastoralist baseline to determine whether it was indeed the land-use by Khoikhoi pastoralists and their livestock that maintained the grassy component of Renosterveld.

Contrary to the hypothesis that Khoikhoi pastoralists maintained a grassy landscape by 1-4 year fire cycles and rest periods, Meadows and Baxter (2001) described the pre-colonial period as being abundant in micro-charcoal fragments coupled with a decline in Poaceae pollen from 1900 BP. These results were suggested to be the result of burning and overgrazing. In the present study, while the high micro-charcoal abundance is evident, there is no decline in Poaceae (Figure 18 and 19). This may not be detected in the VANG core record because it only covers a time period of the last ca. 1300 years. The present study supports the hypothesis that recent land-use change has caused an increase in the shrubby component (Levyns 1956; Newton 2008). However, this has only occurred in the last ca. 69 years at Elandsberg PNR as opposed to the last ca. 200 years. If a pre-1943 benchmark is deemed appropriate, then management will need to aim to reduce the abundance of *Elytropappus rhinocerotis*, which the pollen data indicate is anomalously high compared with any other time in the past ca. 1300 years.

6.5.2. Can the palaeoecological record inform management of disturbance (fire and herbivory)?

The resilience of the Elandsberg PNR and its biodiversity value is probably linked to patchiness. The landscape consists of a range of vegetation types with different post-fire ages. This heterogeneous structure provides a range of habitats for plant and animals species to exist. It also means that the amount of biomass available in the landscape is heterogeneous and fragmented which can act to reduce the likelihood of large-scale fire. Results of this study suggest that fire and grazing regimes over the last ca. 69 years have been inappropriate since this period has had anomalously high levels of disturbance associated with increasing *Elytropappus rhinocerotis*.

Intermediate and variable levels of fire and herbivory are required in order to maintain patchiness and prevent homogenisation of vegetation. There are feedbacks that need to be considered in managing fire and herbivory disturbance. The seasonality of burn and variability of fire interval is also important. For example, a spring fire coupled with herbivory promotes the increase in *Elytropappus rhinocerotis*, whereas an autumn fire coupled with herbivory promotes "Sweet Grassland" (Figure 4; Milton 2007). Regrettably, these aspects could not be distinguished in the palaeo-record and modern ecological experiments are required.

The pollen record shows that abundance of *Elytropappus rhinocerotis* is the highest it has been in the past ca. 1300 years and the modern vegetation survey showed some patches that were highly dominated by *Elytropappus rhinocerotis*, to the exclusion of other species. For these areas, the goal may be to decrease the abundance of *Elytropappus rhinocerotis* and in order to do so frequent fires (fire interval of 3 years or less) are necessary. Levyns (1926, 1929) found that the seeds of *Elytropappus rhinocerotis* are able to persist in the seed bank for 7 years and that they germinate in response to fire. Once they have germinated the plants take three years to mature, so in order to exhaust the seed bank fires should be repeated at three-year intervals (Cowling et al. 1986). However, these frequent fires also favour alien annual grasses which outcompete indigenous perennials. Although grazers will benefit from a compositional state with an increased grass component, this is not ideal for biodiversity conservation. However, if fires are excluded and overgrazing occurs then indigenous perennial grasses would be outcompeted by shrubs that are unpalatable to herbivores and the vegetation would become a species-poor shrubland. This compositional state is therefore undesirable for both grazers and biodiversity.

The management of fire and herbivory also depends on the management goals established for Elandsberg PNR. For example, if managers seek to conserve large indigenous herbivores they would need to use practices that promote the growth of grass for grazers and thicket for browsers. On the other hand, if the aim is to conserve the Geometric Tortoise then West-Coast Renosterveld vegetation diversity needs to be preserved.

The increase in abundance of *Elytropappus rhinocerotis* since ca. AD 1943 seems anomalously high but actually for management purposes this abundance needs to be evaluated at both the patch and landscape level. As well as deciding on overall restoration targets for *Elytropappus rhinocerotis* abundance, the patchiness and heterogeneity need to be considered. A range of patches with different *Elytropappus rhinocerotis* densities with variable fire intervals may be better for biodiversity. *Elytropappus rhinocerotis* is usually the "climax" species in post-fire succession and Walton (2006) identified that that these shrubs can often act as refugia for some geophytes, forbs, hemicryptophytes and dwarf shrubs as the *Elytropappus rhinocerotis* provide protection from over exposure and/or grazing and trampling. So instead of viewing *Elytropappus rhinocerotis* shrubs as "fire-weeds" or "undesirable plants for grazing" or "species-excluders", managers will need to survey patches dominated by *Elytropappus rhinocerotis* and different strategies will be needed in different areas of the reserve. Thus an intermediate level of disturbance is essential. Unfortunately recommendations on the exact fire frequency and herbivory required is not within the scope of the present study.

6.5.3. What can the palaeoecological record say about future resilience?

The present study has shown that recent vegetation changes of West-Coast Renosterveld at Elandsberg PNR are unprecedented and the ecosystem has changed considerably as a result of increased disturbance in the 20th century. Fortunately it seems that no critical threshold has been crossed and the resilience of the system is still intact though it is not clear how close the system is to a climatic or disturbance threshold.

Although the present study identifies that no regime shift has taken place over the last ca. 1300 years at Elandsberg PNR, conservation managers should still be on the alert since it is reported that while some regime shifts are gradual others can be both sudden and dramatic and generally come as a surprise (Walters and Meyers 2004). Previous studies conducted in rangeland livestock-production systems in semi-arid Australia (Walker 1981; Anderies et al. 2002; Fernandez et al. 2002) and Africa (Walker 1981) have noted vegetation shifts as a result of interactions between fire and grazing intensity thresholds. A shift from “desirable” grassy to “undesirable” wooded systems or bare soil was reported in these studies. This is an example of how a shift in societal systems (e.g. increased agricultural pressure, reintroduction of indigenous large herbivores, etc.) can drive a shift in ecosystem state which it is not restricted to farms only and could occur in wildlife reserves as well (Walker 1989; Dublin et al. 1990).

The change in vegetation at the local-landscape level shows an overall dominance of *Elytropappus rhinocerotis* which increased gradually since ca. AD 1943. In order to prevent a future shift to an undesirable alternative stable state which could be classified as “Degraded Renosterveld” largely consisting of *Elytropappus rhinocerotis*, managers are recommended to regulate structure and patchiness which will conserve and build the resilience of the remaining Swartland Shale Renosterveld. Given that fire and herbivory are historical drivers of Renosterveld dynamics and current conceptual models indicate certain compositional states are generally reversible via the correct levels of fire and herbivory, it seems appropriate for managers at Elandsberg PNR to attend to the unprecedented high abundance of *Elytropappus rhinocerotis*.

Another factor to consider is that fire is highly associated with climate (van Wilgen et al. 2010), and therefore anthropogenic-induced climate change also needs to be taken into account. Anthropogenic-induced climate change is marked by continuing increases in temperature and greenhouse gases such as CO_2 (which also affects rainfall and wind run; Hoffman et al. 2011b) which will in turn affect fire. Together with this, the growth in human population is also expected to influence the frequency in wildfire ignitions and thus affect biodiversity conservation. Therefore, managers are recommended to monitor fire frequency and areas that burn too frequently should be protected.

In summary, it is possible to inform restoration targets for West-Coast Renosterveld at Elandsberg PNR since the study has provided a pre- AD 1943 baseline, and better still, a pre-colonial baseline of what the vegetation should look like in its more “pristine” state. The palaeo-record can inform the management of fire an herbivory to an extent. It cannot inform on fire frequency or intensity but it is able to detect that post- AD 1943 has been the highest occurrence of local fires and herbivory. An ecological threshold has not been crossed and previous resilience has not been compromised yet managers need to prevent a regime shift to "Degraded Renosterveld" characteristic of a homogenous, species-poor landscape dominated by *Elytropappus rhinocerotis*, alien plants and bare ground. Resilience should be maintained via intermediate disturbance (varying post-fire ages) that promotes patchiness and adaptive management should involve monitoring at the patch or landscape level of the reserve.

6.6. Future Research

In the present study there was no proxy for climate (such as stable isotopes). An independent climate proxy and/or modelling with historic climate data would aid in the interpretation of climatic influence and interaction with disturbance. Ideally, additional high resolution palaeoecological studies need to be carried out in the West-Coast Renosterveld region in order to verify patterns that have emerged from the present study.

Taxonomic resolution to species level is a priority for future research for a number of reasons. Firstly, in order for palaeoecological studies to make meaningful contributions to conservation on the topic of future resilience of a system, especially within the species-rich CFR, pollen needs to be identified to species level as widely as possible together with monitoring the effects of changing climate on species composition. Secondly, with confirmation through the modern vegetation survey, the present study assumed that Asteraceae *Stoebe/Elytropappus*-type pollen was *Elytropappus rhinocerotis*. Had the system been equally dominated by *Elytropappus rhinocerotis* and *Stoebe* spp it would have made past vegetation reconstruction more complicated. Thus, further resolution to distinguish between *Elytropappus rhinocerotis* and *Stoebe* spp would be beneficial for future studies within Renosterveld. Likewise, *Elytropappus rhinocerotis* was used as the key indicator for Renosterveld vegetation whereas other prominent shrub species such as *Relhania fruticosa* and *Athanasia trifurcata* are also characteristic of Renosterveld (Rebelo 1996). Taxonomic resolution of the Asteraceae family will benefit in interpreting past vegetation change. Pollen types can also be used as climatic and/or disturbance indicators; however, there are some taxa such as Chenopodiaceae/Amaranthaceae which are indicative of both warm, dry conditions (Coetzee 1967; Neumann et al. 2011) and are common as weeds in disturbed environments

(Palgrave 2002). Therefore, there is a need for further modern ecological studies to distinguish between climatic and disturbance indicators that would aid in better interpretation of the palaeo-record.

Furthermore, since there is a greater percentage of natural and intact South-Coast Renosterveld vegetation (von Hase et al. (2003) reported that 12% remains) it would be beneficial to conduct a high resolution palaeoecological study looking at similar proxies (fossil pollen, charcoal, coprophilous spores and phytoliths) in order to create a baseline for South-Coast Renosterveld. This would allow for the comparison between drivers (i.e. climate, fire and herbivory) of vegetation change for West-Coast and South-Coast Renosterveld. Approaching the Overberg Lowlands Conservation Trust (http://www.overbergrenosterveld.org.za/) for future collaborations would be beneficial to this cause since some experimental research (e.g. soil carbon isotopes; Curtis 2013) has already been conducted by the team.

Considering that the present study has provided a pre-colonial baseline of the vegetation compositional state at Elandsberg PNR, the reserve managers could work towards reversing the current state of vegetation, which currently has an unusually high abundance of *Elytropappus rhinocerotis*, associated with increased burning and herbivory in the 20th century. It is currently not clear what frequency and seasonality of burns is appropriate, and what level of herbivory, therefore management experiments are needed that test the effects of different burn and grazing regimes, and respond adaptively to the results.

In order to test the conceptual models of Renosterveld dynamics and the combination of drivers that might cause shifts between alternate stable states, further research which involves setting up of experimental plots with varying degrees of fire and herbivory could be conducted at Elandsberg PNR. This would be beneficial to test the hypotheses before implementing a management regime for the whole reserve and in developing models that can predict future change under different climate, fire and herbivory scenarios. Vegetation communities can often be resilient within limits and therefore no ecological change may happen until a threshold is crossed and this change is often associated with a particular combination of drivers.

7. GENERAL CONCLUSIONS

West Coast Renosterveld is part of the Fynbos biome which is found within the CFR, a globally important and highly threatened biodiversity hotspot (Myers 1990; Low and Rebelo1996; Mittermeier et al. 1998; Goldblatt and Manning 2000; Myers et al. 2000). The Elandsberg PNR is one of the few remaining fragments of West-Coast Renosterveld (Rebelo 1995; Midoko-Iponga et al. 2005), and it supports the threatened and endemic Geometric Tortoise and a number of large indigenous herbivores that have been reintroduced into the area.

