Relative Pollen Productivity Estimates (PPE) and Relevant Source Area of Pollen (RSAP) for key taxa from vegetation communities in Cathedral Peak, KwaZulu-Natal Drakensberg.

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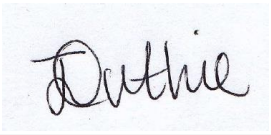
Frontispiece

Abstract

Pollen analysis has proved to be an effective method for elucidating and reconstructing past vegetation patterns, and can be effective in attempting to understand the possible future implications of environmental change. However, 'true' reconstructions of past vegetation patterns and distributions based on pollen analysis have proved elusive due to a number of intrinsic limitations in palynological data interpretations. Perhaps the most pronounced deficiency in interpretation of pollen diagrams used for reconstruction is the fact that no explicit spatial context is discernible for *where* in the wider landscape the pollen originates - consequently, interpretation of pollen diagrams remains innately subjective and predominantly based on intuition. For any given site containing pollen rich sediments, it is important to consider the sources of that pollen, and the means by which it arrived at its preservation site - only by doing this, can one better interpret the pollen assemblage in terms of past vegetation. This research focuses on modern pollen spectra of three vegetation communities (*Themeda* grassland, *Protea* savanna, *Leucosidea* scrubland) in the Cathedral Peak region of the KwaZulu-Natal Drakensberg. The intention is to use models of pollen dispersal and deposition that attach spatial contexts to pollen data extracted from an environment and to link this research to fossil pollen work in the Drakensberg. Fifteen soil surface samples were collected from Cathedral Peak, chemically digested and modern pollen spectra extracted. Vegetation data were collected around each sample point using a 3-tiered ring surveying approach out to a maximum radius of 5 000 m, and distance-weighted using Sutton's taxon-specific weighting method. Fall speeds of dominant taxa were calculated using Stokes Law for spherical pollen grains and Falck's assumption for ellipsoidal grains. Pollen and vegetation data were processed through HUMPOL software suite and Extended R-value analysis to calculate Relevant Source Area of Pollen and Pollen Productivity Estimates for each vegetation community. Results showed the source areas of approximately 150 m for *Themeda* grassland, 100 m for *Protea* savanna and 100 m for *Leucosidea* scrubland. Productivity estimates revealed Poaceae (PPE = 1) to be significantly more productive than herbaceous and shrubs taxa analysed (PPE = 0.00057), yet arboreal taxa were significantly higher in productivity (PPE = 6.5) relative to Poaceae. Findings show pollen models have a very relevant place in South African pollen research and can significantly impact future work by strengthening the foundation from which we base our understanding – the interpretation of results.

Declaration

In my capacity as the researcher and author of the work described in this thesis (with the supervision of Professor Trevor Hill), I recognise and confirm that, to the best of my knowledge, I have completed original work. I declare that where work completed by others has been made use of, it has been duly acknowledged and correctly referenced in the text.

Tristan Duthie: 

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Chapter One

Introduction

1.1. Introduction

In the Quaternary period, the earth's dynamic climate system has fluctuated between glacial and interglacial periods that have resulted in fundamental changes in the environment in response to this climatic instability (Goudie, 1981; van Vuuren *et al*., 2007; Gibbard *et al.*, 2010). It is understood that the earth's climate system and biosphere coexist and are inextricably linked, and that interaction between the two systems is driven primarily by energy from the sun (Foley *et al*., 1998). Moreover, it is increasingly understood that in a broad scope, geographical patterns of climate and vegetation overlap significantly, giving rise to the notions of global biomes (Holdridge, 1967; Fréchette and de Vernal, 2013). Distinct plant functional types each have specific and often limited tolerance ranges to climatic factors in which they can survive, known as climate envelopes, and this information can be used to associate vegetation as a climatic indicator in environmental inquiry (Adams, 2007; Corlett and Westcott, 2013).

Elucidating environmental change of the Quaternary geological period is a salient topic to many branches of the environmental sciences. Considered a period of immense climatic oscillation and resultant vegetation change, environmental scientists have sought to recognise the causes of, and furthermore reconstruct, these past changes over space and time. Palaeoecology has particularly desired to uncover palaeoenvironmental conditions, such as past vegetation compositions of landscapes, from a time preceding the existence of scientific instrumentation and historical environmental monitoring (IPCC, 2013). Quantitative reconstructions based on palaeoecological data are a key resource for obtaining long-term climate variability and vegetation change patterns across a spatial context (Salonen *et al*., 2014). Numerous reconstruction techniques exist that employ a variety of fossil biological proxies to reveal past vegetation and hence climate patterns. This research is concerned with the pollen analysis method – a method which extracts pollen from surface sediments and sediment cores from the stratigraphic column to infer past vegetation conditions (Faegri and Iversen, 1975; Overballe-Petersen *et al.*, 2013).

Palynology, a branch of science with roots in geology, palaeobotany and palaeoecology, is concerned with the study of fossil and live pollen and spores, and can be effectively used to

unearth fundamental information regarding past vegetation community compositions and climates (Steele and Warny, 2013). First introduced by the Swedish naturalist Lennart von Post in 1916, pollen analysis has the primary objective of reconstructing the spatial and temporal variations in vegetation of regional or local environments, and holds an essential place in Quaternary palaeoecology and palaeoclimatology (Faegri and Iversen, 1975; Tarasov *et al*., 2013). It should be noted, however, that researchers from a myriad of different disciplines use the pollen analysis method to various ends, and with differing aims and objectives – its application to specific research questions should therefore be appropriate and relevant to the questions being asked (Moore *et al*., 1991). Nevertheless, the pollen analysis method, in the main, offers researchers from many different backgrounds insight into characteristics of past environments such as *which* plant flora were present, *what* vegetation community or population compositions were like in the wider landscape, and presents an enhanced understanding of inter-taxa interactions (Moore *et al*., 1991). Coupling this knowledge with research on modern plant taxa climate envelopes and environmental tolerances allows inferences about past ecosystems, other palaeoecological circumstances and palaeoclimates (Froyd and Willis, 2008).

There is little doubt that our environment in the present is changing. The prospect of this change being beyond the range of variability to which humankind can respond through adaptation and mitigation strategies, or to which conservation practices are able to develop, provides great impetus for science to reassess whether current scientific techniques or methods for understanding long-term environmental change are effective in offering enhanced understanding of how the environment reacts to variations (Davies and Bunting, 2010). Pollen analysis provides an important historical record of vegetation change, and assuming methodological uniformitarianism holds true, palaeoecological inferences deducted from the past can, with some degree of confidence, be applied to future scenarios (Rana, 2013). This is principally relevant to the omnipresent issue of climate change and the need for reducing uncertainty regarding future climate fluctuations and their impact on the wider ecosystem. Quaternary palynological data can expressly be used to discern the impacts of pre-anthropogenic induced environmental change compared to changes provoked by human activities (Davies and Bunting, 2010).

The pollen analysis method has shown to provide researchers with a means of reconstructing vegetational compositions of the past which significantly facilitates reconstruction of past ecosystem dynamics and climate parameters (Elias and Mock, 2013). Underlying the

application of palynological data, to this end, is dependent on two fundamental assumptions: i) pollen analogues of an environment provide an indication of extant vegetation in the surrounding landscape at a particular time, and ii) the vegetational make-up of a landscape is reflective of the surrounding environment, including wider ecological variables such as climate or edaphic conditions (Moore *et al*., 1991). Even with these assumptions in mind, accurate interpretation of these vegetation records are difficult due to the fact that these pollen materials were deposited preceding direct observation and instrumental verification, and hence scientific record. Moreover, the fact that taxa representation in such archives contrasts considerably because of differences in taxon characteristics such as pollen productivity, pollen dispersal area, and environmental conditions at depositional sites increases the complexity of our interpretations of pollen spectra (Bhattacharya *et al*., 2011). As such, a sound understanding of fossil pollen behaviour in an environment is built on observations, the appreciation of modern pollen-vegetation relationships and the principle of uniformitarianism (Bradley, 1999).

It is evident that a key aim of Quaternary palynology investigations is the quantitative reconstruction of vegetation. It stands to reason that vegetation history, as revealed by pollen spectra, turns out to be more valuable if parameters of vegetation can be analytically quantified over and above qualitative description (Broström, 2002; Sugita, 2007a). It is thus realised that a good understanding of the relationship between pollen analogues retrieved at a site and the surrounding vegetation is paramount for a suitable quantitative reconstruction of past environments (Jackson, 1994). Developments in the theory and techniques of palynological research, and the statistical methods used in interpreting pollen assemblages, have greatly enhanced our ability to quantify pollen-vegetation parameters such as: i) vegetation abundances and compositions in an environment, and ii) pollen productivity, pollen dispersal and deposition characteristics, and have facilitated a shift towards eliminating uncertainties in reconstructions of the spatial distribution of plant species and communities of the past (Broström, 2002).

'True' reconstructions of past vegetation patterns or distributions based on pollen analysis have proved elusive despite advances in palynological theories and techniques. Plants species have differential pollen productivity and dispersal potentials and this leads to biases of representation in the pollen record that one needs to be aware of during pollen diagram interpretation (Prentice, 1988; Jackson, 1994; Sugita, 2007b). Furthermore, environmental factors such as topography, site type and basin size, and surrounding extant vegetation all

affect the composition of the pollen assemblage, especially in terms of dispersal, deposition, preservation and local versus regional pollen influences (Sugita, 2007b). Besides these inherent problems during palynological data interpretation, perhaps the most pronounced deficiency in pollen diagrams used for reconstruction is the fact that no explicit spatial context is discernable for *where* in the wider landscape the pollen comes from - consequently, interpretation of pollen diagrams, to date, "remains innately subjective and based on intuition" (Fyfe, 2013, p.1). In any given site containing pollen rich sediments, it is particulary important to consider the sources of that pollen, and the means by which it arrived at its preservation site - only by doing this, can one better interpret the pollen assemblage in terms of past vegetation (Bunting, 2008; Duffin and Bunting, 2008).

The challenge thus faced by contemporary palynologists has been to develop and supply the study of pollen analysis with improved tools for quantifying past vegetation and reconstruction techniques of palaeoenvironments (Räsänen *et al*., 2007). Developments have predominantly occurred in the formation of predictive mathematical and computer models that simulate and capture broad patterns of pollen and vegetation characteristics, such as pollen dispersal and deposition, and have the objective of improving our understanding of the links between pollen and vegetation, and moreover, our interpretation of long-term palaeoecological records (Bunting, 2008; Bunting and Hjelle, 2010). These models are discussed in detail in Chapter Two. Gaining prominence in pollen research mainly in the last decade, such models have shown to output important quantitative vegetation factors for improving palaeoreconstructions, namely pollen productivity estimate and abundance values, and spatial estimates of pollen source areas (Abraham and Kozáková, 2012).

Pollen research using these computer models has primarily been focused in higher latitude environments, with much work in the northern hemisphere, particularly in areas such as Scandinavia (Norway, Sweden, Finland and Denmark), Switzerland and Britain and USA. To date, there has been one pollen modelling study undertaken in Africa (Duffin and Bunting, 2008), and so it is evident that a major gap in pollen research in Africa exists. In light of this gap, it is the hope that this research will stimulate interest in this area of palynological investigations to strengthen the quality and reliability of interpretations of long term palaeoecological records emanating from South Africa.

1.2. Research aim and objectives

This research aims to use models of pollen dispersal and deposition to investigate and better understand the dispersal characteristics and behaviours of pollen in the Cathedral Peak landscape. In particular, this research has the challenge of taking pollen models primarily developed for European landscapes and testing their relevance and suitability in an African context. Considering that pollen analysis research has no explicit spatial framework in which to contextualise its results, that is to say, no spatial relationship has been deduced between where pollen comes from at its source and where it lands up in an environment, it is important that research goes into unambiguously defining this spatial context. One way of doing this is by comparing modern day pollen records with modern day vegetation through models that delineate the distance pollen travels in a specific landscape. Methods involved in such a task engage three particular areas: i) field techniques that entail collecting both surface soil samples from which to extract pollen assemblages, and vegetation data in tiered field survey methods, ii) laboratory techniques standard to pollen analysis research, namely acetolysis chemical procedures, and iii) computer modelling methods that rely on exclusively designed software to simulate models of pollen dispersal and deposition in a landscape.

Specific objectives of this research are:

1) To extend the existing contemporary pollen reference collection for pollen producing plants in the Cathedral Peak area;
2) Identify, describe and inventory vegetation communities in the Cathedral Peak area so as to create a broad resolution vegetation map of the region;
3) Identify suitable and representative sampling locations where soil surface samples can be extracted;
4) Conduct tiered vegetation surveys around each sampling site;
5) Identify, quantify and analyse modern pollen spectra of the relevant study areas by way of surface samples;
6) Determine the variables required to model pollen dispersal and deposition using the HUMPOL software suite. These include:
    i) The estimated pollen grain fall speeds for the main taxa observed in the pollen and vegetation records;
    ii) The distance-weighted plant abundances of taxa around each sampling point to a maximum distance;

iii) The relative pollen productivity for the main taxa observed in the pollen and vegetation record.

iv) The relevant source area of pollen for both each study site within Cathedral Peak and the wider Cathedral Peak environment.

The intention of this research is to fill a gap in palynological research in southern Africa. An understanding of pollen dispersal and deposition characteristics of different taxa in an environment is essential to reduce uncertainty when reconstructing palaeo-landscapes using pollen data. It is necessary to know how, in relation to pollen source vegetation, pollen is spatially dispersed and deposited at a site of preservation. Only by understanding this is one able to better interpret the pollen assemblage extracted from environments in terms of past vegetation assemblages. Once spatial frameworks are attached to pollen analysis investigations, researchers are able to ensure a more vigorous and robust foundation from which they can understand palaeoecological archive data. Despite this research representing a microcosm of possible environments and palynological research areas in which to test these models, its importance cannot be diminished. Considering pollen research in South Africa is becoming increasingly important to issues such as environmental and climate change, techniques and methods of this branch of science are evolving all the time, growing in new technologies and improving the reliability and confidence of results emanating from research. Pollen modelling therefore has the potential to be a vital research area to palynological studies in South Africa.

Chapter Two

Literature Review

2.1. Introduction

Global environmental change is arguably one of the greatest challenges to face modern civilisation and its pursuit of sustainability into the future (Poortinga *et al.* 2011). The uncertainty of threats posed by environmental change has forced the international community to strengthen the reliability of scientific research in issues such as environmental and climate change, human impacts on the environment and the expected impacts and consequences of these on humankind (Black *et al.*, 2011). As such, much emphasis has been placed on progressing scientific academic fields such as geography and environmental science, biology, botany, ecology, and atmospheric science through understanding how these relate to past environmental changes.

Elucidating environmental changes of the past is significant to many branches of the environmental sciences. Palaeoecology has striven to uncover palaeoenvironmental conditions, such as past vegetation compositions of landscapes, through quantitative environmental reconstructions (Salonen *et al*., 2014). Numerous reconstruction techniques exist that employ a variety of fossil biological proxies to reveal past vegetation and hence climate patterns. Palynology is concerned with the study of fossil and live pollen and spores, and is used to elucidate information relating to past vegetation community compositions and climates (Steele and Warny, 2013). 'True' reconstruction of past vegetation based on pollen analysis has proved difficult however, despite advances in palynological theories and techniques. This relates to issues such as plant species having differential pollen productivities and dispersal potentials, environmental factors such as topography, site type and basin size, and surrounding extant vegetation, which all affect the composition of the pollen assemblage (Prentice, 1988; Jackson, 1994; Sugita, 2007b). Therefore, the test faced by palynologists has been to develop and supply the study of pollen analysis with enhanced tools for quantifying past vegetation and reconstruction techniques of palaeoenvironments (Räsänen *et al*., 2007). Developments have largely occurred in the formation of predictive mathematical and computer models that simulate and capture broad patterns of pollen and vegetation characteristics, such as pollen dispersal and deposition, and have the aim of

improving our understanding and interpretation of long-term palaeoecological records (Bunting, 2008; Bunting and Hjelle, 2010).

This literature review discusses environmental proxy data, in particular pollen analysis, as a basis for elucidating past environmental conditions, and demonstrates how palynological investigations have been strengthened and made more robust through the use of pollen models of dispersal and deposition. Specific sections in this review illustrate the origins of the palaeo-sciences and discuss proxy data as a source of palaeoecological information, highlighting the types of proxy archives used. Thorough explanation is given to pollen analysis, with emphasis on modern pollen analysis, as this proxy is the particular focus of this research. Contemporary South African case studies on modern pollen analysis are highlighted. The review moves onto pollen dispersal and deposition modelling, providing a historical overview of the development of these models to their current state. Research using these pollen models is discussed and related to the specific aim and objectives of this research.

2.2. The changing environment

There is no doubt that our environment is changing: it has changed in the past and will continue to change in the future. Throughout the course of the Earth's history, numerous variations in vegetation cover, biodiversity, geology and soil, hydrology, landforms, sea levels and climate have occurred. Such environmental variations are recognised as manifestations of a set of complex interactions between natural and anthropogenic processes and factors, each of which have, and are, operating at different spatial and temporal scales (Thomas, 2004; Rudel, 2008; Henderson-Sellers, 2012). Pre human-induced global environmental change has predominantly been driven by historical 'natural' processes such as climatic variability that provoke changes in both the abiotic (e.g. chemical composition of the atmosphere and oceans) and biotic (e.g. prevalent vegetation structures and communities, extant species niches and species ranges shifts) components of the bio-physical environment (De Falco *et al.,* 2006; Ericksen *et al.,* 2009). The Quaternary geological period, the last 2.58 million years (Ma) of the Earth's history, is the unit of study that scientific inquiry has increasingly investigated with regards to a more 'naturally induced' state of environmental and climate change, relative to contemporary causes predominantly attributed to anthropogenic influences (Meadows, 2001; Gibbard *et al.,* 2010). Long-term Quaternary climate variations are credited with being caused by external modifications outside of the

Earth's climate system, such as periodic alterations in the geometric configuration of the Earth's orbit around the Sun (the Milankovitch cycles), but are, in part, related to some internal mechanisms such as changes in the Earth's energy budget that cause large-scale changes in oceanic circulation, or volcanic activity that modify the chemical composition of the atmosphere or oceans (Goudie, 1981; Otto *et al.,* 2013).

Despite human-beings having dwelt on Earth for approximately the last 3 million years, human-environment interactions only began to be markedly noticeable approximately 10 000 years ago with the advent of agriculture, and more recently in our history (and perhaps more saliently) with the industrial and medical revolutions (Bocquet-Appel, 2011). The rise of an over-populated global modern civil society equipped with agricultural and technological prowess facilitates large-scale rapid and erratic modification of the landscape and its resources by humankind, the over-exploitation and over-consumption of natural capital such as clean air, water and biodiversity, and the discharge of pollutants and contaminants into nature that have fundamentally altered many of the key biochemical processes of the bio- and geo-sphere necessary to produce and sustain life (Mbow *et al.,* 2008; Ericksen *et al.,* 2009; Martínez *et al.,* 2011). Moreover, these anthropogenic environmental modifications over an extended period of time (i.e. the last 10 000 years) have resulted in unprecedented acceleration in global climatic changes that have left all living organisms - man, animal, and plants alike - exceedingly vulnerable to the uncertainty of change. There is, thus, little doubt that the Earth's environment is changing and humans are responsible (McCarroll, 2010).

Scientific enquiry in the Environmental and Earth Sciences has uncovered a dominant shift in the origin of drivers of global environmental change over the past 10 000 years – a shift from nature-dominated to human-dominated environmental changes (Goudie, 1981; Messerli *et al.,* 2000; Mbow *et al.,* 2008). Messerli *et al.* (2000, p. 459) accordingly suggest that the Earth has, as a result of this shift, reached a critical moment in its history as "we move from a century of rapidly growing human impacts on different environments of our planet, to a century with probable further acceleration in the face of human-induced environmental change… we have to rethink the changing relationship between nature and human beings from the past, through the present towards a future full of uncertainty." More to the point, the 'uncertainty' aspect of change makes it especially complex for humankind to anticipate the direction and magnitude of future environmental change, and so there is little doubt that examination of historical data are crucial in the understanding of plausible future scenarios

and outcomes - that is to say, the past holds the key to the future (Mbow *et al.*, 2008; Kundzewicz, 2011).

2.3. Uniformitarianism – the past, the present and the future

As explained by Hanski (2008), humankind is unable to perceive long periods of time due to our limited cognitive and sensory capacities as a result of biological evolution. Consequently, humans perceive time as logarithmic, meaning past phenomena appear relatively closer together the more distant in time they are, until a point is reached in time where all are homogenized and grouped together in 'the past' (Rull, 2010). As such, humans intuitively perceive the present as a continuous and dynamic progression of events linked by time, while 'the past' represents a group of static and fragmented events that occurred at discrete time intervals (Hanski, 2008; Rull, 2010). This perception of time – that the present is continuous and heading towards the future, but the past is static – has made it very difficult for humans to interpret environmental evidence from the past, and furthermore, to understand and use that evidence to effectively comprehend the outcomes of conceivable future scenarios. In consequence, assumptions of time's influence on natural processes and rates have become standard practice in investigations and research relating to environmental concerns (Lomolino *et al.*, 2006).

Environmental Science is a discipline wherein the concept of time and the influence of past events are implicit in the understanding of the modern world (Rull, 2010). Interpretations of contemporary environmental conditions are considered the outcome of constant action in the present, like those in the past. The principle of Uniformitarianism has emerged as one of the foremost tenets in studies of the Earth and its environment, in particular within the disciplines of geology, biogeography and ecology (Harrison and Bartlein, 2012). Although several variations of the principle exists, in its essence it relays the sentiment that 'the present is key to the past' implying that natural processes observed operating in the present are assumed to be the same as those that have operated in the past, and those that will continue to operate in the future (Tomkeieff, 1962; Weiss, 2007; Orme, 2013;). More to the point, the principle of Uniformitarianism stresses that the past, present and future are not discrete divisions of time, but are rather a continuum through which the environment changes and evolves (Rull, 2010; Harrison and Bartlein, 2012). However, despite widespread adoption of the principle in matters pertaining to the environment and its change through time, since under conditions of uncertainty (with respect to global environmental change) it is not logical to assume that

properties of past processes will remain the same and therefore be applicable in the future, Uniformitarianism is only valid to a limited extent (Rull, 2010; Kundzewicz, 2011).

Anthropogenic pressures notwithstanding, present day conditions of the biosphere are a result of the mutual interactions between ecological and historical factors – that is, ecological factors that account for contemporary biodiversity patterns and extant species' assemblages and niches, and historical factors that reflect long-term processes associated with succession, range shifts, and evolution under the assumption of Uniformitarianism – and each of these agents plays a vital role in shaping our present-day world (Emerson and Gillespie, 2008). The distinction between ecological and historical, however, is often ambiguous and can lead to confusion in determining where the past ends and the present begins (Rull, 2010). As Gosling and Bunting (2008) suggest, it is crucial that this distinction (between past and present) be determined to better interpret the possible future responses of our environment to expected and projected changes. Ecological time (weeks to decades, or occasionally centuries) is considered insufficient to resolve the gradual ecological, biological and chemical dynamics and reactions of the biosphere that occur with change, emphasizing the need for longer temporal perspectives of the past when attempting to appreciate probable future scenarios of environmental change (Jackson, 2001; Jackson and Erwin, 2006). In light of this need, scientific disciplines relevant to the study of the Earth and its environment evolved a new branch of science, palaeo-science.

2.4. *Palaeo*- science

The prefix palaeo-, defined as 'old' or 'ancient' (Birks and Birks, 1980), has had an immense impact on the study of the Earth and its transformation over long time-scales - researchers working in palaeo-sciences thus concern themselves with 'the past', investigating parameters and proxies with reference to long time-scales, and the scientific data they collect relates to a period *a priori* to the availability of technological and instrumental measurement (Bradley, 1999). Disciplines such as geography, zoology, botany, climatology and ecology have all adopted a branched discipline preceded by palaeo- (Rull, 2009; 2010). Of significance to this research is the field of palaeoecology, defined by Birks and Birks (1980) and Birks *et al.* (2010, p.68) as "a branch of ecology that studies the past of ecological systems and their trends in time using environmental proxies, and is principally charged to provide ecological enquiry with a longer temporal scope". Yet, as Rull (2010) critiques, the word palaeo- has the ability to homogenise disciplines into a singular 'community of study' to such an extent that

palaeoecology is regularly confused with other palaeo-disciplines such as palaeoclimatology or palaeoenvironmental reconstructions. Although the reconstruction of prehistoric environments has long been a key objective of palaeoecology, it (palaeoecology) is not synonymous with palaeoenvironmental reconstruction (Sachs *et al.*, 1977; Rull, 1990; Rull 2009). Palaeoenvironmental reconstructions use biological, physical or chemical indicators as proxies, such as fossils or elemental isotopes, and ecological knowledge and expertise is used to reconstruct the physical environment – therefore the objective of a palaeoenvironmental reconstruction need not necessarily be ecological, but can be, for example, climatic (Rull, 2010). Palaeoecological endeavour, however, should by definition have an ecological objective. Nevertheless, despite the subtle disparities between the two, climate certainly is a fundamental part of all natural systems and has a direct link with ecology and palaeoclimate reconstructions are thus exceedingly relevant in palaeoecological examination.

2.5. Proxy data – sources of palaeoecological information

It is appreciated that climate and ecology have an inextricable relationship, as every ecosystem is dependent on climate to some extent (Starfield and Chapin III, 1996; Bradley, 1999). As such, palaeoclimatic and palaeoecological proxy data sources frequently overlap since it is possible to make ecological inference indirectly from climatic data, and vice versa. Therefore, it is necessary to discuss all principal sources of proxy data, whether explicitly ecological or not. A proxy is described as an archive component that can be correlated to an environmental parameter or process and are typically categorised on the foundation of their type (biological, physical, chemical etc) (Fischer and Wefer, 1999; Abrantes *et al.*, 2012). Furthermore, proxy indicators are extensively used as they have the potential to uncover evidence of environmental variation at multiple spatial and temporal scales preceding the existence of scientific instrumentation and historical records (IPCC, 2013). Calibration of proxy indicators against modern instrumental data are required to facilitate a reliable association between the proxy indicator and the environmental (or climatic) variables it is assumed to represent, thereby making available a 'transfer function' that is then used to approximate a quantitative reconstruction of past conditions (IPCC, 2013). Transfer functions are empirically derived equations used to calculate estimates of 'past' conditions from palaeoecological data by way of correlating modern species' assemblages with their fossil assemblages (Simpson, 2007; Balch, 2012). More to the point, and by way of example, if palaeoecologists know that species 'A' is always found in environmental conditions 'X', and subsequently find species 'A' in the fossil record, deduction can be made that the

environmental conditions at that time in the past were analogous to 'X' (Balch, 2012). In sum, palaeoecological studies (including palaeoenvironmental reconstructions using proxy indicators) are essentially motivated by fundamental scientific and societal needs to better understand our environment, especially in terms of being able to discriminate between human-induced and naturally occurring change, with the intention of assisting future predictions of our Earth's response to expected climatic and environmental variations due to relentless anthropogenic pressures (Abrantes *et al.*, 2012).

2.6. Types of natural archives – principal sources of proxy data

Natural systems have an adept archival ability, storing information of events and conditions in their history similar to a computer storing information in its memory – science just has to know where to look to uncover these records. Proxy material acts as a filter, transforming environmental or climatic conditions of a particular time period into a natural record that is stored in the cache of the environment (Bradley, 1999). There are a number of major proxy data sources that have been uncovered in the pursuit of palaeo-science, each differing according to their spatial coverage, temporal resolution and ability to resolve events. All studies of past environments should begin with a broad understanding of the proxy data types available and the methods used in their analyses. The following proxy categories are after Bradley (1999).

2.6.1. Chemical proxy indicators

Considering every constituent of the natural world (atmosphere, biosphere, geosphere, and hydrosphere) has, at its base, a primary elemental composition, it is clear that chemical proxy indicators hold potential for archiving palaeoenvironmental conditions. Chemical proxy data sources involve investigation into the geochemistry of isotopic analysis of elements such as oxygen, hydrogen, nitrogen and carbon, and the extraction of compounds such as carbon dioxide, methane and sulphur dioxide from a range of different environments (Elias and Mock, 2013).

2.6.1.1. Ice core analysis

The accumulation of ice and snow in high latitudes and altitudes (the polar ice caps, glaciers, and ice sheets) of the world provides an indispensible record of palaeoenvironmental conditions. In these regions, snow melt is very low such that snow accumulation has been continuous in various areas for thousands of years. Gas bubbles that are locked in the layered

strata of ice and snow store a mixture of elements that, when extracted and analysed from ice cores, provide comprehensive records of precipitation, temperature, atmospheric composition and evidence of volatile volcanic activity (Bradley, 1999; Elias and Mock, 2013). Essentially, this involves isotope analysis. Isotopes result from variations in the atomic mass of elements - where the number of neutrons in an atom's nucleus varies, but the number of protons and electrons remains constant (Bradley, 1999). For instance, oxygen has 3 naturally occurring isotopes (^{16}O, ^{17}O and ^{18}O) with 8, 9 and 10 neutrons respectively, with ^{16}O being the most abundant. As ^{18}O is 'heavier' than ^{16}O, more energy is required to vaporise it. Therefore the lighter ^{16}O evaporates more easily than ^{18}O, and in turn ^{18}O is preferentially removed in condensation. It is consequently expected that in warmer, wetter climes there would be an excess of ^{18}O, and depletion in colder dryer climates. By unlocking an excess or depletion of an isotope in ice core bubbles, it is possible to infer palaeoclimatic, and hence palaeoenvironmental, conditions (Bradley, 1999).

Progress in isotope analysis is increasingly being made using 'natural isotope recorders' such as speleothems (stalagmites and stalactites), tree-rings, peat bogs, coral and lake sediments (Elias and Mock, 2013). Oxygen, hydrogen, nitrogen, and carbon isotopes are being extracted from organic and inorganic compounds within these mediums and analysed in much of the same manner described above. Isotope analysis is well suited for multi-proxy studies as interpretations based exclusively on isotope data are limited, constrained and uncorrelated (Elias and Mock, 2013).

2.6.2. Biological proxy indicators

To be used as a proxy indicator, a biological proxy must have a number of essential characteristics. These include: rapid reproductive ability; high abundance; it must be easily and consistently identifiable; readily preserved in a suitable environmental medium; and ecologically limited to particular environmental conditions (Elias and Mock, 2013). As such, a number of biological proxy indicators exist.

2.6.2.1. Tree ring analysis

Reading the variations in tree-ring width has long been recognised as a key source of chronological palaeoenvironmental information. Fundamentally, tree-ring analysis involves examining a cross section, from pith to cambium, of a core extracted from a tree's trunk, interpreting the annual growth increments of the couplet early and late wood - namely, the

tree ring. The width of the tree-ring is dependent on several ecological (tree species, tree age, nutrient content of the soil) and climatic variables (sunshine duration, precipitation, temperature, humidity) and these can be inferred from tree-ring analysis (Bradley, 1999). These records can be precisely dated and annually resolved, implying that cross-dating, calibration and verification of tree-ring data is made undemanding in light of a robust and known chronology. However, there are several limitations, these include the relatively short time-scales of variation elucidated by tree-ring data (usually only a couple of centuries at best, and so are inappropriate for millennial enquiry) or sampling bias (as trees are only found in terrestrial environments, and so do not cover large portions of the Earth) (IPCC, 2013). It is therefore most useful to supplement tree-ring analysis with other types of proxy information when estimating past conditions (Elias and Mock, 2013).

2.6.2.2. Faunal and floral fossils

Fossil remnants are a vital proxy indicator for interpreting palaeoenvironmental conditions, and are classified as either macro or micro depending on vestige size. Fossils are a good proxy indicator as they can be found in both terrestrial and marine environments and so supply palaeoenvironmental investigations with a comprehensive database with which to work. Generally, requirements for fossilization of a biological entity entail a durable structure and composition, so either a 'hard' or resilient 'soft' component that does not easily decompose along with a mixture of the right environmental conditions promoting preservation (Elias and Mock, 2013). Furthermore, macro- and micro-fossil information is readily identified through geochemical analyses and microscopy respectively, and furthermore, can be easily compared to a number of existing modern and fossil species' catalogues. Examples of fossil proxy indicators include a list of data sources that comprise: plant and animal macro fossils that are radio-carbon dated, insects, mollusks, diatoms, foraminifera, ostracods - amongst many others – that are generally extracted from sediment cores, and common environmental settings that are conducive to the unearthing of fossil indicators including lake sediments, wetlands, salt marshes and bogs (Bradley, 1999). The value of these indicators lies in being able to quantify an organism's optimum environment using ecological expertise. In revealing a taxon's environmental niche space and tolerance in a modern context, it is possible to link its incidence in a stratigraphic profile (and therefore time) to particular environmental conditions that occurred in the past (Elias and Mock, 2013).

