Patterns of plant species richness and diversity across two habitat types in the Upper Karoo, South Africa

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PTRHAN004

Thesis presented for the degree of Master of Science
in the Department of Biological Sciences
University of Cape Town

MAY 2018

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The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author, and are not necessarily to be attributed to the NRF.

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Acknowledgements

I would like to express my sincere gratitude to my supervisor and mentor, Timm Hoffman (UCT), who has been a kind and supportive presence throughout my journey through this degree. It has been a privilege working with him for the past four years, and learning from him about more than just science. I would also like to thank my co-supervisor, Simon Todd (SAEON), whose expertise in the Nama-Karoo was invaluable during data collection and analysis. My sincere thanks go to Sam Jack, an absolute machine in the field, without whom I am certain my fieldwork experience would not have been the same. Thanks also to Dr Joe McAuliffe from the Desert Botanical Garden in Phoenix, Arizona, for valuable discussion which helped shape the outline of several sections of this thesis. I am indebted to the farmers and landowners on whose property we worked, for their keenness to assist, and their hospitality when it came time to find a place to settle for the evening. Thanks to Dylan Postmas for helping me get started with community ecology and modelling in R, and to Kervin Prayag for always being available to assist when my R code didn't cooperate. Gabriella Leighton, Kervin Prayag, Gina Arena, Samantha Venter, Zander Venter, Kirsten Packer and Simon Power are gratefully acknowledged for their excellent company, support and ability to keep me sane and well-hydrated during the countless tea-times spent together. A heartfelt thank-you to everyone in the Plant Conservation Unit for the comforting space and stimulating discussions over the past few years. I am extremely grateful to my tai chi coach, Peter Williamson, and several members of the UCT Tai Chi Club of 2017 (you know who you are) for the care, support, and lessons they knowingly and unknowingly provided – all the sinking indubitably helped me stay afloat. Finally, I would like to thank my family – especially my mother, Morea Petersen – for the endless supply of love and faith in my ability to achieve my goals.

The MSc bursary, which funded this research and my degree, was awarded through the Foundational Biodiversity Information Programme (FBIP), a joint initiative of the Department of Science of Technology (DST), the National Research Foundation (NRF), and the South African National Biodiversity Institute (SANBI). Further merit funding was awarded by the University of Cape Town, for which I am grateful.

Experience teaches that many curious and minute plants will escape detection, unless sought with more than ordinary attention; and that, by sitting or standing still and carefully looking around, many interesting objects of natural history may be discovered, which otherwise would have been passed unheeded and unknown.

William John Burchell, *Travels in the Interior of Southern Africa* (1824)

Abstract

The Nama-Karoo biome is relatively understudied in terms of its baseline biodiversity. Apart from its rich agricultural land-use history, the region is also under pressure from the development of the Square Kilometre Array, an increased demand for cleaner energy from shale gas fracking and/or other renewable energy installations, and the overarching impacts of global climate change. A reliable baseline inventory of biodiversity for the region is essential if these impacts are to be monitored and managed effectively.

The main aim of this study was to relate fine-scale patterns of plant diversity and community structure to broader-scale vegetation mapping in the Karoo regions. It also investigated the role of several environmental and climatic variables as drivers of species richness, relative cover, and growth form diversity in two habitat types (i.e. plains and rocky dolerite hillslopes), and along a longitudinal environmental gradient. A pairwise floristic survey approach was implemented, using modified Whittaker plots in each habitat type at 30 sites within the shale gas exploration area in the Upper Karoo bioregion. Data were collected on species richness, relative cover, and growth form diversity of the observed vegetation. Soil samples were collected from each Whittaker plot, and climate data were obtained by point sampling from raster layers using GIS.

The results showed that mean species richness was significantly higher ($p < 0.01$) in slope habitats than in plains habitats across the environmental gradient. Trees and woody shrubs had significantly higher species richness ($p < 0.001$) and relative cover ($p < 0.01$) in slope habitats. Low woody shrubs comprised the greatest percentage of growth form diversity in both habitat types in terms of species richness and relative cover, and were the dominant growth form across the longitudinal gradient. At the arid western extent, leaf-succulent shrubs had slightly higher relative cover (~ 25%) in slope habitats compared to other growth forms, apart from low woody shrubs. In the central regions, perennial grasses were more abundant (25 – 60%) in slope habitats, while annual grasses were more abundant (25%) in plains habitats. At the more mesic eastern end of the longitudinal gradient, perennial grasses were dominant (> 50%) in plains habitats.

Cluster analysis, based on species presence data in each habitat type, showed relatively strong correspondence between plant associations in slope habitats and their respective vegetation types as currently defined. These plant associations were spatially aggregated according to their position along the environmental gradient. Little to no correspondence was found between plant associations in plains habitats and their respective vegetation types. These plant associations were interspersed with each other when plotted spatially, and occurred in a repeating pattern in plains habitats across the study area.

Multiple regression models indicated that a combination of climatic and environmental variables, and soil properties significantly predicted overall species richness and relative cover of the five dominant growth forms. Habitat type commonly emerged as a significant predictor for overall species richness and relative cover. Overall dissimilarity, and dissimilarity in the relative cover of five plant functional types between plains and slope habitats, were also predicted by a combination of climatic and environmental variables, and soil properties. These predictors varied greatly between the different response variables, suggesting that different plant functional types are influenced by different drivers, depending on the habitat in which they occur.

Habitat heterogeneity, coupled with local and regional variation in prevailing climate and soils, has consistently emerged as an important driver of plant species richness and relative cover in global drylands research. Measuring richness and diversity within habitats requires a high sampling resolution in both plot size and number. This study has shown that sampling at the 0.1 ha scale (or larger) captures a representative sample of richness and diversity within a given habitat type in the Nama-Karoo biome, where low woody shrubs (< 60 cm tall) are the dominant growth form. In the current vegetation map of South Africa, the vegetation types for the Upper Karoo bioregion are coarse, and hence give the impression of homogeneity in what is in reality a relatively heterogenous landscape. Fine-scale baseline biodiversity data such as are presented in this study may improve the resolution of the existing vegetation map, as well as inform better conservation and management practices in economically important and biologically diverse rangelands in the Nama-Karoo biome, prior to future developments in the region.

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CHAPTER 1: Introduction

1.1 Background & rationale

1.1.1 Introduction

The Nama-Karoo biome (Mucina et al., 2006b) is a grassy dwarf-shrubland that occupies the central elevated interior of South Africa. It is flanked by several other biomes, and comprises floral and faunal components from each, but also contains its own unique floral elements. While the Nama-Karoo biome was occupied by hunter-gatherers for many centuries, the landscape was only utilised for grazing by domestic livestock when the first pastoralists arrived in southern Africa approximately 2000 years ago (Smith, 1999). The arrival of European colonialists in the 18th century introduced new agricultural practices, particularly cultivation, and later, the fencing of farms into many smaller paddocks. The Nama-Karoo landscape has been shaped by both natural and anthropogenic factors, ranging from spatially and temporally variable rainfall, to centuries of changing land-use patterns and practices. Despite this, most parts of the Nama-Karoo biome remain sparsely surveyed for biodiversity.

This chapter provides a review of the Karoo environment, with a general description of the known vegetation structure and prevailing climatic conditions. The determinants of plant diversity in the region are highlighted, and the current and emerging threats to the region are reviewed. Finally, the aims and objectives of the thesis are outlined.

1.1.2 The Nama-Karoo biome as a study area: diverse and data deficient

In terms of baseline biodiversity, the Nama-Karoo biome is one of the most understudied regions in South Africa, and a reliable estimate of the plant diversity of the region is still lacking. Although a variety of floristic surveys have been undertaken to assess the species assemblages present in parts of the region (Cowling and Hilton-Taylor, 1999, 1994; Pienaar et al., 2004), as well as the environmental, climatic, and land-use-related drivers that influence species richness and diversity (e.g. Palmer and Hoffman, 1997), much remains to be understood about how extensively these drivers shape the vegetation in the region. Apart from its rich agricultural land-use history, numerous other anthropogenic pressures are being exerted on the Nama-Karoo. The Square Kilometre Array is one such development that will have an impact on the Nama-Karoo environment over the next few decades (Dewdney et al., 2009; Jonas, 2009). An increased demand for cleaner energy from shale gas fracking or from renewable energy installations also pose novel threats in addition to the global threat of climate change. The need for a reliable baseline inventory of biodiversity for the region is becoming increasingly apparent, if these impacts are to be managed effectively.