This setting is a picturesque view of apparently untransformed West-Coast Renosterveld, though without long-term data it is impossible to know how the landscape has been affected by climate change, fire and herbivory. The sedimentary sequence retrieved from Vangkraal Spring wetland (VANG core), covers the past ca. 1300 years and provides an unprecedented insight into vegetation change during the MCA, LIA and 20th century warming, and the effects of Khoi-San hunter/herders, European settler agriculture and agricultural intensification as well as the transition to a nature reserve. The VANG core provides a better understanding of the interactions between climate change and land-use and consequently its impact on the vegetation.

The pollen data show two statistically significant zones of vegetation assemblages. The first zone called the Hunter-Herder/Settler Agriculture Zone (ca. AD 750-1943) captured the time when the region was occupied by the Khoi-San hunter/herders and the European settlers. It was dominated by Asteraceae long-spine type-1 pollen and other abundant taxa which changed slightly but were relatively stable over this period. The Hunter-Herder/Settler Agriculture Zone was also characterized by relatively low herbivory pressure and low local fire frequency, although regional fires were frequent, intense and highly variable. The second zone called the Agricultural Intensification/Conservation Zone (ca. AD 1943-2012) reflects a period when the region experienced agricultural intensification followed by a transition to nature reserve status. During this period, there was a marked increase in Asteraceae *Stoebe/Elytropappus*-type pollen (*Elytropappus rhinocerotis*) while other abundant taxa remained relatively stable. The Agricultural/Conservation Zone was characterized by relatively high levels of herbivory and high local fire frequency. These pressures continued into the conservation period from AD 1973 to the present.

The pollen, coprophilous spore and macro-charcoal data show that the period after ca. AD 1943 had an unusually high level of the typical Renosterveld shrub, *Elytropappus rhinocerotis*, and was associated with relatively high levels of herbivory and local fire frequency. The changes in vegetation do not seem to coincide with periods of known climate change (i.e. warming since AD 1901 (Haensler et al. 2010)). It therefore seems likely that the above changes in vegetation were probably driven by land-use disturbance such as fire and herbivory. However, the results do not rule out an interaction with climate change.

The VANG core covers three known periods of climate change. These are the warm and arid MCA (ca. AD 900-1400), the cold and wet LIA (ca. AD 1400-1800) and the warm 20th century. Evidence from the pollen record suggests that during the variable climate regimes which characterised the MCA and LIA, the vegetation remained relatively stable, suggesting resilience to these known climatic anomalies. Similarly, vegetation does not appear to have responded to known warming at the start of the 20th century, though further increases in temperatures as a result of more recent climate change may have contributed to the significant change in vegetation since ca. AD 1943. The results suggest that over the past ca. 1300 years, climate change has not been the main driver of vegetation change at Elandsberg PNR.

Before ca. AD 1943, the data suggest less frequent regional fires, lower herbivory and less dominance of *Elytropappus rhinocerotis*. The vegetation remained resilient to land-use during the period when Khoi-San hunter/herders are known to have been in the Cape region and to have used fire to stimulate pasture for livestock grazing. At the Elandsberg PNR site, however, there is little evidence before ca. AD 1943 of herbivory (i.e. no or low amounts of coprophilous spores) and local fires, and there is no decrease in Poaceae. One explanation for the pollen record not showing any significant changes could be that the Khoi-San hunter/herders were using other areas in the region more frequently than the land at Elandsberg PNR. This is evidenced by the high abundance of micro-charcoal in the record which is indicative of regional burning.

European settlers arrived in Cape Town during the mid-17th century and by AD 1800 they had claimed the entire region south of the Orange River (Bergh and Visagie 1985; Hoffman 1997). At Elandsberg PNR changes in land-use after colonial settlement include permanent settlement by a Dutch settler who farmed with cattle, sheep and ostrich, together with the land being used as a horse remount for the British Army around the time of the Second Anglo-Boer War (AD 1899-1902). Even though herbivory was increasing, the vegetation remained stable and the impact from domestic animals was probably less than it was relative to other areas further west and closer to Cape Town (e.g. Princess Vlei, Neumann et al. 2011). The influence of agriculture was relatively subtle at Elandsberg PNR until ca. AD 1943.

Evidence from macro-charcoal and coprophilous spores suggests that changes in land-use since ca. AD 1943 has been the main driver for vegetation change at Elandsberg PNR. Specifically, increased local fires and increased herbivory are associated with agricultural intensification and therefore the increased abundance of *Elytropappus rhinocerotis*. The macro-charcoal and coprophilous spore data suggest that local fires and herbivory increased significantly after ca. AD 1943. This trend continued after the reserve was declared in AD 1973 and large indigenous herbivores were reintroduced.

Recent changes in vegetation in the second half of the 20th century are unprecedented in the ca. 1300 year history of the VANG core. Owing to high land-use disturbance there has been a reshuffling in vegetation dominance which resulted in a Shrubland-type compositional state of Renosterveld, dominated by the unpalatable *Elytropappus rhinocerotis*. However, there is no evidence of a shift to an alternate, degraded, stable state across the whole landscape. This suggests that decreased herbivory and fire may result in the restoration of the vegetation to its pre-AD 1943 compositional state. If current anthropogenic-induced climate change continues there is a possibility that a threshold may be reached in the future since past resilience to changes in climate does not prevent instability under future climate change scenarios. Alternatively there is a possibility of a shift to “Degraded Renosterveld” at the landscape scale if fire is high (or in the incorrect season) and overgrazing occurs immediately after a fire.

In order to inform restoration targets, the palaeo-record has revealed a pre-colonial benchmark which shows an intermediate level of fire and herbivory disturbance maintaining vegetation resilience and an intermediate abundance of *Elytropappus rhinocerotis*. Recommendations concerning the appropriate fire frequencies and herbivory levels necessary for conservation management are not within the scope of the present study. However, the data suggest that levels of burning and herbivory after ca. AD 1943 are greater than those experienced earlier in the historical record and are outside of the previous range of variability. Reduced burning and grazing is recommended, as well as the maintenance of patches of varying post-fire ages and thus varying densities of *Elytropappus rhinocerotis*. Such a heterogeneous patch-mosaic is likely to benefit biodiversity and conserve future resilience. An adaptive approach that incorporates grazing and burning experimental observations and long–term monitoring, as well as a flexible management approach is recommended. An adaptive management approach would aim to adjust fire and herbivory in response to changing vegetation and climate with the aim of preventing an ecological threshold from being crossed with vegetation shifting to an alternative stable state classified as “Degraded Renosterveld”. Management is encouraged to monitor the abundance of *Elytropappus rhinocerotis* and overall biodiversity at the patch and landscape level to ensure Renosterveld biodiversity.

The role of applied palaeoecological research that focuses on a high temporal resolution is important for interdisciplinary studies in ecology as it makes the “past-present-future” link. This is especially important because the present study has shed light on past Renosterveld vegetation dynamics and its interaction with climate, fire and herbivory, which was previously poorly understood due to limited historical records. Palaeoecological results have traditionally had little impact on ecological thinking, although the importance of palaeoecological research for conservation and management has been much discussed in the literature (Gillson and Willis 2004; Willis and Birks 2006; Dearing 2008; Gill-Romera et al. 2010; Birks 2012). The current study demonstrates that bringing together aspects of neoecology and palaeoecology can provide a better understanding of ecosystem patterns and processes, which helps to inform restoration and management. Furthermore, there is uncertainty in the impact that future climate change will have on biodiversity but palaeoecological research can assist in forming the basis for future bioclimatic modelling predictions. Thus the present study can provide great insight for current conservation and restoration management as well as future conservation of the remaining fragments of West-Coast Renosterveld.

Future research is necessary to improve palaeo-datasets such as the use of independent climate proxies and higher pollen taxonomic resolution. These will improve the identification of species changes in response to climate and land-use and therefore provide a more accurate indication of resilience over time. Multiple high resolution study sites are needed within West-Coast Renosterveld to verify baseline conditions. Investigation into baselines of South-Coast Renosterveld will further assist in comparisons between the regions. Linking palaeoecology to neoecology, such as setting up experimental plots with varying degrees of fire and herbivory, will aid in testing conceptual models, verify the palaeo-record and assist current conservation management and restoration interventions.

REFERENCES

Acocks, J. P. H. (1953). Veld types of South Africa (No. 57, Ed. 3).

Adamson, R. S. (1938). The vegetation of South Africa. *The vegetation of South Africa*.

Alley, T. R. (1982). Competition theory, evolution, and the concept of an ecological niche. *Acta Biotheoretica*, 31(3), 165-179.

Anderies, J. M., Janssen, M. A., & Walker, B. H. (2002). Grazing management, resilience, and the dynamics of a fire-driven rangeland system. *Ecosystems*,5(1), 23-44.

Andersen, T., Carstensen, J., Hernandez-Garcia, E., & Duarte, C. M. (2009). Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology & Evolution*, 24(1), 49-57.

Anonymous, (1977) Nature Conservation in the Cape, Cape Town, Department of Nature and Environmental Conservation.

Anonymous, (1997): 3319 Worcester: 1:250.000 Geological Series, Council for Geoscience, Pretoria.

Appleby, P. G., Oldfield, F., Thompson, R., Huttunen, P., & Tolonen, K. (1979). 210Pb dating of annually laminated lake sediments from Finland.

Appleby, P. G. (2001). Chronostratigraphic techniques in recent sediments. In *Tracking environmental change using lake sediments* (pp. 171-203). Springer Netherlands.

Baard, E. H. (1993). Distribution and status of the geometric tortoise< i> Psammobates geometricus</i> in South Africa. *Biological conservation*, 63(3), 235-239.

Bard, E., Raisbeck, G. M., Yiou, F., & Jouzel, J. (1997). Solar modulation of cosmogenic nuclide production over the last millennium: comparison between< sup> 14</sup> C and< sup> 10</sup> Be records. *Earth and Planetary Science Letters*, 150(3), 453-462.

Baxter, A. J., & Meadows, M. E. (1999). Evidence for Holocene sea level change at verlorenvlei, western cape, South Africa. *Quaternary International*,56(1), 65-79.

Becker, C.F. (1996). Experimental training: Elandsberg Private Nature Reserve. National Diploma: Nature Conservation. Cape Technikon.

Behar, D. M., Villems, R., Soodyall, H., Blue-Smith, J., Pereira, L., Metspalu, E., ... & Rosset, S. (2008). The dawn of human matrilineal diversity. *The American Journal of Human Genetics*, 82(5), 1130-1140.

Bengtsson, L., & Enell, M. (1986). Chemical analysis. *Handbook of Holocene palaeoecology and palaeohydrology*, 423-451.

Bennett, K. D. (1994). Confidence intervals for age estimates and deposition times in late-Quaternary sediment sequences. *The Holocene*, 4(4), 337-348.

Bennett, K. D. (1996). Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, 132(1), 155-170.

Bennett, K. D., & Willis, K. J. (2001). Pollen. In Tracking environmental change using lake sediments (pp. 5-32). Springer Netherlands.

Bennion, H., & Appleby, P. (1999). An assessment of recent environmental change in Llangorse Lake using palaeolimnology. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 9(4), 361-375.

Bergh, J. S., & Visagie, J. C. (1985). The Eastern Cape Frontier Zone, 1660-1980: 1660-1980; a Cartographic Guide for Histor. Research. Butterworth.

Berryman, A. A. (2003). On principles, laws and theory in population ecology. Oikos, 103(3), 695-701.

Birks, H. J. B. (2012). Ecological palaeoecology and conservation biology: controversies, challenges, and compromises. *International Journal of Biodiversity science, Ecosystem services & Management*, 8(4), 292-304.

Blaauw, M., van Geel, B., Kristen, I., Plessen, B., Lyaruu, A., Engstrom, D. R., ... & Verschuren, D. (2011). High-resolution< sup> 14</sup> C dating of a 25,000-year lake-sediment record from equatorial East Africa. *Quaternary Science Reviews*, *30*(21), 3043-3059.

Boko, M., Niang, I., Nyong, A., Vogel, C., Githeko, A., Medany, M., ... & Yanda, P. (2007). *Africa*.

Bond, W. J. (2010). Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis. *Plant and soil*, 334(1-2), 47-60.

Bond, W. J., & Parr, C. L. (2010). Beyond the forest edge: Ecology, diversity and conservation of the grassy biomes. *Biological Conservation*, 143(10), 2395-2404.

Bond, W. J., & Van Wilgen, B. W. (1996). Fire and Plants (Population and Community Biology Series 14). *Population and Community Biology*, 263.