2.7. Pollen analysis

2.7.1. Introduction

As pollen analysis is the focus method of this research, it warrants a more comprehensive discussion. Palynology, defined as the study of pollen grains, is concerned with the formation and structure of pollen grains and with their dispersal, deposition, and preservation under specific environmental circumstances (Moore *et al.,* 1991). The fundamental principles of the pollen analysis method provide researchers with a means of reconstructing vegetational frameworks of the past (including plant populations and community assemblages), which facilitates reconstruction of past ecosystem regimes of an environment (Elias and Mock, 2013). According to Bunting (2008), pollen analysis is likely the most widely used proxy indicator for establishing palaeoecological conditions, and moreover, in reconstructing past vegetation dynamics extending long time scales up to millennia. Pollen is a suitable biological proxy as, annually, millions of tons of pollen material is released and dispersed into the atmosphere by the Earth's flowering plants in a concerted effort to reproduce (Bradley, 1999). Pollen grains are extremely small and thus easily dispersed, are produced abundantly and contain a robust outer layer which is resistant to decay (Moore *et al.,* 1991; Bunting, 2008). In particular environmental conditions where decay processes (e.g. pollen oxidation, microbial attack, or extremely dry conditions) are largely absent, this resistant outer layer can be well preserved and trapped in sediment that accumulates steadily over time (Moore *et al.,* 1991; Bradley, 1999; Bunting, 2008; Amami *et al.,* 2010). By coring this stratigraphic sediment and extracting the pollen locked in the layers, one is able investigate how plant community composition and abundances vary over time.

2.7.2. Pollen analysis as a biological proxy

Palaeoecological inference through pollen analysis is achievable in this research due to the following assumptions and characteristics: i) pollen grains possess unique morphological attributes particular to specific families of plants; ii) pollen grains are produced in abundant quantities and dispersed from their source; iii) their robust outer wall makes pollen grains extremely decay resistant (and in turn prone to preservation) in certain environments; and iv) it is assumed that pollen grains reveal the nature of surrounding vegetation present at the time of pollen deposition (Moore *et al.,* 1991).

2.7.3. Pollen grain structure and composition

Pollen grains are exceptionally small particulate matter that range from 10-100μm (along the long-axis) and are protected from a number of decay processes by a 'wall' that is comprised of two layers – the exine and intine. The outer layer, the exine, is a chemically resistant cover comprised of sporopollenin, a biopolymer compound that can withstand the most severe chemical oxidising and reducing agents, such that pollen grains are not destroyed when ground (Bradley, 1999; Bunting, 2008). The inner layer, the intine, is a part of the pollen grain wall comprised of cellulose and is similar in construct to that of a plant cell wall (Moore *et al.,* 1991). Moreover, pollen grains have a unique and very specific morphology, and can be distinctively recognised and attributed to particular plant families or genera based on distinguishing size, shape, physical features, and number of apertures (Faegri and Iversen, 1975). It should however be recognised that pollen identification by light microscopy is limited and difficult to achieve, especially to as high a resolution as plant species level, and so identification has proven to be a complicated aspect in palaeoecological studies (Nakazawa *et al.,* 2013).

2.7.4. Pollen productivity

The source of pollen production is vegetation, and for that reason, a thorough understanding of vegetation bordering a sampling location is essential to the analytical use of pollen data. All plant life that partakes in sexual reproduction produces pollen grains containing the male gamete, and disperses them using a range of mechanisms in an effort to arrive at, and more importantly, fertilise the female structures of other plants (Bradley, 1999; Bunting, 2008). Yet plant species differ considerably in the amount, frequency, and periodicity of pollen produced, and as a result, a pollen signal never perfectly reflects the fraction of plant species in the surrounding vegetation communities at the time of deposition, as some pollen types are under or over represented in the pollen record (Prentice, 1988; Sugita, 1994). Furthermore, vegetation assemblages are dictated by altitudinal, latitudinal and longitudinal prevailing climate parameters that directly influence pollen abundance and periodicity, and hence pollen productivity. Adding complexity to the situation is the issue of scale, where pollen production varies both spatially and temporally, and the pollen record exhibits local and regional influences – these challenges need to be taken into consideration when attempting to discern vegetation patterns from pollen spectra (Prentice, 1988; Bradley, 1999). Therefore a sound understanding of the associations amongst modern pollen rain, vegetation and the broader

environment is critical to the use of fossil pollen data as a proxy for past vegetation dynamics (Minckley *et al.,* 2008).

2.7.5. Pollen dispersal

In any given pollen-rich sediment site, it is essential to consider the sources of that pollen and the means by which it arrived at its preservation site - only by doing this, can one better interpret the pollen assemblage (Moore *et al.,* 1991). Knowledgeable interpretation of pollen assemblages depends on a sound understanding of how pollen grains reach a site of preservation and how it acts upon arrival as this attaches important spatial understanding of pollen behaviour characteristics in an environment (Sjögren *et al.,* 2008). According to Birks and Birks (1980), pollen dispersal is dependent on a number of variables that include atmospheric turbulence, wind speed and direction, grain morphology and weight, and the height and strength of the pollen source. Moreover, considering the variations in pollen morphology (size, shape and weight) between plant species and the variations in climatic factors in different environments, it is not unsurprising that pollen types have differential aptitudes with regard to their aerodynamic and dispersal abilities. There are a number of differing modes of dispersal that facilitate the diffusion of pollen grains into the wider landscape, with the main modes of dispersal being either by wind (anemophily) or by animals or organisms (zoophily). The mode 'chosen' by a plant species has a noticeable effect on the amount of pollen produced, on its diffusibility and a plant taxon's contribution to the pollen assemblage (Bunting, 2008). As Bradley (1999) explains, the quantity of pollen produced is generally inversely proportional to the probability of fertilization success, and so zoophilous species produce orders of magnitude less pollen than anemophilous species. Proportions of species in the pollen assemblage can thus be misleading, and may reflect biases concerning anemophilous species in the surrounding landscape at the time of deposition. Furthermore, since vegetation is heterogeneous and mosaicked, one has to assume a pollen spectrum represents an average vegetation signal of the proximal landscape at a particular point in time, rather than an absolute account of vegetational make-up (Sugita, 1994).

2.7.6. Archives of pollen

Pollen grains are preserved in a selection of materials from which they can be extracted and classified. The interpretation of pollen spectra must take into consideration the nature of the material from which they were extracted since the influx, movement, and preservation of pollen grains differs between sources (Moore *et al.,* 1991). Pollen is predominantly

considered an aeolian deposit and, upon settling where organic and inorganic sediments are amassing, will become a component of the stratigraphic record (Traverse, 1994). Aeolian manipulation of pollen in the Earth's atmosphere advocates that pollen should be found in a range of environments across extensive spatial scales. As such, pollen has been recovered from lake, marsh, alluvial and loess sediments, animal middens and coprolites, archeological sites, estuarine and marine sediments, and glacial and polar ice (Bradley, 1999).

2.7.6.1. Lakes and marshes

Waterlogged sites, such as those provided in lakes and marshes are invaluable sources of palaeoecological evidence due to their ability to effectively preserve a range of materials, including pollen. Pollen arrives at these locations either by wind, carried in precipitation, or inwashed in water that drains over the surface of the surrounding catchment or is supplied by a feeding river (Tauber, 1965). Upon arriving there, since there is an absence of aerobic and biological decay processes, the exine of pollen grains trapped in sediment can be preserved for thousands of years (Bunting, 2008). Matter that is sedimented in lakes and marshes is derived both within and outside the confines of the source itself, that is to say, materials from plants and animals extracted from these sources are *allochthonous* and *autochthonous* and therefore represent both local and regional vegetation patterns (Moore *et al.*, 1991).

Lakes and marshes differ in a number of characteristics such as catchment size and shape, geology, soils and topography, and water depth and nutrient status, and these factors manipulate a source's patterns of pollen influx and sedimentation. Lake and marsh deposits develop in a stratified sequence over time, although bioturbation is a recognized limitation in the surface layers of sediment caused by water turbulence, organisms and plant roots, especially in shallower waters, and thus re-suspension and re-deposition of sediment both laterally and vertically can present problems when interpreting pollen spectra extracted from these sources. Therefore, in the context of pollen analysis investigations, it is assumed that because of lake and marsh processes, pollen is considerably mixed in lake and marsh water, and for that reason, a sediment core extracted at the deepest part of the site is likely the oldest representation of the vegetation structure in the surrounding area (Kangur, 2009).

2.7.6.2. Alluvial sediment and soils

Soil and alluvial materials have been afforded less consideration for pollen analysis as compared to waterlogged sediments because of both the poor preservation of pollen in

aerobic environments and the vertical mixing of the profiles at deposition sites by biological organisms, soil fauna and percolating water (Moore *et al.*, 1991). Pollen arrives at these sites either by wind, carried in precipitation, or in water that drains over the surface of the surrounding catchment (Tauber, 1965). The rate of sedimentation in locations of pollen rich soil and alluvial materials is dependent on a collection of factors, but predominantly upon climate and vegetational composition of the surrounding environment - increased water availability and sparseness of vegetation can lead to an increased sedimentation rate (Moore *et al.*, 1991). However, due to erosion, bioturbation and water percolation, downward movement of pollen in the soil is a major challenge and can cause 'stratified pollen zones' in the profile. In light of this, interpretation of the stratigraphic sequence of pollen in a soil or alluvial core can lead to uncertainties in chronology and such evidence must be prudentially inferred. Nevertheless, these sources of pollen are central to unearthing important and useful palaeoecological evidence and are a significant basis for palaeoenvironmental reconstructions (Gregory, 1983).

2.7.6.3. Animal middens and coprolites

Fossilised animal faecal material has been used as a means of establishing extinct faunal dietary preferences, especially herbivores, and inferences can be made regarding main plant compositions in the surrounding environment at a time in the past (Carrión *et al.*, 2001; Yll *et al.*, 2006). Possible sources of pollen found in faecal matter include: i) pollen directly ingested in food or drink; ii) pollen settling onto food from the atmosphere; or iii) pollen inhaled and swallowed by fauna during respiration (Moore *et al.*, 1991). The value of studying fossilised midden and coprolite materials lies in it allowing palynologists and palaeoecologists to reconstruct poorly known or inaccessible locations, such as extreme arid environments thereby filling a gap in palaeoreconstruction investigations and palaeoecological knowledge (Carrión *et al.*, 2005; Meadows *et al.*, 2010; Chase *et al.*, 2011; 2012).

2.7.6.4. Glacial and polar ice

The investigation of pollen analysis in stratified ice cores is a useful tool in palaeoenvironmental reconstructions of past changes (Liu *et al.*, 2005). Compacted snow in high altitude and latitude regions becomes consolidated as ice over time, thereby amassing a stratified profile within which dust, pollen and other particulates are incorporated and locked (Moore *et al.*, 1991). However, as Bourgeois (2000) reveals, despite innumerable palaeo-

climatic and -environmental studies having been completed using ice cores, much of this work has pertained to geochemistry and isotope analysis, with little consideration for the biological indicators locked in ice, such as pollen, bacteria and diatoms, which have the potential to convey evidence of environmental conditions in the vicinity of the ice caps or glaciers.

2.7.7. Fossil and modern pollen

At this juncture it is necessary to distinguish the difference between fossil and modern pollen assemblages as it pertains to palynological investigations. Pollen analysis is a tool that assists many researchers of varying research backgrounds who have a range of research aims and objectives in problem solving and analytical investigations. Consequently, palynology has many facets or 'study areas' which are investigated under particular research intentions, least of which include fossil and modern pollen assemblages. It is therefore up to the researcher, their research purpose, and intended methodology as to which aspect of palynology they plan on examining (Moore *et al.,* 1991).

2.7.7.1. Fossil pollen

A fundamental aspect of pollen analysis is the study of fossil pollen grains (those pollen grains extracted from ancient or present-day materials) and has predominantly been used as a technique in Quaternary studies to elucidate long term vegetation-climate dynamics and changes (Edwards, 1983). The Quaternary period, formally ratified at 2.58 million years (Ma) ago (Gibbard *et al.,* 2010), is widely acknowledged (and is moreover documented in multiple proxy indicators) as a time of pronounced global climatic variations, with continual changes between glacial, interstadial and stadial conditions. Attributed to the Milankovitch cycles, these climate changes have coincided with variations in the Sun-Earth geometry in phases of approximately 100 000 yr, 40 000 yr and 23 000 yr, correlated with alterations in excentricity, obliquity, and precession of the Earth's orbit respectively, which have manifested in oscillations between warmer and cooler periods in the Earth's history (Kehl, 2009). The Earth's climate is thus a dynamic system, and the marked climate fluctuations that have occurred over the last 2.58 Ma have had an obvious effect on the present environment. Vegetation is viewed as an index of climate – and vice versa - as, at a large scale, the geographical distributions of vegetation assemblages overlap considerably with broad geographical distributions of climatic features such as temperature, precipitation, evapotranspiration etc – this climate-vegetation link is the fundamental parameter underlying

the notion of global biomes (Gavilán, 2005). Consequently, reconstructing Quaternary palaeo-vegetation and palaeo-environmental conditions by means of fossil pollen analysis is primarily concerned with determining and establishing past variations in the environment and climate, and moreover, understanding the mechanisms and causes of these changes prior to scientific record. It therefore follows that only by applying principles and knowledge gained in modern pollen research is it possible to appreciate and understand these mechanisms of change and the dynamics of palaeo-environments within a spatial and temporal framework (Odgaard, 1999).

2.7.7.2 Modern pollen

As already elucidated, fossil pollen preserved in stratigraphic sequences provide a key proxy for understanding past environmental changes. However, accurate interpretation of these records is elusive and difficult due to the fact that these materials were deposited preceding direct observation and instrumental verification, and hence scientific record. Moreover, the fact that species' representation in such archives contrast so significantly because of differentiation in pollen productivity, pollen dispersal area, and environmental conditions at depositional sites increases the complexity of our interpretations of pollen spectra and the subsequent inferences we are able to make from them (Bhattacharya *et al.,* 2011). For these reasons, a primary understanding of patterns and relationships of fossil pollen's behaviour in an environment must necessarily build on observations and appreciation of modern pollen-environment relationships and the principle of Uniformitarianism (Bradley, 1999). In addition, investigation of the associations between modern pollen rain, vegetation and the surrounding environment clarifies the relationships between plant assemblages, pollen dispersal and pollen deposition, and is important for accurate reconstructions and understanding of palaeoenvironments (Niemann *et al.,* 2010; Bhattacharya *et al.,* 2011).

2.7.8. Pollen sampling and analysis

Applications of pollen analysis depend on one's particular research objectives, and in turn, these research questions provide a direction for establishing the most suitable and appropriate sampling method of stratified sequences of pollen source material. Excavation of samples at pollen-rich sites can either occur at exposed locations, such as erosion faces of cliffs or soil, or in circumstances where deposits might be difficult to extract, such as wetland or marine deposits, that requires specialised equipment to recover these samples (Moore *et al.,* 1991). A

collection of sampling apparatus has been used in palynological enquiry, each of which is appropriate for particular source materials, and moreover, relevant for specific tasks.

2.7.8.1. Pollen extracted using cores

At sampling sites where pollen-rich material is hard to reach and recover, cores must be extracted from the site using specialised core sampler instruments. Although not exclusively the case, in the main, core research as it relates to palynology is predominantly used for fossil pollen investigations. Research pertaining to coring sediments to reconstruct palaeoenvironments is based on Walther's Law of Uniformitarianism, which states that, "the various deposits of the same facies areas, and similarly the sum of the rocks of different facies areas are formed beside each other in space, though in cross section we see them lying on top of each other" (Middleton, 1973; Ellison, 2008 p.94). The guidance this conveys to core-based investigations is two-fold: i) the principle directs interpretation of the stratigraphic record that sedimentary divisions increase in age with depth, and ii) the principle guides that one core is representative of an entire basin, and is thus the reason why replication is rarely used in pollen analysis save for instances where high temporal resolution is required (Ellison, 2008). As explained by Moore *et al.* (1991) a range of core samplers have been developed for different environmental conditions. Furthermore, the type of core sampler used is dependent on research objectives, amount of sample needed for investigation, logistics of the site, such as sediment depth and access, and the most limiting factor, equipment availability (Ellison, 2008).

2.7.8.2. Pollen traps and surface samples

Pollen assemblages, recovered from pollen traps and sediment surfaces in particular vegetation communities, are regularly utilised to develop reference sets of modern pollen rain characteristics of those specific vegetation types (Wahl, 2003). These samples are commonly compared with fossil pollen assemblages that were collected in the same spatial area, with the aim of reconstructing the vegetation that produced the fossil pollen spectrum (Davis, 1995; Bamonte and Mancini. 2011). When used in this manner, modern pollen rain samples are called 'analogues' if they closely relate to a fossil pollen assemblage, and the vegetational composition that produced the fossil pollen assemblage can be directly inferred from that vegetation found at its analogue sites (Davis *et al.*, 1998). As such, a comprehensive understanding of the modern pollen rain-vegetation relationship is an important prerequisite for a thorough analysis of past ecosystems and environmental dynamics using pollen data

(Marcos and Mancini, 2012; Jantz *et al.,* 2013). As Bunting (2008) elucidates, there are two fundamental assumptions underlying pollen analysis and environmental reconstructions based on modern pollen-rain; i) modern pollen rain provides an indication of vegetation existing in the surrounding landscape and ii) the contemporary vegetational composition of an area is reflective of the surrounding environment.

Although it is recognised that both aquatic and terrestrial surface samples can be used for pollen analysis, 'surface samples' hereafter refers explicitly to terrestrial. The type of surface material used for pollen sampling must be prudently chosen as the composition of extracted pollen spectra have been shown to differ with environmental conditions, such as sedimentation rates (Moore *et al.,* 1991). Moreover, the positions of surface samples are dependent upon the spatial pattern of vegetation being studied, and hence a major intention of using surface materials should be to relate modern pollen data to its surrounding vegetation. The most common types of surface sample materials used include moss polsters or surface soil samples, and which is used depends on the presence of one or the other at a sampling location. Moss polsters, unconsolidated 'mats' of moss, have been found to be effective natural pollen traps and standard field collection protocol is to extract only the green parts of the polster (Berglund *et al.,* 1986; Broström *et al.,* 2004). Basic interpretation of pollen trapped in moss polsters is that the green part of the polster represents growth, and hence pollen accumulation over a specified time (Moore *et al.,* 1991). Numerous authors have argued over the number of years represented in moss polsters, with consensus reaching anywhere between one and ten years depending on the moss species and its growth rates (Pitkin, 1975; Bradshaw, 1981; Cundill, 1986; Broström *et al.,* 2004). Pollen accumulation is in part a result of the depositional environment, and therefore, pollen content is expected to be present in the soil surface sediment at sampling localities. Surface soil samples involve removing the top few centimeters of soil at a site (usually with the top 2 cm of the soil) using a trowel or spatula (Adam and Mehringer, 1975). There are a number of limitations with surface soil samples as they relate to palynological enquiry however, namely, vague sedimentation rate knowledge and unknown time periods covered by the top 2 cm. Relating pollen data to its surrounding vegetation through the use of surface materials is thus difficult, as we do not accurately know how long a period the samples cover or how far away each pollen type comes from (Xu *et al.,* 2009). Nevertheless despite these difficulties, soil surface samples are extensively used in the study of pollen, vegetation and environment relationships, as these samples are easy to obtain and do not require specialised equipment or materials.

Pollen traps are both an alternative and supplementary way of collecting and sampling modern pollen rain. A range of pollen traps have been engineered for different environments, each with their own aerodynamic characteristics and hence trapping efficiency (Moore *et al.*, 1991). Moreover, the ability of traps to collect modern pollen rain varies with meteorological conditions, most notably wind speed and direction. Essentially, the basic mechanics of a pollen trap involves some form of a container with an aperture or open area covered in a screen or netting through which pollen blows into, filters and collects in a synthetic fibre such as acetate fibre. The trap is either placed at ground level or some predefined height above the surface of the vegetation, depending on the type of trap used. This is a simplistic explanation of pollen trap engineering however, and a number of various pollen trap types and modified trap types exist - typical traps include the Tauber trap, the Cundill trap, the Oldfield and modified Oldfield traps, and the newer Behling trap (For a comprehensive discussion on trap typology see Tauber, 1974; Cundill, 1986; Hill, 1992; Behling *et al.*, 2001; Jantz and Behling, 2011; Jantz *et al.*, 2013).

The use of pollen traps over surface samples helps to overcome the uncertainties of using surface materials, especially in terms of quantitative investigations regarding pollen productivity and pollen accumulation rates since traps provide pollen accumulation over a known time (Barnekow *et al.*, 2007). Yet, both pollen traps and surface sediments do not explicitly provide information on pollen dispersal and deposition characteristics. In either case, whether a pollen trap or surface material is used, the aims of such research has frequently been to obtain a better reference or basis for interpretation of fossil pollen assemblages (Tonkov *et al.*, 2001). In interpreting pollen diagrams of fossil pollen sequences of the Quaternary, and perhaps more importantly in quantitatively reconstructing palaeoenvironments, it is crucial to know whether a taxon, whose pollen is recorded in the sediment, occurred in the vicinity of a site or at some distance away (Tonkov *et al.*, 2001). One potential approach in achieving such information is to model pollen-vegetation relationships, a recent research theme in pollen analysis that has lead to the development of models of pollen dispersal and deposition that are shown to capture and represent the broad patterns of pollen deposition in relation to surrounding vegetation (Bunting, 2008; Bunting *et al.*, 2008a; Bunting and Hjelle, 2010). These models have been developed with the aim of facilitating a more secure and robust basis for improving our understanding and interpretation of long-term palaeoecological archives.

2.7.9. Palynological case studies and research

A primary goal of palynological research has been to reconstruct palaeo-environments as precisely as possible using fossil pollen evidence. However, to achieve this, an understanding of how contemporary vegetation is represented in the modern pollen rain of an environment, is required (Reese and Liu, 2005). It therefore follows that modern pollen studies are crucial to improving the interpretation of fossil pollen spectra in terms of palaeoenvironmental reconstructions. Quantitative reconstructions of past environmental variables, such as climate or vegetation composition, has been facilitated by applying transfer functions to modern pollen rain and its relationship to the surrounding vegetation (Schäbitz *et al.*, 2013). Pollen transfer functions involve models developed to depict association between modern pollen spectra to present abundances of vegetation in a landscape. Assuming uniformitarianism of environmental conditions through time, the model is then used to reconstruct past environmental parameters from fossil pollen analogues (Paus, 2013). Three standard pollen transfer function approaches are commonly used in pollen analysis investigations (after Paus, 2013):

i) Modern Analogue Technique (MAT) – see Simpson *et al.* (2007)
ii) Weighted Averaging (WA)/ Weighted Averaging Partial Least Squares (WA-PLS) – see Bjune *et al.* (2010)
iii) Probability Density Functions (PDF) – see Kühl *et al.* (2010)

The importance of understanding modern pollen rain-vegetation relationships by way of transfer functions for improving past environmental reconstructions cannot be overstated. As modern pollen spectra is the focus of this research, past and present studies on fossil pollen investigations in South Africa will not be reviewed.

2.7.9.1. South African modern pollen research

While a plethora of pollen analysis literature exists in South Africa, the majority of it concerns fossil pollen investigations of the Quaternary period. Little contemporary work, in comparison, has been undertaken on modern pollen rain and its relationship to surrounding vegetation to better understand palaeoenvironmental reconstructions. While some palynological literature in South Africa focuses exclusively on modern samples and the pollen rain data extracted from there, modern pollen rain enquiries are infrequent and usually secondary in a study to those cored materials used to extract fossil pollen assemblages. This

emerges as a significant gap in palynological research in South Africa considering the robust interpretative basis that modern pollen analysis provides in contextualising fossil pollen studies and subsequent reconstructions (Scott *et al*., 2012).

To date, Hill (1992) has assembled the most comprehensive review of modern pollen studies in Cathedral Peak. Hill's PhD thesis primarily concentrated on critically assessing and understanding the relationship and interaction between contemporary pollen rain and surrounding vegetation in environs of Cathedral Peak. This involved collection of modern pollen rain by way of both pollen traps and soil surface samples, and adjacent vegetation community data to answer the critical question of whether modern pollen rain can be related to the vegetation communities from which it derives. It was found by Hill (1992) that modern pollen spectra examined using trap and soil surface sample mediums in the Cathedral Peak region provide a good indication of local and regional vegetation community assemblages. Hill's (1992) work drew fundamentally on early work pertaining to modern pollen analysis undertaken in South Africa by Coetzee and van Zinderen Bakker (1952) and van Zinderen Bakker (1955; 1982), all of which examined modern pollen spectra in particular landscapes and its relationship to the surrounding vegetation to augment fossil pollen investigations.

Cadman (1990) and Cadman and Dames (1993) used atmospheric sampling methods to extract modern pollen spectra from the atmosphere in Johannesburg and Pretoria, and Durban, respectively. The purposes of these studies were to assess and examine the pollen components in the air of these major cities in South Africa for medicinal purposes, but also to deduce the vegetational biomes of these modern pollen assemblages. Moreover, these studies were specifically done with airspora and their allergenic ramifications in mind considering the population densities of these areas. Cadman (1990) found that Johannesburg and Pretoria pollen spectra reflect the wider grassland and savanna biomes in which they are found, and Cadman and Dames (1993) found that Durban's pollen spectra, rather than reflecting those taxa expected in the wider sub-tropical environment, showed a vegetational community made up of exotic and cultivated vegetation.

As already highlighted, most palynological studies in South Africa have the primary objective of long term investigations using fossil pollen, and only on the odd occasion are these investigations supplemented by modern pollen samples and data. Important authors pertaining to pollen research in South Africa include work done by Backwell *et al.* (2014), Baxter and Meadows (1999), Finch and Hill (2008), Meadows (1988; 1989; 2001; 2010),

Metwally *et al.* (2014), Neumann (2008), Norström (Norström *et al.*, 2009; Norström *et al.*, 2014), Scott (1979; 1982; 1986; 1990; Scott *et al.*, 2009), Truc *et al.* (2013) and Valsecchi *et al.* (2013). This is by no means an exhaustive list of work undertaken by important authors, but rather serves as a point of departure on some important fossil pollen works by them.

2.8. Modelling/simulation approach to quantitative reconstruction of past landscapes

2.8.1. Introduction

A key aim in Quaternary palaeoecology and palynology has been the quantitative reconstruction of vegetation, and it stands to reason that vegetation history (as elucidated by pollen spectra) turns out to be more useful if parameters of vegetation can be analytically quantified over and above qualitative description (Broström, 2002; Sugita, 2007a). It is recognised that a comprehensive understanding of the relationship between pollen analogues retrieved at a site and the surrounding vegetation is paramount for a suitable quantitative reconstruction of past environments (Jackson, 1994). Developments in the theory and techniques of pollen analysis, and the statistical methods used in interpreting pollen assemblages (both fossil and modern), over the last decade in particular, have enhanced our ability to quantify pollen-vegetation parameters – these parameters include: vegetation composition and abundance, pollen productivity, dispersal and deposition characteristics, and ultimately a precisely as possible reconstruction of the spatial distribution of plant species and communities (Broström, 2002). However, 'true' quantification of vegetation based on pollen analysis has proved elusive despite advances in palynological theory and technique. First, various plants species have differential pollen productivity and dispersal potentials, and this leads to biases of representation in the pollen record that one needs to take cognizance of during pollen diagram interpretation (Prentice, 1988; Jackson, 1994; Sugita, 2007b). Second, it is exceedingly difficult to identify pollen grains at a high taxonomic resolution (species or genus level) regardless of advancements in taxonomical identification techniques (Punt *et al.*, 2003). Third, environmental factors such as site type, basin size, surrounding vegetation, landscape structure, and topography all affect the composition of the pollen assemblage, in particular in terms of dispersal, deposition, preservation and local versus regional pollen influences (Sugita, 2007b). Consequently, interpretation of pollen diagrams remains innately subjective and based on intuition (Fyfe, 2013). Nevertheless, in spite of these challenges, it is still considered the best suited ecological technique to achieve palaeoenvironmental reconstructions (Gaillard *et al.*, 2008). The challenge therefore faced by contemporary

palynologists has been to develop and supply the study of pollen analysis with improved tools and means of quantifying past vegetation and reconstruction techniques of palaeoenvironments (Räsänen *et al.*, 2007). These developments have occurred in the formation of predictive mathematical and computer models that simulate and capture broad patterns of pollen and vegetation characteristics, such as pollen dispersal and deposition, with the aim of improving our understanding of the links between pollen and vegetation, and moreover, our interpretation of long-term palaeoecological records (Bunting, 2008; Bunting and Hjelle, 2010).

2.8.2. A historical review of the models of pollen dispersal and deposition

The modelling approach must be recognised as a process of simplification, made useful by its ability to reduce complex systems and phenomena into simpler more manageable components that are easier to understand. Moreover, experiments run through model systems can be measured, manipulated, controlled, and replicated, providing insight into real-world features and systems that would otherwise be near impossible to fully comprehend (Bunting and Middleton, 2005). However, it is appreciated that model simplification of the environment cannot be considered a true reflection of reality, as it breaks a complex system into singular properties viewed in isolation that lack connectivity, and models ought to always be tested against empirical data (Bunting and Middleton, 2005). Therefore, modelling of environmental phenomena must be cognizant of the fact that this approach is used as an effective tool that develops and improves knowledge and understanding, rather than supplying definitive and precise data on such complex systems.

2.8.2.1. Davis' *R*-value model

Davis' *R*-value model developed in 1963 is considered the origin point of contemporary pollen dispersal and deposition models (Gaillard *et al.*, 2008). The *R*-value model was built on one of the most fundamental assumptions of the pollen analysis method, which states that the "number of a given type of pollen deposited at a site is directly correlated with the corresponding abundance of that species in the surrounding vegetation within a correctly chosen sampling radius/source area" (Davis, 1963 p. 898; Prentice, 1985). Understanding that differential abundances, pollen productivities and dispersal mechanisms of species resulted in significant disparities between the percentages of species in current vegetation assemblages and pollen being deposited at a sampling site, Davis (1963) sought to devise an algebraic model to demonstrate the relationship between pollen and vegetation percentages of a species

at a site by transforming pollen percentages into relative abundances of a taxon, denoted by *R*-value. This *R*-value (r_i) was taxon specific and could be derived using the following equation:

$$p_{ik} = r_i \times v_{ik}$$

where p_{ik} is the abundance of taxon *i* in the pollen assemblage at sampling site *k* and v_{ik} is the abundance of taxon *i* in the surrounding vegetation within a specific area A_n (Broström, 2002). The *R*-value would then be employed as a 'correction factor', whereby a species' fossil pollen count (or percentage) is divided by the *R*-value to calculate the relative abundance percentages of that species against all other species found at the site (Davis, 1963; Parsons and Prentice, 1981). Davis's *R*-value model made it possible to infer the frequencies of species in vegetation communities from the percentage data of pollen extracted from sampling points. However, a number of problems were associated with the Davis's model, namely with regards to issues of spatial scale for specification of the plant abundances, so in other words the spatial extent of vegetation from which to extract data (Gaillard *et al.*, 2008). The *R*-value model did not take into account pollen data from 'background' sources (i.e. that pollen data extracted outside of area A_n) which if overlooked can have considerable impacts on estimations of *R*-values (Parsons and Prentice, 1981; Broström, 2002; Gaillard *et al.*, 2008). Moreover, as the background component of pollen fluctuates between the size of area surveyed, species' *R*-values will differ between regions. It is for these reasons that Davis's model suffered significant difficulties in application and failed in its general use (Parsons and Prentice, 1981; Broström, 2002; Gaillard *et al.*, 2008).