1.1.2.1 Mapped vegetation of the Karoo

The South African National Vegetation Map recognises two biomes in the Karoo: the Succulent Karoo, and the Nama-Karoo (Mucina and Rutherford, 2006). The Succulent Karoo biome includes Namaqualand, the Hantam, Tanqua and Roggeveld region, as well as the Little Karoo (Mucina et al., 2006a). This biome is comprised of flat to gently rolling hills, with most of the area being < 800 m above sea level. Smaller areas of the Succulent Karoo also occur along the western escarpment, after which it transitions into the Desert biome to the north, the Fynbos biome to the south and south-east, and the Nama-Karoo biome to the north and east (Mucina et al., 2006a). As its name suggests, the Succulent Karoo biome is characterised by leaf-succulent dwarf shrub vegetation (Werger, 1986; Van Rooyen, Theron and Grobbelaar, 1990; Rutherford and Westfall, 1994; Milton et al., 1997; Mucina et al., 2006; Van der Merwe and Van Rooyen, 2011), and is recognised by the IUCN as a biodiversity hotspot (Mittermeier et al., 2011; Myers et al., 2000).

The Nama-Karoo biome extends along the central plateau of the western interior of South Africa and into south-eastern Namibia (Mucina et al., 2006). This biome is landlocked and is located between the Succulent Karoo, Desert, Savanna, Grassland, Albany Thicket and Fynbos biomes. In some cases the Nama-Karoo biome transitions relatively gradually into adjacent biomes (such as at the interface between the Nama-Karoo biome and some parts of the Desert and Grassland biomes) and shares floristic and climatic affinities with these adjacent biomes (Desmet et al., 2006; Mucina et al., 2006). However, in other areas such as the ecotone between the Nama-Karoo and Fynbos biomes, the boundary is more distinct (Mucina et al., 2006). The

Nama-Karoo biome is dominated by dwarf shrubs from the families Asteraceae and Fabaceae and grasses (Poaceae). The flora of the Nama-Karoo has notable genus-level affinities with the biomes which surround it (Hilton-Taylor, 1987; Rutherford et al., 2006). Despite this, and unlike the Succulent Karoo, the Nama-Karoo biome does not represent a centre of endemism (Van Wyk and Smith, 2001). The Upper Karoo Hardeveld vegetation type, within the greater Upper Karoo bioregion of the Nama-Karoo biome, has the highest local endemism in the region (Mucina et al., 2006). The Upper Karoo bioregion, which will be described later, forms the focus of this study.

1.1.2.2 Climate

Limited and highly variable rainfall is characteristic of most arid and semi-arid regions (Chesson et al., 2004; Noy-Meir, 1973; Sala et al., 1988; Webb et al., 1978), and the same applies to the wider Karoo region. On a broad scale, there is a uniform decrease in mean annual rainfall from east to west across the central plateau in South Africa (Desmet and Cowling, 1999). At finer scales, trends in rainfall seasonality are apparent. The eastern parts of the Nama-Karoo biome are dominated by summer rainfall derived from sources further to the north and east of the region (Illius, 2000). Over the western interior, this grades into a predominantly winter rainfall regime, such as in the south- and south-western mountains and along the coast in the Succulent Karoo biome, with Mediterranean climates prevailing (Desmet and Cowling, 1999; Illius, 2000; Pienaar et al., 2004). Variations in rainfall influence the observed species composition of any given plant community (Westoby, 1980). Differences in the amount of rainfall, the duration and time of occurrence of the wet season, and the degree of intensity of individual rainstorms may all contribute to differences in plant distribution and cover (Desmet and Cowling, 1999; Westoby, 1980), both directly and indirectly.

The rainfall regime of a region affects both the biotic and abiotic components. An important difference between the winter and summer rainfall regimes in the wider Karoo region is the reliability of rainfall events. Areas with winter rainfall regimes, such as the Succulent Karoo biome, receive rainfall from circumpolar westerlies. Because of this, they are more reliable in terms of rainfall events than their summer rainfall regime counterparts in the Nama-Karoo (Desmet and Cowling, 1999) which receive rainfall predominantly from convective thunderstorm activity. These differences have important implications for plant community structure and dynamics that prevail throughout the region.

One of the leading theories in plant ecology is the idea that on a global or continental scale, climate is the principal driver governing the distribution of vegetation types, with various other physical and biological variables influencing vegetation at local scales (Cowling and Hilton-Taylor, 1994; Retuerto and Carballeira, 2004). Physical and biological variables are largely involved in generating heterogeneity in the landscape, enabling species to converge on their niche preferences and make use of the resulting microhabitats. The degree to which heterogeneity in a landscape is expressed, however, is largely dependent on scale (Pickett and Cadenasso, 1995). On a local scale, the occurrence of a given community of plants depends on how it responds to available microclimates (Retuerto and Carballeira, 2004). Numerous studies have provided evidence of how species richness and growth form diversity are affected by competition, facilitation and/or niche separation in terms of water and nutrient availability (Aarssen, 1984; Aguiar and Sala, 1999; Armas and Pugnaire, 2005; Silvertown, 2004; Silvertown et al., 2015). The influence of soil properties (Medinski et al., 2010; Schmiedel et al., 2015; Schmiedel and Jürgens, 1999), as well as exposure to direct sunlight (Tilman, 1988) have also been described. These examples are not exhaustive, and much research is still required to ascertain which climatic factors are responsible for the observed floral distribution patterns. The associated physiological mechanisms underlying the adaptations to various niches are also poorly understood (Grace, 1987). These adaptations are crucial, particularly in arid and semi-arid regions, where limitations to growth are common, and where climate change may worsen the already harsh growing conditions for plant communities.

1.1.2.3 Future climate scenarios for the Karoo

Climate change scenarios projected by the IPCC suggest that the interior of South Africa may experience an increase in average temperatures of 3 - 6°C (Ziervogel et al., 2014), accompanied by uncertain changes in precipitation. Climate change scenarios projected for the Karoo region include an increase in the magnitude (Hewitson and Crane, 2006) and variability (Mason et al., 1999) of rainfall events, as well as an increase in the duration of dry spells (Hewitson, 1996). High variability of rainfall can result in drought, which may consequently alter the diversity, cover, abundance and composition of plant communities through mortality (Westoby et al., 1989). Moreover, biomes in the Karoo region are anticipated to experience reductions in their geographic distributions under hotter and drier climatic conditions (Rutherford et al., 1999). Therefore, determining and understanding the climatic drivers of plant diversity and cover in the Karoo is necessary for managing the potential impacts of climate change on the vegetation of a region for which not much data exist.

1.1.2.4 Vegetation and geomorphology

According to the National Vegetation Map (Mucina et al., 2006), the Nama-Karoo biome is comprised of three main bioregions: Bushmanland and West Griqualand, the Lower Karoo, and the Upper Karoo.

The Bushmanland and West Griqualand bioregion consists of six vegetation types, all of which are confined to the Northern Cape province (Mucina et al., 2006). Characteristic to this bioregion are the ‘white’ grasses of the genus *Stipagrostis*, with patchy occurrence of low tree species including *Senegalia mellifera* and *Aloidendron dichotomum* on rocky hill and sandy foot-slope habitats. The Lower Karoo bioregion consists of four vegetation types, which occur predominantly in the Western and Eastern Cape provinces. These vegetation types are comprised largely of a matrix of diverse dwarf shrubland species, with scattered low trees, drought-resistant and less palatable grasses, and some leaf-succulent elements from the families Aizoaceae and Crassulaceae.

The Upper Karoo bioregion, with an area of approximately 120 535 km^2, is among the three largest bioregions in South Africa, with most of the Nama-Karoo biome belonging to this bioregion. Despite its large area, it consists of only four vegetation types: Western Upper Karoo, Upper Karoo Hardeveld, Northern Upper Karoo, and Eastern Upper Karoo. Drought-resistant grasses of the genera *Eragrostis*, *Aristida* and *Stipagrostis* are common in these vegetation types, and occur amongst a matrix of spiny, microphyllous and leaf-succulent dwarf shrubland species. As in the Lower Karoo, some low tree species (e.g. *S. mellifera*) can be found on the rocky hills and sandy soils near large river systems.

The Nama-Karoo biome is considered to be relatively geologically and environmentally homogeneous compared to the surrounding biomes (Mucina et al., 2006). The scattered rocky hills, mesas and inselbergs are distinctive and noteworthy features of the otherwise homogeneous Hardeveld habitat of the region (Dean and Milton, 1999; Partridge, 1997). These features are capped by or wholly comprised of dolerite (fine- to medium-grained dark, intrusive igneous rock), while the surrounding plains and lowland habitats are dominated by shale and sandstone (fine- and medium-grained sedimentary rock) (Palmer and Hoffman, 1997).