Bonnefille, R., & Riollet, G. (1980). Pollens des savanes d'Afrique orientale. CNRS.

Booi, N. (2011). Structure and function of heuweltjies across a rainfall gradient in the South-Western Cape (Doctoral dissertation, Stellenbosch: University of Stellenbosch).

Boonzaier, E. (Ed.). (1996). The Cape herders: a history of the Khoikhoi of southern Africa. New Africa Books.

Botha, C. G. (1924). Note on early veld burning in the Cape Colony. *South African Journal of Science*, 21, 351-352.

Boucher, C. (1980). Notes on the use of the term" Renosterveld. Bothalia, 13, 237.

Boucher, C., & Moll, E. J. (1981). South African mediterranean shrublands. *Ecosystems of the world*.

Boycott, R. C., & Bourquin, O. (1988). The South African tortoise book: a guide to South African tortoises, terrapins and turtles (p. 148). Johannesburg: Southern Book Publishers.

Brooks, M. L., D'antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTOMASO, J. M., ... & Pyke, D. (2004). Effects of invasive alien plants on fire regimes. *BioScience*, 54(7), 677-688.

Buck, C. E., Christen, J. A., & James, G. N. (1999). BCal: an on-line Bayesian radiocarbon calibration tool. *Internet archaeology*, 7.

Bulpin, T. V., & Rennie, H. (1983). *Discovering Southern Africa*. Books of Africa.

Burchell, W. J. (1822). *Travels in the interior of southern Africa (Vol. 1)*. Longman, Hurst, Rees, Orme, and Brown, Paternoster-Row.

Burney, D. A., Robinson, G. S., & Burney, L. P. (2003). Sporormiella and the late Holocene extinctions in Madagascar. *Proceedings of the National Academy of Sciences*, 100(19), 10800-10805.

Change, C. (2007). Synthesis Report: Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change Core Writing Team.

Chase, B. M., & Meadows, M. E. (2007). Late Quaternary dynamics of southern Africa's winter rainfall zone. *Earth-Science Reviews*, 84(3), 103-138.

Chase, B. M., Quick, L. J., Meadows, M. E., Scott, L., Thomas, D. S., & Reimer, P. J. (2011). Late glacial interhemispheric climate dynamics revealed in South African hyrax middens. *Geology*, 39(1), 19-22.

Chase, B. M., & Thomas, D. S. (2007). Multiphase late Quaternary aeolian sediment accumulation in western South Africa: timing and relationship to palaeoclimatic changes inferred from the marine record. *Quaternary International*, 166(1), 29-41.

Cincotta, R. P., Wisnewski, J., & Engelman, R. (2000). Human population in the biodiversity hotspots. *Nature*, 404(6781), 990-992.

Clark, R. L. (1982). Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et spores*, 1982.

Clarke, K. R., & Warwick, R. M. (1994). Change in marine communities: an approach to statistical analysis and interpretation.

Clements, F. E. (1916). *Plant succession: an analysis of the development of vegetation* (No. 242). Carnegie Institution of Washington.

Colles, A., Liow, L. H., & Prinzing, A. (2009). Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters*, 12(8), 849-863.

Connell, J. H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. *Ecology and evolution of communities*, 460, 490.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American naturalist*, 1119-1144.

Cooke, C. K. (1965). Evidence of human migrations from the rock art of southern Rhodesia. *Africa*, 35(03), 263-285.

Cornett, R. J., Chant, L. A., Risto, B. A., & Bonvin, E. (1994). Identifying resuspended particles using isotope ratios. *Hydrobiologia*, 284(1), 69-77.

Cowling, R. M., Cartwright, C. R., Parkington, J. E., & Allsopp, J. C. (1999a). Fossil wood charcoal assemblages from Elands Bay Cave, South Africa: implications for Late Quaternary vegetation and climates in the winter-rainfall fynbos biome. *Journal of Biogeography*, 26(2), 367-378.

Cowling, R. M., & Heijnis, C. E. (2001). The identification of Broad Habitat Units as biodiversity entities for systematic conservation planning in the Cape Floristic Region. *South African Journal of Botany*, 67(1), 15-38.

Cowling, R. M., & Holmes, P. M. (1992). Endemism and speciation in a lowland flora from the Cape Floristic Region. *Biological Journal of the Linnean Society*,47(4), 367-383.

Cowling, R. M., Pierce, S. M., & Moll, E. J. (1986). Conservation and utilisation of South Coast Renosterveld, an endangered South African vegetation type. *Biological Conservation*, 37(4), 363-377.

Cowling, R. M., Pierce, S. M., & Paterson-Jones, C. (1999b). *Namaqualand: a succulent desert*. Fernwood Press.

Cowling, R. M., Pressey, R. L., Lombard, A. T., Heijnis, C. E., Richardson, D. M., & Cole, N. (1999c). Framework for a conservation plan for the Cape Floristic Region. IPC Report, 9902.

Cowling, R. M., & Pressey, R. L. (2003). Introduction to systematic conservation planning in the Cape Floristic Region. *Biological Conservation*,112(1), 1-13.

Cowling, R. M., Procheş, Ş., & Partridge, T. C. (2009). Explaining the uniqueness of the Cape flora: incorporating geomorphic evolution as a factor for explaining its diversification. *Molecular Phylogenetics and Evolution*, 51(1), 64-74.

Cowling, R. M., Richardson, D. M., & Mustart, P. J. (1997). Fynbos. *Vegetation of Southern Africa*.

Cronin, T. M., Dwyer, G. S., Kamiya, T., Schwede, S., & Willard, D. A. (2003). Medieval warm period, little ice age and 20th century temperature variability from Chesapeake Bay. *Global and Planetary Change*, 36(1), 17-29.

Cronje, D. (1998). Bewaringsplan vir Elandsberg Natuurreservaat. Department Natuurbewariging.Universiteit van Stellenbosch.

Crowley, T. J. (2000). Causes of climate change over the past 1000 years.*Science*, 289(5477), 270-277.

Cupido, C. F. (2005). Assessment of veld utilisation practices and veld condition in the Little Karoo (Doctoral dissertation, Stellenbosch: University of Stellenbosch).

Curtis, O. E. (2013). Management of Critically Endangered renosterveld fragments in the Overberg, South Africa.

Davis, O. K., & Shafer, D. S. (2006). < i> Sporormiella</i> fungal spores, a palynological means of detecting herbivore density. Palaeogeography, Palaeoclimatology, *Palaeoecology*, 237(1), 40-50.

Deacon, H. J. (1992). Southern Africa and modern human origins. Philosophical Transactions of the Royal Society of London. Series B: *Biological Sciences*,337(1280), 177-183.

Deacon, H. J., Deacon, J., Brooker, M., & Wilson, M. L. (1978). The evidence for herding at Boomplaas Cave in the southern Cape, South Africa. *The South African Archaeological Bulletin*, 39-65.

Deacon, H. J., Jury, M. R., & Ellis, F. (1992). Selective regime and time. *The ecology of Fynbos: nutrients, fire and diversity*, 6-22.

Deacon, J., & Lancaster, N. (1988). Late Quaternary palaeoenvironments of southern Africa. Clarendon press.

Deacon, J., Lancaster, N., & Scott, L. (1984). *Evidence for Late Quaternary climatic change in southern Africa*. Vogel JC (Ed.), 391-404.

Dean Jr, W. E. (1974). Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sedimentary Research*, 44(1).

Dearing, J. A. (2008). Landscape change and resilience theory: a palaeoenvironmental assessment from Yunnan, SW China. *The Holocene*,18(1), 117-127.

Donaldson, J., Nänni, I., Zachariades, C., & Kemper, J. (2002). Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. *Conservation Biology*, 16(5), 1267-1276.

Drake, J. A. (1990). The mechanics of community assembly and succession. *Journal of Theoretical Biology*, 147(2), 213-233.

Driver, A., Desmet, P. G., Rouget, M., Cowling, R. M., & Maze, K. (2003). Succulent Karoo Ecosystem Plan: biodiversity component technical report. Cape Conservation Unit Report No. CCU, 1(03).

Dublin, H. T., Sinclair, A. R. E., & McGlade, J. (1990). Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology*, 59(3), 1147-1164.

Duffin, K. I., Gillson, L., & Willis, K. J. (2008). Testing the sensitivity of charcoal as an indicator of fire events in savanna environments: quantitative predictions of fire proximity, area and intensity. *The Holocene*, 18(2), 279-291.

Dupont, L. M., Linder, H. P., Rommerskirchen, F., & Schefuß, E. (2011). Climate-driven rampant speciation of the Cape flora. *Journal of Biogeography*,38(6), 1059-1068.

Eakins, J. A., & Morrison, R. T. (1978). A new procedure for the determination of lead-210 in lake and marine sediments. *The International Journal of Applied Radiation and Isotopes*, 29(9), 531-536.

Ekblom, A., Gillson, L., & Notelid, M. (2011). A Historical Ecology of the Limpopo and Kruger National Parks and Lower Limpopo Valley. *Journal Archaeol Ancient History*, *1*, 1-29.

Ekblom, A., Gillson, L., Risberg, J., Holmgren, K., & Chidoub, Z. (2012). Rainfall variability and vegetation dynamics of the lower Limpopo Valley, Southern Africa, 500AD to present. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *363*, 69-78.

Elphick, R. (1977). Kraal and castle: Khoikhoi and the founding of white South Africa (pp. 141-148). New Haven: Yale University Press.

Elphick, R., & Giliomee, H. B. (Eds.). (1989). *The Shaping of South African Society*: 1652-1840. Maskew Miller Longman.

Erdtman, G. (1960). *The acetolysis method. A revised description*. Svensk Bot. Tidsk, 54, 561-4.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... & Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*,333(6040), 301-306.

Fagerlind, F. (1952). *The real signification of pollen diagrams*. Botaniska Notiser, 105, 185-224.

Fairbanks, D. H. K., Thompson, M. W., Vink, D. E., Newby, T. S., Van den Berg, H. M., & Everard, D. D. 2. (2000). The South African land-cover characteristics database: a synopsis of the landscape. *South African Journal of Science*, 96(2).

Fernandez, R. J., Archer, E. R. M., Ash, A. J., Dowlatabadi, H., Hiernaux, P. H. Y., Reynolds, J. F., ... & Wiegand, T. (2002). Degradation and recovery in socio-ecological systems: a view from the household/farm level. *Global desertification: do humans cause deserts*, 297-323.

Finsinger, W., & Tinner, W. (2005). Minimum count sums for charcoal concentration estimates in pollen slides: accuracy and potential errors. *The Holocene*, 15(2), 293-297.

Fish, K.B. (1988). Comparative vegetation study of a ploughed and an unploughed site in a disturbed Renosterveld community. Unpublished 3rd year project: Botany Department, University of Cape Town.

Forster, P. (2004). Ice Ages and the mitochondrial DNA chronology of human dispersals: a review. Philosophical Transactions of the Royal Society of London. Series B: *Biological Sciences*, 359(1442), 255-264.

Forsyth, G.G., Van Wilgen, B.W., Ruddock, G., Nel, J.L., Le Maitre, D.C., Smith, C., Cullinan, C., & Chapman, R.A. (2000). A fire management plan for the Cape Peninsula National Park. Report no. ENV-S-C 2000-111, CSIR, Stellenbosch.

Fowler, R. (1999). Conservation tillage research and development in South Africa. *Conservation tillage with animal traction*. ATNESA, Harare, 51-60.

Fretwell, S. D. (1972). *Populations in a seasonal environment* (No. 5). Princeton University Press.

Froyd, C. A., & Willis, K. J. (2008). Emerging issues in biodiversity & conservation management: the need for a palaeoecological perspective. *Quaternary Science Reviews*, 27(17), 1723-1732.

Gelorini, V., Ssemmanda, I., & Verschuren, D. (2012). Validation of non-pollen palynomorphs as paleoenvironmental indicators in tropical Africa: contrasting~ 200-year paleolimnological records of climate change and human impact. *Review of Palaeobotany and Palynology*, 186, 90-101.

Gelorini, V., Verbeken, A., van Geel, B., Cocquyt, C., & Verschuren, D. (2011). Modern non-pollen palynomorphs from East African lake sediments. *Review of Palaeobotany and Palynology*, 164(3), 143-173.