2.8.2.2. Andersen's model

The most salient disadvantages of Davis' *R*-value model were the absence of a clearly identified source area of pollen and the lack of recognition of the considerable effect of the background pollen component on calculating *R*-values (Livingstone, 1968; Parsons and Prentice, 1981; Broström, 2002). In light of these limitations, Andersen (1970) proposed a linear model for expressing the pollen-vegetation relationship that would estimate a background pollen component, which was expressed using the following equation:

$$p_{ik} = r_i \times v_{ik} + p_{0i}$$

where p_{ik} is the abundance of taxon *i* in the pollen assemblage at sampling site *k*, v_{ik} is the abundance of taxon *i* in the surrounding vegetation within a specific area A_n, r_i is the inferred

R-value for taxon *i* and p_{0i} is the background pollen component outside of the surveyed area A_n (Broström, 2002; Soepboer *et al.,* 2007). Expressed in linear graphical representation (Figure 2.1), r_i is the pollen productivity representation factor (slope coefficient) of taxon *i* and p_{0i} is the y-intercept for taxon *i* (i.e. the background pollen loading) (Broström, 2002).

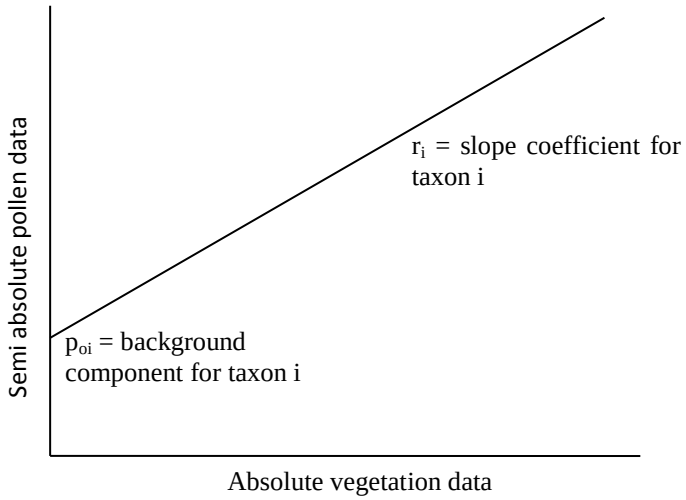

Figure 2.1. The pollen-vegetation relationship for taxon i in Andersen's (1970) linear model. The slope coefficient is the pollen productivity representation factor (r_i) and the y-intercept denotes the background pollen component (p_{0i}).

While Andersen's model significantly enhanced palynologists understanding of the pollen-vegetation relationship, the input parameters of the model were difficult to obtain as it required absolute or semi-absolute pollen data, such as pollen accumulation rates (PARs – pollen per unit volume of sediment per unit time), and pollen percentage data are not appropriate for the model (Prentice and Parsons, 1983; Soepboer *et al.,* 2007; Gaillard *et al.,* 2008).

Utilisation of pollen and vegetation percentage data in Andersen's linear model results in what is known as the Fagerlind effect. Pollen and vegetation data can only be expressed by linear regression if there are no dominant taxa in the data, but that is rarely the case (Gaillard *et al.,* 2008). According to Fagerlind (1952), there is a mathematical expectation of non-linearity between vegetation and pollen conveyed as percentages. The Fagerlind effect implies that a linear relationship becomes non-linear when absolute measured data are converted to proportional data because of taxon interdependencies that are subsequently created – i.e., an increase in the vegetation percentage of taxon *i* need not necessarily imply an increase in the pollen percentage of the same taxon *i*, and vice versa (Broström, 2002; Gaillard *et al.,* 2008). In other words, a taxon not only relies on its own abundance in a pollen dataset but also on the abundances of those taxa it shares the dataset with. As Broström

(2002) explains, this effect can be particularly salient when there is a taxon with abundances greater than 30% in a dataset. Therefore, the Fagerlind effect needs to be corrected for so as to enhance the goodness of fit between the two dataset variables (Gaillard *et al.,* 2008).

2.8.2.3. The Extended *R*-value model (ERV model)

The Extended *R*-value (ERV) model was developed by Parsons and Prentice (1981) and Prentice and Parsons (1983) for percentage pollen and vegetation data in place of semi-absolute or absolute data as used in Andersen's model, and integrates a correction factor that removes the Fagerlind effect (Broström, 2002). The model expresses the pollen-vegetation relationship as a linear regression, used to estimate pollen productivity α_i and the background pollen component z_i, represented by the slope and y-intercept respectively (Broström, 2002; Gaillard *et al.,* 2008). The generic equation for the ERV model is expressed as:

$$p_{ik} = \alpha_i \times v_{ik} \times f_k + z_i$$

where p_{ik} is the pollen deposition in percentage and v_{ik} is the percentage vegetation abundance of taxon *i* at site *k*. The standard equation for the ERV model divides pollen deposition into two parts; i) a variable component $\alpha_i \times v_{ik}$ that corresponds to pollen of taxon *i* sourced within a specific radius from the pollen deposition point (source area), and ii) a constant background pollen component z_i that represents pollen sourced from outside this specified radius (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Broström, 2002). The pollen productivity for taxon *i* denoted by α_i is usually calculated relative to all other taxa included the dataset, one of which is set to unity (i.e. to one) (Broström, 2002). The parameter f_k is a site specific variable that compensates for the Fagerlind effect (Prentice and Webb III, 1986; Broström, 2002). The evolution of the ERV model in pollen-vegetation investigations led to the development of three ERV sub-models based on differences in pollen and vegetation data input format for the model, and the definition of the background pollen component (Figure 2.2) (Sugita, 1994). ERV model 1 and 2 were proposed by Parsons and Prentice (1981) and Prentice and Parsons (1983) respectively, and differed based on assumptions regarding the background component of pollen z_i. These ERV models use vegetation and pollen proportion data. ERV model 1 assumes a taxon-specific background pollen component for each taxon *i* that is constant relative to the total influx of pollen at a site (Parsons and Prentice, 1981), whereas ERV model 2 assumes a taxon-specific background pollen component for each taxon *i* that is a constant relative to the total plant abundance around a site (Prentice and Parsons, 1983). ERV model 3 was proposed by Sugita (1994) and

can be utilised if pollen proportion and absolute plant abundance data is available, and assumes that there is a constant background pollen component between different sites. Gaillard *et al.* (2008) suggests that similar results should be obtained from the three different ERV models if the background pollen loading is low relative to the total pollen loading at a sampling site. Therefore, ERV model 1 and 2 must be used while only pollen and vegetation percentage data are available, and ERV model 3 should be used when pollen proportions and absolute plant abundance data are available (Broström, 2002; Gaillard *et al.*, 2008). Broström (2002) points out that there is no apparent motive for choosing ERV model 1 over 2 (or vice versa), and that both should be used simultaneously to see if they provide comparable model outputs (i.e. relative pollen productivity α_i and background pollen component z_i to deduce their robustness).

When modelling parameters of the pollen-vegetation relationship, researchers attempt to capture the pollen samples 'view' of the landscape (Webb III *et al.*, 1981). Distance weighting of vegetation data should therefore be applied when using ERV models to estimate relative pollen productivity and background pollen loading, so as to account for the empirical observation that plants situated closer to a sampling location contribute more pollen than those situated further away (Duffin and Bunting, 2008). There are a variety of techniques used to distance weight plant abundances:

i) Weight the vegetation by dividing plant abundances by the distance *d* between the pollen sample point and the plant $1/d$ (Prentice and Webb III, 1986);
ii) Weight the vegetation by dividing plant abundances by the square of distance *d* between the pollen sample point and the plant $1/d^2$ (Webb III *et al.*, 1981; Calcote, 1995; Gaillard *et al.*, 2008);
iii) Employ Sutton's taxon-specific distance weighting that takes into consideration dispersal ability (size, weight and fall speed) of pollen grains for a specific taxon (Sugita, 1993; Broström, 2002).

Broström *et al.* (2004) argue that the weighting method chosen for a study can be interpreted at subjective, based on which taxa are chosen for modelling, appropriateness of weighting method to the data, and best-fit between pollen-vegetation data. While Duffin and Bunting (2008) suggest that all three weighting methods should be applied and compared to find the most mathematically suitable option, Sutton's taxon-specific was expressly chosen for this research based on it being the most ecologically appropriate option (and thus making the

most ecological sense as opposed to mathematical sense) since it takes into consideration pollen grain geometry and fall speeds of individual taxa. It is perhaps a future recommendation for similar studies to compare the three distance weighting methods determine if there is any significant difference between them.

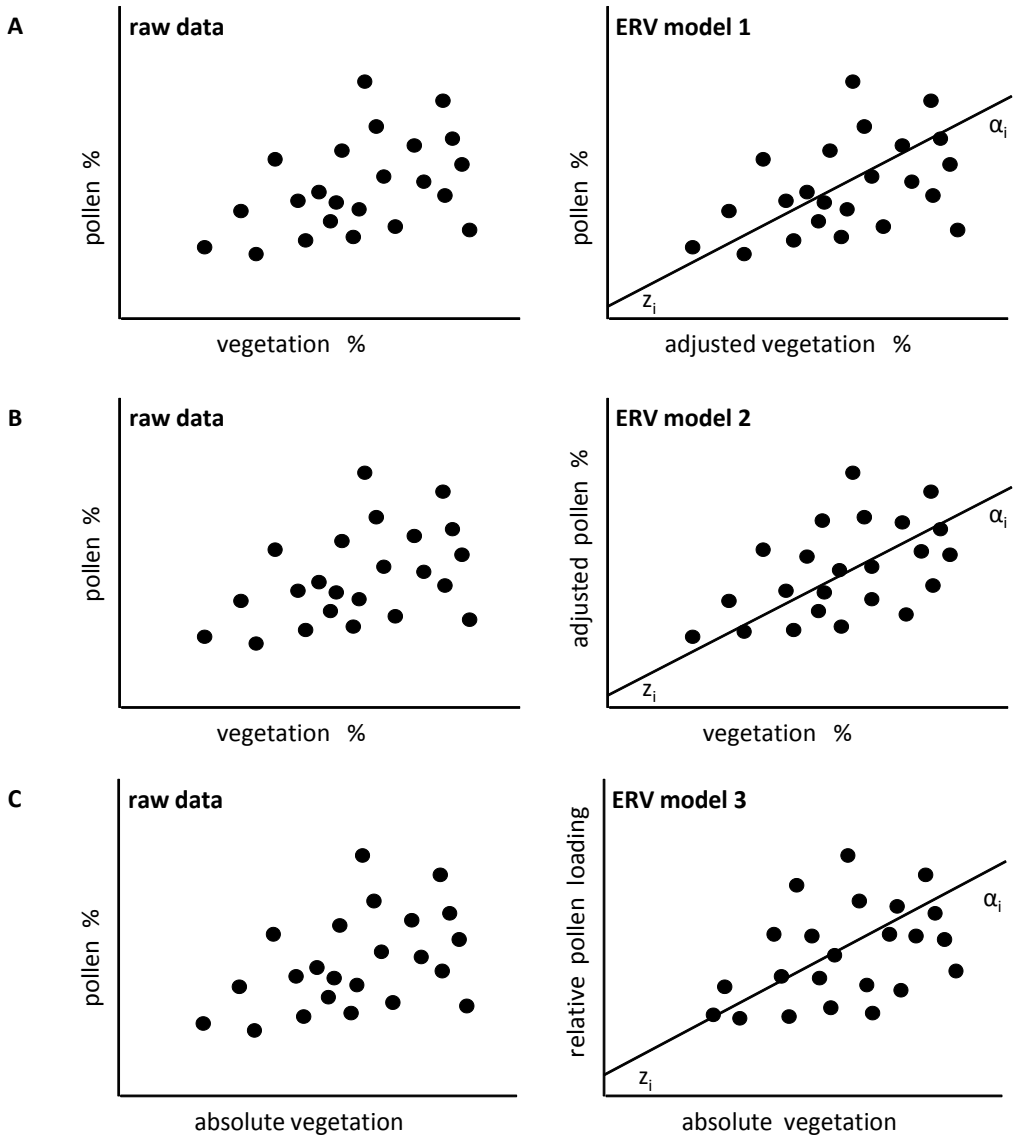

Figure 3.2. The Extended R-value (ERV) models are used to estimate the pollen productivity α_i and background component z_i for taxon I from coupled pollen and vegetation data. Raw data of the pollen-vegetation relationship of taxon i is shown in the first column, and the goodness-of-fit for model specific adjusted data to the ERV linear model is shown in the second column, A) ERV model 1, B) ERV model 2 and C) ERV model 3 (Broström, 2002).

2.8.2.4. The Prentice-Sugita model

In 1985, Prentice developed a mathematical model prompted by a need for quantitative theory to explain pollen analogue characteristics such as pollen production, and dispersal and

deposition behaviours, in addition to having the capacity to predict pollen source areas and other representation characteristics of basins of various sizes (Prentice, 1985). Mathematically complex, the Prentice model of pollen dispersal and deposition simulates pollen loading of a taxon at a deposition site originating from plants of that same taxon in the surrounding region. The basic Prentice model is denoted by the following equation:

$$y_{ik} = \alpha_i \int_R^{Zc} x_{ik}(z) g_i(z) dz + \omega_i$$

where y_{ik} is the pollen loading of taxon *i* at site *k*, α_i is the pollen productivity of taxon *i*, $x_{ik}(z)$ is the average plant abundance of taxon *i* at distance *z* from the centre of the basin, $g_i(z)$ is a pollen dispersal and deposition function for taxon *i* at distance *z* from the centre of the basin based on Sutton's particle settling equation (Sutton, 1953), R is the radius of the basin, Z_c is the distance from the centre of the basin to the outer edge of the vegetation survey and ω_i is the background pollen component of taxon *i* (Bunting and Middleton, 2005). However this model of pollen dispersal and deposition is only suitable for explaining vegetation-pollen relationships in environments where it is assumed the horizontal movement of pollen after deposition in negligible, such as in undisturbed bogs (Gaillard *et al.*, 2008). Sugita (1993, 1994) modified the Prentice model to account for the pollen-vegetation relationship in environments where mixing and disturbances redistribute deposited pollen, such as lakes. This modified model is termed the Prentice-Sugita model, and illustrates the relationship between pollen loading in a sedimentary basin and four factors that affect it: pollen productivity, pollen dispersal, the spatial distribution of plants in the basin, and basin size (Prentice, 1985; Sugita, 1993; Sugita, 1994; Broström, 2002). Furthermore, the Prentice-Sugita model has six fundamental assumptions (Broström, 2002; Gaillard *et al.*, 2008), namely:

i) The sampling basin (e.g. lake or bog) is a circular opening in a surrounding closed canopy. Basin size is indicated by the radius measurement of a basin.
ii) Pollen dispersal is constant in all directions.
iii) The dominant pollen transportation agents are wind above the canopy level and gravity below the canopy level.
iv) Each taxon has a constant pollen productivity.
v) The spatial distribution of each plant taxon is described as a function of distance from a location found directly in the centre of a basin.

vi) Crosswind-integrated deposition of pollen in a basin is defined as a function of distance from a source plant that is derived from a diffusion model of small particles from a ground level source – mainly determined by wind speed and species-specific fall speeds of pollen grains (Sutton, 1953).

The basic Prentice-Sugita model is expressed by the following simplified linear model:

$y_{ik} = \alpha_i \text{ x } \psi_{ik} + \omega_i$

where y_{ik} is the pollen loading of taxon *i* at site *k*, α_i is the pollen productivity of taxon *i*, ψ_{ik} is the distance weighted plant abundance of taxon *i* at site *k*, and ω_i is the background pollen component of taxon *i* (Duffin and Bunting, 2008). In addition, Sugita (1994) introduced the concept of spatial heterogeneity into the conversation of the spatial extent represented by pollen analogues, and proposed the idea of Relevant Source Area of Pollen (RSAP) (Hellman *et al.,* 2009). It is recognised that pollen grains can potentially be transported many kilometers from their source by the wind and therefore it is often difficult to identify the source area of pollen (Gaillard *et al.,* 2008). Essentially, Sugita (1994) demonstrated that the goodness of fit (as adjudged by the coefficient of determination r^2 of linear regression) of vegetation and pollen data to the ERV model, and the correlation between vegetation abundances of a taxon surrounding sampling locations and the pollen loading of that taxon found at a site, will increase with increasing distance up to a certain point, and thereafter will not continue to improve – i.e. an asymptote is reached (Sugita, 1994; Broström, 2002; Hellman *et al.,* 2009). In other words, the RSAP is defined as the distance beyond which the correlation between pollen loading at a site and vegetation abundances in the surrounding landscape do not continue to improve, even with increased sampling distances (Broström, 2002; Gaillard *et al.,* 2008). This implies that pollen coming from outside the RSAP is from the 'background' pollen component, and is constant between sites (Sugita, 1994). The concept of RSAP is useful in illustrating the influences of taxonomic dispersal differentials and basin size on the spatial scale represented in pollen archives. These influences theoretically include: i) the better dispersed the pollen type, the larger the RSAP, and ii) the larger the basin size, the larger the RSAP (Gaillard *et al.,* 2008).

2.8.2.5. Computer simulation models – POLLSCAPE and HUMPOL

The POLLSCAPE computer simulation approach and software suite was developed by Shinya Sugita (Sugita, 1994, Sugita *et al.,* 1999; Broström, 2002), and its successor, the

HUMPOL software suite was developed by Dr Jane Bunting and Richard Middleton (Bunting and Middleton, 2005). Both computer packages employ Prentice (1985) and Sugita (1994) mathematical model options, and enable the user to simulate parameters of pollen dispersal, deposition and assemblages in heterogeneous landscapes (Gaillard *et al.,* 2008). Data required for input into these simulation software suites include pollen assemblages estimates, and abundance and spatial distribution data of plant taxa from hypothetical or real landscapes (Sugita, 1994; Broström, 2002; Broström *et al.*, 2005; Bunting and Middleton, 2005). The simulation procedure broadly consists of four steps (Gaillard *et al.,* 2008): i) landscape design from mapped or simulated data; ii) extraction of sample-specific weighted vegetation data relative to sampling sites; iii) simulation of pollen loading at each sampling location; and iv) RSAP, pollen productivity and background pollen component estimation through a comparison of vegetation and pollen data for each sampling site using ERV models.

2.8.2.5.1. POLLSCAPE

POLLSCAPE was initially devised to simulate pollen dispersal and deposition in closed forest systems with the assumption that the predominant agent of pollen transport is wind above the canopy level (Gaillard *et al.,* 2008). As described below, POLLSCAPE has four sub-units of simulation (Figure 2.3) (after Sugita, 1994).

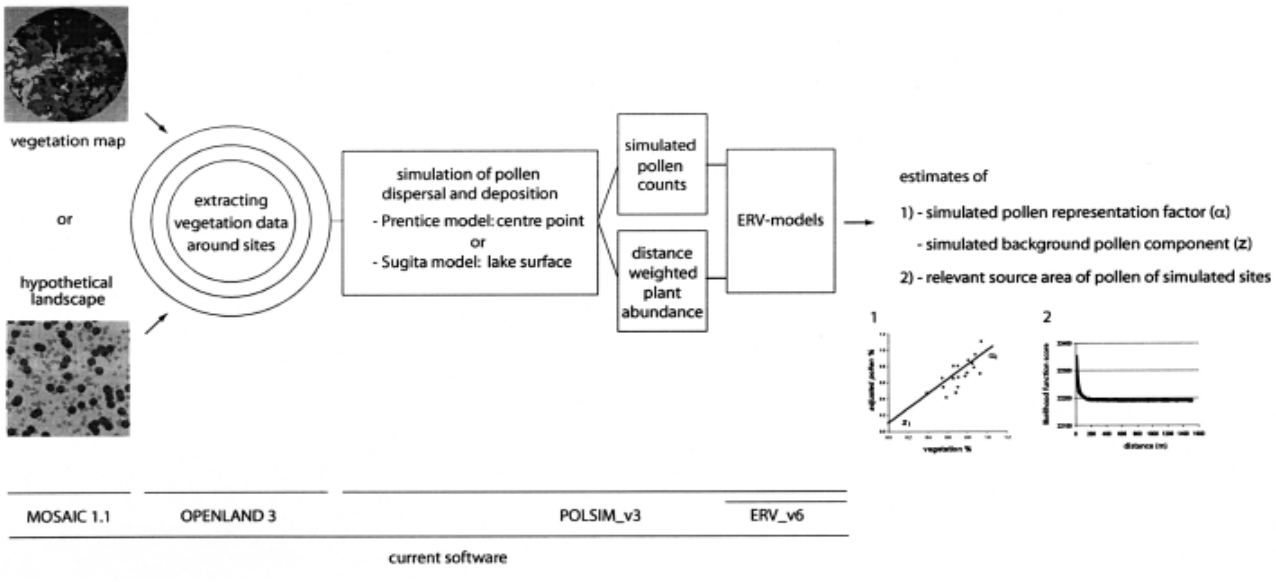

Figure 2.3. The POLLSCAPE software package for pollen simulation modelling in heterogeneous vegetation landscapes. Illustrated is the simulation model process from input to output and the various sub-unit programs used to achieve each step (Sugita, 1994).

The POLLSCAPE software package has three sub-unit computer programs used to execute each of the simulation stages (Figure 2.3). Stage 1 is performed using MOSAIC 1.1 to create

hypothetical or real vegetation distribution maps of a landscape and is known as landscape design (Middleton and Bunting, 2004). Stage 2 employs OPENLAND3 to extract vegetation data relative to each sample location in the format required by POLSIM_v3 in Stage 3 and 4 (Eklof *et al.*, 2004; Gaillard *et. al.*, 2008). POLSIM_v3 simulates pollen loading at each sampling point using dispersal and deposition models and ERV analysis, and outputs modelled pollen counts, RSAP estimation parameters, relative pollen productivity estimates and background pollen component (Gaillard *et al.*, 2008). Sugita (2007b) later developed the program ERV_v6 to run ERV analysis in the POLLSCAPE suite (Stage 4).

A number of fundamental assumptions underlie the basis of the POLLSCAPE modelling approach. First, average vegetation composition is determined in a sequence of incremental rings outwards from the sampling point that assumes vegetation is one-dimensional (constant height) and that wind direction is constant in all directions (Bunting and Middleton, 2005). Second, it assumes a deposition basin is a circular opening in a closed canopy of vegetation and simulates pollen loading as a singular point in the centre of that opening. Any non-circular basins are approximated circular using the OPENLAND3 program (Bunting and Middleton, 2005). Third, it assumes the landscape composition is uniform to a distance beyond the surveyed area, and therefore the background pollen component is estimated from within the modelled study area. This assumption is sound in areas where topography, climate, soils, and thus vegetation are uniform over large distances – yet in mosaic landscapes this assumption is problematic (Bunting and Middleton, 2005). These assumptions have, however, restricted the application and flexibility of POLLSCAPE modelling, such as not taking into consideration differentials in pollen source height (e.g. between trees and shrubs), variations in air movement and turbulence caused by topography, surface roughness and degree of openness of the landscape (Gaillard *et al.*, 2008).

2.8.2.5.2. HUMPOL

HUMPOL (HUll Method of POLlen simulation) software suite was developed by Dr Jane Bunting and Richard Middleton from Hull University, England (Bunting and Middleton, 2005). Considered to be successor to POLLSCAPE, HUMPOL software is considered a more flexible approach to pollen dispersal and deposition modelling (Gaillard *et al.*, 2008). HUMPOL organizes the stages of simulation slightly differently to POLLSCAPE (Figure 2.4) (Bunting and Middleton, 2005).

<table>
<tr><th>Simulation Stage</th><th>POLLSCAPE</th><th>HUMPOL</th></tr>
<tr><td>Prepare vegetation data (empirical or simulated)</td><td colspan="2">Create Idrisi image file (MOSAIC, GRIDIN) and definition files (taxon fall speed and Relative Pollen Productivity, communty composition) (SURVEY AND POLSACK)</td></tr>
<tr><td>Define sampling points. Convert vegetation data into a series of point pollen sources characterised by composition and position</td><td>OPENLAND3</td><td rowspan="2">POLLFLOW</td></tr>
<tr><td>Apply a weighting algorithm to simulate the pollen loading at the sample point from each point source and sum them (adding appropriate background pollen deposition terms)</td><td>Polsim_v3</td></tr>
<tr><td>Estimation of pollen productivity, background pollen component and Relevent Source Area of Pollen</td><td>ERV_v6</td><td>POLERV</td></tr>
</table>

Figure 2.4. Schematic representation of the sub-unit programs used in both POLLSCAPE and HUMPOL for each of the stages in the pollen dispersal and deposition simulation modelling process (Bunting and Middleton, 2005).

Stage 1 is performed using MOSAIC5 to create hypothetical or real vegetation distribution maps and to prepare the vegetation data. GRIDIN, a HUMPOL utility, can be employed to translate maps produced in standard GIS packages such as ArsGIS into the raster layout required by HUMPOL (Bunting and Middleton, 2005; Gaillard *et al.*, 2008). POLFLOW is used for simulations of pollen assemblages at single sampling points, and extracts percentage vegetation data (Stage 2) and illustrates pollen loadings and sample locations using dispersal and deposition models (Stage 3), and outputs a file that contains the input data required for ERV analysis (Bunting and Middleton, 2005; Gaillard *et al.*, 2008). The HUMPOL utility POLERV can be used to extract data from the output file for ERV analysis (Bunting and Middleton, 2005; Gaillard *et al.*, 2008).

2.8.2.6. Palaeoenvironmental reconstruction

Once the stages of the simulation process are complete and all data outputted from the software are available, it is then possible to quantitatively reconstruct past vegetation

composition, using approaches such as Landscape Reconstruction Algorithm (LRA) (Sugita, 2007a; Sugita, 2007b) or the Multiple Scenario Approach (MSA) (Figure 2.5) (Bunting *et al.*, 2007, 2008b; Bunting and Middleton, 2009). The LRA is an approach to quantitative landscape reconstruction that uses both a modeling and simulation strategy, and is employed for local and regional scale reconstructions (Gaillard *et al.*, 2008). Within the LRA, there are two models, LOcal Vegetation Estimates (LOVE) and Regional Estimates of VEgetation Abundance from Large Sites (REVEALS) that are used to produce estimates of past vegetation compositions from pollen assemblages in regions of ($\leq$ 100 km^2) and (10^4 - 10^5 km^2) respectively (Sugita, 2007a, 2007b). The MSA uses a mixture of pollen dispersal and deposition modelling, GIS approaches and statistical techniques to reconstruct likely past vegetation compositions of the landscape from pollen assemblages (Gaillard *et al.*, 2008). The MSA methodology is designed to generate multiple ecologically distinct vegetation reconstructions of past landscapes from pollen assemblages that attempts to address the ambiguity of equifinality (the realisation that different landscapes can produce similar pollen signals) in pollen diagram interpretation (Bunting and Middleton, 2009). The basic MSA process involves the following: vegetation data and ecological process data are combined with other known landscape data (e.g. topography and altitude data) into a GIS to produce a number of possible vegetation maps. Models of pollen dispersal and deposition are then used to simulate pollen assemblages at a known sample location for each of the possible maps. Thereafter, these simulated assemblages are statistically compared to actual past pollen assemblages from the same area to identify which of the possible maps can be considered the most likely reconstruction of past vegetation (Bunting and Middleton, 2009).

It must be stated here that neither the LRA nor MSA are used in this research as it is not the intention, and moreover, beyond the scope of the study to reconstruct past landscapes. The intention of this research is to calculate variables such as PPE and RSAP using pollen models to determine spatial characteristics of pollen dispersal and deposition in the Cathedral Peak landscape, thus employing ERV models and the HUMPOL software suite.

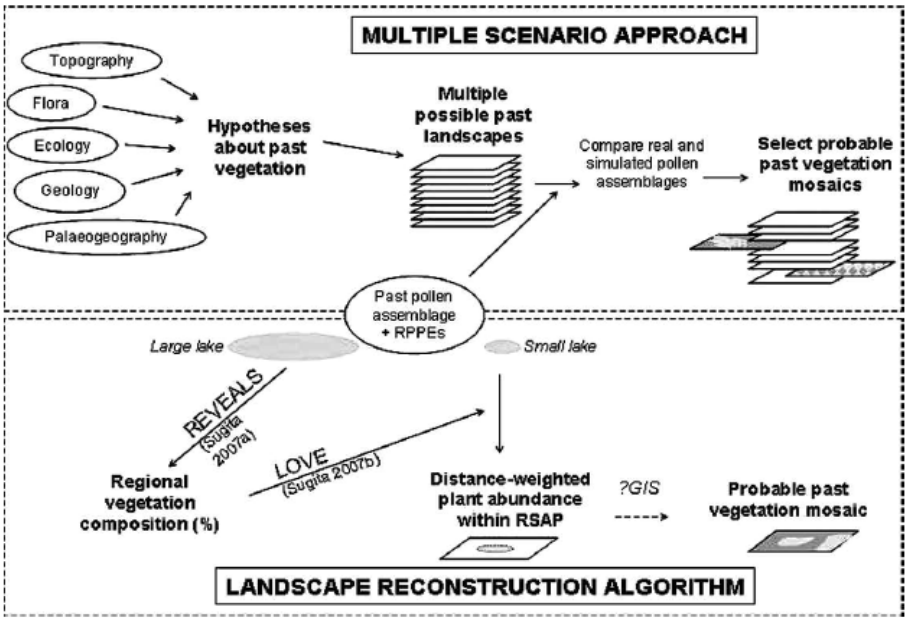

Figure 2.5. Schematic comparison of the Multiple Scenario Approach and Landscape Reconstruction Algorithm (Bunting and Middleton, 2009).

2.8.3 Pollen dispersal and deposition modelling research

2.8.3.1. Global research

Origins of pollen modelling were theoretically developed in the 1960s beginning with Davis' R-value model, progressing to Andersen's model in the 1970s and then Extended R-value models in the 1980s. Despite this 50 year history, pollen research pertaining to modelling dispersal and deposition characteristics has mainly risen in the last decade (Abraham and Kozáková, 2012).

Many regions of Europe have employed models of pollen dispersal and deposition to calculate PPE and RSAP for specific environments using ERV models. These include England (Bunting *et al.*, 2005), Finland (Räsänen *et al.*, 2007), Sweden (Broström *et al.*, 2004; Sugita *et al.*, 1999; von Stedingk *et al.*, 2008), Norway (Hjelle, 1998), Denmark (Nielsen, 2003), Switzerland (Mazier *et al.*, 2008; Soepboer *et al.*, 2007) and the Czech Republic (Abraham and Kozáková, 2012). These studies have attempted to use modern pollen and vegetation data in association with ERV models to obtain reliable and representative PPE and RSAP values to quantify past vegetation assemblages, and moreover to reconstruct past landscapes. In the USA, PPE and RSAP have been calculated for key taxa in forest hollows (Calcote, 1995), and in Asia key desert and desert-steppe taxa PPE and RSAP values determined (Li *et al.*, 2011). Pollen modelling studies have predominantly been European based, with little work having been attempted in Africa, Asia and the Americas

relative to Europe. This is understandable considering Europe is where the HUMPOL suite was developed and improved. The challenge is now to validate these pollen models by investigating whether they are suitable, and moreover, appropriate for pollen studies in other parts of the world (Duffin and Bunting, 2008).

2.8.3.2. South African research

To date, there has been one pollen modelling study undertaken in Africa. Duffin and Bunting (2008) have calculated RSAP and PPE for southern Africa savanna taxa in the Kruger National Park. Specifically, this study involved using HUMPOL to analyse modern pollen analogues from 34 surface sediment samples in association with its surrounding vegetation to run ERV analysis on key savanna taxa and to thus calculate the PPE and RSAP for the research site (Duffin and Bunting, 2008). The aim of this research was to present these PPE and RSAP estimates as a basis for improved interpretation of past and future fossil pollen archives collected from the savanna biome. This aim is in similar vein to the aim and objectives of this research, and so Duffin and Bunting's work was a key text. Duffin and Bunting (2008) illustrated that the HUMPOL suite and associated pollen models of dispersal and deposition can be suitably used in an African context. Nevertheless, it is apparent that there is a lack of pollen modelling work in South Africa and the hope is that this research will stimulate interest in this area of palynological investigations. Moreover, Duffin and Bunting's work supplied a fundamental basis on which appropriate methods and techniques were drawn to suit the aim and objectives of this work.

2.9. Conclusions

Pollen analysis is recognised as an effective proxy for storing palaeoecological archive data from a time preceding the science of direct observation and instrumental verification, and hence scientific record. Quaternary palynology, over the last decade, has tended to focus on vegetation reconstructions of past environments and landscapes. Specifically, enhanced techniques and methods of quantitative vegetation reconstructions have been developed to provide reliable and robust approximations of vegetation compositions and land cover at a variety of spatial scales, or to test hypotheses regarding long-term changes regarding vegetation and climate in both a temporal and spatial context (Reitalu *et al.,* 2014). Necessarily however, a fundamental understanding of patterns and relationships of past vegetation and its behaviour in an environment must necessarily build on observations and appreciation of modern vegetation dynamics in an environment, and recognition of the

principle of Uniformitarianism (Marquer *et al.,* 2014). 'True' quantification of vegetation based on pollen analysis has proved complicated despite advances in palynological techniques and methods for a variety of reasons such as plants species having differential pollen productivity/dispersal potentials, the difficulty in identifying pollen grains at a high taxonomic resolution and environmental factors such as site type, basin size, surrounding vegetation, landscape structure, and topography that influence the composition of the pollen assemblage. Consequently, interpretation of pollen diagrams remains subjective and based on intuition. Nevertheless, in spite of these challenges, it is still considered the best suited ecological technique to achieve palaeoenvironmental reconstructions (Gaillard *et al.,* 2008).