The hills (known in Afrikaans as *'koppies'*) created by the dolerite intrusions are fragmented in the landscape, but these intrusions are what make the Karoo region unique (Glazewski and Esterhuyse, 2016). Due to their rocky nature and elevation, these features provide greater heterogeneity in habitat and microclimates than the surrounding matrix (Pienaar et al., 2004), and support higher species richness and diversity, in both fauna and flora (Burke et al., 2003; Pienaar et al., 2004). Overall, local endemism of the Nama-Karoo biome is relatively low compared to the surrounding biomes. The Upper Karoo Hardeveld, however, hosts a higher number of local endemics (17 endemic species) than any other vegetation unit in the Nama-Karoo biome (Mucina et al., 2006). This comparatively low level of endemism suggests that the Nama-Karoo biome is relatively young, but may also be related to the noteworthy environmental and geological homogeneity of the region (Mucina et al., 2006).

1.1.3 Richness and diversity responses to environmental gradients and disturbance

Land-use and land degradation have been popular themes in the literature on the arid zones of South Africa. Historically, ecological research in the Karoo has focused primarily on the impacts of livestock grazing on vegetation. The study of fence-line contrasts between communal and commercial rangelands (Todd and Hoffman, 2009, 1999), or contrasts between heavily grazed and lightly grazed biodiversity observatories (Bossdorf et al., 2000; Hanke et al., 2014) have been among the most popular recent approaches. The eastern Karoo in particular has been extensively researched in terms of the effects of livestock on vegetation structure (Du Toit et al., 2006; Du Toit, 1996; Vorster et al., 1983) and on the development of grazing index values for Karoo plants (Du Toit, 1995; Du Toit et al., 1995). The number of livestock as well as the management strategy have both been suggested to have a significant impact on the eastern Karoo landscape, even when other sources of variability (e.g. variation in rainfall) are removed (Archer, 2004). Studies from the eastern Karoo also suggest that fire can significantly alter vegetation structure and composition, to a similar degree as grazing and herbivory (Du Toit et al., 2015, 2014). Furthermore, studies have focused not only on the vegetation, but also on the physical soil properties, including impacts of various stocking rates on infiltration rate, compaction, and bulk density (van N. du Toit et al., 2009), which in turn influence vegetation structure and patterns.

While many studies have investigated the impacts of livestock on the landscape and vegetation structure, few studies have looked at the spatial patterns of plant biodiversity. Even fewer have catalogued the baseline diversity of vegetation. A study by Palmer and Cowling (1994) noted a coarse change in the floristic species gradients from west to east across a topo-moisture gradient, and variations in the dominance of different growth forms on different substrates (sandstone vs dolerite). Phytosociological studies conducted in the Nama-Karoo biome have also given some insight into the spatial patterns of species diversity and vegetation structure (Palmer, 1989; Rubin and Palmer, 1996; van der Walt, 1980). The contributions made by John Acocks are also noteworthy in that his research not only produced the first comprehensive map of vegetation types (*'veld types'*) for South Africa (Acocks, 1953), but also influenced national perspectives on degradation in the country, notably through the development and introduction of the 'expanding Karoo' concept. The expanding Karoo concept consists of two related hypotheses (Hoffman et al., 1999). The first hypothesis suggests that prior to the colonisation of the Karoo by European settlers, the semi-arid interior was generally grassier than at present. The second warns that Karoo shrublands have expanded eastward into the grasslands as a result of selective grazing by livestock and poor land-use practices (Meadows, 2003). Contemporary research still explores the nexus between grazing and climate, and provides an important baseline for climate change research (Masubelele et al., 2015).

Determining how the vegetation of a region is influenced by the prevailing climatic and environmental conditions is important for many reasons and can be explored in several different ways. Natural gradients have traditionally been used to investigate and assess ecological dynamics across a range of spatial scales, most notably in the context of climate change. These include the analysis of vegetation patterns in relation to temperature (Bragazza et al., 2013; de Sassi and Tylianakis, 2012; Koch et al., 1995; Retuerto and Carballeira, 2004; Townsend et al., 1995), elevation and altitude (Amundson et al., 1989; Breshears et al., 2008; Erschbamer et al., 2009; Ooi et al., 2012; Randin et al., 2009; Williams et al., 2003), and precipitation (Austin, 2002; Austin and Sala, 2002; Austin and Vitousek, 1998; Stanton et al., 1994).

Natural environmental gradients investigated in the Karoo include gradients of moisture and aridity (Burke et al., 2003; Cowling et al., 1994a), and elevation, altitude and topography (Burke, 2001). However, the sampling methods used in many of these studies were restricted to a single habitat type. A study by Cowling et al. (1994), however, was different in that it highlighted the dichotomy in functional diversity and species diversity between two habitat types: rocky hills and loamy plains in the Nama-Karoo biome. The result of their study suggested that habitat type and, more specifically, habitat heterogeneity plays an important role in shaping vegetation structure and composition. Despite rocky hills occupying a significant proportion of the landscape in the Nama-Karoo biome, it is likely that they provide important niches for the establishment and survival of certain sensitive species, and therefore support higher species richness (Burke et al., 2003; Pienaar et al., 2004). Functional diversity, i.e. the number of plant functional groups present in a specified area (Díaz and Cabido, 2001; Tilman, 2001) also offers a level of resilience to a landscape, since different functional types have different dynamics, and respond differently to different pressures. Therefore, understanding not only the patterns of plant species, but also plant functional types (PFTs), across a range of spatial scales within different habitat types, would provide better insight into the resilience of a landscape.

Related to niche theory is the understanding that vegetation structure and pattern can be expressed at a range of different spatial scales. As such, species richness at one scale is not necessarily linearly correlated with species richness at another scale, particularly in heterogeneous landscapes with many different habitat types. In the Nama-Karoo biome, alpha (α) and beta (β) diversity is low (Mucina et al., 2006). According to a study by Cowling and Hilton-Taylor (1999), plant species densities in the Nama-Karoo ranged from 22 – 76 species at the 0.1 ha (1000 m^2) scale. A study of the influence of sampling effort and scale of sampling in the semi-arid Succulent Karoo biome suggested that although broad-scale patterns of species richness could still be estimated with poor sampling effort, finer-scale floristic relationships were sensitive to poor sampling effort (Burke, 2007). In heterogeneous landscapes, such as can be observed in the Nama-Karoo biome, the probability of fine-scale floristic relationships being missed because of poor sampling effort (e.g. too broad-scale) is therefore quite high. Extrapolating patterns of species richness across a heterogeneous landscape could mask finer-scale patterns of species richness unique to certain areas, and could therefore undermine our understanding of the true biodiversity within the region, leaving it vulnerable to disturbance.

1.1.4 The energy sector and its prevalence in South Africa

Uranium and natural shale gas are two key mineral resources in the Karoo that have attracted the attention of both national and international energy companies. The acquisition of shale gas by means of hydraulic fracturing (hereafter referred to as ‘fracking’) is a process that is new to South Africa, but has been undertaken by numerous countries across the world. While many countries have benefitted from fracking, several countries, including Brazil, France, and Scotland have banned fracking activities altogether (Du Toit, 2016). Multiple case studies from the United States of America and the United Kingdom suggest that fracking has the potential for a large environmental disturbance footprint. Sensitivity studies conducted in the greater Karoo region have also indicated the potential impacts of exploratory fracking on the biodiversity of the region (Todd et al., 2016). Despite the high levels of uncertainty in the estimates of the volume of recoverable shale gas, the economic opportunities that could potentially be created by shale gas exploration and acquisition in South Africa render the enterprise appealing.

In April 2011, a moratorium on shale gas exploration was imposed by the South African government, following objections by various activist groups and local communities in the Karoo. The moratorium was later lifted in 2012, and the South African government has since made public commitments to proceed with the development of shale gas in the Karoo (CSIR, 2015). A 24-month long strategic environmental assessment (SEA) was commissioned in 2015, with the objective of, *inter alia*, developing policy options and guidelines for site specific assessments to be implemented if applications for environmental authorisation for shale gas development are submitted to any relevant authority (CSIR, 2015).

The Karoo BioGaps Project, led by the South African National Biodiversity Institute (SANBI), was developed in response to the need for more detailed information on biodiversity patterns within the Karoo as identified through the shale gas SEA. The primary objective of the Karoo BioGaps Project, to which the present study contributes, is to address the deficiency of biodiversity data for the Nama-Karoo biome prior to the potential large-scale disturbances caused by exploratory fracking. Understanding the biodiversity of the region pre-disturbance will allow for better conservation management, monitoring and rehabilitation practices after disturbance from fracking, and indeed other future developments, has occurred.