Gill, J. L., Williams, J. W., Jackson, S. T., Lininger, K. B., & Robinson, G. S. (2009). Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science*, 326(5956), 1100-1103

Gillson, L. (2002). *Vegetation change in East African elephant habitat* (Doctoral dissertation, University of Oxford).

Gillson, L., & Ekblom, A. (2009). Untangling anthropogenic and climatic influence on riverine forest in the Kruger National Park, South Africa. *Vegetation History and Archaeobotany*, 18(2), 171-185.

Gillson, L., & Hoffman, M. T. (2007). ECOLOGY: Rangeland Ecology in a Changing World. *Science*, 1136577(53), 315.

Gillson, L., & Willis, K. J. (2004). 'As Earth's testimonies tell': wilderness conservation in a changing world. *Ecology Letters*, 7(10), 990-998.

Gil-Romera, G., López-Merino, L., Carrión, J. S., González-Sampériz, P., Martín-Puertas, C., López Sáez, J. A., ... & Stefanova, V. (2010). Interpreting Resilience through Long-Term Ecology: Potential Insights in Western Mediterranean Landscapes. *Open Ecology Journal.*

Gil-Romera, G., Scott, L., Marais, E., & Brook, G. A. (2006). Middle-to late-Holocene moisture changes in the desert of northwest Namibia derived from fossil hyrax dung pollen. *The Holocene*, 16(8), 1073-1084.

Goldblatt, P., & Manning, J. (2000). Cape plants: a conspectus of the Cape flora of South Africa. National Botanical Institute.

Goldblatt, P., & Manning, J. C. (2002). Plant diversity of the Cape region of southern Africa. *Annals of the Missouri Botanical Garden*, 281-302.

Graf, M. T., & Chmura, G. L. (2006). Development of modern analogues for natural, mowed and grazed grasslands using pollen assemblages and coprophilous fungi. *Review of Palaeobotany and Palynology*, 141(1), 139-149.

Greig-Smith, P. (1979). Pattern in vegetation. *The Journal of Ecology*, 755-779.

Grove, J. M. (2004). *Little ice ages: ancient and modern* (Vol. 1). Taylor & Francis.

Gugerli, F., Parducci, L., & Petit, R. J. (2005). Ancient plant DNA: review and prospects. *New Phytologist*, 166(2), 409-418.

Haensler, A., Hagemann, S. and Jacob, D. (2010). Climate history of Namibia and western South Africa. In: *Biodiversity in southern Africa. Volume 2: Patterns and processes at regional scale* [Schmiedel, U., Jürgens, N. (eds.)]. Klaus Hess Publishers, Göttingen and Windhoek.

Haensler, A., Hagemann, S., & Jacob, D. (2011). The role of the simulation setup in a long-term high-resolution climate change projection for the southern African region. *Theoretical and applied climatology*, 106(1-2), 153-169.

Halpern, A. B. W., & Meadows, M. E. (2013). Fifty years of land use change in the Swartland, Western Cape, South Africa: characteristics, causes and consequences. *South African Geographical Journal*, 95(1), 38-49.

Hannah, L., Midgley, G. F., Lovejoy, T., Bond, W. J., Bush, M. L. J. C., Lovett, J. C., ... & Woodward, F. I. (2002a). Conservation of biodiversity in a changing climate. *Conservation Biology*, 16(1), 264-268.

Hannah, L., Midgley, G. F., & Millar, D. (2002b). Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, 11(6), 485-495.

Hannah, L., Millar, D., Thuiller, W., & Booth, A. (2003). Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation*, 112(1), 87-97.

Hanski, I. (1991). Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, 42(1-2), 17-38.

Hays, J. D., Imbrie, J., & Shackleton, N. J. (1976, December). Variations in the Earth's orbit: Pacemaker of the ice ages. American Association for the Advancement of Science.

Heijnis, C. E., Lombard, A. T., Cowling, R. M., & Desmet, P. G. (1999). Picking up the pieces: a biosphere reserve framework for a fragmented landscape–The Coastal Lowlands of the Western Cape, South Africa. *Biodiversity & Conservation*, 8(4), 471-496.

Heiri, O., Lotter, A. F., & Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of paleolimnology*, 25(1), 101-110.

Henshilwood, C. (1996). A revised chronology for pastoralism in southernmost Africa: new evidence of sheep at c. 2000 bp from Blombos Cave, South Africa.*Antiquity*, 70(270), 945-949.

Higgins, S. I., Azorin, E. J., Cowling, R. M., & Morris, M. J. (1997). A dynamic ecological-economic model as a tool for conflict resolution in an invasive-alien-plant, biological control and native-plant scenario. *Ecological Economics*, 22(2), 141-154.

Hilton-Taylor, C. (1996). *Red data list of Southern African plants*. National Botanical Institute.

Hirzel, A. H., & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, 45(5), 1372-1381.

Hoffman, M. T. (1997). Human impacts on vegetation. *Vegetation of southern Africa*, 507-534.

Hoffmann, J. H., Moran, V. C., & Van Wilgen, B. W. (2011a). Prospects for the biological control of invasive Pinus species (Pinaceae) in South Africa. *African Entomology: Biological control of invasive alien plants in South Africa* (1999-2010): Special Issue 2, 19, 393-401.

Hoffman, T., & Ashwell, A. (2001). Nature divided: land degradation in South Africa. University of Cape Town Press.

Hoffman, M. T., Cramer, M. D., Gillson, L., & Wallace, M. (2011b). Pan evaporation and wind run decline in the Cape Floristic Region of South Africa (1974–2005): implications for vegetation responses to climate change. *Climatic Change*, 109(3-4), 437-452.

Hogg, A. G., Hua, Q., Blackwell, P. G., Niu, M., Buck, C. E., Guilderson, T. P., ... & Zimmerman, S. R. (2013). SHCAL13 SOUTHERN HEMISPHERE CALIBRATION, 0-50,000 YEARS CAL BP. *Radiocarbon*, 55(4).

Illius, A. W., & O'connor, T. G. (1999). On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, 9(3), 798-813.

Ingegnoli, V. (1991). Human influences in landscape change: thresholds of metastability. *Terrestrial and aquatic ecosystems: perturbation and recovery*, 303-309.

Jacobs, Z., Roberts, R. G., Galbraith, R. F., Deacon, H. J., Grün, R., Mackay, A., ... & Wadley, L. (2008). Ages for the Middle Stone Age of southern Africa: implications for human behavior and dispersal. *Science*, 322(5902), 733-735.

Jamieson, M. A., Trowbridge, A. M., Raffa, K. F., & Lindroth, R. L. (2012). Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant physiology*, 160(4), 1719-1727.

Jarman, M. L. (1986). Conservation priorities in lowland regions of the fynbos biome. Foundation for Research Development: CSIR.

Jarzen, D. M., & Elsik, W. C. (1986). Fungal palynomorphs recovered from recent river deposits, Luangwa Valley, Zambia. *Palynology*, 10(1), 35-60.

Johnson, T. C., Barry, S. L., Chan, Y., & Wilkinson, P. (2001). Decadal record of climate variability spanning the past 700 yr in the Southern Tropics of East Africa. *Geology*, 29(1), 83-86.

Keay-Bright, J., & Boardman, J. (2007). The influence of land management on soil erosion in the Sneeuberg Mountains, Central Karoo, South Africa. *Land degradation & development*, 18(4), 423-439.

Kehinde, T., & Samways, M. J. (2012). Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agriculture, Ecosystems & Environment*, 146(1), 162-167.

Kemper, J., Cowling, R. M., & Richardson, D. M. (1999). Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biological Conservation*, 90(2), 103-111.

Klein, R. G. (1974). A provisional statement on terminal Pleistocene mammalian extinctions in the Cape biotic zone (Southern Cape Province, South Africa). Goodwin Series, 39-45.

Koekemoer, M. (2002). Systematics of the Metalasia group in the Relhaniinae (Asteraceae-Gnaphalieae) (Doctoral dissertation, Rand Afrikaans University).

Kraaij, T., Cowling, R. M., & Van Wilgen, B. W. (2013). Fire regimes in eastern coastal fynbos: Imperatives and thresholds in managing for diversity. *Koedoe*,55(1), 01-09.

Krebs, C. J. (2009). *Ecology; the experimental analysis of distribution and abundance*.

Krug, R. M., Krug, C. B., Midoko Iponga, D., Walton, B. A., Milton, S. J., Newton, I. P., ... & Shiponeni, N. N. (2004). Reconstructing West Coast Renosterveld: past and present ecological processes in a Mediterranean shrubland of South Africa. In *Proceedings of the 10th MEDECOS Conference* (pp. 120-132).

Krug, C. B., & Krug, R. M. (2007). Restoration ofOld Fields in Renosterveld: A Case Study in a Mediterranean-type Shrubland ofSouth Africa. *Old fields: dynamics and restoration of abandoned farmland*, 265.

Kruger, F. J. (1979). South African heathlands. *Ecosystems of the world*.

Kruger, F. J. (1984). Effects of fire on vegetation structure and dynamics. In *Ecological effects of fire in South African ecosystems* (pp. 219-243). Springer Berlin Heidelberg.

Kruger, A. C., & Shongwe, S. (2004). Temperature trends in South Africa: 1960–2003. *International Journal of Climatology*, 24(15), 1929-1945.

Lambrechts, J. J. N. (1998). Natural resources and farming in the Tygerberg. *The Tygerberg: the story of Tygerberg Hills and the towns of Parow*, 112-126.

Lee, S., & Crous, P. W. (2003). New species of< i> Anthostomella</i> on fynbos, with a key to the genus in South Africa. *Mycological research*, 107(3), 360-370.

Le Maitre, D. C., Van Wilgen, B. W., Chapman, R. A., & McKelly, D. H. (1996). Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *Journal of Applied Ecology*, 161-172.

Levyns, M. R. (1926). A preliminary note on the Rhenoster Bush (Elytropappus Rhinocerotis) and the germination of its seed. *Transactions of the Royal Society of South Africa*, 14(4), 383-388.

Levyns, M. R. (1929). Guide to the Flora of the Cape Peninsula.

Levyns, M. R. (1935). Veld-burning experiments at Oakdale, Riversdale. *Transactions of the Royal Society of South Africa*, 23(3), 231-243.

Levyns, M. R. (1956). Notes on the biology and distribution of the rhenoster bush. *South African Journal of Science*, 52, 141-143.

Levyns, M. R. (1972). The Rhenosterbush. *Veld & Flora*, 2(1), 7-9..

Licciardi, J. M., Schaefer, J. M., Taggart, J. R., & Lund, D. C. (2009). Holocene glacier fluctuations in the Peruvian Andes indicate northern climate linkages. *Science*, 325(5948), 1677-1679.

Louys, J., Wilkinson, D. M., & Bishop, L. C. (2012). Ecology needs a paleontological perspective. In *Paleontology in Ecology and Conservation* (pp. 23-38). Springer Berlin Heidelberg.

Lovejoy, T. E., & L. Hannah. (2005). Climate change and biodiversity (pp 479-479) ST - *Climate change and biodiversity*. Yale University Press.

Low, A.B. & Rebelo, A.G. (1996). *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism: Pretoria.

Lowe, J. J., & Walker, M. J. (1997). Reconstructing quaternary environments (2nd ed., p. 446). Londres: Longman.

Lundqvist, N. (1972). Nordic Sordariaceae s. lat.

Ludwig, D., Walker, B., & Holling, C. S. (1997). Sustainability, stability, and resilience.

MacArthur, R. H. (1957). On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the United States of America*, 43(3), 293.

Macaulay, V., Hill, C., Achilli, A., Rengo, C., Clarke, D., Meehan, W., ... & Richards, M. (2005). Single, rapid coastal settlement of Asia revealed by analysis of complete mitochondrial genomes. *Science*, 308(5724), 1034-1036.

MacDowell, C. R. (1988). Factors affecting the conservation of Renosterveld by private landowners (Doctoral dissertation, University of Cape Town.).

Maher Jr, L. J. (1972). Nomograms for computing 0.95 confidence limits of pollen data. *Review of Palaeobotany and Palynology*, 13(2), 85-93.

Mahler, B. J., Van Metre, P. C., & Callender, E. (2006). Trends in metals in urban and reference lake sediments across the United States, 1970 to 2001.*Environmental Toxicology and Chemistry*, *25*(7), 1698-1709.