Models that estimate broad patterns of pollen and vegetation characteristics, such as pollen dispersal and deposition, have been developed with the aim of improving our understanding of the links between pollen and vegetation, and moreover, our interpretation of long-term palaeoecological records (Bunting, 2008; Bunting and Hjelle, 2010). Gaining prominence in pollen research in the last decade, these models have shown to produce important quantitative vegetation information for improving palaeoreconstructions, namely pollen productivity estimate and abundance values, and spatial estimates of pollen source areas (Abraham and Kozáková, 2012). Pollen research using these computer models has primarily been focused in higher latitude environments, with much work being undertaken in the northern hemisphere, particularly in areas such as Norway, Sweden, Finland, Denmark, Switzerland and Britain and USA, as this is where these models have been developed for particular landscapes. To date, there has been one pollen modelling study undertaken in Africa (Duffin and Bunting, 2008), thus there is a gap in pollen modelling research in South Africa. It is therefore the intention of this research to test these models in a South African context so as to link this research to ongoing and future fossil pollen work in the Drakensberg, which is a region that can tell us much about past environments as a consequence of steep environmental gradients.

Chapter Three

Methods

3.1. Study area

The research was carried out at the Ezemvelo KZN Wildlife Research Centre located in the Cathedral Peak region of the KwaZulu-Natal Drakensberg (Figure 3.1). The research centre is situated at latitude 28^{o} 56’ 26” S and longitude 29^{o} 14’ 06” E, and is approximately 30 km southwest of Winterton in the Okhahlamba Local Municipality, KwaZulu-Natal (Ezemvelo KZN Wildlife, 2014).

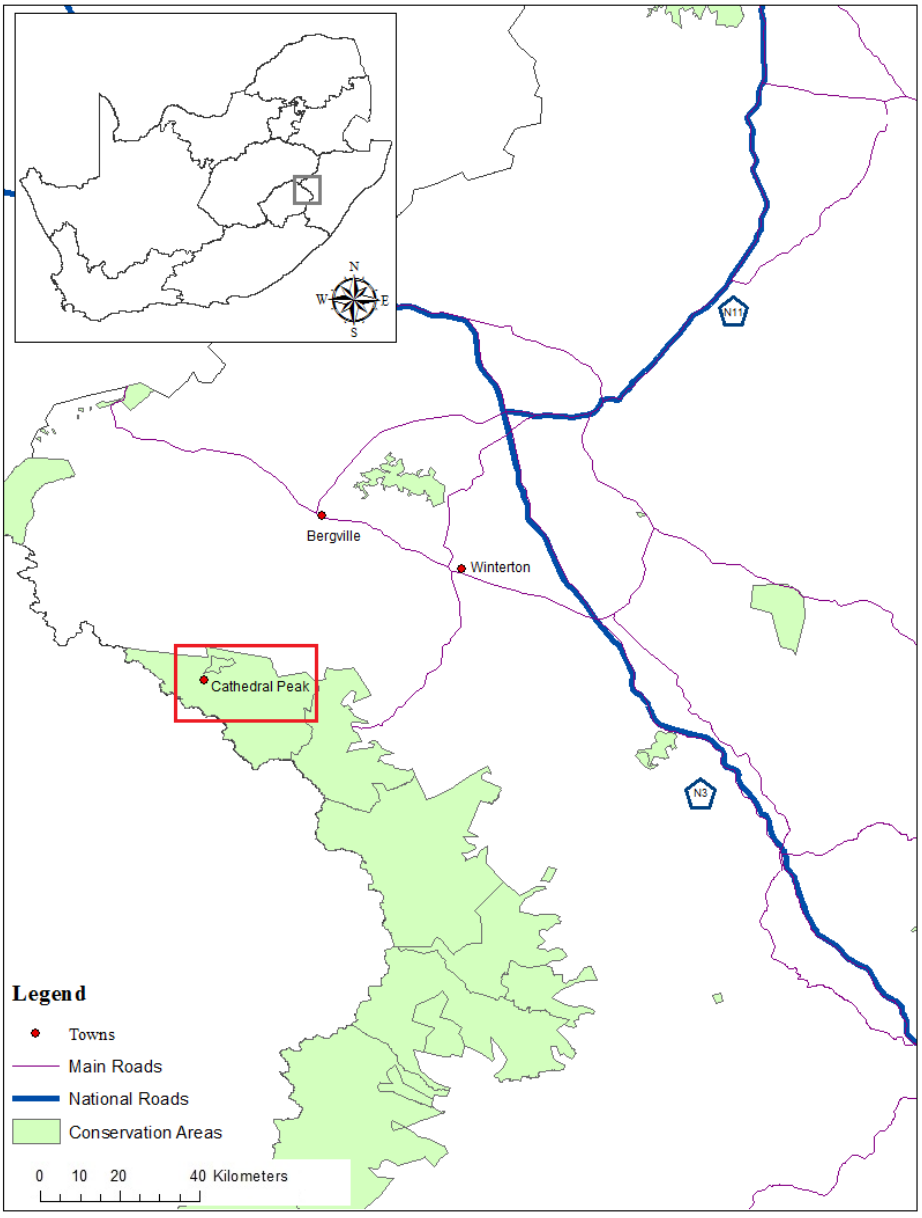

Figure 3.4. Cathedral Peak study site situated in the KwaZulu-Natal Drakensberg.

The Cathedral Peak region of the KwaZulu-Natal Drakensberg is an area frequented by researchers for various research purposes. Current studies being conducted at the research centre and within the Cathedral Peak catchments include: fire monitoring schemes in grassland management, alternative water management designs, and most notably, investigation into, and long-term monitoring of, the impact of climate change on the seasonality of water flow in an area of significant water importance to South Africa (SAEON, 2014). In addition to its considerable fresh water value, Cathedral Peak maintains substantial ecological biodiversity significance. The region has remarkably diverse topography and steep altitudinal gradients that exists over a relatively short spatial area, and these have resulted in a topographically complex and ecologically diverse and unique landscape with over 13 unique vegetation communities present in a confined geographical area (Hill, 1996). As such, past ecological research in the area has centred around plant community descriptions, community classifications, the effects of alien invasive species on indigenous ecology and the effects of climate and environmental changes on the migration of vegetation along altitudinal gradients (Hill, 1996).

For the purposes of this research, three vegetation communities were chosen as study sites within the surrounding environs of Cathedral Peak, that is the *Themeda* grassland, *Protea* savanna and *Leucosidea sericea* scrubland. Killick (1963) categorises the KwaZulu-Natal Drakensberg vegetation according to three distinct altitudinal zones, namely: i) Montane zone (1280 – 1829 m a.s.l), ii) Sub-alpine zone (1830 – 2865 m a.s.l) and iii) Alpine zone (2866 – 3353 m a.s.l). Motivations for choosing the three specific vegetation communities were manyfold. First, selection was broadly based on Killick's montane vegetation classification and communities selected went according to these altitudinal gradients. Second, dominant vegetation communities represented in the region were chosen. Third, those vegetation communities most sensitive to shifts in composition or altitude with a change in environmental or climatic conditions were selected. Finally, the presence of pre-existing vegetation and/or pollen data on the three chosen vegetation communities from previous research facilitated a comparison with new data collected in this research.

The wider study area covering all three sites lies in mountainous terrain. Predominant vegetation compositions of the Cathedral Peak region were categorised into altitudinal zones by Killick (1963). In the Montane zone, *Podocarpus latifolius* forest, *Protea* savanna and *Themeda*-dominated sourveld grassland dominate. The Sub-alpine zone is predominated by grasslands (*Themeda triandra* grasslands, *Rendlia altera* grasslands, Sub-alpine and

Themeda-temperate grasslands) and scrublands (*Leucosidea sericea* scrublands, boulder scrub and sub-alpine fynbos). The Alpine zone consists of Alpine grasslands, *Erica-Helichrysum* heathlands and Alpine sedge meadows (Killick, 1963; Hill, 1996). Although this vegetation classification is useful in terms of altitudinal differentiation, it is relatively out-dated for current use. Work of Everson *et al.* (1990) and O'Connor (2005) illustrates the species diversity and importance of montane grasslands and vegetation communities in the area. However, the most up-to-date vegetation mapping of the area has been done by Mucina and Rutherford (2011), who, with the use of a comprehensive vegetation index key, describe the Cathedral Peak area in altitudinal progression from Drakensberg Foothill Moist Grassland (Gs 10 – index key code) to Northern Drakensberg Highland Grassland (Gd 5), then to uKhahlamba Basalt Grassland (Gd 7) and finally, Drakensberg Afroalpine Heathland (Gd 10) at the highest altitudes.

The range of altitudes covering all three study sites varies between 1300 – 2000 m a.s.l. Mean annual rainfall in this altitudinal range fluctuates between 700 -1500 mm, culminating in the summer months between October and March. Main sources of precipitation include orographically induced thunderstorms, line thunderstorms and large scale mid-latitude cyclones that move from the Atlantic across southern Africa in an easterly direction bringing cold fronts (Tyson *et al.*, 1976). Further climate characteristics of the Cathedral Peak area include mean annual air temperatures of 16 ^{o}C, with winter presenting especially challenging climatic conditions, with temperatures regularly falling below 0 ^{o}C, resulting in frost, ice and snow occurrences. Snowfalls take place in the region on an average of eight times per annum, and occur mostly in the Alpine zone which adds to the total amount of mean annual precipitation in the area (Tyson *et al.*, 1976). Wind plays an important role in the area as frequent 'berg winds' blow down the escarpment towards the coastline, warming as they descend according to the dry adiabatic lapse rate. These warm winds are a key factor in fire hazard warnings in grassland management and general monitoring of vegetation communities in the Cathedral Peak area as they are especially prevalent during the dry season (Nänni, 1969).

Land-use surrounding the wider environment is predominantly related to altitude. Conservation areas are situated within the Sub-alpine and Alpine zones, most notably the Maloti-Drakensberg Trans-frontier Park bordering Lesotho (UNESCO, 2014). In conjunction with conservation areas there are several hotels, camping sites, and tourist activities close to Cathedral Peak. As a result, infrastructure is better developed here than in other rural areas in

the region as there are adequately tarred roads, electricity supply, and running water. In the foothills and Montane zone, land-use mainly relates to commercial agriculture, subsistence farming and small rural villages and towns.

3.2. Methods

3.2.1. Introduction

Modern pollen and vegetation data were collected, quantified, and analysed with the aim of investigating the dispersal and deposition relationship between the two – how far from a pollen source does that pollen travel in an environment? The purpose thereof is to explicitly attach a spatial context to pollen analysis studies so that one is able to secure a more robust basis for improving the interpretation of long-term palaeoecological records and therefore eliminating uncertainty in environmental reconstructions.

Methods employed in this research involve three distinct categories, namely: field methods, laboratory methods and computer modelling methods (Figure 3.2), which are described in detail in this chapter.

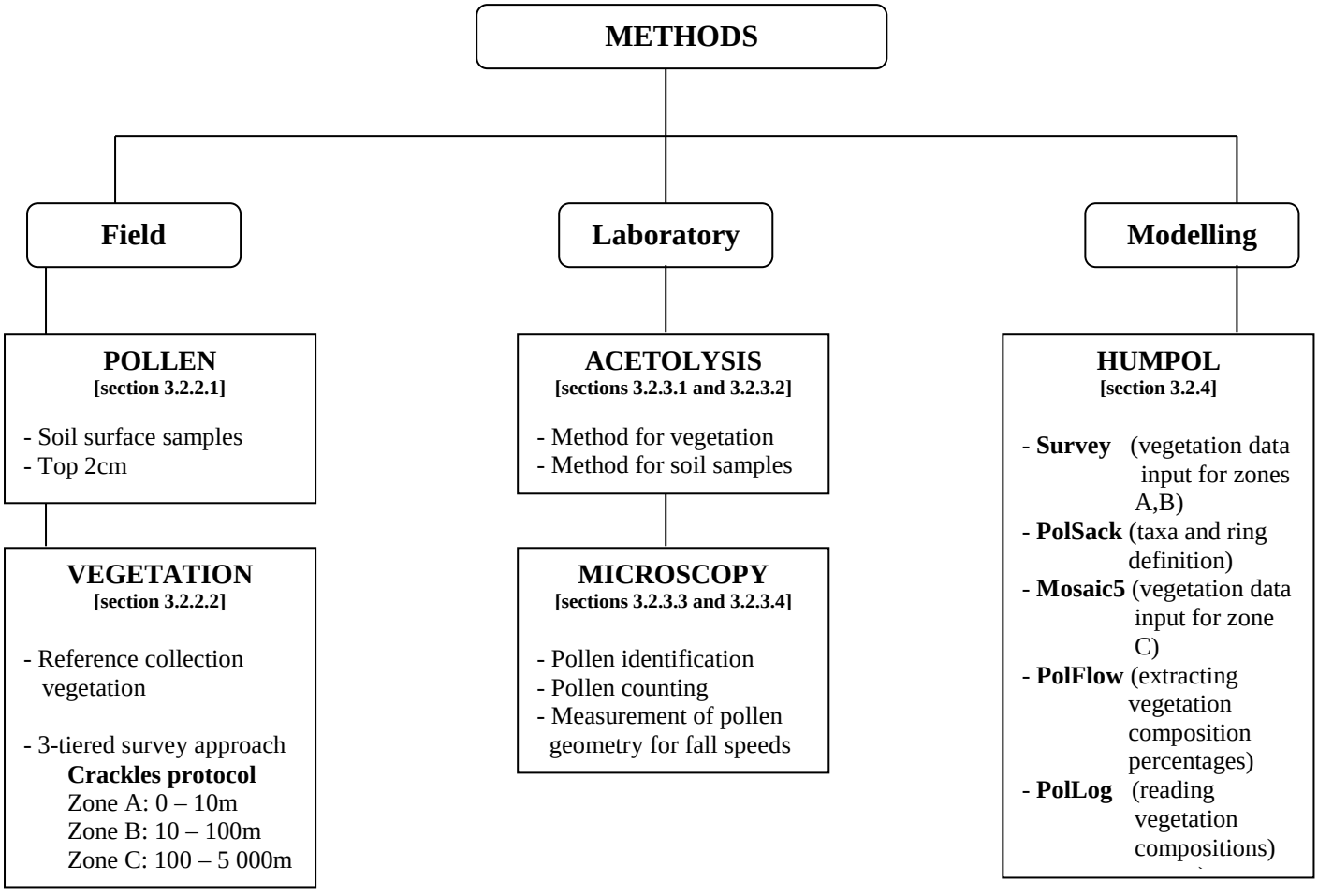

Figure 3.2. Schematic breakdown of methods used in this research – Field, Laboratory and Modelling.

3.2.2. Field methods

Field data were collected from environments surrounding the Ezemvelo KZN Wildlife Research Centre in Cathedral Peak from 10th – 16th November 2013. Three distinct and unique vegetation communities were selected for collecting pollen and vegetation data for modelling based on multiple criteria (see above chapter 3.1), namely: *Themeda* grassland, *Protea* savanna and *Leucosidea sericea* scrubland. Pollen modelling methodology requires both pollen and tiered-vegetation data at each sample point in the field.

3.2.2.1. Pollen data

This research is concerned with investigating modern pollen analogues, and as such, no coring techniques (which are primarily used to remove fossil pollen data) were used. Modern pollen assemblages are usually collected using pollen traps, soil surface samples or moss polsters. The process of collecting pollen from the surface of a landscape, whether it is by way of trap apparatus, moss polsters, or soil samples is standard procedure in establishing modern pollen spectra in relation to its surrounding vegetation (Adam and Mehringer, 1975; Xu *et al.,* 2009). All of these modern pollen sampling media have strengths and weaknesses in their ability to effectively capture representative pollen assemblages of the surrounding environment, and the technique used depends on, *inter alia*; research objectives, research cost, availability of equipment, availability of time for the research project, and physiographic context of the surrounding environment.

Moss polsters, due to their physical architecture, have been shown to be natural and effective pollen traps (Räsänen *et al.,* 2004). Different moss species have certain growth rates per annum, and if these are known, absolute values of modern pollen accumulation rates per year can be calculated (Broström *et al.,* 2004). The limitation of moss polsters, however, is that they ordinarily grow in wet, shady, and cooler climes, and so are only common in very specific environments such as forests or at higher latitudes. Moss polsters were not used in this research primarily due to their absence in the Cathedral Peak region. Pollen traps are commonly used to collect modern pollen analogues. Pollen traps have been given significant attention regarding modern pollen assemblages, especially in terms of their usefulness in being able to identify variations in seasonal pollen production and dispersal patterns due to the fact that they yield pollen composition and accumulation rates for a specified time period, e.g. seasonally or interannually (Xu *et al.,* 2009; Jantz *et al.,* 2013; Huusko and Hicks, 2009). A disadvantage of pollen traps lies in the expense of some types of trap equipment, and more

saliently, the time traps need to accumulate pollen which can range anywhere between one to ten years depending on research objectives (Räsänen *et al.,* 2004; Räsänen *et al.,* 2007; Xu *et al.,* 2009).

Soil surface samples were used in this research as they are readily available in most environments and are easily and quickly collected. Soil surface samples are a function of complex sedimentation rates and other environmental factors in the wider environment, and it is thus difficult to attach a temporal context to the pollen extracted from them – this poses difficulties when absolute values are required for understanding results (Xu *et al.,* 2009). Nevertheless, Jantz *et al.* (2013) point out that soil surface samples are an adequate media from which to extract a comprehensive and detailed pollen assemblage indicative of the vegetation in the surrounding landscape. Soil surface samples are shown to represent average modern pollen assemblages of a few years depending on sedimentation rates, and are effective in exploring relationships between these modern spectra and contemporary vegetation inventories (Zhao and Herzschuh, 2009).

Site selection for surface sampling within each of the three distinct vegetation communities under investigation was based on random sampling methods. Mazier *et al.* (2008) and Abraham and Kozáková (2012) show the importance of random sampling with regards to pollen modelling research to obtain reliable relevant source area of pollen (RSAP) and pollen productivity estimate (PPE) values. A total of five samples in each of the three distinct vegetation communities were randomly selected resulting in an overall sample count of 15 sample sites. A further constraint decided upon for site selection was that samples had to be at least 400 m away from one another so as to create a 'buffer zone' of at least 2x the distance of zone B between sample points (see below chapter 3.2.2.2 for further explanation) (Figure 3.3).

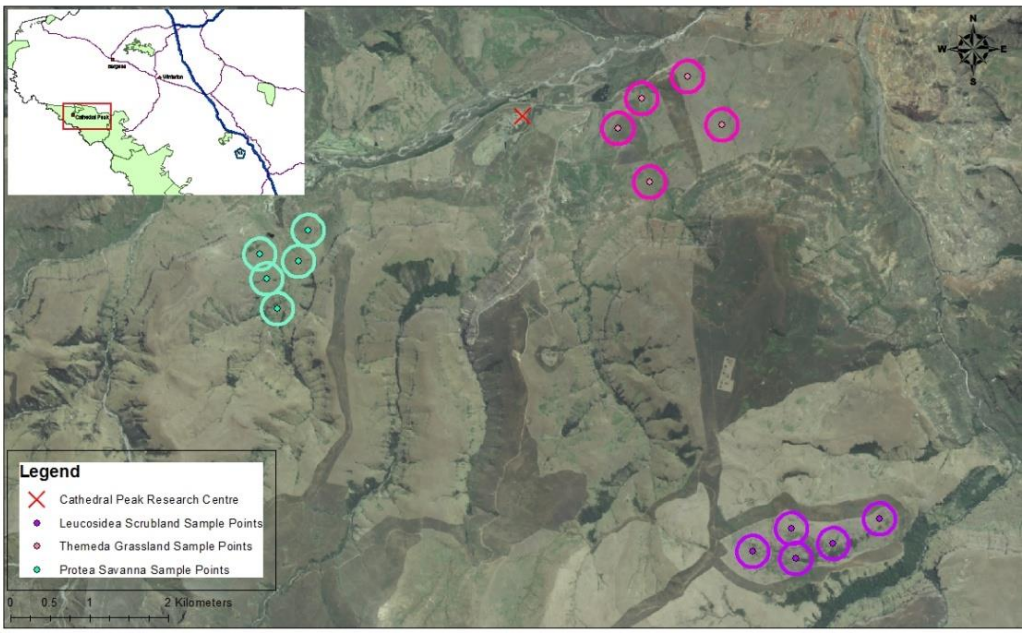

Figure 3.3. Sample Point locations for the three study areas situated in the environs of Cathedral Peak.

The central sampling point of each of the 15 sample locations was randomly placed with the aid of a vegetation map and ArcGIS 10.2 software. From this vegetation map, a hand-held Garmin eTrex 10 GPS was used to locate these sample points on the ground. At each sample site, the upper 2 cm of surface soil was collected using the tip of a hand trowel, placed in a brown paper bag and mixed. This followed the methods described by Adam and Mehringer (1975) and Bunting *et al.* (2013) for extracting modern pollen surface samples. The surface sample bags were then taken to the University of KwaZulu-Natal (UKZN) Palaeoecology laboratory in Pietermaritzburg for pollen extraction by chemical analysis methods.

3.2.2.2. Vegetation data

3.2.2.2.1. Reference collection vegetation

The vegetational composition of environs in the Cathedral Peak region has been shown to be diverse and complex (Killick, 1963; Hill, 1996). Work done by Hill (1992) established a reference collection of pollen and vegetation types in the area, but needed updating to be considered reliable for use in 2014. To this end, a thorough vegetation identification and collection survey was conducted in September 2013 of all main and common plant types in the Cathedral Peak area and taken back to the UKZN Palaeoecology laboratory, where the vegetation was prepared for chemical processing to produce updated pollen reference slides used in pollen identification and fall speed calculation (pollen grain geometry measurements).

3.2.2.2.2. Crackles vegetation protocol

For the collection of vegetation data surrounding each sample point, a 3-tiered surveying approach, known as the Crackles vegetation protocol as described by Bunting *et al.* (2013), was used to compile the vegetation inventory (Appendix 1). Bunting *et al.* (2013) have developed this detailed and specialised vegetation protocol exclusively for pollen modelling research, not only to simplify an overtly complicated task such as vegetation surveying, but also to standardise the way in which vegetation data is collected to facilitate comparison of results between modelling studies. This vegetation protocol is now standard practice in pollen modelling research as it allows for vegetation data to be distance-weighted, which is a critical variable in ERV analysis and calculation of RSAP and PPE values.

Mazier *et al.* (2008) show that to obtain reliable values in ERV analysis, vegetation surveys need to extend beyond the RSAP. Considering RSAP is an outcome of ERV analysis and often not available at the vegetation survey stage, a common approach is to simulate, using

HUMPOL software, an environment similar to the one in which the research is taking place to estimate a possible RSAP so that one is able to deduce how far the vegetation survey needs to extend (Sugita, 1994). Bearing in mind that pollen modelling research has only once been undertaken in South Africa (Duffin and Bunting, 2008), there is no environmental reference in which to run these simulations that estimate RSAP at the outset. Vegetation surveys were therefore done to the maximum possible distance that the available data allowed, that being 5 000 m around each sample point.

Present day vegetation around each sample location was surveyed according to the Crackles vegetation protocol (Appendix 1), with the purpose of comparing contemporary vegetation assemblages with modern pollen spectra extracted by way of soil surface samples. This protocol takes into consideration the assumption that vegetation closer to a sample point contributes more significantly to the pollen assemblage than those plants further away. The Crackles vegetation protocol therefore uses a ring-based approach to collecting vegetation data, which places theoretical concentric rings around each sample site at specified distances to allow for distance-weighting (Duffin and Bunting, 2008; Mazier *et al.,* 2008; Bunting *et al.,* 2013). Thus, the vegetation surveying method is partitioned into three zones (A, B, C), with a comprehensive vegetation survey done in zone A, an intermediate vegetation survey done in zone B, and GIS and remote sensing techniques used to extract broad-scale vegetation data from maps in zone C (Figure 3.4).

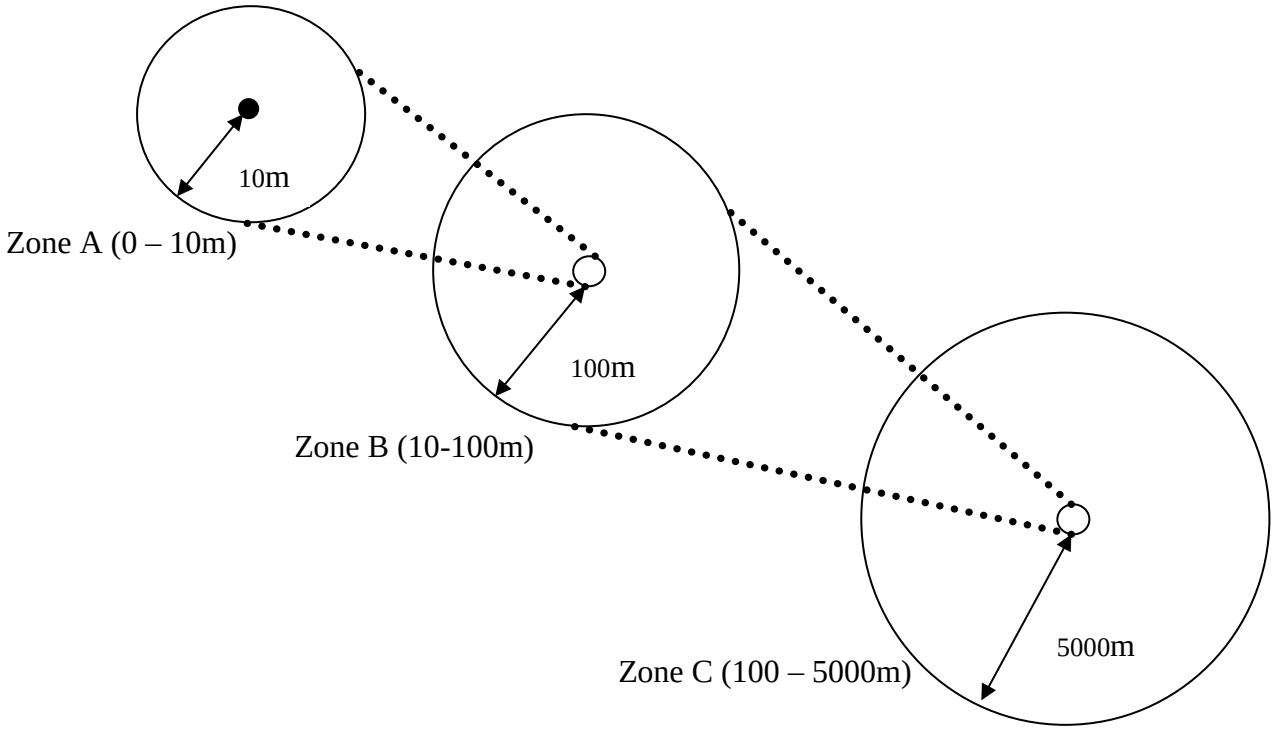

Figure 3.4. Three-tiered surveying approach as defined by the Crackles vegetation protocol (Bunting *et al.*, 2013).

1. Zone A (0-10m)

A detailed vegetation survey was completed according to the Crackles vegetation protocol for distances between 0 – 10m around each sample point located by the use of hand-held Garmin eTrex 10 GPS device (Appendix 1). Concentric ring boundaries in zone A are located at distances of 0.5m, 1.5m, 3m, 6m, and 10m, resulting in a total of five rings in zone A (Figure 3.5). Vegetation was identified and visually estimated from above using $1m^2$ quadrats placed at the mid-point in each ring in N, E, S, W directions. Additional quadrats were placed in the outer ring in NE, SE, SW and NW directions. This resulted in vegetation estimations for a total of 21 quadrats in zone A (Figure 3.5). All plants surveyed were identified to the species level where possible (Appendix 5).

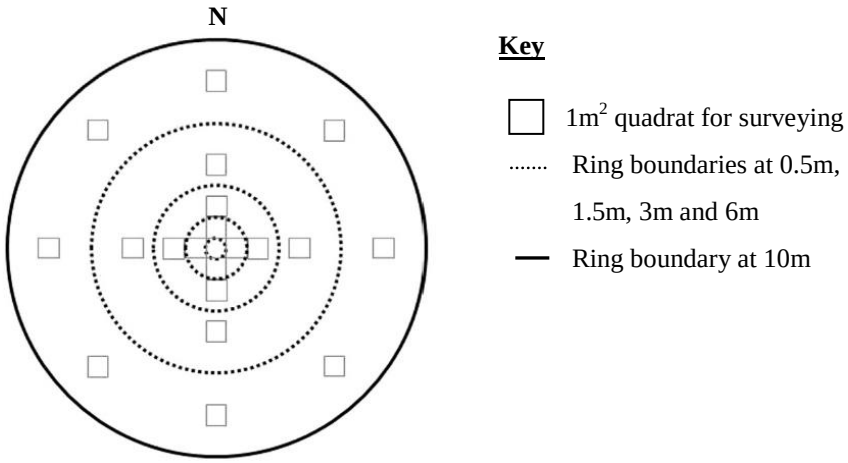

Figure 3.5. Zone A surveying strategy (0-10m). Indicated are the ring widths and quadrat placements for vegetation sampling (Bunting *et al.*, 2013).

2. Zone B (10-100m)

An intermediate vegetation survey was completed according to the Crackles vegetation protocol for distances between 10 – 100m around each sample point (Appendix 1). Concentric ring boundaries in zone B are located at 10m intervals from 10 to 100m, resulting in a total of nine rings in zone B (Figure 3.6). Vegetation in zone B was field sketched in these 10m ring intervals with the use of existing vegetation maps, ArcGIS 10.2 software, and by way of transect walks out to 100m every 30^o bearing from the sampling point, starting at N as 0^o. A total of 12 transect walks were done around each sample point using a compass and a hand-held GPS to record distance along the transect line. Distance along each of the transect lines where vegetation communities changed distinctly was noted and marked on the field sketch, and then joined by eye once all transect walks had been completed (Appendix 1). Unique vegetation communities were then identified and characterised, and four random

quadrats of $1m^2$ were surveyed and recorded in each distinct community. All plants surveyed were identified to the species level where possible.

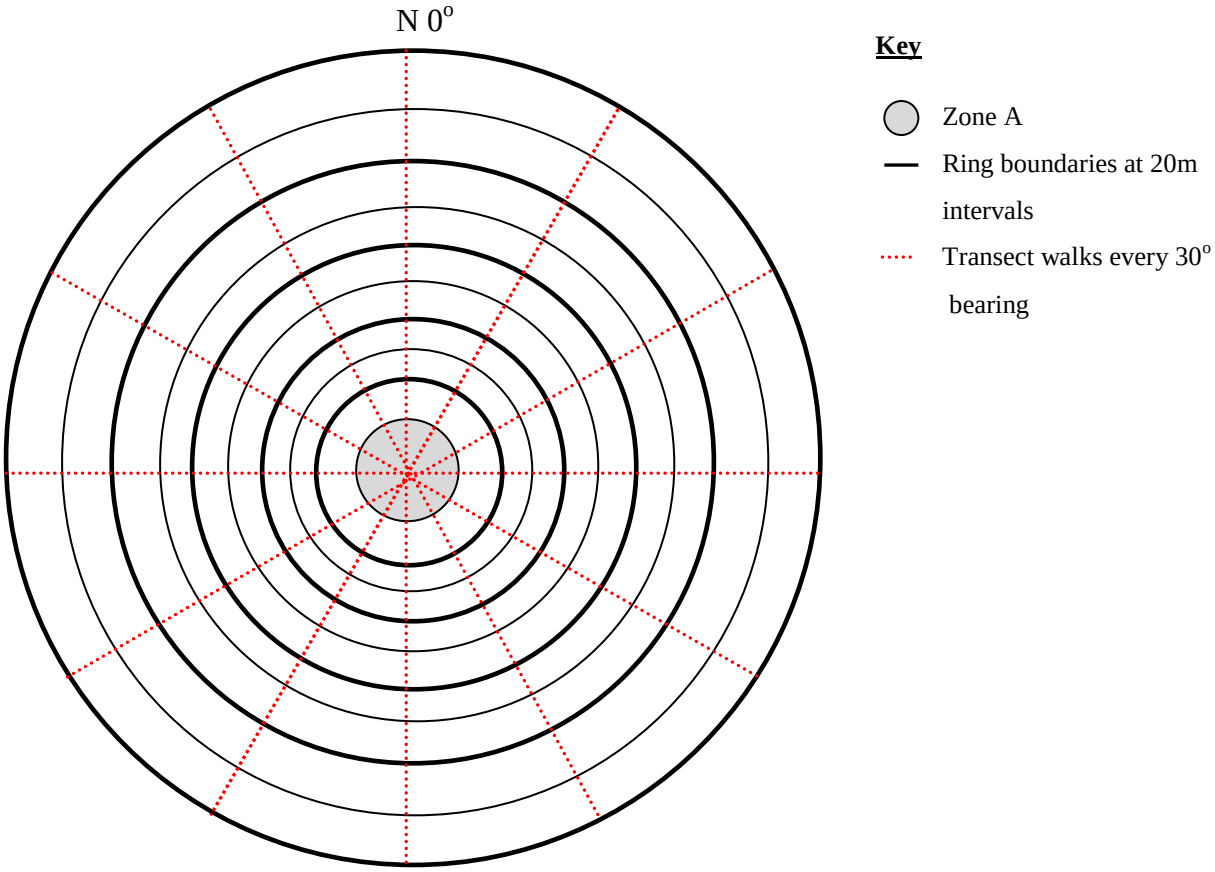

Figure 3.6. Zone B surveying strategy (10-100m). Indicated are the ring widths every 10m from 10-100m, and transect walks every 30° bearing (Bunting *et al.*, 2013).