1.2 Aims and objectives

The primary aims of this study are as follows:

(i) To determine the species richness, relative cover and growth form diversity of the vegetation in the Upper Karoo bioregion by conducting floristic surveys in two main habitat types (i.e. plains and slope habitats) at 30 selected sites in the Karoo region, with the objective of:
investigating how species richness, relative cover and growth form diversity in plains and slope habitats relate to known diversity patterns at the 1000 m^2 (0.1 ha) scale in the Nama-Karoo and other biomes;

(ii) To relate fine-scale plant diversity and community structure to broader-scale vegetation mapping in the Karoo regions, with the objective(s) of:
   a. investigating variation in patterns of plant species richness at various spatial scales, and
   b. determining how the observed plant associations relate to the current mapped vegetation types in the Karoo region;

(iii) To investigate the role that environmental and climatic variables might play in influencing species richness, relative cover and growth form diversity within each of the two sampled habitat types and along the sampled environmental gradient.

CHAPTER 2: Methods

2.1 Study area

2.1.1 Sample site selection within the shale gas exploration area in the Karoo

This study was conducted within the shale gas exploration area (SGEA) in the Karoo region of South Africa (Fig. 1). The SGEA is a large area of approximately 171 811 km^2, consisting of three main precincts (western, central, and eastern) which extend into the Western Cape, Northern Cape, and Eastern Cape provinces. Although the precise locations within the SGEA where exploration activities may occur have not yet been designated, it has been suggested that the Nama-Karoo biome will be most disturbed by these activities (Todd et al., 2016).

Sampling sites within the SGEA were selected at a broad scale to ensure adequate representation and spatial coverage of the study area. Although potential sampling sites were frequently identified based on satellite imagery, these were verified and refined in the field to ensure consistency in sampling site selection. A total of 30 representative sites were selected based on the presence of suitable dolerite hills/koppies and adjacent plains, as well as the accessibility of the sites. The dolerite hills in the southern segment of the SGEA, located below the escarpment, were not large enough to sample. Sites were a minimum of 30 km apart from one another, spread across the western, central, and eastern precincts of the SGEA.

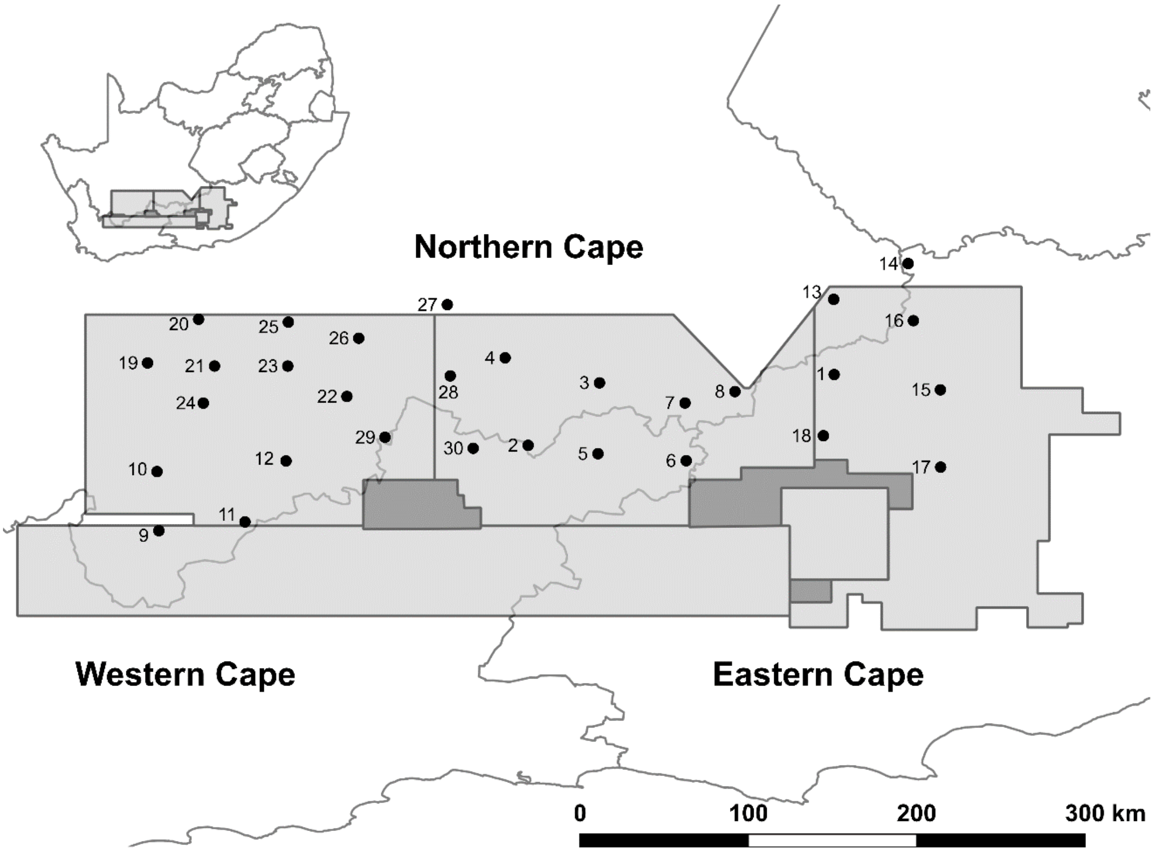

Figure 1: Sample sites (numbered) in the shale gas exploration area (SGEA) in the Karoo region, South Africa. Light shaded areas indicate the western, central, and eastern SGEA precincts. Dark shaded areas indicate exclusions from the SGEA.

2.1.2 Selecting habitat types within sample sites

Data were collected from the 30 selected sites between March 2016 and April 2017, shortly after the summer rainfall seasons. Delaying field sampling after rains allowed for sufficient plant growth for species-level identification and more representative sampling. A paired approach was used at each of the 30 sites to sample two main habitat types: dolerite hill slopes, and their adjacent plains. Slopes were sampled on south-, east- or southeast-facing aspects to maintain consistency across sites and to minimise the number of variables that could potentially influence the structure and composition of the communities investigated. Sample sites were also located along a longitudinal environmental gradient that is arid in the west (Fig. 2A) and mesic in the east (Fig. 2B), across which vegetation patterns could be compared.