Mann, M. E., Zhang, Z., Rutherford, S., Bradley, R. S., Hughes, M. K., Shindell, D., ... & Ni, F. (2009). Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, 326(5957), 1256-1260.

Manning, J., & Goldblatt, P. (2012). Plants of the Greater Cape Floristic Region 1: The Core Cape Flora. Pretoria (ZA): SANBI. xiv.

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, 405(6783), 243-253.

Marloth, R. (1908). The plant formations of the Cape'. *Report of the South African Association for the Advancement of Science*, 6, 246-251.

Marks, S. (1972). Khoisan resistance to the Dutch in the seventeenth and eighteenth centuries. *Journal of African History*, 13(1), 55-80.

Massee, G., & Salmon, E. S. (1901). Researches on coprophilous fungi. *Annals of Botany*, (2), 313-357.

Mayewski, P. A., Rohling, E. E., Curt Stager, J., Karlén, W., Maasch, K. A., David Meeker, L., ... & Steig, E. J. (2004). *Holocene climate variability.Quaternary Research*, 62(3), 243-255.

McCormac, F. G., Hogg, A. G., Blackwell, P. G., Buck, C. E., Higham, T. F., & Reimer, P. J. (2004). SHCal04 Southern Hemisphere calibration, 0–11.0 cal kyr BP.

McCune, B., Grace, J. B., & Urban, D. L. (2002). *Analysis of ecological communities* (Vol. 28). Gleneden Beach, Oregon: MjM software design.

McDowell, C. (1995). Grazing and renosterveld management. *The sustainable use and management of Renosterveld remnants in the Cape Floristic Region*. CCU Report, 95(4), 63-80.

McDowell, C., & Moll, E. (1992). The influence of agriculture on the decline of West Coast Renosterveld, south-western Cape, South Africa. *Journal of Environmental Management*, 35(3), 173-192.

McDowell, N. G. (2011). Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant physiology*, 155(3), 1051-1059.

Meadows, M. E. (1999). Biogeography: changing places, changing times. *Progress in physical geography*, 23(2).

Meadows, M. E. (2001). The role of Quaternary environmental change in the evolution of landscapes: case studies from southern Africa. *Catena*, 42(1), 39-57.

Meadows, M. E. (2003). Soil erosion in the Swartland, Western Cape Province, South Africa: implications of past and present policy and practice. *Environmental Science & Policy*, 6(1), 17-28.

Meadows, M. E. (2006). Global change and southern Africa. *Geographical Research*, 44(2), 135-145.

Meadows, M. E., & Baxter, A. J. (2001). Holocene vegetation history and palaeoenvironments at Klaarfontein Springs, Western Cape, South Africa. The *Holocene*, 11(6), 699-706.

Meadows, M. E., Baxter, A. J., & Parkington, J. (1996). Late Holocene environments at Verlorenvlei, Western Cape Province, South Africa. *Quaternary International*, 33, 81-95.

Meadows, M. E., Chase, B. M., & Seliane, M. (2010). Holocene palaeoenvironments of the Cederberg and Swartruggens mountains, Western Cape, South Africa: pollen and stable isotope evidence from hyrax dung middens. *Journal of arid environment*s, 74(7), 786-793.

Meadows, M. E., & J. M. Sugden. (1991). A vegetation history of the last 14 000 years on the Cederberg, south-western Cape Province. *South African Journal Of Science* 87, 34-43.

Meadows, M. E., & Sugden, J. M. (1993). The late Quaternary palaeoecology of a floristic kingdom: the southwestern Cape South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 101(3), 271-281.

Meine, C. (1999). Editorial: It's about Time: Conservation Biology and History.

Mellars, P. (2006). Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. *Proceedings of the National Academy of Sciences*, 103(25), 9381-9386.

Meyer, E.H.F. (1875). On the geographical distribution of plants in South Africa. (Translated by H. Bolus). Juta: Cape Town.

Midgley, G. F., Chapman, R. A., Hewitson, B., Johnston, P., De Wit, M., Ziervogel, G., ... & Forsyth, G. G. (2005). A status quo, vulnerability and adaptation assessment of the physical and socio-economic effects of climate change in the Western Cape. Report to the Western Cape Government, Cape Town, South Africa. CSIR Report No. ENV-SC, 73.

Midgley, G., Rutherford, M., & Bond, W. J. (2001). The heat is on… impacts of climate change on plant diversity in South Africa. *National Botanic Institute, Cape Town, South Africa*.

Midgley, G. F., & Thuiller, W. (2007). Could anthropogenic climate change threaten biodiversity in Namaqualand. *Journal of Arid Environments*, 70, 615-628.

Midoko-Iponga, D., Krug, C. B., & Milton, S. J. (2005). Competition and herbivory influence growth and survival of shrubs on old fields: Implications for restoration of renosterveld shrubland. *Journal of Vegetation Science*, 16(6), 685-692.

Mighall, T. M., Foster, I. D., Rowntree, K. M., & Boardman, J. (2012). Reconstructing recent land degradation in the semi-arid karoo of South Africa: a palaeoecological study at compassberg, eastern cape. *Land Degradation & Development*, 23(6), 523-533.

Miller, C. S., Doss, P. K., Thompson, L. D. P., & Baedke, S. J. (1991). *Land-based vibracoring and vibracore analysis: tips, tricks, and traps.* Department of Natural Resources, Geological Survey.

Mills, A. J., Birch, S. J. C., Stanway, R., Huyser, O., Chisholm, R. A., Sirami, C., & Spear, D. (2013). Sequestering carbon and restoring renosterveld through fallowing: a practical conservation approach for the Overberg, Cape Floristic Region, South Africa. *Conservation Letters*, 6(4), 255-263.

Milne, B. T., Johnson, A. R., Keitt, T. H., Hatfield, C. A., David, J., & Hraber, P. T. (1996). Detection of critical densities associated with pinon-juniper woodland ecotones. *Ecology*, 77(3), 805-821.

Milton, S.J.(2007). Rapid Assessment Method for Renosterveld. Unpublished report submitted to WWF, Stellenbosch, for the Renosterveld Assessment Workshop, Worcester, 23 July 2007.

Mittermeier, R. A., Myers, N., Thomsen, J. B., Da Fonseca, G. A., & Olivieri, S. (1998). Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation biology*, 12(3), 516-520.

Moll, E. J., & Bossi, L. (1984). Assessment of the extent of the natural vegetation of the fynbos biome of South Africa. *South African journal of science*.

Moll, E. J., Campbell, B. M., Cowling, R. M., Bossi, L., Jarman, M. L., & Boucher, C. (1984). *Description of major vegetation categories in and adjacent to the Fynbos biome*. National Scientific Programmes Unit: CSIR.

Molles, M. C. (2008). *Ecology: Concepts and Applications*. McGraw Q Hill Companies. Inc., New York, 169.

Mooney, S. D., & Tinner, W. (2010). *The analysis of charcoal in peat and organic sediments*. Mires & Peat, 7.

Moore, P. D., Webb, J. A., & Collison, M. E. (1991). *Pollen analysis*. Blackwell scientific publications.

Mucina, L., & Rutherford, M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.

Mullins, J., & Emberlin, J. (1997). Sampling pollens. *Journal of Aerosol Science*, 28(3), 365-370.

Munsell, A. H. (1942). Munsell book of color.

Musil, C. F., Milton, S. J., & Davis, G. W. (2005). The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies: research in action. *South African Journal of Science*, 101(7 & 8), p-337.

Myers, N. (1990). The biodiversity challenge: expanded hot-spots analysis. *Environmentalist*, 10(4), 243-256.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853-858.

Neumann, F. H., Scott, L., & Bamford, M. K. (2011). Climate change and human disturbance of fynbos vegetation during the late Holocene at Princess Vlei, Western Cape, South Africa. *The Holocene*, 21(7), 1137-1149.

Newton, I. P. (2008). *Recent Transformations in West-Coast Renosterveld: Patterns, Processes and Ecological Significance* (Doctoral dissertation, University of the Western Cape).

Newton, I. P., & Knight, R. S. (2005). The use of Landsat imagery for the identification of the remaining West Coast Renosterveld fragments, Western Cape Province, South Africa. *South African Journal of Botany*, 71(1), 67-75.

Noble, I. R., Gill, A. M., & Bary, G. A. V. (1980). McArthur's fire-danger meters expressed as equations. *Australian Journal of Ecology*, 5(2), 201-203.

Oosthoek, J., & Gills, B. K. (2005). Humanity at the crossroads: The globalization of environmental crisis. *Globalizations*, 2(3), 283-291.

Orsi, A. J., Cornuelle, B. D., & Severinghaus, J. P. (2012). Little Ice Age cold interval in West Antarctica: evidence from borehole temperature at the West Antarctic ice sheet (WAIS) divide. *Geophysical Research Letters*, 39(9).

Palgrave, K. C., (2002). *Trees of southern Africa*. Struk. Cape Town, 1212 pp.

Parducci, L., Suyama, Y., Lascoux, M., & Bennett, K. D. (2005). Ancient DNA from pollen: a genetic record of population history in Scots pine. *Molecular Ecology*, 14(9), 2873-2882.

Parkington, J., Cartwright, C., Cowling, R. M., Baxter, A., & Meadows, M. (2000). Palaeovegetation at the last glacial maximum in the western Cape, South Africa: wood charcoal and pollen evidence from Elands Bay Cave. South African Journal of *Science*, 96(11), 543-546.

Pauw, A. (2004). Variation in pollination across a fragmented landscape at the Cape of Africa (Doctoral dissertation, University of Cape Town).

Penn, N. (1987). The frontier in the western Cape, 1700–1740. Papers in the prehistory of the Western Cape, South Africa. *International Series*, 332, 462-503.

Power, H. C., & Mills, D. M. (2005). Solar radiation climate change over Southern Africa and an assessment of the radiative impact of volcanic eruptions. *International journal of climatology*, 25(3), 295-318.

Prager, A., Barthelmes, A., Theuerkauf, M., & Joosten, H. (2006). Non-pollen palynomorphs from modern Alder carrs and their potential for interpreting microfossil data from peat. *Review of Palaeobotany and Palynology*, 141(1), 7-31.

Prentice, C. (1988). *Records of vegetation in time and space: the principles of pollen analysis. In Vegetation history* (pp. 17-42). Springer Netherlands.

Pressey, R. L. (1994). Ad hoc reservations: forward or backward steps in developing representative reserve systems?. *Conservation biology*, 8(3), 662-668.

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in ecology & evolution*, 22(11), 583-592.

Quick, L. J., Chase, B. M., Meadows, M. E., Scott, L., & Reimer, P. J. (2011). A 19.5 kyr vegetation history from the central Cederberg Mountains, South Africa: palynological evidence from rock hyrax middens. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 309(3), 253-270.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Radloff, F. G. T. (2008). The ecology of large herbivores native to the coastal lowlands of the Fynbos Biome in the Western Cape, South Africa (Doctoral dissertation, Stellenbosch: Stellenbosch University).

Ramsey, C. B. (1995). Radiocarbon calibration and analysis of stratigraphy; the OxCal program. *Radiocarbon*, 37(2), 425-430.

Raper, D., & Bush, M. (2009). A test of< i> Sporormiella</i> representation as a predictor of megaherbivore presence and abundance. *Quaternary Research*,71(3), 490-496.

Rebelo, A. G. (1992). Red Data Book species in the Cape Floristic Region: threats, priorities and target species. *Transactions of the Royal Society of South Africa*, 48(1), 55-86.

Rebelo, A. G. (1995). Renosterveld: conservation and research. In *The sustainable use and management of Renosterveld remnants in the Cape floristic region: proceedings of a symposium* (pp. 32-42).

Rebelo, A.G. (1997). Conservation. In R.M Cowling, D.M. Richardson and S.M. Pierce, *Vegetation of southern Africa*: 571-590. Cambridge University Press, Cambridge.

Rebelo, A. G., Boucher, C., Helme, N., Mucina, L., Rutherford, M. C., Smit, W. J., Powrie, L. W., Ellis, F., Lambrechts, J. J., and Scott, L. (2006). Fynbos biome. in L. Mucina, and M. C. Rutherford, editors *The vegetation of South Africa, Lesotho and Swaziland. South African* National Biodiversity Institute, Pretoria, South Africa. Strelitzia (pp.53–219).