3. Zone C (100-5 000m)

Vegetation data beyond 100m from each sample point was extracted from digitised aerial photographs and previous vegetation data of the Cathedral Peak region (Hill, 1992; Hill, 1996). Zone C of the Crackles vegetation protocol is relativiely subjective in that there are no set guidelines regarding the distances for ring-width or total ring number to be used. Research objectives and availability of large-scale vegetation data are the major influencing factors as to the number of rings, ring-width, and maximum vegetation survey extent chosen by the researcher for this zone (Broström *et al.*, 2004; Duffin and Bunting, 2008; Bunting *et al.*, 2013).

For the purpose of this research, a large-scale resolution vegetation map of the Cathedral Peak region and surrounding catchments was created from existing ground-truthed vegetation data and current aerial photography of the area (Figure 3.7). Full-colour aerial photography was obtained in digital format from the Surveyor-General in Mowbray, Cape Town, covering the Cathedral Peak region (Figure 3.7 A). Latest available coverage for the area was 2011 imagery with a pixel resolution of 0.5 m^2. In association with ground-truthed vegetation data provided by Hill (1992; 1996) (Figure 3.7 B), an interactive, on-screen heads-up approach was used to digitise vegetation community assemblages from the aerial photography for Cathedral Peak and the surrounding catchments (Figure 3.7 C, D). On-screen, heads-up digitising refers to a method of digitisation whereby the user focuses on the computer screen and uses the mouse cursor to manually trace features and create a new map layer from a scanned map or image (Haddock, 1998). Once the large-scale vegetation map layer had been created, all vegetation communities were classified and taxon data was input into the meta-data of this layer.

Due to Cathedral Peak's proximity to Lesotho, aerial photography available for the area could only extend to a 5 000 m radius beyond each sample point without interruption or missing data. Thus, the broad resolution map used to extract vegetation data for zone C reached a maximum areal extent of 10 km^2. Within this maximum extent, a total of 49 rings were chosen at 100 m intervals and used to extract vegetation community data for distance-weighting.

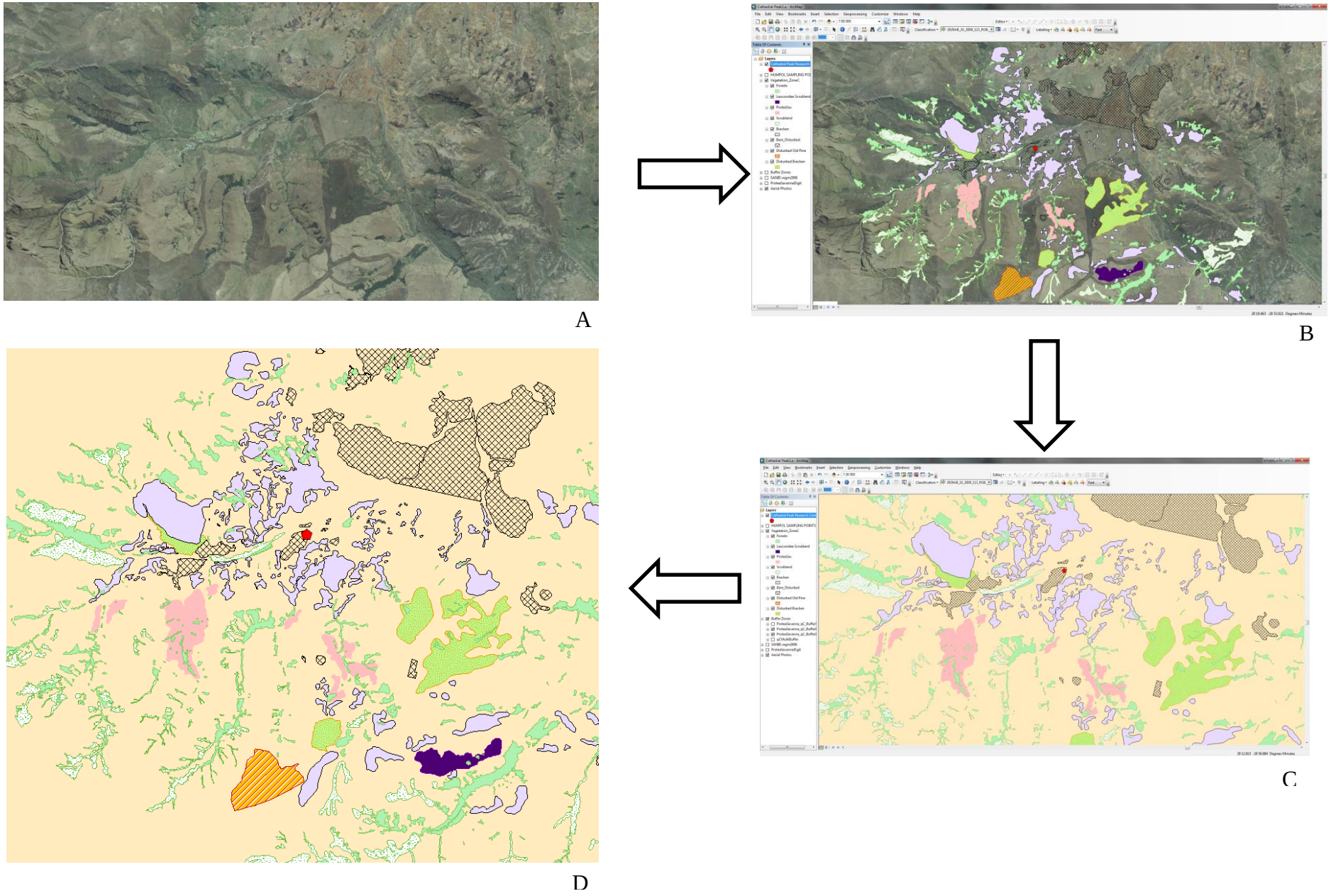

Figure 3.7. Zone C surveying strategy (100-5 000m). Large-scale vegetation map of 10km^2 [D] created from aerial photography [A] and digitised using ground truthed data [B], [C].

3.2.3. Laboratory methods

Laboratory methods included chemical processing of vegetation and soil mediums, and identification and counting of the processed pollen using light microscopy. The chemical processing of vegetation and soil surface samples follows two separate methods.

3.2.3.1. Reference collection vegetation

Vegetation collected from the Cathedral Peak environment was processed in the Palaeoecology laboratory at the University of KwaZulu-Natal in Pietermaritzburg, and followed standard methods as described by Moore *et al.* (1991) and Hill (1996). Pollen was extracted from plant specimens using chemical means which progressively boil the sample in hot alkali sodium hydroxide, filtering it through a 180 μm sieve by light crushing of the plant material, boiling the sieved material in a mixture of sulphuric and acetic acid (acetolysis mixture), washing it with distilled water and then staining the specimen with aqueous Safranine. Once chemical analysis was complete, the specimen was mounted onto pollen slides using glycerine jelly and sealed (Appendix 2). This method was repeated for all plants collected in the field, and three replica slides were made of each species.

3.2.3.2. Soil surface samples

Soil surface samples collected from Cathedral Peak were processed in the UKZN Palaeoecology laboratory in Pietermaritzburg, and followed standard methods as described by Moore *et al.* (1991), Hill (1996) and Duffin and Bunting (2008). Pollen was extracted from 5g of surface soil using chemical means which progressively boil the sample in hot alkali sodium hydroxide to remove humic acids from the sample, filtering it through a 180μm sieve by light crushing of the soil material, washing it with hydrochloric acid to remove carbonates, treating it with hydrofluoric acid to remove silicates, boiling the sample in acetolysis mixture to remove polysaccharides and washing the sample with distilled water. Thereafter, the sample was stained with aqueous Safranine, dehydrated using tertiary butyl alcohol and silicone oil added. This polleniferous oil was then mounted onto pollen slides using a glass rod and sealed (Appendix 3). This method was repeated for all soil surface samples, and three replica slides were made of each sample.

3.2.3.3. Pollen identification and counting

Once pollen slides had been prepared, pollen identification and counting was conducted. Depending on research objectives and the chemical processing method that is followed, the number of pollen grains counted differs significantly between studies (Mourelle and Prieto, 2012). Previous literature on modern and fossil pollen studies have shown researchers to count to 250, 300, 400, 500 or 1 000 pollen grains for a variety of reasons (Hill, 1996; Broström *et al.,* 2004; Duffin and Bunting, 2008; Wei *et al.,* 2011). For the purpose of this research, statistical techniques were used to establish an appropriate pollen count. One of the processed soil surface samples from each of the *Themeda* grassland, *Protea* savanna and *Leucosidea* scrubland communities were chosen to run an Analysis of Variance (Anova) and assess if there was any significant difference between a sample count of 250, 500 and 1 000 pollen grains in each community. Pollen in each representative community sample was counted to 250, 500 and 1 000 pollen grains at x63 magnification using a Leica DM750 light microscope and identified and verified using the African Pollen database and UKZN Pollen repository specific to Cathedral Peak taxa. It must be noted that pollen identification using light microscopy is not often possible beyond the family level or genera level of a taxon at best, and thus pollen was identified predominantly at the family level of taxon classification.

In all three communities it was found that no statistically significant difference existed between the population means of pollen counts of 250, 500 and 1 000 at the level of significance where $\alpha = 0.05$ (Appendix 4). As such, it was deemed sufficient to count the remaining samples to a minimum of 250 pollen grains. Pollen sums for the remaining samples were counted and identified at x63 magnification using a Leica DM750 light microscope, with the African Pollen database and UKZN Pollen repository specific to Cathedral Peak employed as identification catalogues.

3.2.3.4. Calculation of taxa fall speeds

A critical variable for applying Sutton's taxon-specific formula to calculate distance-weighting of vegetation data relies on the estimation of pollen grain fall speeds of the main taxa under concern (Duffin and Bunting, 2008). Broadly, pollen grains are categorised into two shape classes – spherical and ellipsoidal. Fall speeds are estimated using Stokes Law for spherical grains (Equation 3.1) and Falck's Assumption for ellipsoidal grains (Equation 3.2) (Gregory, 1973).

$$v_s = \frac{2r^2 \cdot g(\rho_0 - \rho)}{9\mu}$$ **Equation 3.1. Stokes Law**

where

v_s = spherical settling velocity (cm s^{-1})

r = pollen grain radius (cm)

g = acceleration due to gravity constant taken as 981cm s^{-2}

ρ_o = grain density (cm^{-3}) taken as $1cm^{-3}$

ρ = air density (cm^{-3}) taken as 1.27×10^{-3} cm^{-3}

μ = dynamic viscosity (cm^{-1} s^{-1}) taken as 1.8×10^{-4} cm^{-1} s^{-1}

$$v_e = v_s \sqrt[3]{\frac{a}{b}}$$ **Equation 3.2. Falck's Assumption**

where

v_e = ellipsoidal settling velocity (cm s^{-1})

v_s = spherical settling velocity (cm s^{-1})

a = major axis (cm)

b = minor axis (cm)

Pollen grain geometries were measured using a Leica DM750 light microscope at x40 magnification for all the dominant taxa from Cathedral Peak. Spherical grains were measured along one axis only, recording a diameter measurement, whereas ellipsoidal grains were measured along their major and minor axis and these measurements were recorded. For each taxon, a total of 50 random pollen grains were measured using pollen reference slides, and an average diameter (spherical) and major and minor axis (ellipsoidal) measurement was calculated.

3.2.4. Computer modelling methods

The HUMPOL (Hull Method of Pollen dispersal and deposition model) software suite has been specifically developed for the purposes of combining pollen dispersal and deposition models with computing power to facilitate the simulation of a spatial context of pollen dispersal and deposition in a landscape, and the simulation of pollen signals in relation to past

vegetation that supports vegetation reconstructions on palaeoecological investigations (Bunting, 2014). HUMPOL suite consists of multiple software programs used in this research, namely: SURVEY, POLSACK, MOSAIC5, POLFLOW, POLLOG and POLERV. These programs were used to prepare and input the processed vegetation and pollen data into a digital format which the dispersal and deposition models could be applied to (Figure 3.8).

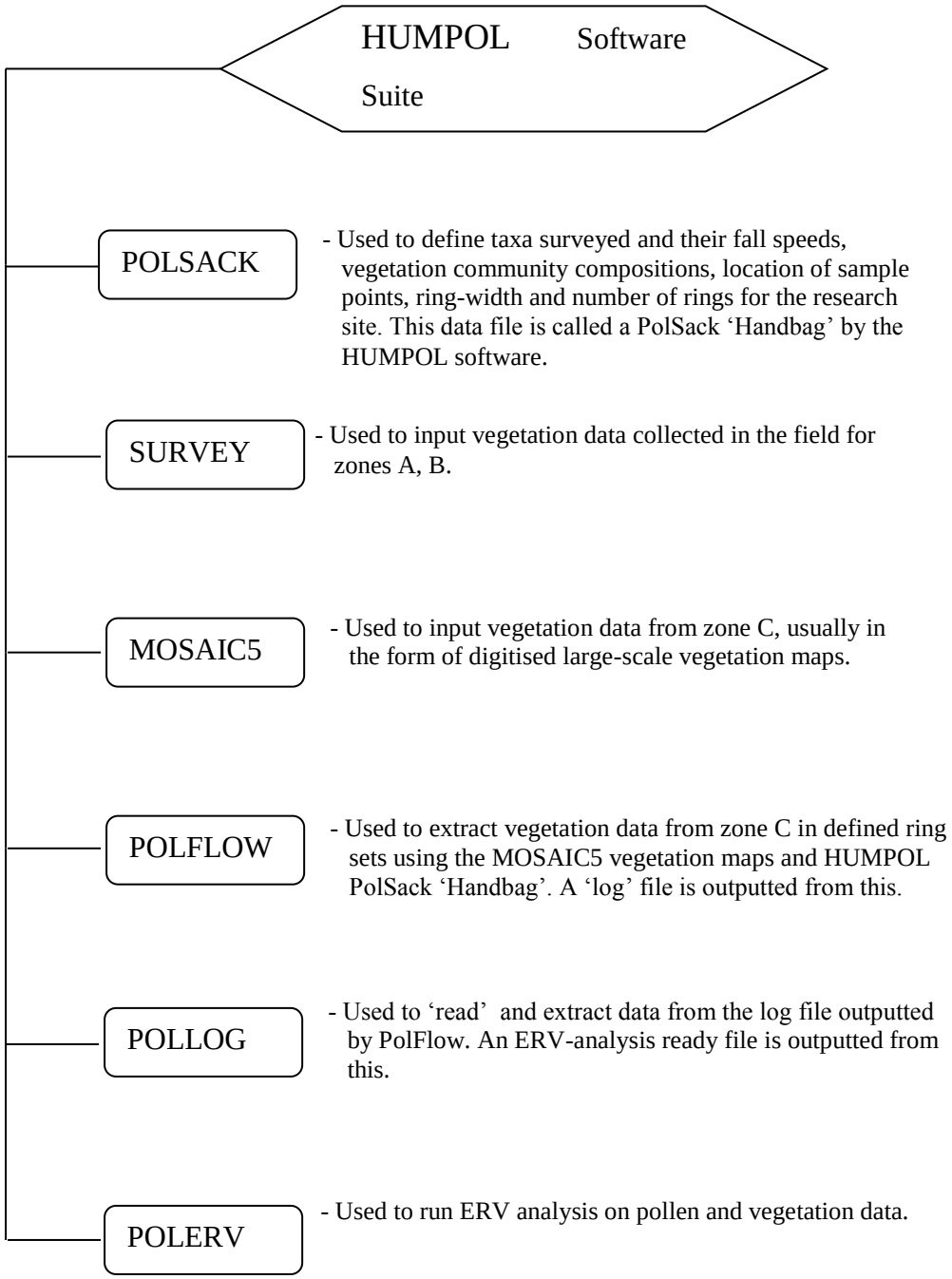

Figure 3.8. An illustration of the utility software comprising the HUMPOL software suite and their purpose.

3.2.4.1. Input of vegetation data – zones A, B

The first step in the modelling process is to input the vegetation data for zones A and B, and to use the HUMPOL software to calculate the distance-weighting in rings for each taxon. This required at the outset that a POLSACK data collection file be created which defined important research information such as the taxa present and their fall speeds that will be modelled, community compositions, sample point locations and ring data (ring width and number of rings) of the research area. In addition, a taxon dictionary file, of all plant taxa found in the research area, was created using notepad. Zone A and B vegetation data was inputted using SURVEY, which allows the user to enter their vegetation data into the 21 defined quadrats of zone A, and upload their field sketch map as a scanned image and attach vegetation data to it (Figure 3.9). Once all vegetation data had been input, distance-weighting was calculated using Sutton's taxon-specific weighting method in Excel.

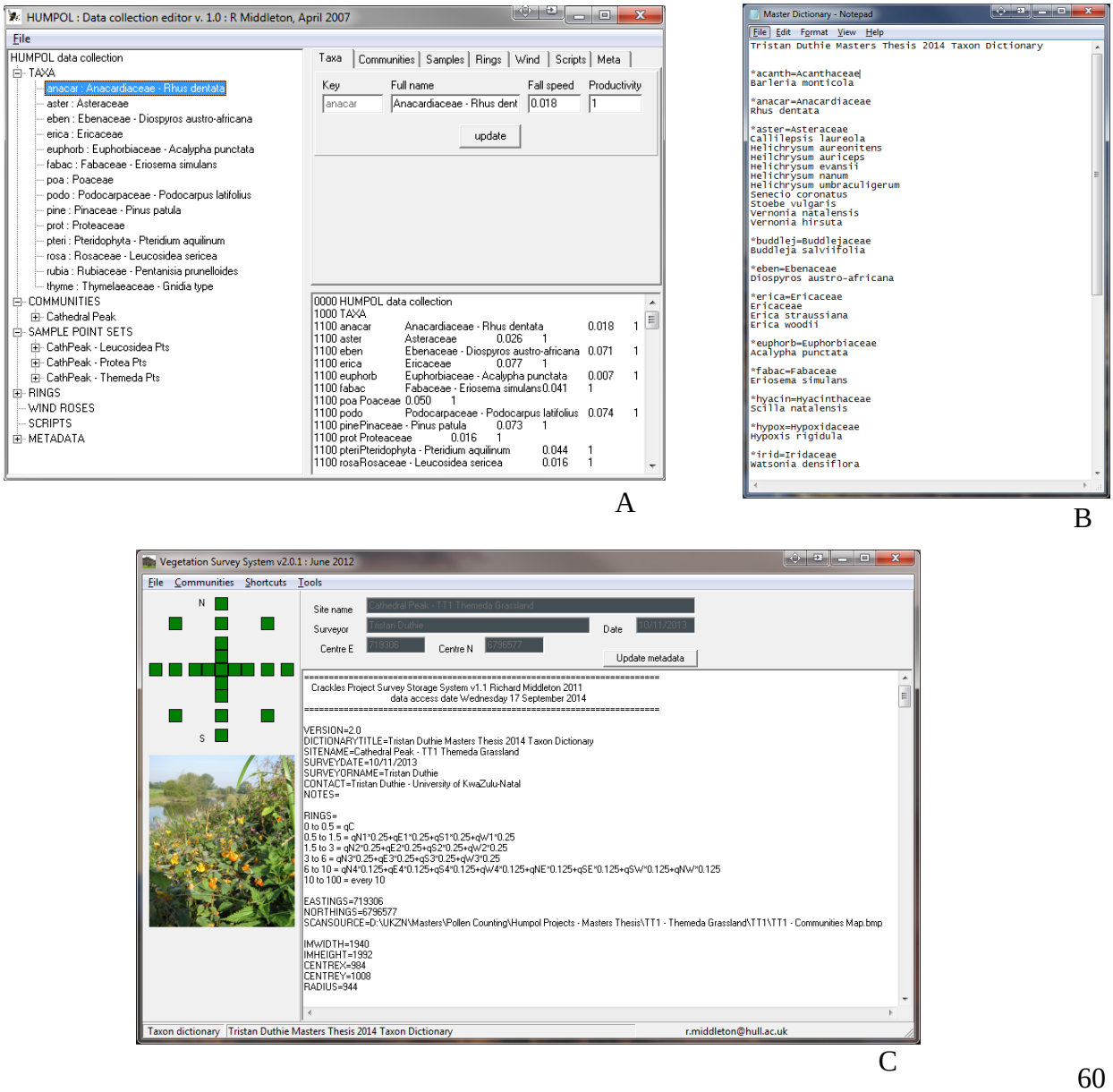

Figure 3.9. POLSACK [A] utility used to define research criteria, taxon dictionary created in notepad [B], and SURVEY [C] used to input zones A and B vegetation data.

3.2.4.2. Input of vegetation data – zone C

Zone C vegetation data was processed from digitised aerial photography using MOSAIC5, whereby vegetation communities were traced into MOSAIC5 from the large-scale vegetation map created, and then classified with existing vegetation data of the Cathedral Peak research area. This was done to a maximum radius of 5 000m around each sample point. Once all zone C vegetation had been input, POLFLOW and POLLOG were used to extract and read taxon percentages in each of the rings out to 5 000m (Figure 3.10). Thereafter, distance-weighting was calculated using Sutton's taxon-specific weighting method in Excel.

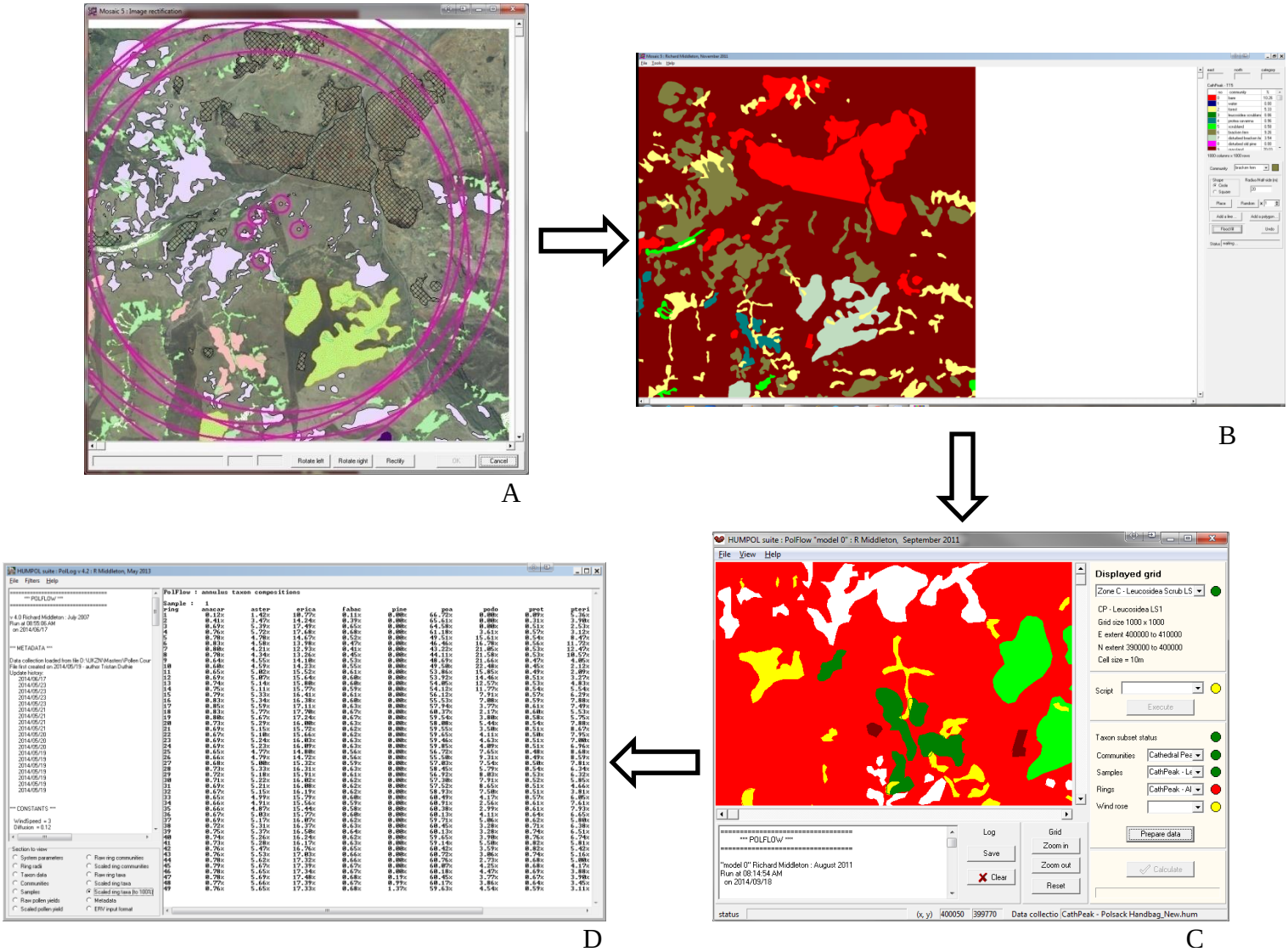

Figure 3.10. MOSAIC5 [A, B] utility used to trace and define vegetation communities for zone C, POLFLOW [C] used to extract vegetation data in defined ring sets, and POLLOG [D] used to read the POLFLOW log file.

3.2.4.3. ERV Analysis and RSAP and PPE calculations

Selection of taxa for ERV analysis and modelling is based on two suggested requirements, that is: i) those taxa chosen for modelling need to be present in both the pollen and vegetation data. Taxa where pollen or plant data is absent from the dataset, or where pollen and plants occur at a low frequency in only a few samples need to be removed from the datasets, and ii) the number of taxa chosen for ERV analysis should be half the number of samples collected in the field (Bunting and Hjelle, 2010). As the purpose of this research was to calculate individual RSAP for the *Themeda, Protea and Leucosidea* vegetation communities, selection criteria for taxa chosen for ERV analysis was based on presence in both the pollen and vegetation data in all five of each communities subsamples. Those taxa chosen for ERV modelling were then input in to an ERV analysis ready data file from POLLOG, which contains sample number, ring data, pollen data and the calculated distance weightings of each taxon out to 5 000m. This data file was run through POLERV, where ERV model 1, 2 or 3 can be chosen, the reference taxon for PPE values can be set and the number of iterations defined (Figure 3.11). The output of POLERV was transferred to excel to calculate RSAP and PPE values for the modelled taxa.

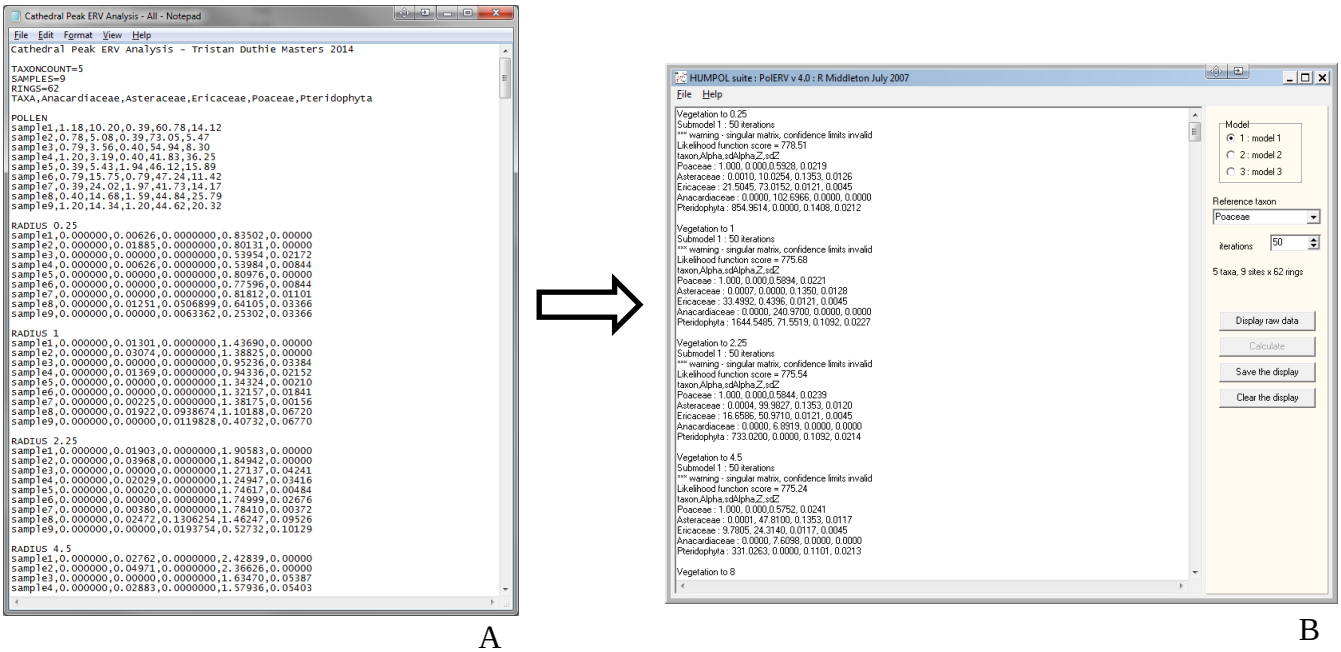

Figure 3.11. ERV-analysis ready file containing taxon, ring, pollen and distance weighted vegetation data [A]. This file is then run through the POLERV utility [B] to calculate RSAP and PPE values.

3.2.5. Conclusions

Methodologies used in data collection for pollen research have implicit complexities that entail reliability and appropriateness of sampling strategies, pollen identification and counting ability, and the extensive time periods it takes to complete these procedures in the laboratory. Methods employed in this research entailed three main areas, namely: field, laboratory, and computer modelling techniques. Field methods were used to collect both soil surface samples (from which to extract modern pollen spectra) and distance weighted vegetation data according to the specialised Crackles vegetation protocol. Laboratory methods involved chemical processing of vegetation and soil materials, and microscopy work for pollen identification, counting and pollen fall speed measurements. Computer modelling methods utilised the HUMPOL software suite to model pollen dispersal and deposition characteristics i.e. RSAP and PPE values, in the three chosen vegetation communities under consideration. These methods were considered reliable and appropriate as they have been specifically created and adapted for pollen modelling investigations - which is the core focus of this research.

Chapter Four

Results

4.1. Introduction

This chapter describes the results that were produced to address research aims and the associated objectives. Fifteen soil samples from Cathedral Peak were chemically processed, extracting pollen types and pollen counts to establish the modern pollen spectra of the area. Vegetation inventories around each sample point were collected in a 3-tiered surveying approach, known as the Crackles vegetation protocol, to compare modern vegetation assemblages to modern pollen rain assemblages. Taxon fall speeds were calculated to apply an ecologically relevant distance-weighting to the tiered vegetation data, which is a required step in running the ERV analysis models and calculating PPE values. ERV analysis was subsequently run and RSAP and PPE values calculated.