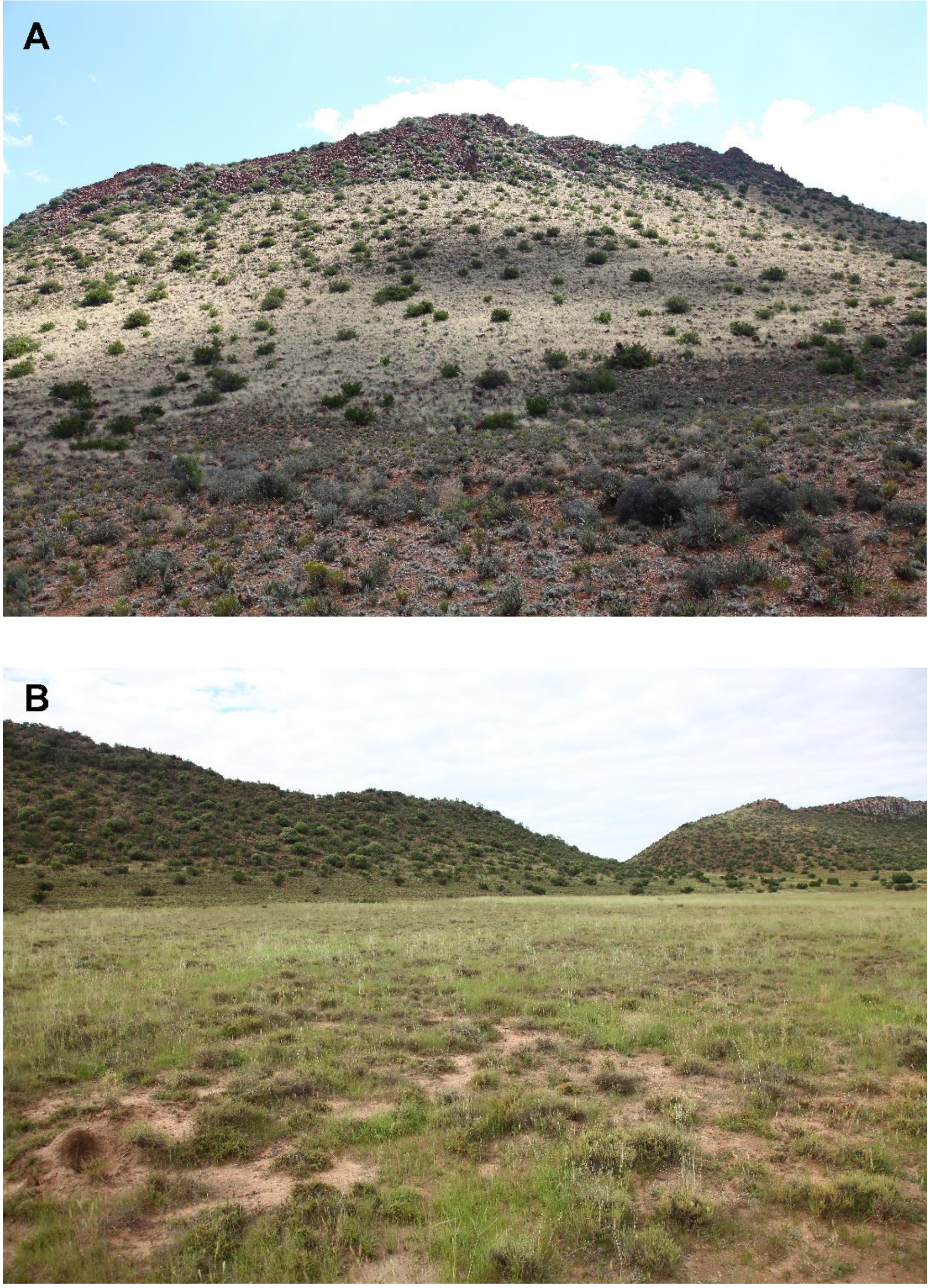

Figure 2: Photographs of selected sample sites at **(A)** the arid end (Site 27) and **(B)** the mesic end (Site 14) of the study area, demonstrating differences in habitat types. In both photographs, the sampled plains habitat is visible in the foreground, while the sampled slope habitat is visible in the background.

2.2 Data collection

2.2.1 The modified Whittaker plot sampling method

The modified Whittaker plot vegetation sampling method (*sensu* Stohlgren et al. 1995) was implemented. The modified Whittaker plot method is a multi-scale sampling approach which involves a 1000 m^2 (0.1 ha) rectangular plot containing ten regularly spaced 1 m^2 plots around the internal perimeter, two 10 m^2 plots in opposite diagonal corners, and one central 100 m^2 plot (Fig. 3). This method provides a more realistic comparison of community species richness and diversity than do single-scale sampling methods (Whittaker, 1977), and magnifies the influence of spatial scale on local patterns of species richness (Podani et al., 1993; Stohlgren et al., 1995). Relating species to their area of occurrence also provides the most accurate representation when measuring diversity and richness. When measuring dominance, using species cover values is often most effective (Shmida, 1984). This makes the modified Whittaker plot sampling method appropriate for the purposes of this study.

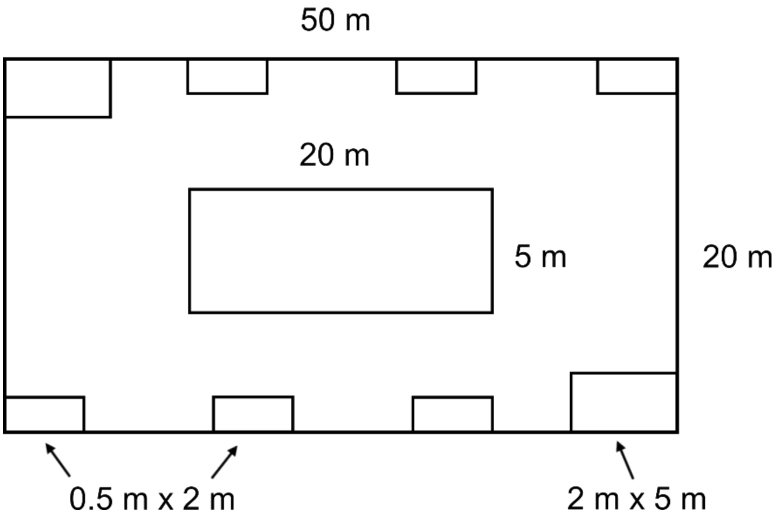

Figure 3: Modified Whittaker plot, *sensu* Stohlgren et al. (1995).

2.2.2 Assessing the relative cover and richness of species and growth forms

Two modified Whittaker plots were sampled at each site, one on the plains and one on the slope. Within each of the ten peripheral 1 m^2 subplots, total live vegetation cover, total bare ground, and total rock cover were estimated as a percentage of the subplot area. Individual species cover values were estimated as a percentage of total live vegetation cover for each species observed in each subplot. Lichen, moss, fungi and unidentifiable seedlings were not included in the assessment. For each of the larger subplots, all new species observed were recorded, and the presence of previously recorded species was noted. Species cover data for the ten 1 m^2 subplots were then averaged to obtain a mean cover value for each species per habitat type per site.

Each species was assigned to one of five plant functional types (PFTs): woody shrub, perennial grass/sedge, annual grass, forb/geophyte/parasite, or succulent shrub. PFTs were defined based on life history (annual or perennial), growth form (shrub, grass or herbaceous forb) and succulence (succulent or non-succulent) (Hanke et al., 2014). These PFTs and their corresponding species were then grouped into 13 growth forms: tree (> 2 m), tall woody shrub (> 60 cm), low woody shrub (< 60 cm), liana, leaf-succulent shrub, stem-succulent shrub, dwarf succulent, annual grass (Family: Poaceae), perennial grass (Family: Poaceae), sedge (Family: Cyperaceae), annual forb, perennial forb, or geophyte. A separate category (‘Other’) was created for plants that were parasitic or otherwise could not be assigned to any other growth form. Average species richness and relative cover was calculated for each growth form.

2.2.3 Collecting biophysical data on site

A slope gradient index (0 = flat, 1 = gentle, 2 = moderate, 3 = steep) was recorded on site. GPS coordinates and elevation were recorded at all four outer corners of the modified Whittaker plot using a using a Garmin GPSMAP 64s GPS device. One bulk soil weighing up to 400 g was collected from each Whittaker plot by sampling soil from ten random locations within each Whittaker plot using a hand trowel. Once transported back to the processing laboratory at the University of Cape Town, soil samples were sieved to a particle size of 2 mm, then oven dried at 40 °C for 24 hours. Analyses were performed to extract several biophysical variables for each plot (Table 1).

2.2.4 Extracting climate and environmental data using GIS

Climate and environmental data were obtained from raster files from the Computing Centre for Water Research (CCWR) database. Data on vegetation types and bioregions were obtained from a vector file of the vegetation map of South Africa (Mucina and Rutherford, 2006), available on the South African National Biodiversity Institute's (SANBI) website. Data were extracted for each sample site using Quantum GIS 2.18.0 (Las Palmas de G.C.). All layers used in QGIS used geographic coordinate system WGS84 and EPSG:4326 as a spatial reference.

Table 1: Climatic and biophysical variables extracted and analysed.

Variable measured	Abbreviation	Units
Climatic		
Mean annual precipitation	MAP	mm
Mean annual pan evaporation	MPAN	mm
Water stress during hottest month (January)	WS	
Mean annual number of days with heavy frost	Frost	days
Mean annual temperature	MAT	°C
Maximum temperature of the hottest month (January)	MaxHot	°C
Minimum temperature of the coldest month (July)	MinCold	°C
Biophysical		
Soil fertility	SF	
Sand (of total soil texture)		%
Silt (of total soil texture)		%
Clay (of total soil texture)		%
Resistance (electroconductivity)	EC	Ω (ohm)
pH		
[Ca]		$\mathrm{cmol_c/kg}$
[Mg]		$\mathrm{cmol_c/kg}$
[Na]		mg/kg

[K]		mg/kg
[P]		mg/kg
Ammonium (NH_4)	NH4	%

Soil texture was measured by three-fraction particle size (i.e. sand, silt, and clay). Calcium (Ca), magnesium (Mg), sodium (Na), potassium (K) and phosphorus (P) concentrations were extracted by soil washing with citric acid (Bassi et al., 2000). All soil analyses were conducted by Elsenburg Laboratories in Stellenbosch, South Africa.

2.3 Data analysis

All statistical analyses were performed using the R statistical environment (R Development Core Team, 2011), and all plots were generated using the R package *ggplot2* (Wickham, 2016), unless otherwise stated.

2.3.1 Determining basic diversity patterns

2.3.1.1 Species richness and growth form diversity

Species richness (i.e. number of species present) and relative cover of each species were calculated for each habitat type per site using cover data obtained from the 1 m^2 subplots. Soil properties between habitat types were tested for significant differences using paired Student’s t-tests. To determine the influence of habitat on overall species richness, a paired Student’s t-test was done on species richness for plains and slope habitats. Data were tested for normality using Shapiro-Wilks normality tests. Model validation (testing normality) was done by quantile-quantile (Q-Q) plots and frequency histograms, as well as Shapiro-Wilks tests on the residuals for each model. A visual assessment of homoscedasticity was done by linear regression of the residuals against predicted values.