Rebelo, A. G., Holmes, P. M., Dorse, C., & Wood, J. (2011). Impacts of urbanization in a biodiversity hotspot: conservation challenges in Metropolitan Cape Town. South *African Journal of Botany*, 77(1), 20-35.

Reyers, B., Fairbanks, D. H. K., Van Jaarsveld, A. S., & Thompson, M. (2001). Priority areas for the conservation of South African vegetation: a coarse-filter approach. *Diversity and Distributions*, 7(1-2), 79-95.

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

Roberts, N., Meadows, M. E., & Dodson, J. R. (2001). The history of mediterranean-type environments: climate, culture and landscape. *The Holocene*, 11(6), 631-634.

Rouget, M., Richardson, D. M., & Cowling, R. M. (2003a). The current configuration of protected areas in the Cape Floristic Region, South Africa—reservation bias and representation of biodiversity patterns and processes. *Biological Conservation*, 112(1), 129-145.

Rouget, M., Richardson, D. M., Cowling, R. M., Lloyd, J. W., & Lombard, A. T. (2003b). Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation*, 112(1), 63-85.

Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., ... & Rutherford, M. C. (2004). South African National Spatial Biodiversity Assessment 2004. Technical report. *Volume 1: Terrestrial component*.

Rosenthal, Y., Linsley, B. K., & Oppo, D. W. (2013). Pacific ocean heat content during the past 10,000 years. *Science*, 342(6158), 617-621.

Ross, R. (1983). The first two centuries of colonial agriculture in the cape colony: A historiographical review∗. *Social Dynamics*, 9(1), 30-49.

Rull, V. (1990). Quaternary palaeoecology and ecological theory. Orsis: organismes i sistemes, 5, 91-111.

Rull, V. (2010). Ecology and Palaeoecology: Two Approaches, *One Objective.Open Ecology Journal*.

Rutherford, M. C., & Westfall, R. H. (1994). *Biomes of southern Africa: an objective categorization*. National Botanical Institute.

Schaefer, J. M., Denton, G. H., Kaplan, M., Putnam, A., Finkel, R. C., Barrell, D. J., ... & Schlüchter, C. (2009). High-frequency Holocene glacier fluctuations in New Zealand differ from the northern signature. *Science*, 324(5927), 622-625.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856), 591-596.

Schloms, B. H. A., Ellis, F., & Lambrechts, J. J. N. (1983). Soils of the Cape coastal platform. *Fynbos palaeoecology: a preliminary synthesis*. FRD, CSIR, Pretoria, 70-86.

Schnitzler, J., Barraclough, T. G., Boatwright, J. S., Goldblatt, P., Manning, J. C., Powell, M. P., ... & Savolainen, V. (2011). Causes of plant diversification in the Cape biodiversity hotspot of South Africa. *Systematic Biology*, 60(3), 343-357.

Scholz, C. A., Johnson, T. C., Cohen, A. S., King, J. W., Peck, J. A., Overpeck, J. T., ... & Pierson, J. (2007). East African megadroughts between 135 and 75 thousand years ago and bearing on early-modern human origins. *Proceedings of the National Academy of Sciences*, 104(42), 16416-16421.

Schulze, R. E., & Maharaj, M. (1997). *South African atlas of agrohydrology and-climatology*. Water Research Commission.

Scott, L., & Bousman, C. B. (1990). Palynological analysis of hyrax middens from southern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*,76(3), 367-379.

Scott, L., & Cooremans, B. (1992). Pollen in recent Procavia (hyrax), Petromus (dassie rat) and bird dung in South Africa. *Journal of Biogeography*, 205-215.

Scott, L., & Woodborne, S. (2007a). Vegetation history inferred from pollen in Late Quaternary faecal deposits (hyraceum) in the Cape winter-rain region and its bearing on past climates in South Africa. *Quaternary Science Reviews*,26(7), 941-953.

Scott, L., & Woodborne, S. (2007b). Pollen analysis and dating of Late Quaternary faecal deposits (hyraceum) in the Cederberg, Western Cape, South Africa. *Review of Palaeobotany and Palynology,* 144(3), 123-134.

Sealy, J. (2010a). Isotopic evidence for the antiquity of cattle-based pastoralism in southernmost Africa. *Journal of African Archaeology*, 8(1), 65-81.

Sealy, J. (2010b). The origins of khoekhoen cattle pastoralism: new insights from bone chemistry. *The Digging Stick*. Vol. 28(2), 5-8

Shiponeni, N. N. (2003). Dispersal of seeds as a constraint in revegetation of old fields in Renosterveld vegetation in the Western Cape, South Africa(Doctoral dissertation, Stellenbosch: Stellenbosch University).

Shiponeni, N. N., & Milton, S. J. (2006). Seed dispersal in the dung of large herbivores: implications for restoration of Renosterveld shrubland old fields. *Biodiversity & Conservation*, 15(10), 3161-3175.

Singer, R., & Weiner, J. S. (1963). Biological aspects of some indigenous African populations. *Southwestern Journal of Anthropology*, 168-176.

Skead, C. J. (1980). *Historical mammal incidence in the Cape Province*.ORDER, 7, 17-1.

Skelton, R. P., West, A. G., Dawson, T. E., & Leonard, J. M. (2013). External heat-pulse method allows comparative sapflow measurements in diverse functional types in a Mediterranean-type shrubland in South Africa. *Functional Plant Biology*, 40(10), 1076-1087.

Smith, A. B. (1983). Prehistoric Pastoralism in the South-western Cape, South Africa. *World Archaeology*,15, 79-89.

Smith, A. B. (1992a). Origins and spread of pastoralism in Africa. *Annual Review of Anthropology*, 125-141.

Smith, A. B. (1992b). *Pastoralism in Africa: origins and development ecology*. Hurst & Company.

Smith, D. G. (1987). A Mini-Vibracoring System: RESEARCH METHOD PAPER. *Journal of Sedimentary Research*, 57(4).

Snow, C. P. (1960). The two cultures and the scientific revolution. Cambridge: University Press.

Specht, R. L., & Moll, E. J. (1983). Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In *Mediterranean-type Ecosystems* (pp. 41-65). Springer Berlin Heidelberg.

Stager, J. C., Mayewski, P. A., White, J., Chase, B. M., Neumann, F. H., Meadows, M. E., ... & Dixon, D. A. (2012). Precipitation variability in the winter rainfall zone of South Africa during the last 1400 yr linked to the austral westerlies. *Climate of the Past*, 8(4).

Stander, M. (1988). A comparative study of coastal Renosterveld communities subjected to grazing by wild game. Unpublished 3rd year project: Botany Department, University of Cape Town.

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K. S., & Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, 297(5585), 1292-1296.

Stockmarr, J. (1971). Tablets with spores used in absolute pollen analysis. *Pollen et spores*, 1971.

Stow, G. W. (1905). *The native races of South Africa*. London: Swan Sonnenschein

Sugita, S. (1994). Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology*, 881-897.

Sullivan, S., & Rohde, R. (2002). On non-equilibrium in arid and semi-arid grazing systems. *Journal of Biogeography*, 29(12), 1595-1618.

Suyama, Y., Kawamuro, K., Kinoshita, I., Yoshimura, K., Tsumura, Y., & Takahara, H. (1996). DNA sequence from a fossil pollen of Abies spp. from Pleistocene peat. *Genes & genetic systems*, 71(3), 145-149.

Swift, M. J., Izac, A., & van Noordwijk, M. (2004). Biodiversity and ecosystem services in agricultural landscapes—are we asking the right questions?. *Agriculture, Ecosystems & Environment*, 104(1), 113-134.

Szabo, P., & Hedl, R. (2011). Advancing the integration of history and ecology for conservation. *Conservation Biology*, 25(4), 680-687.

Talbot, W. J. (1947). *Swartland and Sandveld: A survey of land utilization and soil erosion in the western lowland of the Cape Province*. Oxford University Press.

Tansley, S. (1982). Koppie Conservation Project. *Wildlife Society of Southern Africa and the South African Nature Foundation*, Rondebosch, 1-100.

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

Thom, H.B. (1952). *Journal of Jan van Riebeeck Volume 1*, 1651-1655. AA Balkema: Cape Town.

Thom, H.B. (1954). *Journal of Jan van Riebeeck Volume 2*, 1656-1658. AA Balkema: Cape Town.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427(6970), 145-148.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press.

Toggweiler, J. R., & Russell, J. (2008). Ocean circulation in a warming climate.*Nature*, 451(7176), 286-288.

Troels-Smith, J. (1955). Karakterisering af lose jordarter. *Characterization of unconsolidated sediments*.

Turpie, J., Winkler, H., Spalding-Fecher, R., & Midgley, G. (2002). Economic impacts of climate change in South Africa: a preliminary analysis of unmitigated damage costs. Energy and Development Research Centre, University of Cape Town, Cape Town.

Tyson, P. D. (1999). Late-Quaternary and Holocene palaeoclimates of Southern Africa: a synthesis. *South African Journal of Geology*, 102(4).

Tyson, P. D., Preston-Whyte, R. A., & Preston-Whyte, R. A. (2000). *weather and climate of southern Africa*. Oxford University Press.

Tyson, P. D., Karlén, W., Holmgren, K., & Heiss, G. A. (2000). The Little Ice Age and medieval warming in South Africa. *South African Journal of Science*,96(3).

van Geel, B. (1986). Application of fungal and algal remains and other microfossils in palynological analyses. *Handbook of Holocene palaeoecology and palaeohydrology*, 24, 497-505.

van Geel, B., & Aptroot, A. (2006). Fossil ascomycetes in Quaternary deposits.*Nova Hedwigia*, 82(3-4), 3-4.

van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G., & Hakbijl, T. (2003). Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi. Journal of *Archaeological Science*, 30(7), 873-883.

van Wilgen, B. W., Forsyth, G. G., De Klerk, H., Das, S., Khuluse, S., & Schmitz, P. (2010). Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *Journal of Applied Ecology*,47(3), 631-638.

van Wilgen, B. W., Forsyth, G. G., & Prins, P. (2012). The management of fire-adapted ecosystems in an urban setting: the case of Table Mountain National Park, South Africa. *Ecology & Society*, 17(1).

Verboom, G. A., Archibald, J. K., Bakker, F. T., Bellstedt, D. U., Conrad, F., Dreyer, L. L., ... & Nowell, T. L. (2009). Origin and diversification of the Greater Cape flora: Ancient species repository, hot-bed of recent radiation, or both?. *Molecular Phylogenetics and Evolution*, 51(1), 44-53.

Vermeulen, T. (2010). Plant water relations of Elytropappus Rhinocerotis with specific reference to soil restrictions on growth (Doctoral dissertation, Stellenbosch: University of Stellenbosch).

Vetter, S. (2005). Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments*, 62(2), 321-341.

Vlok, J. H. (1988). Alpha diversity of lowland fynbos herbs at various levels of infestation by alien annuals. *South African Journal of Botany*, 54(6), 623-627.

Von Hase, A., Rouget, M., Maze, K., & Helme, N. (2003). A fine-scale conservation plan for Cape lowlands renosterveld: technical report. *Report CCU*,2(03).

Von Hase, A., Rouget, M., & Cowling, R. M. (2010). Evaluating private land conservation in the Cape Lowlands, South Africa. *Conservation Biology*, 24(5), 1182-1189.

Walker, B. H. (1981). Stability Properties Of Semiarid Savannas In Southern African Game Reserves.

Walker, B. (1989). Diversity and stability in ecosystem conservation. *Conservation for the twenty-first century*, 121-130.

Walker, B., & Meyers, J. A. (2004). Thresholds in ecological and socialecological systems: a developing database. *Ecology and society*, 9(2), 3.

Walker, L. R., & Del Moral, R. (2003). *Primary succession and ecosystem rehabilitation*. Cambridge University Press.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., ... & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*,416(6879), 389-395.

Walton, B. A. (2006). Vegetation patterns and dynamics of renosterveld at Agter-Groeneberg conservancy, Western Cape, South Africa (Doctoral dissertation, Stellenbosch: University of Stellenbosch).

Warburton, M., Schulze, R. E., & Maharaj, M. (2005). Is South Africa’s temperature changing? An analysis of trends from daily records, 1950–2000.*Climate change and water resources in southern Africa: studies on scenarios, impacts, vulnerabilities and adaptation*, 275-295.