4.2. Pollen analysis

Pollen identification and counting results are illustrated (Table 4.1), with a total of 40 taxon families identified from 15 samples of a minimum count of 250 pollen grains from each. Samples 1-5 were taken from the *Themeda* grassland, samples 6-10 from the *Protea* savanna, and samples 11-15 from the *Leucosidea sericea* scrubland.

4.2.1. *Themeda* grassland: samples 1 – 5

Pollen analysis of samples 1-5 from the *Themeda* grassland community reveal the consistently high and dominant pollen type to be Poaceae (55-73%), with constant presence of Pteridophyte spores (5-15%), and Asteraceae pollen (5-10%) across all sites (Table 4.1). These herbaceous taxa are common and, moreover, indicative of the grassland environment in which they are found, and suggest that the modern pollen spectra of the *Themeda* grassland has a clear relationship to its surrounding vegetation. At these sites, Anacardiaceae, Cyperaceae and Pinaceae pollen grains are also recorded in significant quantities (Table 4.1). Anacardiaceae can be explained by the omnipresence of *Searsia dentata* shrubs in the surrounding grassland landscape from where the samples were extracted, and Cyperaceae reflects the presence of aquatic-type environments, explained by a nearby wetland and

Table 4.4. Identified and counted pollen data for all 15 soil surface samples collected from the Cathedral Peak region. Illustrated are the final percentage data for each identified taxon family in each sample. TT = *Themeda*-dominated grassland, PS = *Protea* savanna, and LS = *Leucosidea* scrubland.

			Identified Taxon [Family Level] Percentage Data																																								
		Sample Number	Amaranthaceae	Anacardiaceae	Apiaceae	Aquifoliaceae	Asteraceae	Begoniaceae	Boraginaceae	Campanulaceae	Caryophyllaceae	Celastraceae	Chenopodiaceae	Commelinaceae	Cornaceae	Cyatheaceae	Cyperaceae	Dipsacaceae	Ebenaceae	Ericaceae	Euphorbiaceae	Fabaceae	Fabaceae (Mimosoideae)	Geraniaceae	Iridaceae	Labiatae	Lycopodiaceae	Malvaceae	Moraceae	Myricaceae	Myrtaceae	Palmaceae	Pinaceae	Poaceae	Podocarpaceae	Polygalaceae	Proteaceae	Pteridophyte Spores	Rosaceae (Leucosideae)	Rubiaceae	Schropulariaceae	Thymelaceae	Unidentified
TT	**1**	1	0.38	2.68	0.00	0.00	9.96	0.00	0.00	0.00	0.00	0.00	1.53	16.86	0.38	0.00	2.30	0.00	0.00	0.00	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	1.15	55.17	0.00	1.53	0.00	5.75	0.00	0.00	0.00	0.38	0.77
	2	2	0.00	1.18	0.00	0.00	10.20	0.00	0.00	0.00	0.00	0.00	0.00	1.18	0.78	0.00	1.96	0.00	0.00	0.39	0.78	0.00	0.00	4.31	0.00	0.00	0.00	0.00	0.00	0.00	0.78	0.00	3.53	60.78	0.00	0.00	0.00	14.12	0.00	0.00	0.00	0.00	0.00
	3	3	1.56	0.00	0.00	0.00	8.95	0.00	0.00	0.39	0.00	0.00	0.00	1.95	0.00	0.39	2.72	0.00	0.00	0.00	0.00	0.00	0.39	0.78	0.00	1.17	0.00	0.00	0.00	0.00	0.00	0.00	1.95	62.26	1.17	0.00	0.00	14.79	0.00	0.00	0.00	0.00	1.56
	4	4	0.00	0.79	0.40	0.00	7.91	0.00	0.00	0.00	0.00	0.00	1.19	0.00	0.00	0.79	2.77	0.00	1.19	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	1.98	67.98	0.79	0.00	0.40	9.88	0.00	0.00	1.98	0.00	0.79
	5	5	0.00	0.78	0.00	0.00	5.08	0.00	0.00	0.00	0.00	0.39	0.78	0.00	0.78	0.78	4.30	0.00	0.39	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.78	0.00	3.52	73.05	0.78	0.00	0.00	5.47	0.00	0.00	0.00	0.78	1.95
PS	**1**	6	0.00	0.00	0.00	0.39	6.25	0.00	0.00	1.95	0.00	0.00	0.00	0.00	2.34	0.39	0.00	0.00	0.39	0.39	0.00	0.00	0.78	0.00	0.39	0.00	0.00	0.00	0.00	0.00	0.39	0.00	5.08	57.81	2.34	0.00	9.38	11.33	0.00	0.00	0.00	0.00	0.39
	2	7	0.00	0.79	0.00	0.00	3.56	0.00	0.00	2.37	0.00	0.00	0.00	0.00	0.00	0.79	9.49	0.00	0.79	0.40	0.00	1.58	0.79	0.00	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.40	1.19	54.94	1.19	0.40	6.32	8.30	0.00	0.00	0.00	0.40	1.98
	3	8	0.00	0.39	0.00	0.00	4.28	0.00	0.00	0.39	0.00	0.00	1.56	0.00	1.56	0.78	3.50	0.00	0.39	0.00	0.00	0.78	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.00	1.95	0.00	2.33	56.81	0.39	0.00	8.17	14.40	0.00	0.00	0.00	0.00	1.56
	4	9	0.00	1.20	0.00	0.00	3.19	0.00	0.00	0.00	0.00	0.00	0.40	0.00	3.19	0.80	2.79	0.00	0.40	0.40	0.00	0.40	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.00	1.20	41.83	0.80	0.00	5.58	36.25	0.00	0.00	0.00	0.00	0.40
	5	10	0.00	0.39	0.00	0.00	5.43	0.00	0.00	0.78	1.55	0.00	0.00	0.00	0.00	0.78	3.88	0.00	0.00	1.94	0.00	3.10	0.00	0.00	0.39	0.00	0.00	0.00	0.00	0.78	1.16	0.00	3.88	46.12	1.94	0.00	9.69	15.89	0.00	1.94	0.00	0.00	0.39
LS	**1**	11	0.00	0.79	0.00	0.00	15.75	0.00	0.00	0.00	0.00	0.39	0.39	0.00	0.39	0.00	3.54	0.00	1.97	0.79	0.00	1.18	0.39	0.00	0.00	0.00	1.97	0.00	0.00	0.00	0.39	0.00	2.36	47.24	0.00	0.00	0.00	11.42	10.63	0.00	0.00	0.00	0.39
	2	12	0.00	0.00	0.00	0.00	18.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.79	3.19	0.80	0.00	1.99	0.00	0.00	0.00	0.40	0.80	0.00	0.00	0.40	0.00	0.40	0.00	0.00	1.59	54.98	0.00	0.00	0.00	9.56	2.79	0.00	0.40	0.00	1.59
	3	13	0.00	0.39	0.00	0.00	24.02	0.00	0.40	0.00	0.00	0.00	0.00	0.00	1.97	0.39	2.36	1.97	1.97	1.97	0.00	0.00	0.00	0.39	1.18	0.00	0.00	0.00	0.00	0.00	0.39	0.00	1.57	41.73	0.00	0.00	0.00	14.17	1.57	0.00	0.00	0.79	3.15
	4	14	0.00	0.40	0.00	0.00	14.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.97	0.00	0.00	1.59	0.00	1.59	0.40	0.40	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.79	44.84	0.00	0.79	0.00	25.79	2.38	0.00	0.00	0.00	1.98
	5	15	0.00	1.20	0.00	0.00	14.34	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.40	3.59	5.58	0.00	1.20	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.40	0.80	0.40	0.00	0.00	44.62	0.00	0.00	0.40	20.32	1.99	0.00	0.00	0.00	3.59

stream system in the sample area. The presence of exotic Pinaceae is interesting especially considering the closest known Pinaceae plantation is approximately 6.9 km away, but isolated pine trees were observed invading nearby surrounding grasslands. This raises interesting questions of local versus regional influences observable in the modern pollen assemblage.

4.2.2. *Protea* savanna: samples 6 – 10

Pollen data from samples 6-10 from the *Protea* savanna indicates that the main taxa are Asteraceae (3-6%), Poaceae (41-57%), and Proteaceae (5-10%) pollen, and Pteridophyte spores (8-36%) (Table 4.1). As with the *Themeda* grassland, these dominant taxa are indicative of the surrounding landscape common to the *Protea* savanna, and therefore the composition of the modern pollen rain reflects the surrounding vegetation. Cyperaceae is present in a range from 2 – 9%, suggesting nearby aquatic environments, expected since a tributary of the Bhemane river runs through the sampling area. Other consistently occuring taxa in the surface pollen assemblages include Pinaceae (1-5%), Campanulaceae (1-3%), Fabaceae (1-3%) and Podocarpaceae (1-3%) (Table 4.1). Of significant interest is Podocarpaceae, which reflects the *Protea* savanna's proximity to patches of surviving indigenous afromontane forest.

4.2.3. *Leucosidea* scrubland: samples 11 – 15

Surface pollen data from samples 11-15 from the *Leucosidea* scrubland all show consistently high and dominant presence of Asteraceae (14-24%) and Poaceae (44-55%) pollen, Pteridophyte spores (9-25%) and lower proportions of Rosaceae pollen (1-10%) (Table 4.1). Vegetation in these landscapes was dominated by grasses, ferns and *Leucosidea sericea*. The main pollen types in the modern pollen spectra are therefore reflective of the surrounding vegetation, and thus modern pollen spectra demonstrate useful association to modern vegetation compositions surrounding the sampling sites. Additional taxa occurring in relatively significant quantities in the surface pollen data includes Ericaceae (<2%) and Cyperaceae (2-4%) (Table 4.1).

4.3. Vegetation

Vegetation surveys were conducted according to the Crackles vegetation protocol devised by Bunting *et al.* (2013), using a 3-tiered surveying approach. Combined averages from all in-depth surveys completed in zone A (0-10m) revealed Poaceae as the dominant plant type encountered at all sampling sites, with much bare ground around *Protea* and *Leucosidea*

sampling sites (Figure 4.1). Pteridophyta had significant presence in the *Leucosidea* and *Protea* communities due to the omnipresence of the bracken fern *Pteridium aqiulinum* in the Cathedral Peak region. As expected, Proteaceae and Rosaceae species were considerable in the *Protea* and *Leucosidea* areas respectively, mainly in the form of *Protea caffra*, *P. roupelliae*, and *Leucosidea sericea*. The *Themeda* grassland vegetation primarily consisted of Poaceae and small herbs and shrubs of Acanthaceae (*Barleria monticola*), Asteraceae (*Helichrysum aureonitens, Vernonia natalensis, Senecio coronatus*), Euphorbiaceae (*Acalypha punctata*), and Fabaceae (*Eriosema simulans*).

Zones B and C of the vegetation surveys were completed at a much coarser spatial resolution and therefore more generalisations had to be made. Describing the overall pattern of taxa represented shows that Poaceae is the dominant vegetation cover type in all three studied vegetation communities, interspersed with shrubs and herbs (Asteraceae, Ericaceae, Euphorbiaceae, Fabaceae, Rubiaceae and Thymalaeaceae species). Predominant woody vegetation cover was in the form of patchy indigenous *Podocarpus* type forest species. Higher altitudes and valley areas along river courses are dominated by scrub vegetation (Rosaceae) which was particularly evident in the *Leucosidea* and *Protea* communities, with bracken fern omnipresent throughout all vegetation communities.

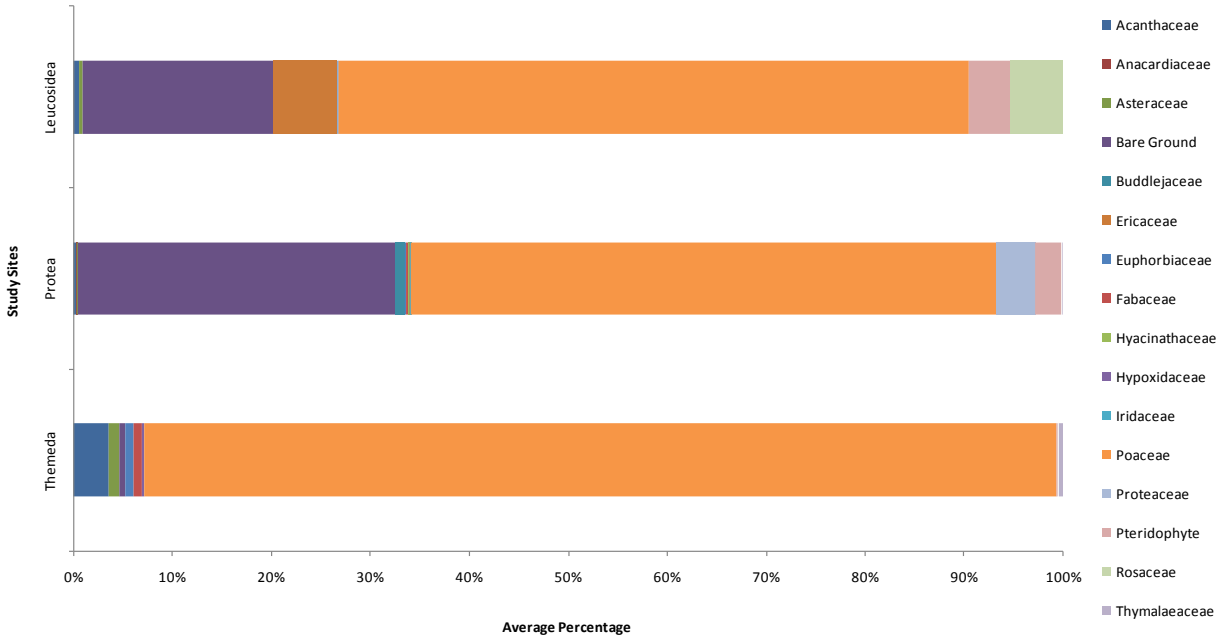

Figure 4.1. Combined average vegetation data for *Themeda, Protea* and *Leucosidea* across all sampling sites in zone A.

4.4. Pollen fall speeds

Fall speeds were estimated using a geometric method based of grain shape for dominant Cathedral Peak taxa. Stokes Law was used for spherical grains, supplemented by Falck's Assumption for ellipsoidal grains. For each taxon, 50 pollen grains were measured, from reference type slides, to provide average values of the dimensions for the calculations (Table 4.2). Values for individual plant species which produce the same palynological type present in the study area were calculated, then averaged to obtain a palynological type mean. In instances where only one species contributing to a palynological type was present in the area, that species' fall speed was used.

Table 4.5. Fall speed calculations of dominant vegetation taxa in the Cathedral Peak region.

Cathedral Peak Taxa		Approx. Shape	Avg Diameter (μm)	Fall Speed (m s^{-1})	Average Fall Speed (m s^{-1})
Poaceae	*Themeda triandra*	Spherical	50.98	0.079	0.050
	Alloteopsis semialata		33.91	0.035	
	Digitaria flaccida		37.44	0.042	
	Panicum natalensis		30.78	0.029	
	Tristachya leucothrix		46.67	0.066	
Asteraceae	*Aster bakeranus*	Spherical	33.21	0.033	0.026
	Helichrysum aureonitens		20.16	0.012	
	Vernonia type		32.62	0.032	
Cornaceae	*Curtisia dentata*	Spherical	16.89	0.009	0.009
Ebenaceae	*Diospyros austro-africana*	Spherical	48.32	0.071	0.071
Ericaceae	*Erica drakensbergensis*	Spherical	33.24	0.033	0.077
	Erica cerinthoides		65.97	0.132	
	Erica straussianna		47.05	0.067	
Euphorbiaceae	*Acalypha punctata*	Spherical	15.48	0.007	0.007
Fabaceae	*Eriosema simulans*	Spherical	36.81	0.041	0.041
Geraniaceae	*Pelargonium type*	Spherical	91.77	0.255	0.255
Rubiaceae	*Pentanisia prunelloides*	Spherical	42.12	0.054	0.054
Thymelaeaceae	*Gnidia kraussiana*	Spherical	25.79	0.020	0.020
Pteridophyte Spores	*Pteridium aquilinum*	Spherical	38.18	0.044	0.044
Proteaceae	*Protea caffra*	Spherical	23.38	0.017	0.017
	Protea roupillae		24.45	0.018	
Anacardiaceae	*Rhus dentata* - *x axis*	Ellipsoidal	26.95	0.018	0.018
	- *y axis*		22.13		
Commelinaceae	*Commelina type* - *x axis*	Ellipsoidal	43.33	0.037	0.037
	- *y axis*		28.61		
Podocarpaceae	*Podocarpus latifolius* - *x axis*	Ellipsoidal	68.52	0.074	0.074
	- *y axis*		38.19		
Pinaceae	*Pinus patula* - *x axis*	Ellipsoidal	64.94	0.073	0.073
	- *y axis*		37.20		
Rosaceae	*Leucosidea sericea* - *x axis*	Ellipsoidal	29.51	0.016	0.016
	- *y axis*		17.98		
Cyperaceae	*Carex austro-africana* - *x axis*	Ellipsoidal	38.49	0.035	0.036
	- *y axis*		30.26		
	Fionia type - *x axis*		37.17	0.037	
	- *y axis*		25.39		

4.5. ERV Analysis – estimating RSAP and PPE

ERV analysis was run using the POLERV utility program of the HUMPOL software suite to estimate Relevant Source Area of Pollen (RSAP) in metres and Pollen Productivity Estimates (PPE) in a unit-less ratio for vegetation communities in the Cathedral Peak region. This was

done on each of the three vegetation communities, that is – three independent ERV analyses were run on *Themeda, Protea* and *Leucosidea* separately. While there are no standard selection criteria of how best to choose taxa for ERV analysis in pollen dispersal and deposition modelling, most pollen modelling research follows two specific advisory rules: i) taxa where pollen or plants are absent from one of the datasets, or where both plant and pollen data of that taxa occurs in low frequency in only a few samples should be removed from ERV analysis, and ii) the number of taxa chosen for ERV analysis should be no more than half the number of samples collected in the field (e.g. Bunting and Hjelle, 2010). While these rules are suggested, they need not be strictly adhered to. More taxa in smaller numbers of samples can be run, however in instances such as this, there will understandably be greater uncertainties in any solutions the model finds compared to studies with larger sample numbers. For ERV models to run, a minimum of three taxa and samples are required for the algorithm find solutions. Due to the high species diversity of vegetation communities in Cathedral Peak over relatively short spatial scales (a function of altitude) coupled with the aforementioned standardised selection rules, only a small subset of the total number of taxa recorded were chosen for ERV analysis. Particular selection criteria of taxa used for the purposes of ERV analysis in this research were based on taxon presence in both the pollen and vegetation data in all five of each of the *Themeda, Protea* and *Leucosidea* communities subsamples. All analyses used ERV models 1 and 2 in the running of ERV analysis to evaluate if they provide comparable model outputs, running only Sutton's taxon-specific distance weighting.

4.5.1. *Themeda* grassland

Taxa chosen for ERV analysis, based on their presence in all five samples, were Poaceae, Pteridophyta and Asteraceae, with Poaceae set as the reference taxon. Bunting *et al.* (2013) state that there are three important criteria for choosing a taxon as the reference: i) the reference taxon must be common in every sample, ii) the reference taxon must have a good range of values in both the pollen and vegetation data in datasets, and iii) the reference taxon should have an anticipated PPE value in the middle of the range of taxa studied. While the third criterion is difficult to discern until the ERV analysis has been run (as PPE's are an outcome of ERV analysis), the first two are easily distinguishable by examining the data one has collected. Poaceae was common in all *Themeda* samples and had a good range of pollen data and distance-weighted values. RSAP is defined as that point along the curve (of likelihood function score plotted against distance of vegetation survey) where an asymptote is

reached, and is used as a measure to discern the distance around a sampling point beyond which the fit of the ERV model to the pollen-vegetation provided does not improve. In other words, within the RSAP, both the amount of a plant species and its position relative to a sample point can affect the pollen signal. Beyond the RSAP, only the amount of a plant species matters in terms of influencing the pollen signal, not its distribution.

The *Themeda* grassland shows a RSAP of approximately 150 m. Both ERV models demonstrate similar RSAPs (Figure 4.2), suggesting both models adequately fit the data. PPE values are used to show proportional values of pollen representation of taxa in a pollen assemblage in a given area of vegetation, and are important variables for quantitative reconstruction purposes of past vegetation communities and their abundances. In terms of PPE values obtained from ERV analysis, model 2 illustrates better fit to the data because of having the lower likelihood function score values, and is therefore chosen as the ERV model to base results on (Table 4.3). Final PPE values were calculated by taking an average of the alpha coefficients (outputted from ERV analysis) from the chosen RSAP to the furthest point of the vegetation survey (i.e. 5 000 m). Calculated PPE values show that relative to Poaceae (PPE = 1), Asteraceae pollen (PPE = 0.00026) producing plant species are substantially less productive in terms of pollen production than grasses, whereas Pteridophyte (PPE = 3.14) are significantly higher palynomorph producers. In other words, $1m^2$ of Asteraceae vegetation produces ≈ 3 800 (1/0.00026) times less pollen than $1m^2$ of Poaceae, and $1m^2$ of Pteridophyte vegetation produces ≈ 3 (3.14/1) times more spores than $1m^2$ of Poaceae produces pollen (Figure 4.3). These results are interesting when taking into consideration growth forms and pollination methods of these plant families and how this relates to differential pollen production abilities. Poaceae generally have a singular inflorescence at the end of each module from which pollen is released, whereas Asteraceae plants possess a pseudanthium - clusters of flower heads exhibiting a ‘single’ flower head appearance - and so an assumption exists that Asteraceae would produce more pollen. Yet, Poaceae are anemophilous plants whereas Asteraceae are predominantly zoophilous, and so they have less need to produce masses of pollen and disperse it well (Morhardt and Morhardt, 2004; Perreta *et al,* 2011). Pteridophyte growth forms have multiple pinna on each leaf blade, with dot-clustered sori on the underside which produce many fern spores (Cooke and Racusen, 1988). It is thus expected that Pteridophyta would produce a lot of spores when compared to Poaceae.

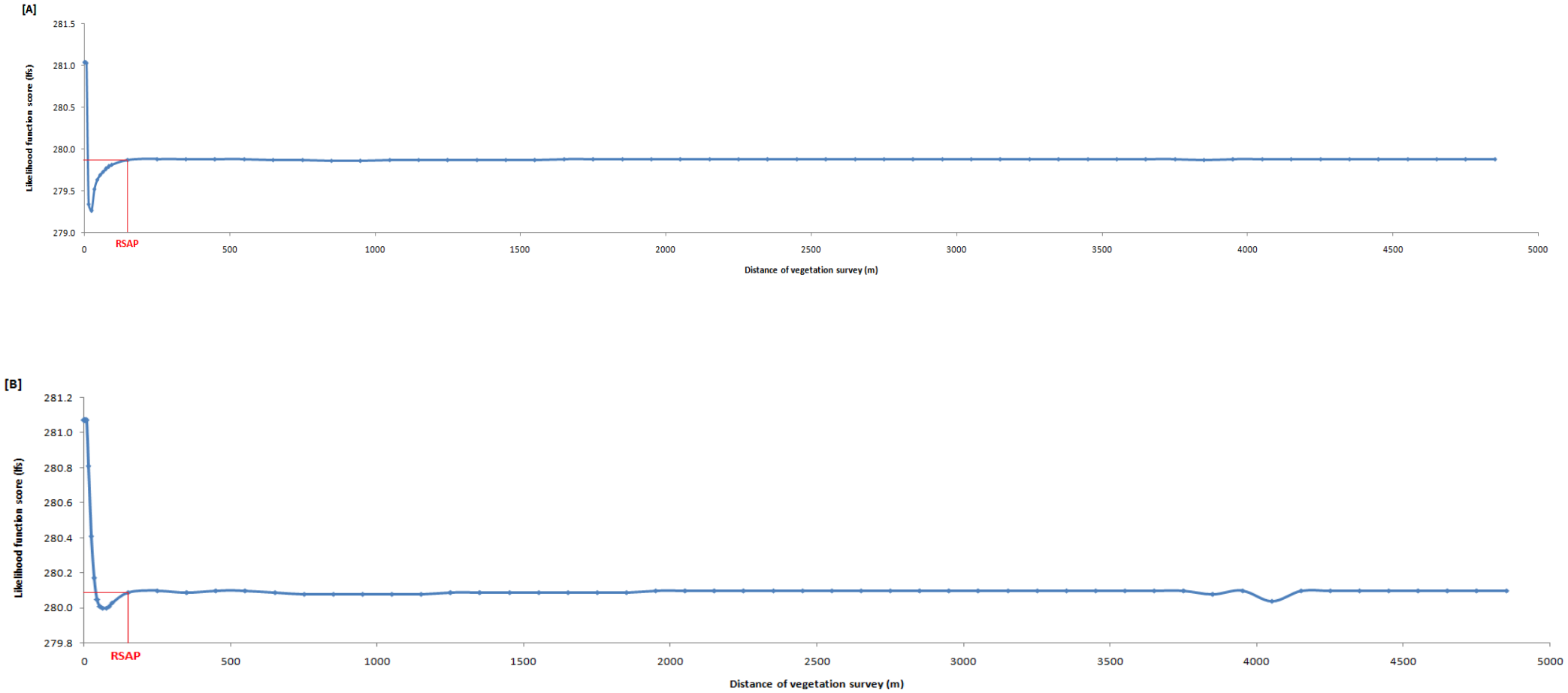

Figure 4.2. ERV analysis output for *Themeda* grassland sampling sites. Illustrated are likelihood function score graphs for pollen-vegetation datasets run with Sutton's taxon specific distance-weighting using ERV model 1 [A] and 2 [B]. RSAP is visually estimated from the graphs where the curve tends to an asymptote.

Table 4.6. Calculated PPE estimates for taxa selected from *Themeda* samples.

PPE Estimates			
	Poaceae	Asteraceae	Pteridophyta
Model 1	1	0.00015	4.60171
Model 2	1	0.00026	3.14094

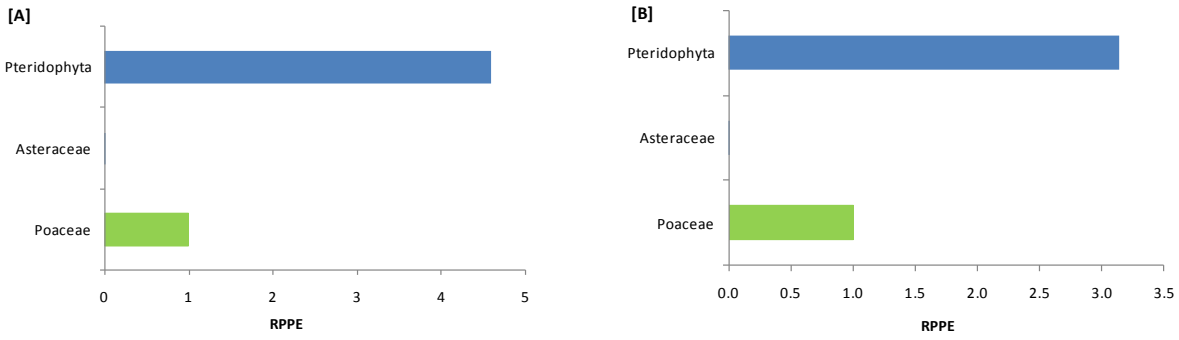

Figure 4.3. *Themeda* PPE values for graphical representation using ERV models 1 [A] and 2 [B].

4.5.2. *Protea* savanna

Taxa chosen for ERV analysis, based on their presence in all five samples, were Poaceae, Pteridophyta, Asteraceae, Proteaceae and Podocarpaceae. As there were more than three taxa for the *Protea* samples, two ERV analyses with four taxa were run, each with Poaceae set as the reference taxon so that results could be directly comparable. ERV analysis 1 consisted of Poaceae, Proteaceae, Podocarpaceae and Pteridophyta, and ERV analysis 2 consisted of Poaceae, Proteaceae, Asteraceae and Pteridophyta (Table 4.4; Figures 4.4, 4.6).

ERV analysis with the first subset of taxa reveals an estimated RSAP of 150 m, with both ERV models producing comparable RSAPs (Figure 4.4) to suggest both models fit the data adequately. ERV analysis with the second subset of taxa provides a RSAP range between 100 and 150 m using model 1 and 2 respectively (Figure 4.6). PPE values obtained from ERV analysis show that model 1 has a better fit to the data because of having the lower likelihood function score values and a more stable likelihood function score plot, and is therefore chosen as the ERV model to base results on (Table 4.4). Final PPE values were calculated by taking an average of the alpha coefficients (outputted from ERV analysis) from the chosen RSAP to the furthest point of the vegetation survey (i.e. 5 000 m). PPE values suggest that relative to Poaceae (PPE = 1), Asteraceae pollen (PPE = 0.00038) and Proteaceae pollen (PPE = 0.22) producing plant species are less productive in terms of pollen production than grasses,

whereas Pteridophyta (PPE = 8.49) and Podocarpaceae pollen (PPE = 6.54) producing species are significantly higher producers. Specifically, $1m^2$ of Asteraceae vegetation produces ≈ 2 600 (1/0.00038) times less pollen than $1m^2$ of Poaceae and $1m^2$ of Proteaceae vegetation produces ≈ 4.5 (1/0.22) times less pollen than $1m^2$ of Poaceae, while Podocarpaceae produces ≈ 6.5 (6.5/1) times more pollen than $1m^2$ of Poaceae and Pteridophyte produces ≈ 8.5 (8.49/1) times more spores than $1m^2$ of Poaceae produces pollen (Figure 4.5). These results are again interesting when taking into consideration growth forms and pollination methods of these plant families and how this influences pollen production. While Poaceae was explained as having a singular inflorescence at the end of each module from which pollen is released, and Asteraceae possessing clusters of flower heads, Proteaceae have multiple inflorescences consisting of several cushioned flowers and follicles condensed into one compacted head like structure (Collins and Rebelo, 1987). One would therefore assume much like Asteraceae, that due to having a cluster of flower heads that produce pollen, Proteaceae would be higher pollen producers when compared to Poaceae. Yet, when taking into consideration pollination methods, it is noted that Poaceae are anemophilous plants while Proteaceae are zoophilous, and so the need to produce masses of pollen and disperse it well are lowered. Pteridophyte growth forms were shown to have multiple pinna on each leaf blade, under which dot-clustered sori produce many fern spores for reproduction (Cooke and Racusen, 1988). Podocarpaceae growth forms have ovulate cone structures containing pollen on the ends of all vegetative shoots on their needle-like leaf apparatus (Tomlinson *et al.*, 1991). Moreover, Podocarpaceae are anemophilous thus produce masses of pollen for dispersal. It is thus expected that Pteridophyta and Podocarpaceae would produce a lot of spores and pollen, respectively, when compared to Poaceae.

Table 4.4. Calculated PPE estimates for taxa selected from *Protea* samples using ERV models 1 and 2. Results of both taxa subsets have been combined into one table.

PPE Estimates					
	Poaceae	Podocarpaceae	Proteaceae	Pteridophyta	Asteraceae
Model 1	1	6.54313	0.22356	8.49329	0.00038
Model 2	1	5.13538	0.00050	9.51827	0.00057

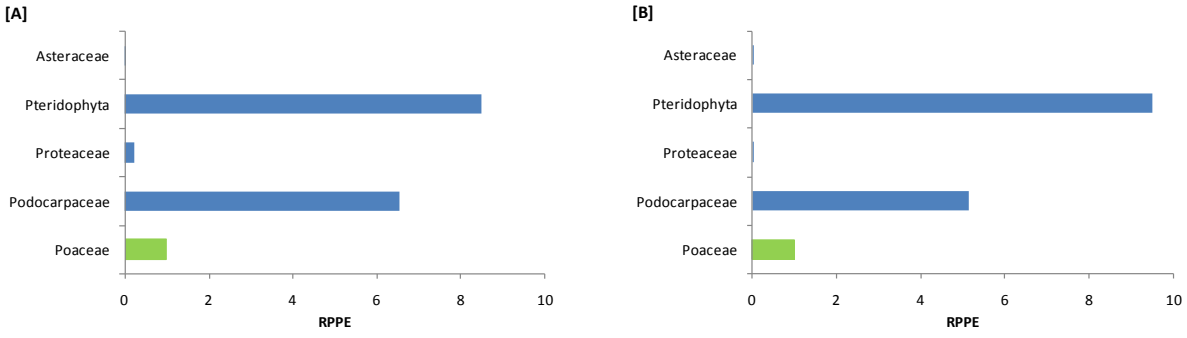

Figure 4.5. *Protea* PPE values for graphical representation using ERV models 1 [A] and 2 [B].