To determine whether growth form diversity varied between plains and slopes within each site, paired Student’s t-tests were done on the richness and relative cover of each growth form. To provide a visual display of the incidence of growth forms across all 30 sites, radial plots were drawn for each site. The five growth forms with the highest relative cover in both habitat types were used to maximise visual impact. The relative percent cover of each of the five dominant growth forms per site in each habitat type was averaged for six longitudinal bands comprising the entire study area. Radial plots were then generated using these values and arranged by longitude using the *fmsb* package in R (Nakazawa, 2018), to investigate trends in the relative percent cover of growth forms at broad spatial scales from west to east across the proposed environmental gradient. These plots provided a simple visual comparison of growth forms in each habitat type within a single longitudinal band, as well as across the environmental gradient.

2.3.1.2 Diversity patterns over different spatial scales

To investigate how overall species richness changed with increasing plot size in the modified Whittaker plots, species-area relationships were shown using box-and-whisker plots of species richness per habitat type. A species accumulation curve was drawn using the R package *vegan* (Oksanen et al., 2016) for each habitat type. The ‘random’ method of species accumulation was used to avoid any bias with the order in which sites were sampled. Values were obtained using observed species cover from the 1 m^2 subplots, with 999 permutations. The difference in slopes of species accumulation for plains and slope habitats was tested using a paired Student’s t-test on the permutated data. The species accumulation curves were also fitted with 95% confidence interval ribbons based on the permutated data using the *Hmisc* package in R (Harrell, 2018). Significant differences in slopes are indicated if the confidence interval ribbons do not overlap.

Additive diversity partitioning was used to determine the scale at which the highest proportion of the total species richness was found. Gamma (γ) diversity, i.e. the total species richness at a specified spatial scale, can be partitioned into alpha (α) diversity, i.e. the average number of species that occur within a sample, and beta (β) diversity, i.e. the average number of species that are absent from a sample (Crist et al., 2003; Veech et al., 2002). Therefore, $\gamma = \alpha + \beta$ (Wagner et al., 2000). Diversity was calculated for all five plot sizes used in the modified Whittaker plot sampling method, such that:

i. α = *average species richness in all 1* m^2 *plots*
ii. β_1= *average species richness in all 10* m^2 *plots* – α
iii. β_2= *average species richness in all 100* m^2 *plots* – β_1

iv. β_3= *average species richness in all 1000* m^2 *plots –* β_2
v. $\gamma = \alpha + \beta_1 + \beta_2 + \beta_3$

These values were then plotted in a stacked bar chart, with the cumulative stacked bar representing *γ*-diversity, to compare which scale of sampling comprised the highest species richness between habitat types.

2.3.1.3 Plant associations and their spatial correspondence with the current vegetation map of South Africa

Hierarchical cluster analysis was done using R's *cluster* package, to determine whether plant associations (i.e. a group of plants with a strong phytosociological affinity to one another based on floristic composition, physiognomy, and ecological circumstances (Becking, 1957; Flahault and Schröter, 1910)) were formed on plains and slopes. Agglomerative nesting with a flexible beta value of -0.5 was used. K-means clustering was then used to assign an individual sample site to clusters based on the length of the branches of the resultant cluster dendrograms. In addition, sites were colour-coded according to their cluster membership and overlaid on a map of the bioregions of South Africa (Mucina and Rutherford, 2006) in QGIS, using their geographic coordinates. This allowed for a visual representation of the spatial distribution of the clusters. It also allowed for a visual assessment of the correspondence between sites belonging to the same cluster and their respective bioregions.

Relative percent cover of each of the five dominant growth forms was calculated for each cluster in each habitat type based on relative cover data from the 1 m^2 subplots. These values were then plotted in a stacked bar chart for comparison of clusters within and between habitat types.

2.3.1.4 Visualising patterns of plant diversity on plains and slopes

The differences in species richness and diversity in each habitat type at the 1 m^2 scale was shown by non-metric multidimensional scaling (NMDS) using R's *vegan* package, based on mean relative cover values of observed species. Data were relativised by maximum values per species to standardise the observed species cover values and reduce the variation introduced by rare and small-habited species. Bray-Curtis dissimilarity was used as the measure for original distance, because it is not affected by the number of null values between samples. An assessment of the stress in relation to dimensionality (i.e. number of axes) concluded that a 3-dimensional solution produced the lowest overall stress values for plains and slope habitats. However, the minimum stress values were on the higher end of the acceptable range of stress values (10 < *stress* < 20), according to Kruskal's (Kruskal, 1964) and Clarke's (Clarke, 1993) rules of thumb (McCune et al., 2002). Analysing each habitat type independently improved these stress values and resulted in better ordinations that were ultimately used for interpretation.

Points in the NMDS scatterplots were grouped according to cluster membership based on hierarchical clustering. Using the climatic and biophysical variables extracted and calculated for each site, each NMDS scatterplot was overlaid with fitted vectors as a visual representation of which variables influenced the ordination of points. Thereafter, a matrix of Kendall correlations between species cover and each of the climatic and biophysical variables was generated to determine the strength and direction of these relationships.

2.3.2 Exploring potential biophysical predictors of diversity

2.3.2.1 Attributing drivers of species richness and growth form diversity

Multiple regression was used to evaluate the relationship between overall species richness, and various climatic and biophysical variables. Data from both plains and slope habitats were included in the same set of linear models. To achieve the most parsimonious model, a subset of predictor variables was selected from the maximal model (i.e. the total set of climatic and biophysical variables (Table 1)) by forward and backward stepwise selection based on exact Akaike information criteria (AIC), using R's *MASS* package (Ripley et al., 2017). Longitude was included as a predictor variable in the maximal model, to serve as a proxy for the environmental gradient. The same was done when evaluating the relationship between the relative cover of the five dominant growth forms (independently) and the climatic and biophysical variables. Those variables which significantly ($p < 0.05$) predicted the overall species richness and relative cover of the dominant growth forms were then plotted against overall species richness and respective relative cover of each growth form, so that these relationships could be visually inspected and validated.

2.3.2.2 Investigating the response of plant associations on plains and slopes across a climatic and environmental gradient

To assess how similar the two habitat types were to each other with respect to species assemblages, the Bray-Curtis distances between sites in plains and slope habitats was calculated using a presence-absence species matrix. This was calculated for overall species richness, as well as within each of five key PFTs. Multiple regression was used to assess whether species assemblages and plant functional diversity on plains and slopes converged or diverged (i.e. became more, or less, similar) across the environmental gradient.

CHAPTER 3: Results

3.1 Basic diversity patterns

3.1.1 Species richness and growth form diversity

Overall species richness was higher in slope habitats (mean = 45.9, range: 20 – 73, n = 30) than in plains habitats (mean = 36.5, range: 11 – 59, n = 30). A paired Student's t-test suggested that mean species richness was significantly higher ($t = 3.53$, $p < 0.01$) in slope habitats than in plains habitats (Fig. 4).

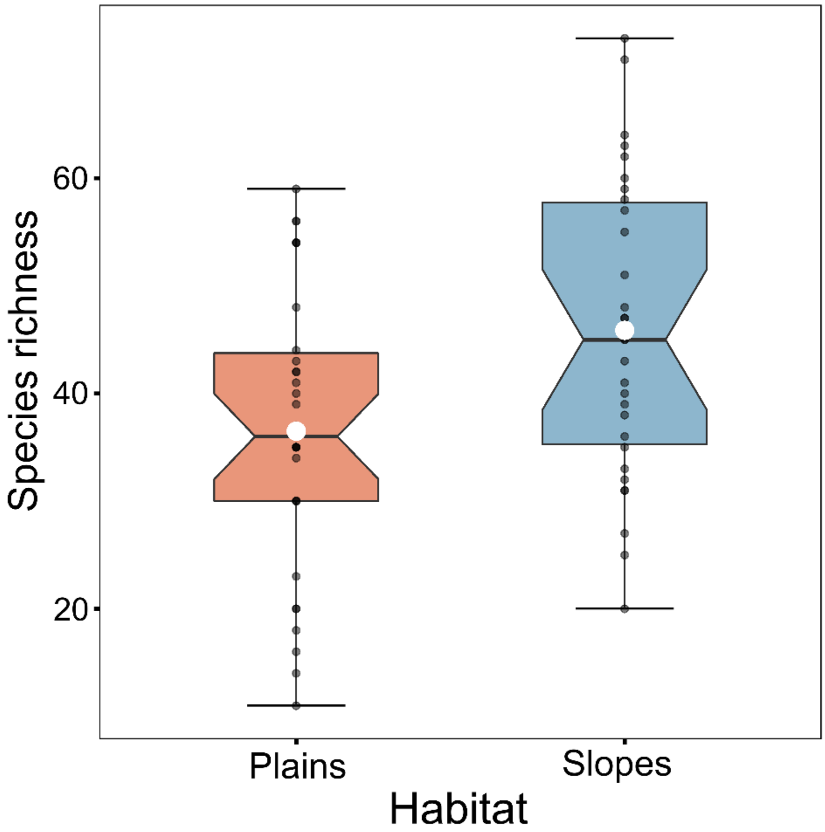

Figure 4: Box and whisker plots of species richness found in plains and slope habitats at 30 sites (0.1 ha scale) in the SGEA. Mean values are indicated by a white dot. Notches indicate significant difference in medians if notches do not overlap.