Webb III, T., Howe, S. E., Bradshaw, R. H. W., & Heide, K. M. (1981). Estimating plant abundances from pollen percentages: the use of regression analysis. *Review of Palaeobotany and Palynology*, 34(3), 269-300.

Wells, M. J., Poynton, R. J., Balsinhas, A. A., Musil, K. J., Joffe, H., Van Hoepen, E., & Abbott, S. K. (1986). history of introduction of invasive alien plants to southern Africa. In *Ecology and management of biological invasions in southern Africa: proceedings of the National Synthesis Symposium on the Ecology of Biological Invasions*/edited by IAW Macdonald, FJ Kruger, AA Ferrar.

Werger, M. J. A. (1978). *Biogeographical division of southern Africa* (pp. 145-170). Springer Netherlands.

West, A. G., Dawson, T. E., February, E. C., Midgley, G. F., Bond, W. J., & Aston, T. L. (2012). Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa. *New Phytologist*, 195(2), 396-407.

Westphal, E. O. (1963). The linguistic prehistory of southern Africa: Bush, Kwadi, Hottentot, and Bantu linguistic relationships. *Africa*, 33(03), 237-265.

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional ecology*, 3(4), 385-397.

Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5(9), 475-482.

Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences*, 104(14), 5738-5742.

Willis, K. J., & Birks, H. J. B. (2006). What is natural? The need for a long-term perspective in biodiversity conservation. *Science*, 314(5803), 1261-1265.

Wood, J. R., & Wilmshurst, J. M. (2013). Accumulation rates or percentages? How to quantify< i> Sporormiella</i> and other coprophilous fungal spores to detect late Quaternary megafaunal extinction events. *Quaternary Science Reviews*, 77, 1-3.

Wooding, B. (2011). Game Management Plan for Elandsberg Nature Reserve. Unpublished Management Report. Elandsberg Private Nature Reserve.

Woodward, F. I., & Williams, B. G. (1987). Climate and plant distribution at global and local scales. In *Theory and models in vegetation science* (pp. 189-197). Springer Netherlands.

Wu, J. and Loucks, O. (1995). From Balance of Nature to Hierarchical Patch Dynamics: a Paradigm Shift in Ecology. *The Quarterly Review of Biology*, 70, 439–466.

Zhang, W., Ricketts, T. H., Kremen, C., Carney, K., & Swinton, S. M. (2007). Ecosystem services and dis-services to agriculture. *Ecological economics*,64(2), 253-260.

Zhou, L. J., Pei, K. Q., Zhou, B., & Ma, K. P. (2007). A molecular approach to species identification of Chenopodiaceae pollen grains in surface soil. *American journal of botany*, 94(3), 477-481.

APPENDICES

Appendix 1. Table A1*: *Area (ha) transformed for cereal cultivation (barley, oats, rye, wheat, maize and lucerne) between 1911 and 1988 in seven magisterial districts (Hopefield, Malmesbury, Morreesburg, Piketberg, Tulbagh, Vredenburg and Wellington) on the west coast of the Fynbos biome. Data are from Agricultural Censuses.

Year	Barley (ha)	Oats (ha)	Rye (ha)	Wheat (ha)	Maize (ha)	Lucerne (ha)	Total area (ha)
1911	9173.504	80755.56	17461.54	61972.65	194.0171	116.2393	169673.5
1918	8883.761	68307.69	15485.47	84887.18	236.7521	33.33333	177834.2
1923	7572.65	79586.32	18214.53	88779.49	214.5299	0	194367.5
1928	5023.932	67088.03	17760.68	88307.69	93.16239	77.77778	178351.3
1939	5447.863	60917.09	20747.01	141263.2	200	154.7009	228729.9
1939	5447.863	60917.09	20747.01	141263.2	200	154.7009	228729.9
1946	5320.513	58220.51	24885.47	144036.8	86.32479	1317.094	233866.7
1951	6993.162	44737.61	12078.63	165067.5	65.81197	1980.342	230923.1
1956	5008.547	40905.13	0	159164.1	630.7692	2029.06	207737.6
1961	5763.248	41855.56	0	194373.5	64.95726	2562.393	244619.7
1965	6550.427	42326.5	0	186788	371.7949	1511.111	237547.9
1971	6090.598	50198.29	1708.547	218187.2	788.0342	739.3162	277712.0
1976	5999.145	46540.17	2958.12	188392.3	608.547	1985.47	288386.0
1981	4000.855	43177.78	3798.291	186986.3	214.5299	7164.103	287050.0
1983	4194.872	40489.74	2352.137	207116.2	1121.368	0	298671.0
1988	4026.496	35585.47	0	253895.7	350.4274	2962.393	347280.0

Appendix 2.1. Information on Lycopodium spore tablets

***Production*:**

Spore tablets for calibration of pollen analyses have earlier been produced and distributed by Dr Jens Stockmarr, Copenhagen. In October 1980 this business was taken over by the

Department of Quaternary Geology in Lund. It is performed as an official commission approved by the University of Lund. A new batch, No. 483216, is now produced and calibrated and tablets are available. The tablets were manufactured in Denmark.

Lycopodium spore tablets (batch 483216) (September 2004):

Lycopodium spore tablets can be dissolved in water or in HC1, but not in NaOH. For this study the *Lycopodium* spore tablets were prepared in a slightly different way compared to that described by Stockmarr (1971, 1973). The tablets comprises mainly of sodium bicarbonate together with polyvinylpyrilidon and polyethyleneglycol, thus they had to be carefully washed away with water and finally with diluted HCl before further treatment. The spores were acetolysed. The spore concentration was determined with an electronic particle counter,

Coulter Counter ZB (cf.Stockmarr 1973) with a tube size of 140 pm. Preparation included 100 samples of five tablets each that were taken from different places in the batch. These samples were prepared by dissolving the tablets in Isoton II NaCl solution in 100 ml flasks, with 20 counts each of 0.5 ml were made on each sample.

Results of the calibration for 5 tablets showed the following concentration:

X = 92914; sd = ± 3820; V = ± 4.1 %. Thus the Lycopodium spore concentration for one tablet is: X = 18583.

Appendix 2.2. Script for PCA analysis.

```
setwd("C:/")
require(vegan) # loading vegan
vg2<-read.csv("C:/vang.csv", row.names=1) # reading in the 2% threshold data from the
VANGKRAAL site
vg2 #printing the data to screen
vg_nd<-vg2[,-1] #removing the depth column from analysis
vg_nd #printing output without depth

#alternative 2
```

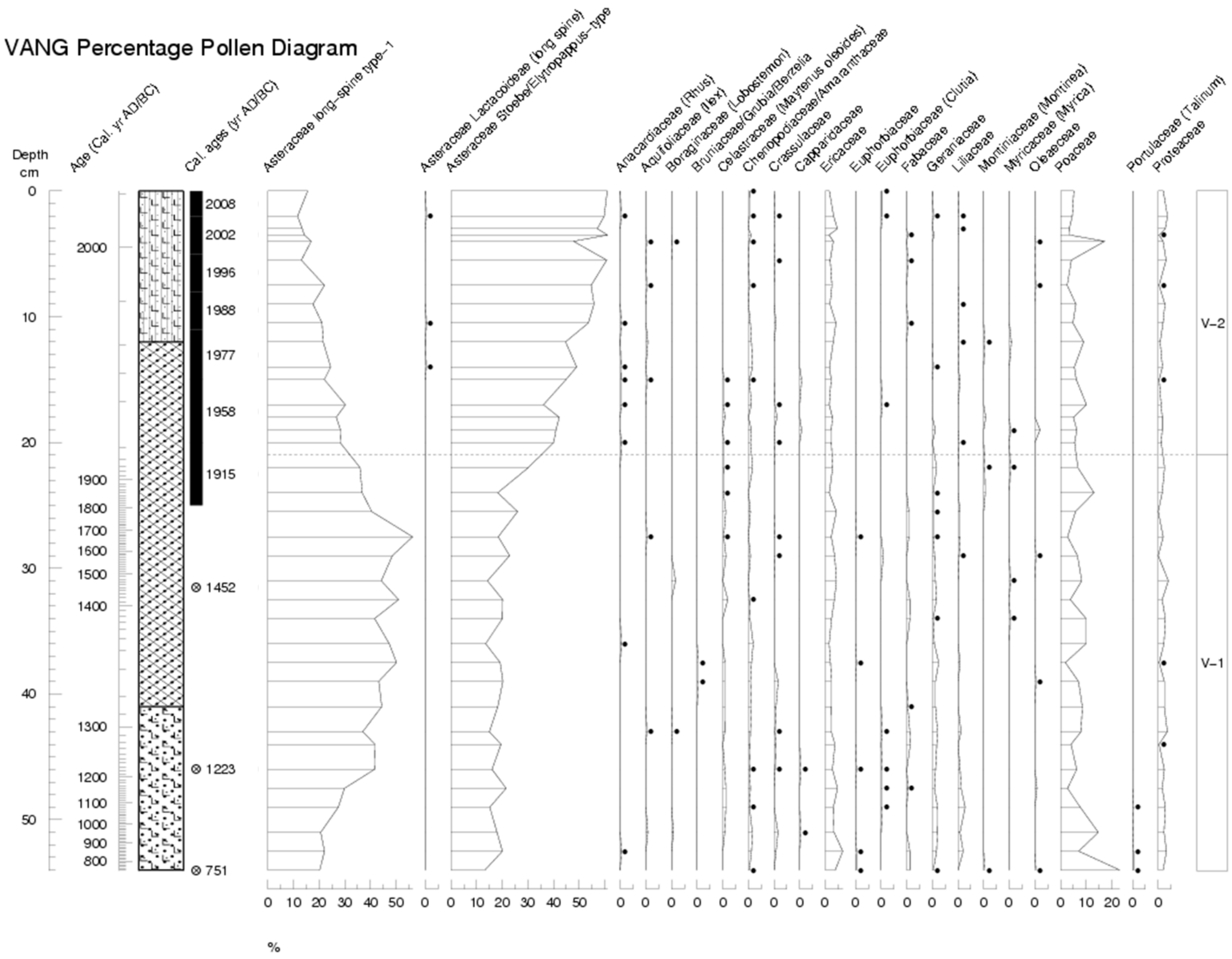
```
layout(1)
vang<-rda(vg_nd, scale=TRUE) # running the pca
scl<-1 #setting the scale for the distance biplot
bplot <- ordipointlabel(vang, pch = c(18, 3)) #setting the labels for the species and site scores
orditkplot(bplot, pch=1) # plotting and editing the final PCA plot
```

Appendix 3. Table A2: Table with R^2 values and corresponding sediment accumulation rates. R^2 values as a function of background ^{210}Pb level subtracted. Note that the R^2 value and corresponding accumulation rate associated with the VANG core is marked with an asterisk.