4.5.3. *Leucosidea* scrubland

Pollen and spore taxa chosen for ERV analysis, based on their presence in all five samples, were Poaceae, Pteridophyta, Ericaceae, and Rosaceae, with Rosaceae set as the reference taxon. The *Leucosidea* scrubland appears to have an RSAP of approximately 100 m from the source. Both ERV models demonstrate comparable RSAP values (Figure 4.7), suggesting that both models fit the data adequately. PPE values obtained from ERV analysis illustrate that model 1 has a better fit to the data because of having the lower likelihood function score values and a more stable likelihood function score plot, and is therefore chosen as the ERV model to base results on (Table 4.5). PPE values were calculated by taking an average of the alpha coefficients (outputted from ERV analysis) from the chosen RSAP to the furthest point of the vegetation survey (i.e. 5 000 m). PPE values show that relative to Rosaceae (PPE = 1), Poaceae pollen (PPE = 0.28) and Ericaceae pollen (PPE = 0.16) producing plant species are less productive in terms of pollen production than Rosaceae, whereas Pteridophyta (PPE = 7.04) are higher palynomorph producers. Specifically, $1m^2$ of Poaceae produces ≈ 3.5 (1/0.28) times less pollen than $1m^2$ of Rosaceae and $1m^2$ of Ericaceae vegetation produces ≈ 6 (1/0.16) times less pollen than $1m^2$ of Rosaceae, and Pteridophyte produces ≈ 7 (7.04/1) times more spores than $1m^2$ of Rosaceae produces pollen (Figure 4.8).

Taking into consideration growth forms and pollination methods of these plant families and how this relates to differential pollen production abilities is necessary to contextualise the PPE results. Rosaceae generally have a bunched collection of individual flower heads made up of a few stamens that produce pollen, and so the bunched nature of the many small flowers results in an expectation of a fair amount of pollen being produced (Chacoff *et al.*, 2007). As already explained, Poaceae generally have a singular inflorescence at the end of each from which pollen is released, and so less pollen is expected to be produced when compared to Rosaceae. Ericaceae flowers are mostly tubular, consisting of stamens within the urn-like shaped flower that produces pollen, and usually occur in bunches on branches surrounded by needle-like spines (Navarro, 2001). Moreover, Rosaceae and Poaceae are anemophilous plants, whereas Ericaceae are zoophilous and the need to produce a mass of pollen and disperse it well is lowered. Pteridophyte growth forms show ferns to have multiple pinna on each leaf blade, under which dot-clustered sori produce many fern spores (Cooke and Racusen, 1988). It is thus evident that Pteridophyta are high spore producers based on growth form.

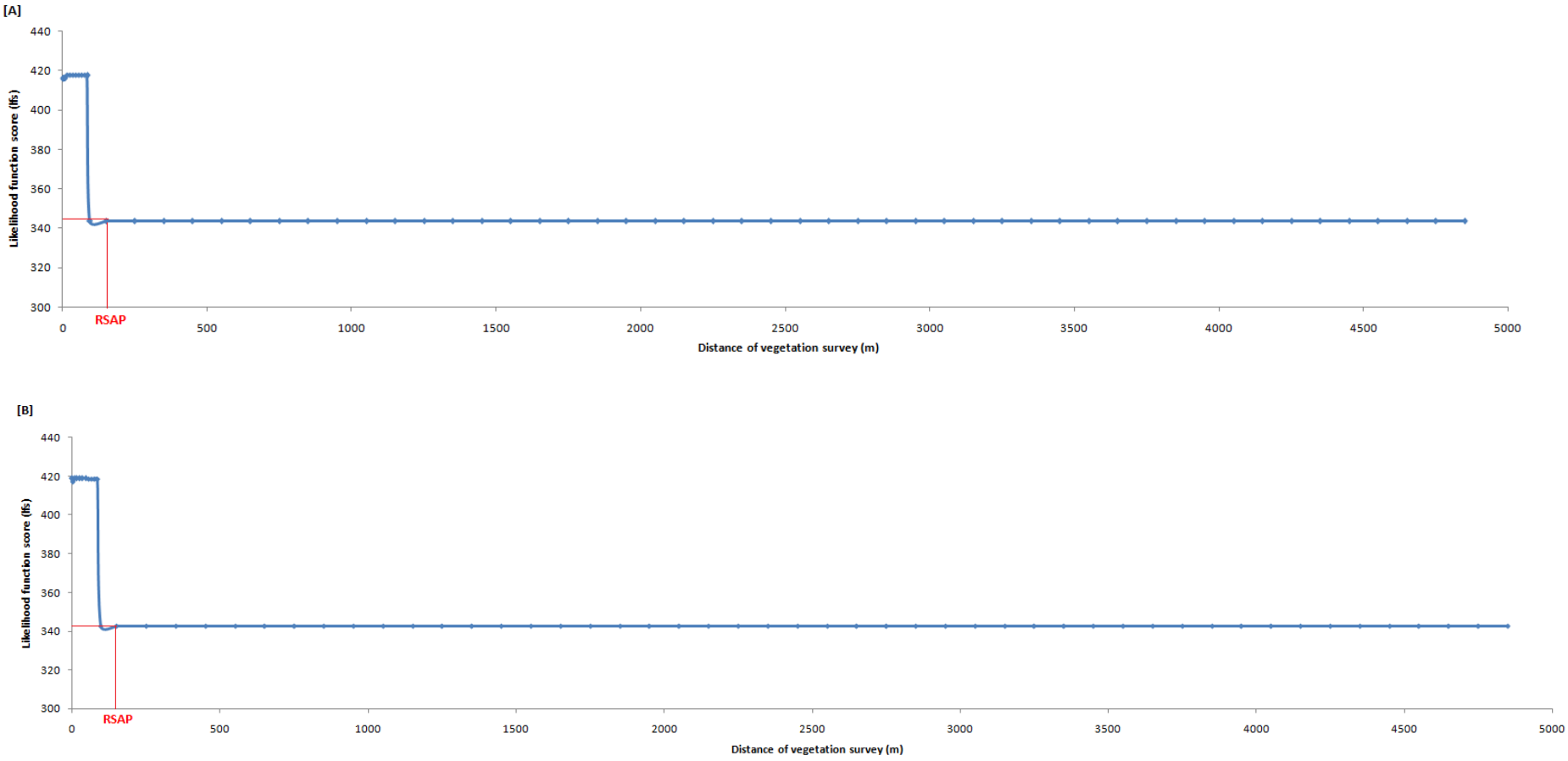

Figure 4.4. ERV analysis output for *Protea* savanna sampling sites. Illustrated are likelihood function score graphs for pollen-vegetation datasets run with Sutton's taxon specific distance-weighting using ERV model 1 [A] and 2 [B] for the first subset of taxa – Poaceae, Proteaceae, Podocarpaceae and Pteridophyta. RSAP is visually estimated from the graphs where the curve tends to an asymptote.

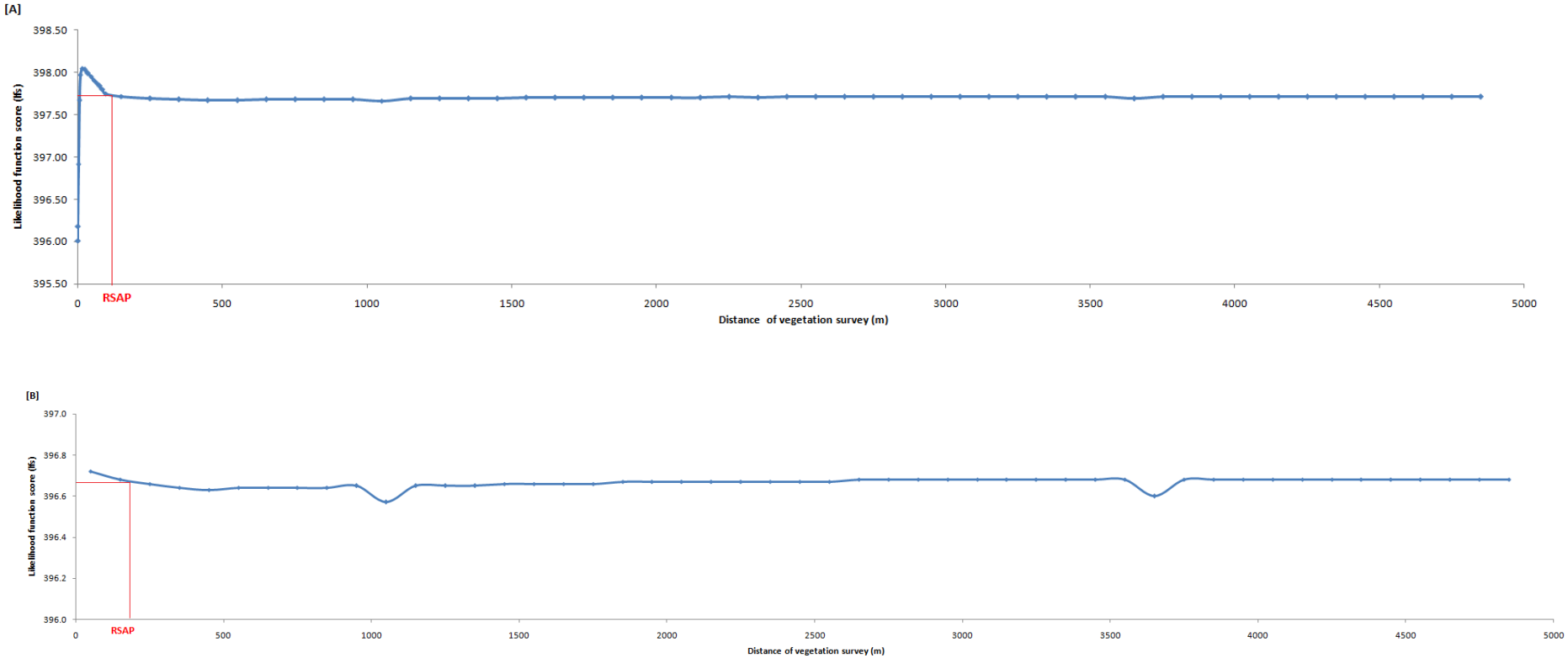

Figure 4.6. ERV analysis output for *Protea* savanna sampling sites. Illustrated are likelihood function score graphs for pollen-vegetation datasets run with Sutton's taxon specific distance-weighting using ERV model 1 [A] and 2 [B] for the second subset of taxa – Poaceae, Proteaceae, Asteraceae and Pteridophyta. RSAP is visually estimated from the graphs where the curve tends to an asymptote.

Table 4.5. Calculated PPE estimates for taxa selected from *Leucosidea* samples. Results of both taxa subsets have been combined into one table.

PPE Estimates				
	Rosaceae	Poaceae	Pteridophyta	Ericaceae
Model 1	1.00000	0.28499	7.04411	0.16911
Model 2	1.00000	0.00052	14.85367	1.14274

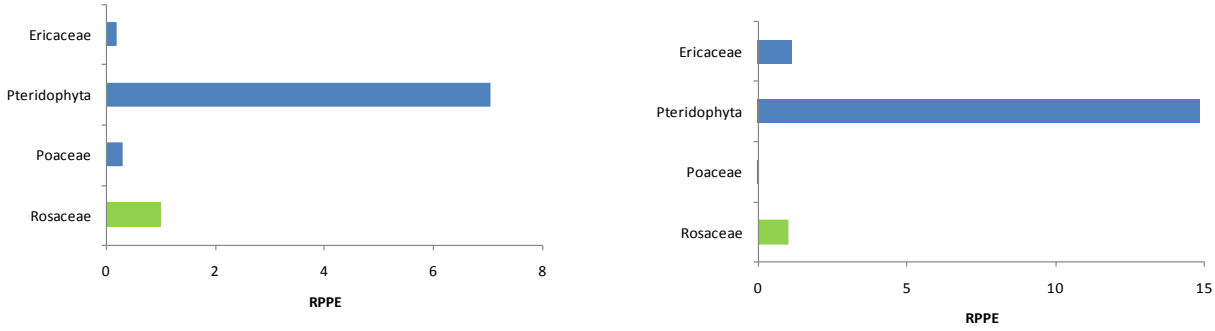

Figure 4.8. *Leucosidea* PPE values for graphical representation using ERV models 1 [A] and 2 [B].

Table 4.6. Summary of ERV analysis results for all three Cathedral Peak vegetation communities studied.

Summary of Results									
Vegetation Community	ERV Model	RSAP	PPE						
			Asteraceae	Ericaceae	Poaceae	Podocarpaceae	Proteaceae	Pteridophyta	Rosaceae
Themeda	1	≈ 150 m	0.00015	-	1	-	-	4.60171	-
	2	≈ 150 m	0.00026	-	1	-	-	3.14094	-
Protea	1	≈ 100 - 150 m	0.00038	-	1	6.54313	0.22356	8.49329	-
	2	≈ 100 - 150 m	0.00057	-	1	5.13538	0.0005	9.51827	-
Leucosidea	1	≈ 100 m	-	0.16911	0.28499	-	-	7.04411	1
	2	≈ 100 m	-	1.14274	0.00052	-	-	14.85367	1

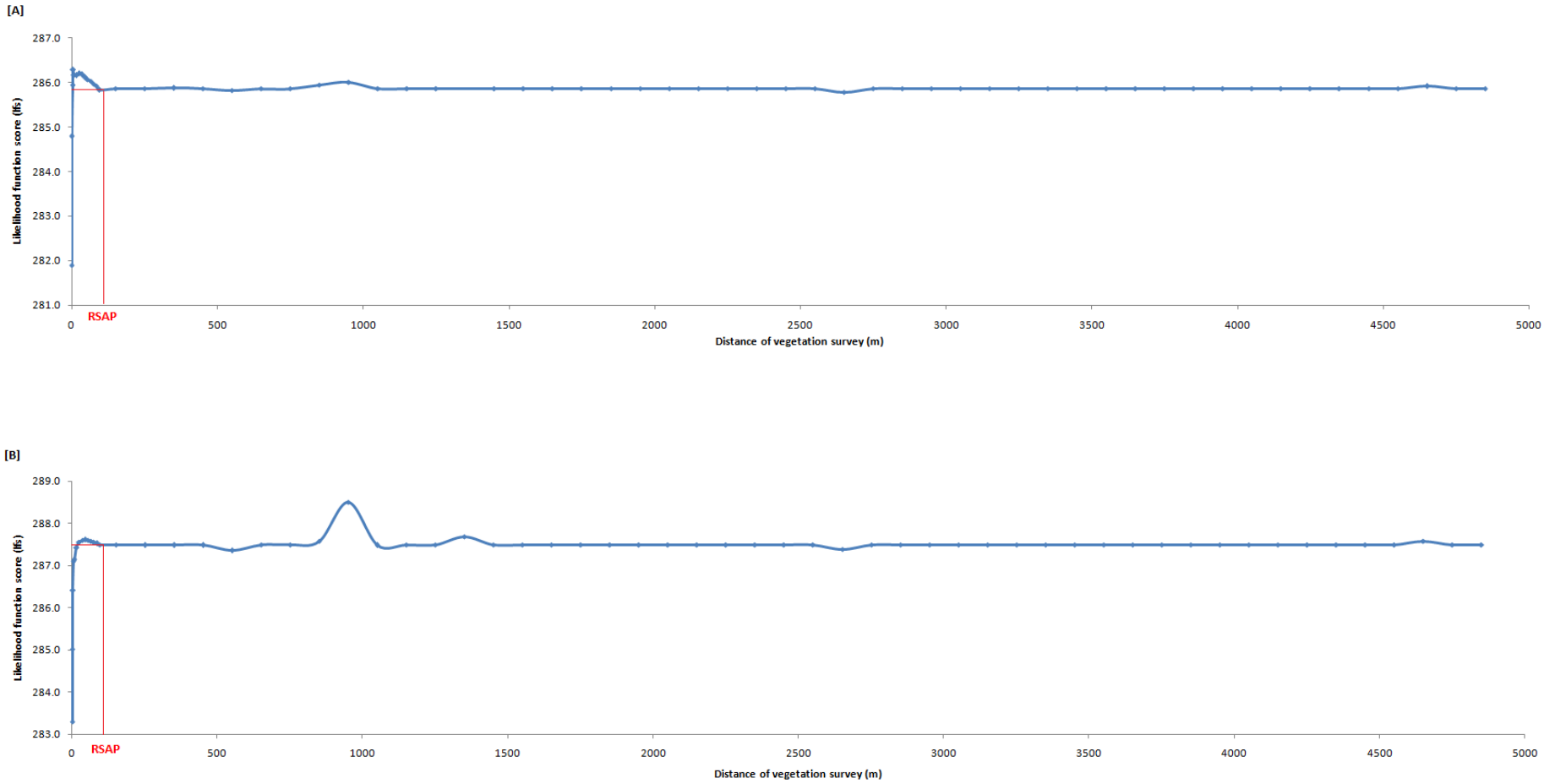

Figure 4.7. ERV analysis output for *Leucosidea* scrubland sampling sites. Illustrated are likelihood function score graphs for pollen-vegetation datasets run with Sutton's taxon specific distance-weighting using ERV model 1 [A] and 2 [B]. RSAP is visually estimated from the graphs where the curve tends to an asymptote.

4.6. Conclusions

Pollen analysis of 15 surface soil samples collected from a *Themeda* grassland, *Protea* savanna and *Leucosidea* scrubland in the Cathedral Peak region revealed all pollen assemblages were dominated by Poaceae, with substantial presence of Pteridophyta and Asteraceae. Proteaceae and Rosaceae were co-dominant in the *Protea* savanna and *Leucosidea* scrubland pollen assemblages respectively. Outcomes from the field surveyed vegetation data supported these results. Geometric dimensions of 50 pollen grains of several Cathedral Peak taxa were randomly measured using reference type slides, calculating individual fall speeds of each taxon. Aggregate fall speeds of palynomorphic types were then calculated for dominant Cathedral Peak taxa to apply Sutton's taxon-specific weighting in ERV analysis. Finally, ERV models were applied to the pollen and vegetation results in order to establish RSAP for the *Themeda, Protea* and *Leucosidea* communities separately, and calculate PPE values for dominant taxa from each (Table 4.6).

Chapter Five

Discussion

5.1. Introduction

To develop the use of pollen models in an Afro-montane context, modern pollen and modern vegetation data was run through ERV analysis for 15 sample locations from Cathedral Peak. The intention here is to critically discuss those results produced in Chapter Four and the methods used, in addition to providing recommendations for future work. Moreover, to contextualise this discussion, a link to theory and literature relayed in Chapter Two is required as this places the discussion within the context of Cathedral Peak and highlights the relevance that these results hold to South African palynological, and ultimately, palaeoecological studies.

5.2. Pollen analysis

At the outset, it must be recognised that pollen identification errors will always transpire in research pertaining to pollen analysis due to inherent difficulties in being able to identify taxa at a higher resolution than the family or genus level. Furthermore, counting inconsistencies occur in pollen analysis due to human error, especially if multiple people are undertaking the counting process. In consequence, a single researcher will often do all the counting and this can take an inordinate amount of time to complete.

Fifteen surface soil samples were located using a stratified random sampling strategy, taking five samples from three distinct vegetation communities in the Cathedral Peak landscape, namely: *Themeda* grassland, *Protea* savanna and *Leucosidea* scrubland. Pollen assemblages from all surface samples were dominated by Poaceae pollen, reflecting the general situation of Cathedral Peak in the Grassland biome of South Africa (Mucina and Rutherford, 2011). Bracken fern was pervasive throughout all environments in the Cathedral Peak region, supported by significant trilete spore quantities in the pollen and spore spectra in all samples.

Assemblages from each of the three habitats were distinct, reflecting differences in the observed vegetation. *Themeda* grassland sites contained scattered herbaceous and shrub species, and pollen assemblages reflected this by all containing multiple grains of Asteraceae, Cyperaceae and Anacardiaceae (Chapter 4 – Table 4.1). The *Protea* savanna samples came from isolated bands of *Protea* vegetation in and amongst grassland habitat. Pollen

assemblage reflected this by containing various grains of Proteaceae, Asteraceae, Cyperaceae and Podocarpaceae (Chapter 4 – Table 4.1). The pollen inventory extracted from the *Protea* savanna reflects its isolated context within a wider landscape of predominantly grassland. *Proteaceae* is expected as common in the *Protea* savanna, with Cyperaceae pollen abundance possibly being explained by the presence of a watercourse through the middle of the vegetation community, and *Podocarpus* pollen abundance explained as a result of the nearby indigenous forests surrounding the sample sites.

Samples from the *Leucosidea* scrubland came from isolated islands of scrub-type vegetation within a wider grassland environment. Pollen assemblages revealed this by containing grains of Rosaceae, Ericaceae and Asteraceae pollen (Chapter 4 – Table 4.1). Modern pollen spectra extracted from the *Leucosidea* scrubland demonstrates a useful association to modern vegetation compositions surrounding the sampling sites, as those taxa exhibiting in the modern pollen spectra were reflective of *in-situ* vegetation assemblages.

5.2.1. Pollen analysis: limitations and recommendations

All modern pollen spectra extracted from soil surface samples in the *Themeda* grassland, *Protea* savanna and *Leucosidea* scrubland appear to show a direct relationship to surrounding modern vegetation inventories. This outcome is enhanced by the fact that all sampling locations had been selected randomly. While sampling strategy of this research emerges as adequate, the number of samples chosen is criticised. Broström *et al.* (2005) and Mazier *et al.* (2008) discuss the importance of random sampling strategies in an environment to ensure optimum and reliable RSAP and PPE calculations. Furthermore, Duffin and Bunting (2008) illustrate how ERV analysis and the outcomes of pollen models are noticeably improved in terms of consistency and reliability when the number of samples used in modelling is significant. While sample locations in this research were randomly located, the collection of only 15 samples was not optimal. Considering the ERV models only need three samples to run, 15 was sufficient for the purposes of this research, however, model results perceptibly had greater uncertainties than a study with a high number of sample points. Future research recommendations are to have a focused collection of a ‘target’ number of samples (i.e.’target’ number should refer to the maximum number of samples possible that is balanced by the time and effort it takes to collect them) to enhance the dependability and certainty of RSAP and PPE. Another recommendation would be to supplement modern pollen spectra extracted from surface soil samples with pollen trap data, such that a definite temporal attribute can be

attached to the modern pollen rain data, and results can be better interpreted and understood in both a spatial and temporal context. Pollen traps were not used in this research due to the time-period needed to collect data from these apparatus, which was beyond the time allocation of this project (e.g. Hicks and Hyvärinen (1999) show how depending on particular sedimentary environments, it can take between 5 – 10 years to gain any meaningful results from collection of pollen assemblages using pollen trap apparatus). Nevertheless, the scope and time frames of future longer term research, such as PhD studies, could benefit from using both methods of collection of modern pollen rain.

5.3. Vegetation

A 3-tiered vegetation survey approach, known as the Crackles vegetation protocol, was used to collect modern vegetation data around each sampling location. This protocol employs virtual 'rings' at specified distances radiating from each sample point, where inner rings in zone A are used to collect more detailed vegetation data close to the sample point and outer rings in zones B and C to collect broader scaled vegetation data. This approach allows vegetation data to be spatially placed in relation to its corresponding sample point, and moreover, to be appropriately distance-weighted, which is a vital aspect of running ERV models on pollen and vegetation data. Distance weighting allocates surveyor effort according to the relative importance of plants as potential pollen sources, so taking into account that plants closer to a sample site contribute more directly to the pollen signal than those further away – that is to say, distance weighting allows for 'pollen's eye-view' of vegetation around it, rather than just a map view of vegetation. For the purposes of this research, Sutton's taxon-specific weighting was used to calculate vegetation distance-weightings as it was deemed the most ecologically appropriate method as it considers taxon fall-speeds based on pollen morphology and other aerodynamic characteristic of an environment such as average wind speed, and therefore places in context pollen dispersal and deposition patterns. This means that through using Sutton's taxon-specific weighting, explicit dispersal and deposition characteristics of pollen in a particular environmental setting are better understood because environment specific wind speeds are used and taxon-specific fall speeds employed in the model. This is especially useful when comparing, and furthermore trying to understand, how far pollen is dispersed in different environmental contexts, each with their own set of wind dynamics, topography and vegetation assemblages.

Detailed vegetation surveys completed in zone A showed Poaceae as the dominant vegetation type surrounding all sample locations, with much bare ground around *Protea* and *Leucosidea* sample points. While no domestic animals were apparent in these vegetation communities, a possible explanation for the bare ground could be the excess of tourist footpaths and hiking trails in these areas. Pteridophyta were significantly present in all communities due to the omnipresence of the bracken fern throughout the Cathedral Peak landscape. Proteaceae and Rosaceae vegetation was considerable in the relevant habitats respectively, mainly in the form of *Protea caffra, P. roupelliae*, and *Leucosidea sericea*. The *Themeda* grassland vegetation primarily consisted of Poaceae and small herbs and shrubs of Acanthaceae (*Barleria monticola*), Asteraceae (*Helichrysum aureonitens, Vernonia natalensis, Senecio coronatus*), Euphorbiaceae (*Acalypha punctata*), and Fabaceae (*Eriosema simulans*).

Zones B and C of the vegetation were surveyed at a broader spatial resolution and data collected in these areas were generalised from random quadrat information and digitised aerial photography. The generalised pattern of taxa represented shows that Poaceae was the prevailing vegetation cover type in all three vegetation communities under investigation, interspersed with shrubs and herbs (Asteraceae, Ericaceae, Euphorbiaceae, Fabaceae, Rubiaceae and Thymalaeaceae species). Woody vegetation cover was in the form of patchy indigenous *Podocarpus* type forest species. Higher altitudes and valley areas along river courses are dominated by scrub vegetation (Rosaceae) which was particularly evident in the *Leucosidea* and *Protea* communities. The modern vegetation data extracted for all three vegetation zones around every sample point showed a positive correlation to modern pollen spectra extracted from these sites.

5.3.1. Vegetation data collection: limitations and recommendations

While the Crackles vegetation protocol has a set procedure for collecting detailed vegetation data from zone A (0-10m) and fairly detailed vegetation from zone B (10-100m), zone C is more flexible in the approach used, depending on the availability of pre-existing maps, aerial photography and other remote sensed sources. Due to Cathedral Peak's vicinity to Lesotho and the consequent lack of availability of aerial photography for parts of this this area, zone C could only extend to a maximum coverage of 5 000 m radius around each site using aerial photographs and ground-truthed data. Once broad scaled vegetation data is available for zone C, it is then up to the researcher to define the 'ring' distances in zone C based on their own discretion. For the purposes of this research, zone C was classified in rings of 100 m from the

edge of zone B out to the defined 5 000 m radius. Duffin and Bunting (2008) and Bunting *et al.* (2013) illustrate how definition of ring distance can influence RSAP estimations, and choosing too broad a ring size can affect where RSAP becomes clear on the RSAP curve (i.e.. that point at which an asymptote is reached). While 100 m rings defined in this research work in being able to adequately define RSAP curves, estimated RSAPs are in the order of 1-200m in the studied vegetation zones, so more accurate estimates could be obtained if narrower rings were used in the inner parts of zone C (e.g. 50 m width rings between 100 and 1000 m).

5.4. Pollen fall speeds

Pollen fall speeds based on grain morphology were calculated from 50 randomly selected pollen grains on reference type slides for dominant vegetation taxa found in environs of Cathedral Peak (Chapter 4 – Table 4.2). Stokes Law was used for taxa where pollen grains were considered spherical and Falck's Assumption for taxa where grains were considered ellipsoidal. A number of African Savanna taxa fall speeds have been calculated by Duffin and Bunting (2008), and many common European taxa fall speeds have been calculated (Mazier *et al.,* 2008). Duffin and Bunting (2008) point out the notable size distribution differences, and hence fall speeds, of African and European taxa of a common family, and is believed to be a manifestation of past climatic pressures across Europe and its subsequent influence on species diversity. For example, Poaceae, a cosmopolitan taxon in almost all environments of the world (over 12 000 species have been identified worldwide) has a documented size difference in grains between species (Schüler and Behling, 2011). This pattern is observable in the individual fall speeds of species of a same family calculated for this research (Chapter 4 – Table 4.2, see Poaceae). It is therefore perceivable that tropical and subtropical species of a common plant family would have significantly varying average fall speeds based on multiple species as compared to the temperate species of that family, such as those found in Europe, based on only a few species present. Schüler and Behling (2011) suggest that pollen preparation and processing techniques, depending on the chemicals used, can alter pollen grain size. Potassium hydroxide treatments used in association with acetolysis have been shown to significantly increase pollen grain size, and hydrofluoric acid treatment has been seen to modify grain size (Schüler and Behling, 2011).

Average pollen fall speeds for a subset of dominant taxa groups in Cathedral Peak vegetation communities used in this research were calculated. Poaceae was estimated at 0.050 ms^{-1}, Asteraceae at 0.026 ms^{-1}, Pteridophyta at 0.044 ms^{-1}, Proteaceae at 0.017 ms^{-1} and Rosaceae

at 0.016 ms^{-1}. In comparison to those African savanna taxa fall speeds calculated by Duffin and Bunting (2008) for the Kruger National Park, Poaceae was estimated at 0.019 ms^{-1} which is significantly lower than the 0.050 ms^{-1} fall speed calculated in this research, which is more aligned to European estimates of Poaceae at 0.035 ms^{-1} (Broström, 2002; Mazier *et al.*, 2008). This is an interesting result considering the two African estimates appear most unrelated, but may relate to altitudinal differences between the Drakensberg and Kruger National Park, and thus past and present climate influences on species in these areas. Moreover, these differences may relate to the fact that the same plant, chemically treated differently, might produce different fall speed estimates and a lack of taxonomic discrimination possible between some taxa in different places can result in different fall speed estimations.

5.4.1. Pollen fall speeds: limitations and recommendations

Future recommendations would be for research to explore the possibility of calculating pollen taxon fall speeds using "fresh" pollen material rather than chemically dehydrated or acetolysised pollen material. This would possibly represent more accurate and reliable reflections of fall speeds of species under investigation, as fresh pollen is the actual material dispersed in nature. Improved fall speeds would then have direct influence on taxon-specific distance weighting of vegetation data, ERV analysis results and thus RSAP and PPE calculations (Bunting *et al.,* 2013).

5.5. ERV analysis – estimating RSAP and PPE

ERV analysis was run separately on each of the three Cathedral Peak vegetation communities to estimate Relevant Source Area of Pollen (RSAP) for each community, and to calculate Pollen Productivity Estimate (PPE) values for dominant taxa from each community. ERV analysis was run using sub-models 1 and 2 only, as these models use pollen and vegetation percentage data (as was collected in this research), whereas sub-model 3 was not used as it requires absolute vegetation data (Gaillard *et al.,* 2008). While RSAP values from sub-model 1 and 2 were of similar value, PPE values were markedly different, and the most appropriate model to the data was chosen according to which model showed PPE values with the closest fit to one another, i.e. PPE values closest together (Broström, 2002).

RSAP values appear to be reasonably uniform across all three communities, with estimates ranging between 100 – 150 m from the source: *Themeda* grassland RSAP was estimated at

150 m, *Protea* savanna RSAP at 150 m, and *Leucosidea* scrubland RSAP at 100 m. This implies that pollen coming from outside the RSAP is from the 'background' pollen component, and is assumed constant between sites – that is to say, the pollen signal of sample sites in this research are predominantly influenced by source vegetation abundance and distribution from within a 100 – 150 m radius (Sugita, 1994).

The concept of RSAP is useful in illustrating the influences of taxonomic dispersal differentials and basin size on the spatial scale represented in pollen archives that are collected. These influences theoretically include: i) the better dispersed the pollen types, the larger the RSAP, and ii) the larger the basin size, the larger the RSAP (Gaillard *et al.*, 2008). A low RSAP of 100 – 150 m for these Cathedral Peak vegetation communities could thus reflect the smaller and more confined sedimentary basin sizes that are a function of topography in montane regions. Bunting *et. al.* (2013) suggest that it is not uncommon in pollen modeling research for RSAP to reflect at the boundary between vegetation surveying strategies of zones B and C. It is therefore recommended that future research employ finer-grained vegetation surveys between 100-500 m to increase the precision on where RSAP occurs and decrease the influence of zone boundary changes.