Patterns of growth form diversity varied between plains and slope habitats in both richness and relative cover. Paired Student's t-tests showed that the woody component had significantly higher species richness (trees: $t = -6.06$, $p < 0.001$; tall woody shrubs: $t = -4.28$, $p < 0.001$) and relative cover (trees: $t = -2.28$, $p < 0.05$; tall woody shrubs: $t = -2.80$, $p < 0.01$) in slope habitats than in plains habitats (Table 2). Annual grasses showed the inverse trend, with significantly higher species richness ($t = 3.01$, $p < 0.01$) and relative cover ($t = 3.28$, $p < 0.01$) in plains habitats than in slope habitats. Of the forbs, annual forbs ($t = 2.83$, $p < 0.01$) had significantly higher species richness in plains habitats, while geophytes had significantly higher species richness in slope habitats ($t = -2.71$, $p < 0.05$). Low woody shrubs contributed the most to growth form diversity in both plains and slope habitats in both species richness (plains: 36.26%, slopes: 36.77%) and relative cover (plains: 50.61%, slopes: 45.67%). Annual forbs (12.97%), perennial grasses (12.24%), and perennial forbs (10.68%) had the next highest species richness values in plains habitats. In slope habitats, species richness values were relatively similar for perennial forbs (11.63%), perennial grasses (11.26%) and geophytes (11.19%). All succulent shrub growth forms (dwarf succulents, leaf- and stem-succulent shrubs) showed low representation in richness and relative cover for both plains and slope habitats, with no significant difference between the two habitat types. Other growth forms with low richness and relative cover were lianas, which were absent from plains habitats, and parasites, which were not present in any of the 1 m^2 plots, resulting in their relative cover values not being recorded.

Table 2: Percentage contribution to species richness (i.e. species count) and relative cover by each growth form to the total species richness within each habitat type (0.1 ha scale), and the results of a paired Student's t-test (95% confidence interval) on species richness and relative cover between habitat types for each growth form.

*Significance levels: n.s. = not significant; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

	Richness			***Relative cover***		
	Plains	**Slopes**	**Significance**	**Plains**	**Slopes**	**Significance**
Woody plants						
Trees	0.18	2.47	***	0.00	3.69	*
Tall woody shrubs	2.10	4.29	***	0.38	4.55	**
Low woody shrubs	36.26	36.77	n.s.	50.61	45.67	n.s.
Lianas	0.00	0.22	n.s.	0.00	0.67	n.s.
Succulent shrubs						
Leaf-succulent shrubs	5.30	5.23	n.s.	6.12	3.15	n.s.
Stem-succulent shrubs	1.19	1.24	n.s.	0.07	0.12	n.s.
Dwarf succulents	2.47	2.69	n.s.	0.38	0.68	n.s.
Grasses						
Annual grasses	5.11	2.25	**	10.50	1.20	**
Perennial grasses	12.24	11.26	n.s.	22.00	24.30	n.s.
Sedges	0.55	0.58	n.s.	0.50	0.10	n.s.
Forbs						
Geophytes	9.41	11.19	*	1.41	3.53	n.s.
Annual forbs	12.97	8.28	**	4.83	1.87	n.s.
Perennial forbs	10.68	11.63	n.s.	3.17	10.34	n.s.
Other						
Parasitic plants	0.18	0.36	n.s.	0.00	0.00	n.s.
Not classified	1.37	1.53	n.s.	0.04	0.23	n.s.

3.1.2 Habitat-level differences in soil and growth form dominance

Habitat-level differences in soil properties were observed in soil texture, with percent sand ($t = 2.17$, $p < 0.05$) and silt ($t = -2.92$, $p < 0.01$) of total soil texture showing significant differences between plains and slope habitats (Table 3). Soil chemistry was largely similar between the two habitat types, except for resistance ($t = 2.41$, $p < 0.05$) and percent ammonium ($t = -6.14$, $p < 0.001$), which were significantly different between the two habitat types.

Table 3: Mean ± standard deviation values of soil physical and chemical properties in plains and slope habitat types, and the results of paired Student's t-tests (95% confidence interval) on soil properties between habitat types.

*Significance levels: n.s. = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.*

		Plains	**Slopes**	**Significance**
Sand	(%)	81.20 ± 7.45	78.60 ± 6.55	*
Silt	(%)	7.93 ± 3.50	9.73 ± 3.05	**
Clay	(%)	10.87 ± 4.13	11.67 ± 3.76	n.s.
pH		5.93 ± 0.86	5.67 ± 0.59	n.s.
Resistance	Ω (ohm)	1167.67 ± 536.82	930.00 ± 512.58	*
[Ca]	$\mathrm{cmol_c/kg}$	6.10 ± 8.38	6.89 ± 7.39	n.s.
[Mg]	$\mathrm{cmol_c/kg}$	2.58 ± 1.19	3.09 ± 0.74	n.s.
[Na]	mg/kg	22.47 ± 6.84	27.33 ± 14.54	n.s.
[K]	mg/kg	201.60 ± 61.91	181.90 ± 64.38	n.s.
[P]	mg/kg	84.27 ± 68.03	76.57 ± 31.34	n.s.
Ammonium (NH_4)	%	0.04 ± 0.03	0.10 ± 0.05	***

Apart from the pattern of varying growth form dominance between habitat types, patterns of growth form dominance were observed across broad spatial scales (Fig. 5). The five dominant growth forms cumulatively comprised 92.3% of the total relative cover in plains habitats, and 84.6% in slope habitats. Overall, growth form dominance between plains and slope habitats was fairly similar, with specific growth forms having higher relative cover depending on geographic location along the longitudinal gradient. Low woody shrubs appeared to be the dominant growth form across the entire study area, in both habitat types. In the western regions (approximately 20°E), leaf succulent shrubs had slightly higher relative cover (approximately 25%) in slope habitats compared to other growth forms except low woody shrubs, with 75% relative cover. Further east (approximately 22°E - 24°E), perennial grasses were more abundant (25 – 60%) in slope habitats, while annual grasses were more abundant (25%) in plains habitats (around 23°E). In the east (approximately 25°E), dominance then switched from annual grasses to perennial grasses (> 50%) in plains habitats, with much lower relative cover in low woody shrubs than the more western longitudes of the study area, while perennial forbs increased in relative cover (> 25%) in slope habitats.