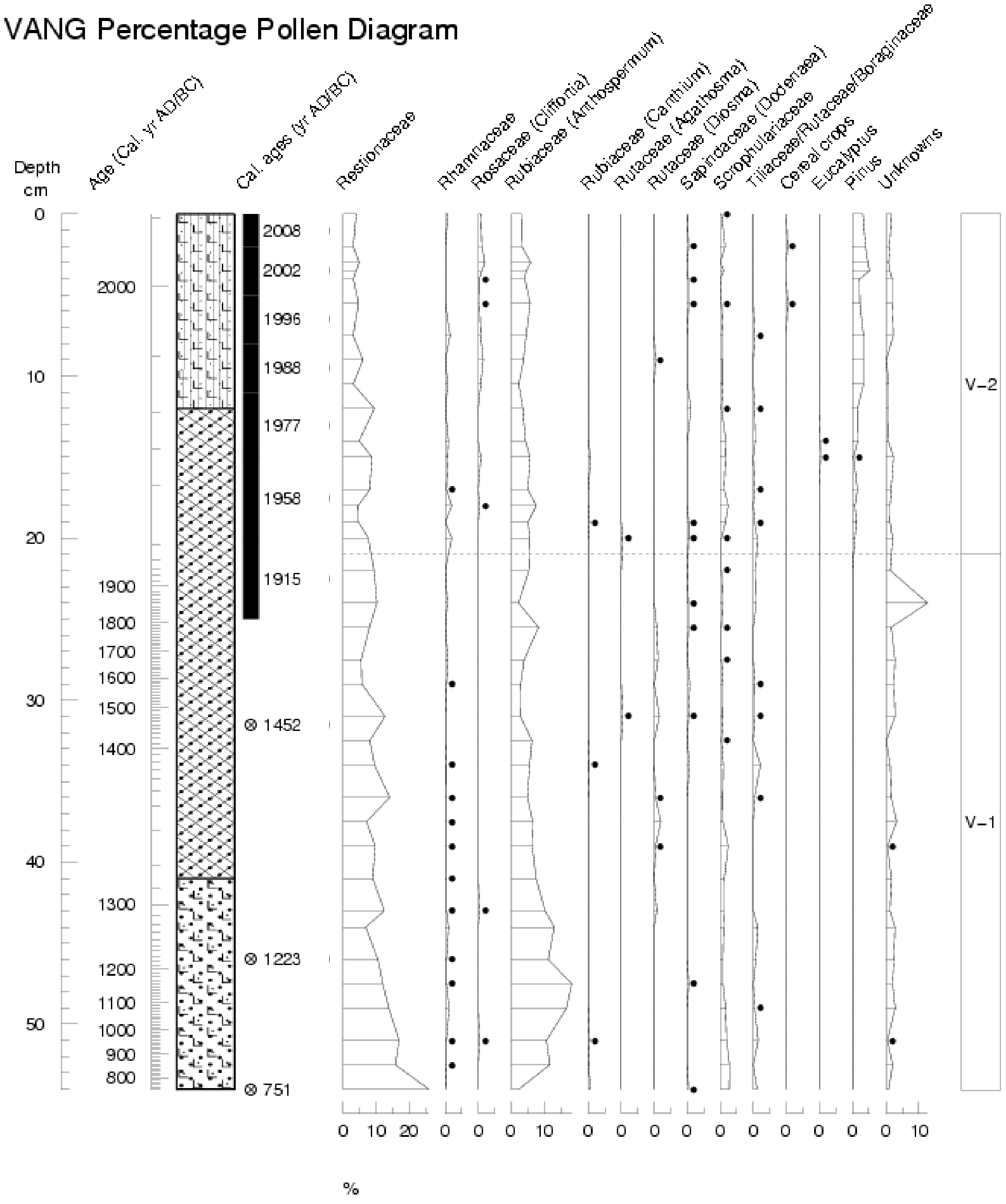
***Background ^{210}Pb level* (DPM/g)**	**R^2**	**Sediment Accumulation Rate (g/cm^2/yr)**	**Slope 'm'**	**Y intercept 'b'**
0.0000	0.9676	1.2280	-39.511	106.486
0.0865	0.9667	1.2098	-38.924	104.787
0.1729	0.9658	1.1914	-38.333	103.087
0.2594	0.9647	1.1729	-37.738	101.385
0.3458	0.9636	1.1543	-37.138	99.681
0.4323	0.9625	1.1355	-36.533	97.974
0.5187	0.9612	1.1165	-35.923	96.264
0.6052	0.9599	1.0974	-35.308	94.550
0.6916	0.9585	1.0781	-34.687	92.833
0.7781	0.9570	1.0586	-34.060	91.111
0.8645	0.9554	1.0389	-33.426	89.384
0.9510	0.9536	1.0190	-32.785	87.651
1.0375	0.9517	0.9988	-32.137	85.911
1.1240	0.9497	0.9784	-31.480	84.163
1.2105	0.9475	0.9577	-30.814	82.408
1.2970	0.9452	0.9367	-30.138	80.642
1.3835	0.9426	0.9154	-29.451	78.865
1.4700	0.9398	0.8936	-28.752	77.076
1.5565	0.9368	0.8715	-28.041	75.272
1.6430	0.9335	0.8490	-27.315	73.452
1.7295*	0.9298*	0.8259*	-26.573*	71.613*

Appendix 4. Figure A1: Complete percentage diagram for all pollen taxa from the VANG core. The pollen sum included terrestrial and unknown pollen. Black dots represent taxa with 5% threshold, which would otherwise not be visible in this figure. Pollen zones are calculated by Psimpoll using a 2% threshold and are indicated by the dashed line and boxes V-1 and V-2 to the far right of the diagram.

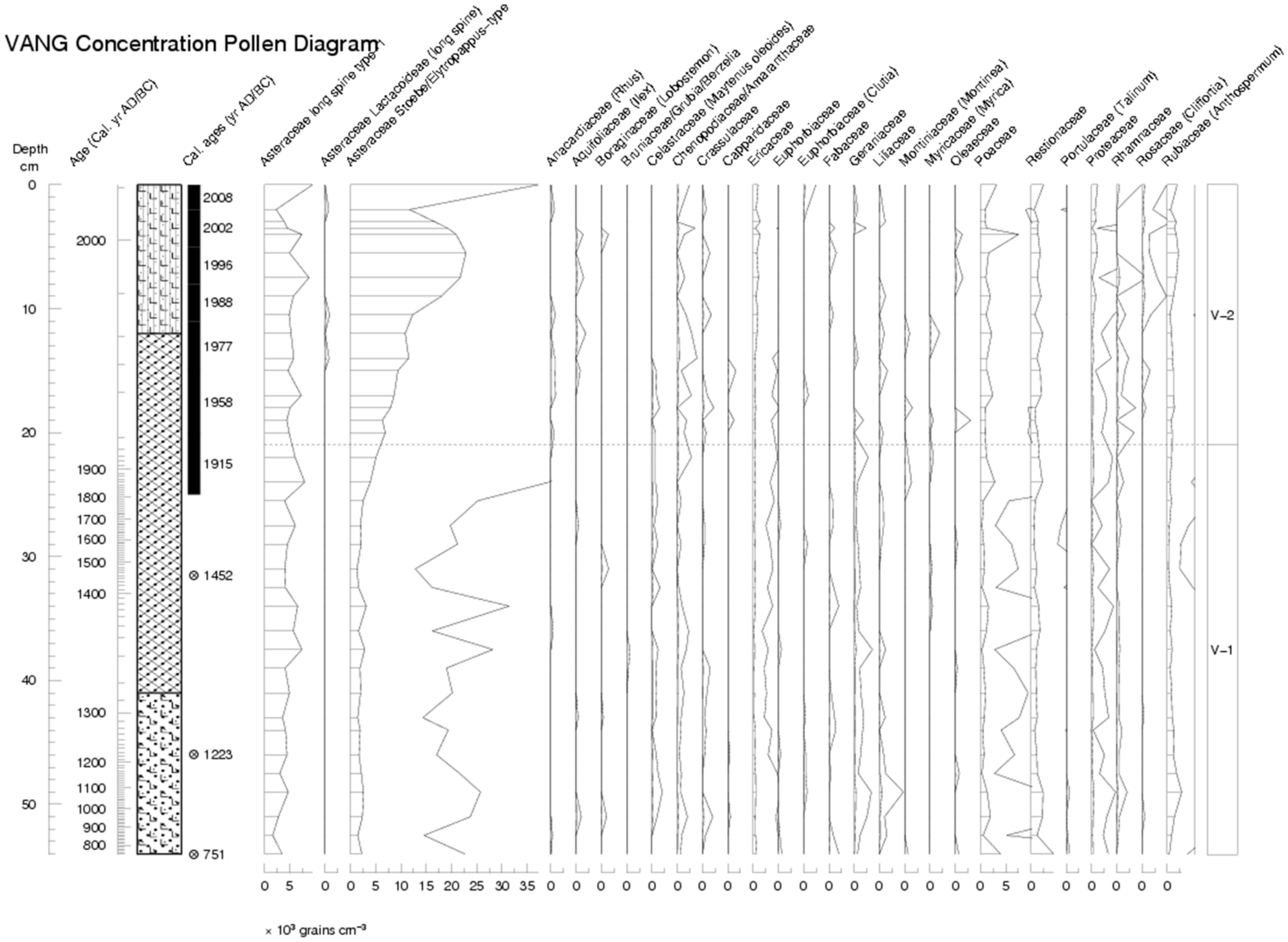
Appendix 5. Figure A2: Complete concentration pollen diagram for taxa from the VANG core. The pollen sum included terrestrial and unknown pollen. x10 exaggeration is shown since concentration values are often low for most taxa. Pollen zones are calculated by Psimpoll using a 2% threshold and are indicated by the dashed line and boxes V-1 and V-2 to the far right of the diagram.



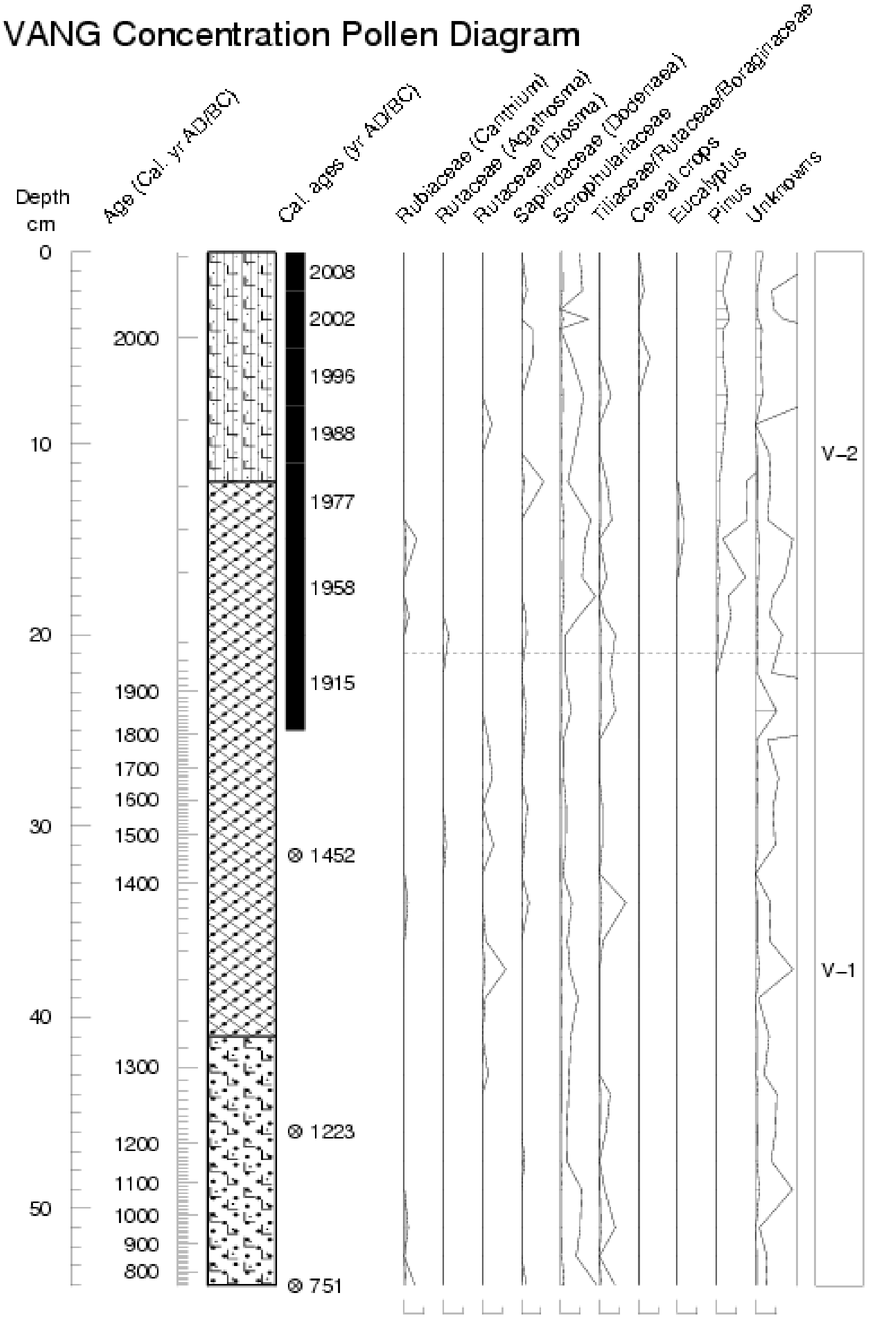
Appendix 4. Figure A1: Complete pollen percentage diagram for the VANG core.



Appendix 4. Figure A1: Complete pollen percentage diagram for the VANG core (continued).



Appendix 5. Figure A2: Complete pollen concentration diagram for the VANG core.



Appendix 5. Figure A2: Complete pollen concentration diagram for the VANG core (continued).