While RSAP is useful in showing how a pollen signal is influenced by both pollen source plants abundance and geographical location relative to a sample point, inferences must also be made regarding regional versus local influences to pollen assemblages. Traditional fossil pollen work attempts to intuitively divide pollen sums into regional and local pollen so as to discern regional and local source vegetation influences respectively. It must be noted that whilst RSAPs for the three studied vegetation communities all lie within approximately 150 m of sample points, signifying an important local influence of source plants into the pollen sums, it is not being suggested that local influx is more important or influential than regional influx. More to the point, what RSAP is representing is a spatial context around a sample location from which researchers can deduce the influence of source vegetation abundance *and* location has on the pollen sum. That is to say, RSAP is not suggesting the majority of pollen comes from source plants within 150 m of the sample location, but rather within 150m of the sampling location (i.e. local pollen influence), source plant abundance *and* geographical location influences the pollen assemblage, and thus >150 m represents background pollen (i.e. regional pollen influence) where only source plant abundance is important. It is still important, however, to resolve the contributions and influences that local and regional pollen influxes have on a pollen assemblage.

PPE values were obtained for modelled taxa from three vegetation communities. PPE values are an important data for improving the reconstruction of past landscapes as they provide a means of quantifying past vegetation abundances of taxa in environments (Abrahams and Kozáková, 2012). While palaeoreconstruction was not the purpose here, PPE values provide important insights into pollen productivity abilities of taxa and their representation in the pollen archive from certain vegetation communities.

PPE values obtained from the *Themeda* grassland show that Asteraceae pollen (PPE = 0.00026) producing species are much less productive in terms of pollen production relative to Poaceae pollen (PPE = 1) producing species, whereas Pteridophyta (PPE = 3.14) are relatively higher palynomorph producers. Particularly, $1m^2$ of Asteraceae vegetation produces ≈ 3 800 times less pollen than $1m^2$ of Poaceae, and $1m^2$ of Pteridophyta vegetation produces ≈ 3 times more pollen than $1m^2$ of Poaceae (Chapter 4 – Table 4.3). The abovementioned PPE values further suggest that in a given pollen assemblage taken from the *Themeda* grassland, Asteraceae is under-represented as there is theoretically a high quantity of vegetation of this taxon in a landscape which reflects only in a low abundance in the pollen spectra, and Pteridophyta is over-represented as there is theoretically a low quantity of vegetation of this taxa and this reflects in a high abundance in the pollen spectra.

PPE values obtained from the *Protea* savanna show that Asteraceae and Proteaceae plants are less productive in terms of pollen production relative to *Poaceae* in a known area of vegetation, whereas Pteridophyta and Podocarpaceae are significantly higher pollen producers in a same sized area of vegetation. In addition, $1m^2$ of Asteraceae vegetation produces ≈ 2 600 times less pollen than $1m^2$ of Poaceae and $1m^2$ of Proteaceae vegetation produces ≈ 4.5 times less pollen than $1m^2$ of Poaceae, while Podocarpaceae produces ≈ 6.5 times more pollen than $1m^2$ of Poaceae and Pteridophyta produces ≈ 8.5 times more pollen than $1m^2$ of Poaceae (Chapter 4 – Table 4.4). These PPE values suggest that in a given pollen assemblage taken from the *Protea* savanna, Asteraceae and Proteaceae are under-represented as there is theoretically a high quantity of vegetation of this taxon in a landscape which reflects only in a low abundance in the pollen spectra, and Pteridophyta and Podocarpaceae are over-represented as there is theoretically a low quantity of vegetation of these taxa and this reflects in a high abundance in the pollen spectra.

PPE values obtained from the *Leucosidea* scrubland show that relative to Rosaceae, Poaceae and Ericaceae plants are less productive in terms of pollen production in a known area of

vegetation, whereas Pteridophyta are higher pollen producers in a same sized area of vegetation. Specifically, $1m^2$ of Poaceae produces ≈ 3.5 times less pollen than $1m^2$ of Rosaceae and $1m^2$ of Ericaceae vegetation produces ≈ 6 times less pollen than $1m^2$ of Rosaceae, and Pteridophyta produces ≈ 7 times more pollen than $1m^2$ of Rosaceae (Chapter 4 – Table 4.5). Moreover, PPE values suggest that in a given pollen assemblage taken from the *Leucosidea* scrubland, Poaceae and Ericaceae are under-represented as there is theoretically a high quantity of vegetation of this taxon in a landscape which reflects only in a low abundance in the pollen spectra, and Pteridophyta are over-represented as there is theoretically a low quantity of vegetation of this taxa and this reflects in a high abundance in the pollen spectra.

5.5.1. ERV analysis: limitations and recommendations

The number of samples collected for pollen modelling research compromises RSAP and PPE calculations when running ERV models and its subsequent ability to find solutions. The more pollen and vegetation data the models have to run, the more certainty can be placed in their outputs. A recommendation to improve RSAP and PPE calculations would therefore be to have as many samples from as many sites as is possible to enhance the dependability and certainty of ERV analysis results. Furthermore, a recommendation would be to use different distance weighting models to investigate confidence levels in the use of these models and their relevance to site-specific data sets.

5.6. Synthesis and conclusions

The fundamental principles of the pollen analysis method provide researchers with a means of reconstructing past vegetational frameworks and ecosystem regimes of an environment (Elias and Mock, 2013). According to Bunting (2008), pollen analysis is likely the most widely used proxy indicator for establishing palaeoecological conditions, and moreover, reconstructing past vegetation dynamics extending long time scales up to millennia. Consequently, attempts to improve the methods and techniques of collecting pollen data, and moreover, the basis from which we interpret those results have been emphasised in recent research developments. These developments have predominantly occurred in the formation of predictive mathematical and computer models that simulate and capture broad patterns of pollen and vegetation characteristics in a landscape with the aim of improving our understanding of the links between pollen and vegetation, and moreover, our interpretation of long-term palaeoecological records (Bunting, 2008; Bunting and Hjelle, 2010).

Origins of pollen modelling were theoretically developed in the 1960s beginning with Davis' R-value model, succeeded by Andersen's model in the 1970s and then progressing to Extended R-value models in the 1980s. Pollen modeling has, however, predominantly found mainstream interest in Europe since the 2000s. Many regions of Europe have employed models of pollen dispersal and deposition to calculate PPE and RSAP for specific environments using ERV models. These include England (Bunting *et al.,* 2005), Finland (Räsänen *et al.,* 2007), Sweden (Broström *et al.,* 2004; Sugita *et al.,* 1999; von Stedingk *et al.,* 2008), Norway (Hjelle, 1998), Denmark (Nielsen, 2003), Switzerland (Mazier *et al.,* 2008; Soepboer *et al.,* 2007) and the Czech Republic (Abraham and Kozáková, 2012). To date, there has been one study undertaken in Africa. Duffin and Bunting (2008) have calculated RSAP and PPE for southern Africa savanna taxa in the Savanna Biome of the Kruger National Park.

Duffin and Bunting (2008) used ERV models to analyse modern pollen spectra from 34 surface sediment samples in association with its surrounding vegetation to analyse key savanna taxa and thus calculate PPE values and RSAP. A significant difference between this research and Duffin and Bunting's (2008) research lies in the fact that a comparison of all distance-weighting methods were used as opposed to only Sutton's taxon-specific weighting. The RSAP for all sites was estimated at 700 m, which is considerably greater than the approximated 150 m in this study. A key point here is that Duffin and Bunting (2008) sampled small ponds, not soil samples, and so had much larger sampling basins to work with. RSAP differences could also be attributed to the different sampling strategies in zones A and B of the vegetation surveys done between the two research projects or due to the differences in openness of the Kruger National Park landscape and the topographical complexity of Cathedral Peak (Gaillard *et al.,* 2008).

Species' dispersal ability has a direct influence on RSAP estimations as the better dispersed taxa will result in larger RSAP values in a landscape (Gaillard *et al.,* 2008). PPE values of taxa between the two research projects are not so easily compared, as different taxa assemblages exist in these two environments and moreover were used for modelling. The aim of Duffin and Bunting's (2008) research was to present these PPE and RSAP estimates as a basis for improved interpretation of past and future fossil pollen archives collected from the savanna biome. This aim is aligned to objectives of this research, and so Duffin and Bunting's (2008) work was a key text. Considering it is the only study done in South Africa pertaining to ERV analysis and the calculation of PPE and RSAP values for African taxa, it

illustrated that these European developed pollen models of dispersal and deposition can be suitably used in an African context. This research builds on this view, and results attest to the suitability of using these models in African pollen research.

In sum, data extracted from 15 surface soil samples and its associated surrounding modern vegetation inventory in Cathedral Peak were used to run pollen models in an Afro-montane landscape. While model outputs were not 'perfect' as would be the case in an open, homogeneous European landscape (and for which these models were expressly developed), they show that sound and applicable information can be produced for an environment such as Cathedral Peak. Furthermore, results produced in this research suggests that future pollen research in the Cathedral Peak region, particularly those concerning fossil pollen studies and palaeoenvironmental reconstructions, have a reliable tool and resource on which they can supplement, and moreover, base their interpretations on. In this regard, future researchers can use the PPE values determined here for dominant taxa in Cathedral Peak vegetation communities in association with the HUMPOL software suite to simulate numerical past vegetation abundances, and use RSAP estimates to attach spatial attributes to vegetation assemblages when reconstructing past environments. RSAP calculations can also help future research to assess dispersal abilities of taxa in Cathedral Peak, make inferences of basin sizes and how these influence the pollen assemblages extracted from Cathedral Peak environments. This research and its positive findings thus have significant implications and influences for prospective fossil pollen research and palaeoecological science in the Cathedral Peak area.

Chapter Six

Conclusions

6.1. Introduction

The primary aim of this research was to use models of pollen dispersal and deposition developed in flat, open European landscape contexts, and to test their functionality in an African environment. The intention of these models are to investigate and better understand the dispersal and deposition characteristics of pollen in landscape so as to improve the basis from which palaeoecologists are able to reconstruct, and interpret the dynamics of past vegetation assemblages. These models output variables which enable researchers to reduce uncertainty in characteristics such as spatial contexts of source areas of fossil pollen archives or pollen productivities of key taxa – minimising uncertainty in such characteristics of pollen research progresses confidence in our ability to reconstruct the past in a 'least inaccurate' manner as possible and thus advances pollen science and understanding. This research was carried out in a palynologically rich and important area – Cathedral Peak in the KwaZulu-Natal Drakensberg.

The logistics of these models involve comparing modern day pollen records with modern day vegetation through models that delineate the distance pollen travels in an environment. Objectives defined to address the primary aim of this research are set out in Chapter One, all of which have been met within the limits of this project. Specified objectives of this research were:

1) To extend the existing contemporary pollen reference collection for pollen producing plants in the Cathedral Peak area;
2) Identify, describe and inventory vegetation communities in the Cathedral Peak area so as to create a broad resolution vegetation map of the region;
3) Identify suitable and representative sampling locations where soil surface samples can be extracted;
4) Conduct tiered vegetation surveys around each sampling site;
5) Identify, quantify and analyse modern pollen spectra of the relevant study areas by way of surface samples;
6) Determine the variables required to model pollen dispersal and deposition using the HUMPOL software suite. These include:

i) The estimated pollen grain fall speeds for the main taxa observed in the pollen and vegetation records;

ii) The distance-weighted plant abundances of taxa around each sampling point to a maximum distance;

iii) The relative pollen productivity for the main taxa observed in the pollen and vegetation record.

iv) The relevant source area of pollen for both each study site within Cathedral Peak and the wider Cathedral Peak environment.

6.2. Meeting objectives

The first objective of this research was to extend the existing contemporary pollen reference collection for dominant pollen producing plants in the Cathedral Peak area. A vegetation identification and specimen collection survey was conducted in September 2013 of all dominant plant types in the Cathedral Peak area to supplement and update that reference collection of Hill (1992). This vegetation material was then processed at the UKZN Palaeoecology laboratory where reference slides were prepared, and updated to the reference collection so that the reference collection was relevant to 2014.

The second objective was to identify, describe and inventory vegetation communities in the Cathedral Peak area to create a broad resolution vegetation map to extract vegetation data for zone C. Aerial photography was obtained from the Surveyor-General in Mowbray, Cape Town, for the wider Cathedral Peak region, where latest available coverage for the area was 2011 imagery with a pixel resolution of 0.5 m^2. In association with ground-truthed vegetation data provided by Hill (1992; 1996), an interactive, on-screen heads-up approach was used to digitise vegetation community assemblages from the aerial photography for Cathedral Peak and the surrounding environs. Once the large-scale vegetation map layer had been created, all vegetation communities were classified and taxa data was input into the meta-data of this layer, and a broad resolution map of the region was generated.

The third objective of this research was to identify suitable and representative sampling locations from which soil surface samples could be extracted, to obtain representative modern pollen rain spectra of the Cathedral Peak region. For the purposes of this study, three different vegetation communities were chosen as study sites within the surrounding environs of Cathedral Peak - that is, the *Themeda* grassland, *Protea* savanna and *Leucosidea sericea* scrubland. Several motivations were behind choosing the three specific vegetation

communities under investigation. First, selection was broadly based on Killick's montane vegetation classification and communities selected went according to these altitudinal gradients. Second, dominant vegetation communities represented in the region were chosen. Third, those vegetation communities potentially most sensitive to shifts in composition or altitude with a change in environmental or climatic conditions were selected. Finally, the presence of pre-existing vegetation and/or pollen data on the three chosen vegetation communities from previous research (Hill, 1992; 1996) facilitated a comparison with new data collected in this research. Within each of the chosen communities, five samples were collected to represent that vegetation community resulting in a total of 15 samples. These five samples in each of the three distinct vegetation communities were randomly placed and selected in accordance with standard ERV analysis research sampling strategies (Mazier *et al.*, 2008).

The fourth research objective was to conduct tiered vegetation surveys around each sampling site, so as to not only collect a modern inventory of vegetation surrounding each sample location, but also to distance-weight the modern vegetation data which is a key step in ERV analysis and thus the calculation of RSAP and PPE values. A specialised 3-tiered surveying approach, known as the Crackles vegetation protocol as described by Bunting *et al.* (2013), was used to compile the vegetation inventory and this vegetation protocol is now standard practice in most pollen modelling research. Essentially, this vegetation surveying method is partitioned into three zones (A, B, C), where a fully detailed and comprehensive vegetation survey is done in zone A, an intermediate vegetation survey done in zone B, and GIS and remote sensing techniques used to extract basic vegetation data from maps in zone C. In depth surveys were completed in zone A (0-10m) around each sample location, with zones B (10-100m) and C (100-5 000m) surveyed at a much larger spatial resolution and therefore more generalisations went into the collection of this data. Describing the overall pattern of taxa represented in the surveyed vegetation revealed that Poaceae was the dominant vegetation type in all three studied vegetation communities, interspersed with shrubs and herbs (Asteraceae, Ericaceae, Euphorbiaceae, Fabaceae, Rubiaceae and Thymalaeaceae species). Predominant woody vegetation cover was in the form of patchy indigenous *Podocarpus* type forest species. Higher altitudes and valley areas along river courses are dominated by scrub vegetation (Rosaceae) which was particularly evident in the *Leucosidea* and *Protea* communities, with bracken fern (*Pteridium aqulinum*) ubiquitous throughout the vegetation communities.

The fifth objective of this research was to identify, quantify and analyse modern pollen spectra of the relevant study areas extracted from the soil surface samples. The 15 soil samples collected from Cathedral Peak were chemically digested, pollen types identified and pollen counts undertaken to establish the modern pollen spectra of the area. Pollen identification and counting results illustrated a total of 40 taxon families identified from the 15 samples from a minimum count of 250 pollen grains from each. In all samples, Poaceae appeared as the dominant pollen type with Pteridophyta and Asteraceae found to be co-dominant at all sites. This dominance was evident in the collective percentage representation of these taxa in all sites: Poaceae (41-73%), Pteridophyta (5-36%) and Asteraceae (5-24%). In the *Themeda* grassland, Anacardiaceae, Cyperaceae and Pinaceae pollen were observed and are indicative taxa of the grassland setting. Other prevailing taxa pollen extracted from the *Protea* savanna included Proteaceae, Pinaceae, Campanulaceae, Fabaceae and Podocarpaceae. Finally, additional dominant taxa pollen extracted from the *Leucosidea* scrubland include Rosaceae, Ericaceae and Cyperaceae. Overall pollen data from all surface samples proved to have a close reflection to surrounding vegetation assemblages in Cathedral Peak, and furthermore proved to reflect the wider environmental setting of being located in the Grassland biome of South African as defined by Mucina and Rutherford's (2011) vegetation classification.

The sixth objective of this research, and arguably the crux of the entire project, was to determine the variables required to model pollen dispersal and deposition using the HUMPOL software suite. This included pollen fall speeds to be used in taxon-specific distance-weighting of the modern vegetation data, calculation of these actual distance-weighting values, and then to run ERV analysis where calculations of RSAP and PPE were determined. This was undertaken to establish whether pollen dispersal and deposition models are suitable the context of an Afro-montane environment in which pollen research takes place.

Pollen fall speeds were estimated for dominant Cathedral Peak taxa using Stokes Law for spherical grains and Falck's Assumption for ellipsoidal grains from an average of 50 counted and measured pollen grains using pollen reference slides. Values of individual species were averaged to obtain a family level mean used in distance-weighting calculations and ERV analysis. In instances where one species was present in a family group, that fall speed was used to represent the entire family.

Vegetation data was distance-weighted using Sutton's taxon-specific weighting formula as this was deemed the most ecologically appropriate method for the purposes of this research because it takes into account pollen morphology and hence fall speeds, as well as other important atmospheric variables such as average wind speed in an environment.

ERV analysis was run using the HUMPOL software suite to estimate RSAP and PPE for three key vegetation communities in Cathedral Peak. ERV analysis was run individually on each of the three vegetation communities under investigation, using both ERV models 1 and 2 to evaluate if both provide comparable model outputs and if not, to assess which model best suits the data. ERV model 3 was not used as it employs semi-absolute data.

6.3. Synthesis

Interpretation of ERV results has shown that, while the model outputs are not 'perfect' as would be the case in an open, homogeneous and flat landscape, they are perfectly coherent and within the realm of expectations of results from a study with a relatively small amount of samples in a varied landscape, as is the case in this research project. The findings of this study are therefore that developments made in pollen modeling have a very relevant place in South African pollen research and can significantly impact future work by strengthening the foundation from which we base our understanding – the interpretation of results. Further validation of these models in South African pollen research can only further serve to improve our confidence in pollen data, and it is the hope that this research has in the very least informed and sparked interest for future researchers in this new and significant aspect in pollen science.

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Appendices

Appendix 1 – Crackles Vegetation Protocol (Bunting *et al.*, 2013)

1) Locate the sample site (you will be given grid coordinates in advance)
    a. Use a hand-held GPS to get to the general location
    b. Identify a suitable sampling point within the area; if at all possible, this needs to be a moss polster

2) Take the surface sample (or protect the future sampling location)
    a. Take a GPS reading of the actual location
    b. Label sample bag with site, sample code (if specified), collection team, date, coordinates
    c. Collect a palm-sized sample of moss, cutting off plants growing through it and any soil
    d. If the moss sample seems a bit small, or no moss is found, take a separate sample of soil by cutting a mini turf 0.5-1cm thick and about 5cmx5cm in area.
    e. Seal sample into a second outer bag, and put carefully in rucksack.
    f. If you are not sampling on this visit, invert a bucket or other solid container over the sampling point as soon as possible. When removing the 'cap' at the end of the survey, do so carefully and smoothly – the aim is to prevent pollen disturbed by your movements landing on the sample point.

3) Document the point
    a. Take a photo of the record sheet or the sample bag (to record the sample information in the photo record)
    b. Leaving knife or other marker in the sampled point, centre the 1mx1m quadrat with one edge facing north. Stand over the point, facing north (so standing on the south side) and take a photograph of the quadrat on the ground.
    c. Take four photographs of the landscape, looking N, S, E and W from the sample point (make sure you do them in this order so we know what the photographs are).

4) Record the inner 10m circle
    a. Set out markers 10m from the centre point at N, S, E, W
    b. Record the inner quadrat
        i. Use visual estimates of cover, viewed from above. List all the species present in the quadrat, then estimate cover for the minor species (using + for a single plant taking up less than 1% (one quarter of a subdivision), 1-5%, then multiples of 5%), then divide the remaining points between the major species (i.e. each record should add to 100%. Bare ground/rock can be recorded as a category if it has clearly been bare all season).
    c. Lay the marked line from the centre marker to the north marker (line is marked at distances of 0.5, 1.5, 3, 6 and 10m).
    d. Record the four quadrats along the line- centre the quadrat over the line, and position it halfway between the markers.
    e. Search outwards from the outer three (in the wedge NW to NE for 1.5-3 and 3-6, and in the wedge NNW and NNE for 6-10), noting additional species not recorded in the quadrat. Record these species as 'P' – not percentage cover.

f. Move the line to midway between the N and E marker. Check the bearing is approximately NE-SW. Record the 6-10 quadrat and search outwards for missed species (in the wedge NNE-ENE). Missed species should be recorded as 'P'.
g. Move the line to the E marker, record as above... Continue until all quadrats are recorded for the full circle.
h. Use the record sheet to mark off each area as it is logged.
i. Draw in the canopy area of any trees or shrubs on the circle provided.

5) Record the 10-100m ring:
   a. CREATE A MAP:
      i. Using aerial photograph or existing vegetation map, if available, create rough sketch
      ii. If using handheld GPS, label the eastings and northings on the sketch grid from the central point (note: grid squares are 50m x 50m)
      iii. Walk 12 transects, using tape and compass or handheld GPS to mark the positions of community boundaries, and join points 'by eye'
      iv. Note position and species of single trees

   b. CHARACTERISE EACH COMMUNITY
      i. IN OPEN COMMUNITIES
         1. Randomly locate 4 quadrats (1m x 1m) within blocks of relatively homogeneous vegetation
         2. Record each quadrat as described in 4 b i
      ii. IN WOODLAND COMMUNITIES
         1. Define a 6m radius relevée in a stand of relatively homogeneous, representative vegetation
         2. Using marked line, record point data both below and above the line (species present below the line – using a plumb-bob - and above the line – using a mirror) along 8 radial lines (N, NE, E etc.).
         3. Points representing equal areas are placed at 1.2m, 2.9m, 3.85m, 4.6m, 5.2m and 5.75m.
         4. NOTE: map in any clearings or rides, and record their composition as for open communities
      iii. IN MIXED COMMUNITIES (e.g. gorse or birch scrub areas at Allerthorpe)
         1. Set up 6m relevée as described above. Record component present at each point (e.g. gorse or open).
         2. Record composition of each community as appropriate (e.g. for grassy area, use quadrats. For gorse: visual estimate of composition (100% gorse?) will be sufficient.
      iv. HEDGEROWS
         1. Lay out a 30m tape along a representative section of the hedgerow.
         2. Walk the length of the tape noting each species present.
         3. Estimate the abundance of each species along the 30m section of hedgerow that you walked (note: percentages do NOT have to add to 100 in this case as you will have both hedgerow and understorey species – the vegetation is layered).

Appendix 2 – Laboratory Preparation Procedure for Vegetation (Pollen Reference Slides)

(Faegri and Iversen, 1975; Moore *et al.*, 1991 and Hill, 1992)

Chemical Procedure:

1. Place specimen into a 50ml glass centrifuge tube.
2. Add 20ml 10% NaOH to the tube and stir.
3. Heat in water bath (50-60^{o}C) for five minutes, stirring often.
4. Filter through a clean 180μm aperture sieve into a 100ml glass beaker. Lightly crush the material on the screen and wash through with distilled water.
5. Centrifuge at 3500rpm for one minute and decant the supernatant.
6. Transfer the contents to a 10ml centrifuge tube using glacial acetic acid.
7. Stir, centrifuge at 3500rpm for three minutes and decant.
8. Add acetolysis mixture [acetolysis mixture consists of 9 parts acetic acid and 1 part concentrated sulphuric acid]. Stir and place in a heated water bath (50-60^{o}C) for five minutes. Place samples in a cold water bath to stop acetolysis reaction. Centrifuge and decant.
9. Add 5ml glacial acetic acid. Centrifuge and decant.
10. Wash 3-5 times with distilled water, adding 1-5 drops of aqueous Safranine stain into the final wash.
11. Centrifuge and decant.
12. Invert tubes onto blotting paper.

Pollen Slide Procedure:

1. Clean and label slides (replicates of three for each specimen).
2. Pick up pollen grains with a small block of glycerine jelly placed on a dissecting needle. Wipe around the sides of the centrifuge tubes to pick up grains still adhering to the tube.
3. Place glycerine jelly on centre of slide and pass slide over a warm surface to melt the jelly. Caution: Heating plate must be approximately 40-45^{o}C, if hotter the glycerine jelly will boil and damage the pollen grains.
4. Lower a cover slip over the jelly with a dissecting needle. Seal cover slip with clear nail varnish. If the slide is inverted the pollen grains will settle near the cover slip surface, thereby facilitating easier light microscope viewing.

Appendix 3 – Laboratory Preparation Procedure for Soil Surface Samples

(Faegri and Iversen, 1975; Moore *et al.*, 1991 and Hill, 1992)

Chemical Procedure:

1. Place 5g of soil sample into a 50ml glass centrifuge tube
2. Add 20ml 10% NaOH and place in a heated water bath (80-90^{o}C) for 10 minutes, stirring occasionally.
3. Strain and wash through a 180μm aperture sieve using distilled water. This filtration does not retain or cause material to be discarded but rather acts to 'break-down' the material.
4. Centrifuge and decant the supernatant. All centrifuging is performed at 3500rpm for three minutes.
5. Wash five times with distilled water or until the supernatant becomes clear.
6. Wash with 10ml 10% HCl. Centrifuge and decant.
7. Agitate and transfer to 100ml polypropylene tube.
8. In a fume cupboard, treat with 20ml 40% hydrofluoric acid (HF) and place in a water bath for three hours, stir occasionally.
9. Stir, place caps on tubes then centrifuge and decant.
10. Decant sample into 20ml glass centrifuge tubes using 10% HCl. Place in heated water bath for 20 minutes.
11. Centrifuge and decant.
12. Wash with distilled water, centrifuge and decant.
13. Add 10ml glacial acetic acid. Stir, centrifuge and decant.
14. Add acetolysis mixture and place in a heated water bath (50-60^{o}C) for five minutes [acetolysis mixture consists of 9 parts acetic acid and 1 part concentrated sulphuric acid]. Place samples in a cold water bath to stop acetolysis reaction.
15. Stir, centrifuge and decant.
16. Add 10ml glacial acetic acid, centrifuge and decant.
17. Add 9ml distilled water and 1ml NaOH to obtain a neutral pH. Stir, centrifuge and decant.
18. Wash with distilled water three times, adding 1-5 drops of aqueous Safranine stain into the final wash.
19. Add 5ml tertiary butyl alcohol (TBA) into each tube. Stir, centrifuge and decant.
20. Transfer suspension into labelled vials using TBA, centrifuge and decant.
21. Add silicone oil in equal amount to pollen sediment. Store uncapped for 24 hours to allow TBA to evaporate.

Pollen Slide Procedure for Counting and Identification:

1. Stir the polleniferous silicone oil with a clean glass stirring rod until the pollen is evenly suspended.
2. Clean and label slides (replicates of three for each sample).
3. Place a few drops of silicone oil onto a clean slide.
4. Add drops of the polleniferous oil to the slide with a Pasteur pipette.
5. Lower a cover slip over the oil with a dissecting needle. Seal cover slip with clear nail varnish.
6. Relative percentage pollen counts are performed.

Appendix 4 - Analysis of Variance (Anova) Results for Pollen Counting

Hypotheses:

H_0: $\mu_{250} = \mu_{500} = \mu_{1000}$ for pollen counts in *Themeda*, *Protea* and *Leucosidea* communities.

H_a : At least one of the population means is beyond the level of significance $\alpha = 0.05$.

Computed Results:

***Themeda* Grassland**

Groups	*Count*	*Sum*	*Average*	*Variance*
μ_{250}	27	100.1	3.707407	112.0007
μ_{500}	27	100.1	3.707407	131.1592
μ_{1000}	27	100	3.703704	151.8581

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.000247	2	0.000123	9.38E-07	0.999999	3.113792
Within Groups	10270.47	78	131.6726			
Total	10270.47	80				

Computed F value ≈ 9.38E-07 where $\alpha = 0.05$

$F_{crit} \approx 3.11$

Conclusion:

Using F values:

Since $F < F_{crit}$ it is concluded that we accept the null hypothesis at a 5% level of significance.

***Protea* Savanna**

Groups	*Count*	*Sum*	*Average*	*Variance*
μ_{250}	24	100.2	4.175	116.4106522
μ_{500}	24	100	4.166666667	125.4223188
μ_{1000}	24	100.2	4.175	130.7732609

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.001111	2	0.000555556	4.473E-06	0.999996	3.129644
Within Groups	8569.943	69	124.2020773			
Total	8569.944	71				

Computed F value ≈ 4.47E-06 where $\alpha = 0.05$

$F_{crit} \approx 3.13$

Conclusion:

Using F values:

Since $F < F_{crit}$ it is concluded that we accept the null hypothesis at a 5% level of significance.

***Leucosidea* Scrubland**

Groups	*Count*	*Sum*	*Average*	*Variance*
μ_{250}	29	100	3.448276	78.70187
μ_{500}	29	100.2	3.455172	83.79685
μ_{1000}	29	100.1	3.451724	94.70759

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.00069	2	0.000345	4.02E-06	0.999996	3.105157
Within Groups	7201.777	84	85.73544			
Total	7201.777	86				

Computed F value ≈ 4.02E-06 where $\alpha = 0.05$

$F_{crit} \approx 3.10$

Conclusion:

Using F values:

Since $F < F_{crit}$ it is concluded that we accept the null hypothesis at a 5% level of significance.

Appendix 5 – Zone A Vegetation Inventories

Vegetation Inventory

Themeda- dominated Grassland

Family	Species
Acanthaceae	*Barleria monticola*
Anacardiaceae	*Searsia dentata*
Asteraceae	*Callilepsis laureola*
Asteraceae	*Helichrysum aureontiens*
Asteraceae	*Senecio coronatus*
Asteraceae	*Vernonia natalensis*
Euphorbiaceae	*Acalypha punctata*
Fabaceae	*Eriosema simulans*
Hypoxidaceae	*Hypoxis rigidula*
Plantaginaceae	*Plantago lanceolata*
Poaceae	
Pteridophyta	*Pteridium aquilinum*
Rosaceae	*Rubus ludwigii*
Rubiaceae	*Pentanisia prunelloides*
Scrophulariaceae	*Buddleja salviifolia*
Thymelaeaceae	*Gnidia caffra*
Thymelaeaceae	*Gnidia kraussiana*

Vegetation Inventory

Leucosidea Scrubland

Family	Species
Anacardiaceae	*Searsia dentata*
Asteraceae	*Helichrysum aureontiens*
Asteraceae	*Helichrysum auriceps*
Asteraceae	*Helichrysum evansii*
Asteraceae	*Helichrysum nanum*
Asteraceae	*Senecio coronatus*
Asteraceae	*Stoebe vulgaris*
Ericaceae	*Erica straussiana*
Ericaceae	*Erica woodii*
Euphorbiaceae	*Acalypha punctata*
Fabaceae	*Eriosema simulans*
Plantaginaceae	*Plantago lanceolata*
Poaceae	
Pteridophyta	*Pteridium aquilinum*
Rosaceae	*Leucosidea sericea*
Rosaceae	*Rubus ludwigii*
Rubiaceae	*Pentanisia prunelloides*

Vegetation Inventory

Protea Savanna

Family	Species
Acanthaceae	*Barleria monticola*
Anacardiaceae	*Searsia dentata*
Asteraceae	*Callilepsis laureola*
Asteraceae	*Helichrysum aureontiens*
Asteraceae	*Helichrysum nanum*
Asteraceae	*Helichrysum umbraculigerum*
Asteraceae	*Senecio coronatus*
Asteraceae	*Stoebe vulgaris*
Asteraceae	*Vernonia natalensis*
Euphorbiaceae	*Acalypha punctata*
Fabaceae	*Eriosema simulans*
Hyacinthaceae	*Scilla natalensis*
Hypoxidaceae	*Hypoxis rigidula*
Iridaceae	*Watsonia densiflora*
Plantaginaceae	*Plantago lanceolata*
Poaceae	
Proteaceae	*Protea caffra*
Proteaceae	*Protea roupillae*
Pteridophyta	*Pteridium aquilinum*
Rosaceae	*Rubus ludwigii*
Rubiaceae	*Pentanisia prunelloides*
Scrophulariaceae	*Buddleja salviifolia*
Thymelaeaceae	*Gnidia caffra*
Thymelaeaceae	*Gnidia kraussiana*