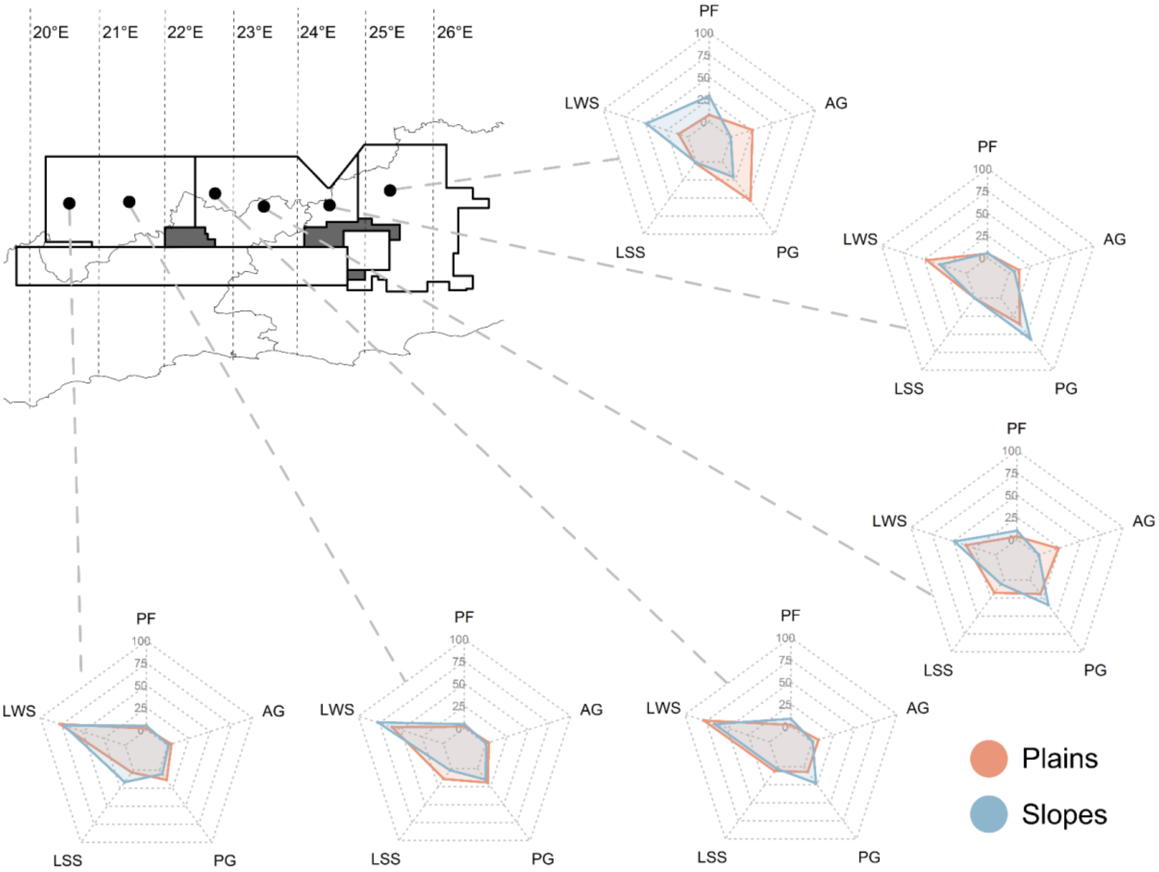

Figure 5: Radial plots showing relative percent cover of the five most abundant growth forms on slopes and plains (1 m^2 scale) across the study area summarised for all sites within one-degree longitudinal bands. **PF** = perennial forbs, **AG** = annual grasses, **PG** = perennial grasses, **LSS** = leaf-succulent shrubs, **LWS** = low woody shrubs.

3.1.3 Diversity patterns over space

3.1.3.1 Species accumulation at different scales

Total species richness at the 1 m^2 and 10 m^2 scale in the modified Whittaker plots was very similar for both plains and slope habitats, but species richness was higher on the slopes at the 100 m^2 and 1000 m^2 scale (Fig. 6).

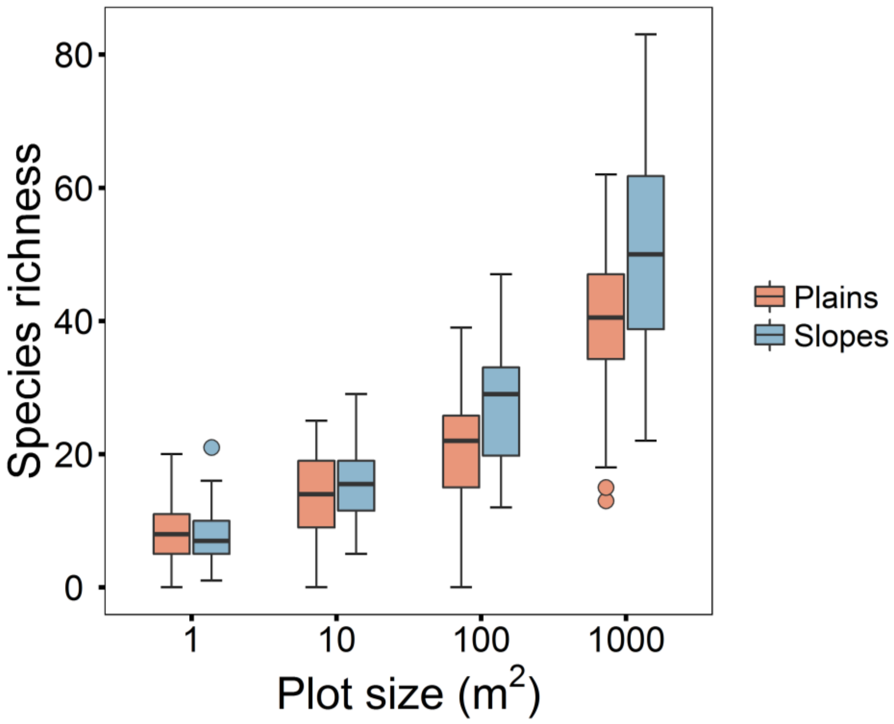

Figure 6: Species area curve boxplots showing overall species richness per plot size within modified Whittaker plots.

Species accumulation was consistently higher in slope habitats than in plains habitats across all sites (Fig. 7). The species accumulation curves diverge as number of sites increases, with significant difference between the slopes of the curves ($t = -17.31$, $p < 0.001$). The 95% confidence interval ribbons for the species accumulation curve with 999 permutations were too narrow to be seen on the plot, further indicating that the slopes were highly significantly different from each other.

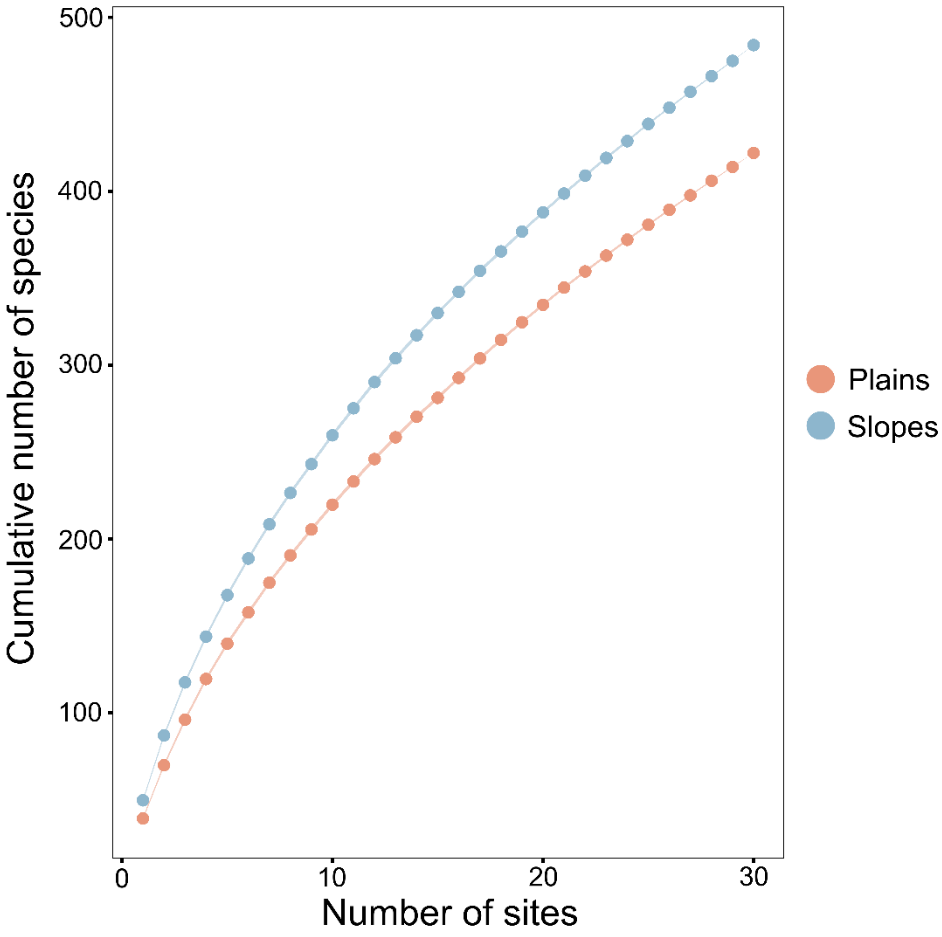

Figure 7: Species accumulation curves for plains and slope habitats with 95% confidence interval ribbons. Confidence interval ribbons indicate significant difference in slopes if ribbons do not overlap. Confidence interval ribbons are not visible on the graph because the slopes of the curves (*k* = 999 permutations) are highly significantly different from each other.

3.1.3.2 Additive diversity partitioning

Gamma (γ) diversity refers to the additive diversity at the 0.1 ha scale (i.e. within one plot), while β-diversity refers to additive diversity at finer sampling scales comprising the total γ-diversity, based on additive diversity partitioning theory (Crist et al., 2003; Veech et al., 2002). At the smallest sampling scale within a plot (α-diversity), species richness is very similar between plains and slope habitats (Fig. 8). This ratio increases at larger sampling scales (β_1, β_2, β_3 and γ), reaching up to 1.3 times more species on the slopes (n = 50.27) than on the plains (n = 39.70) at the γ-diversity level. Most of the diversity in both plains and slope habitats is derived from γ-diversity, at the 0.1 ha plot scale.

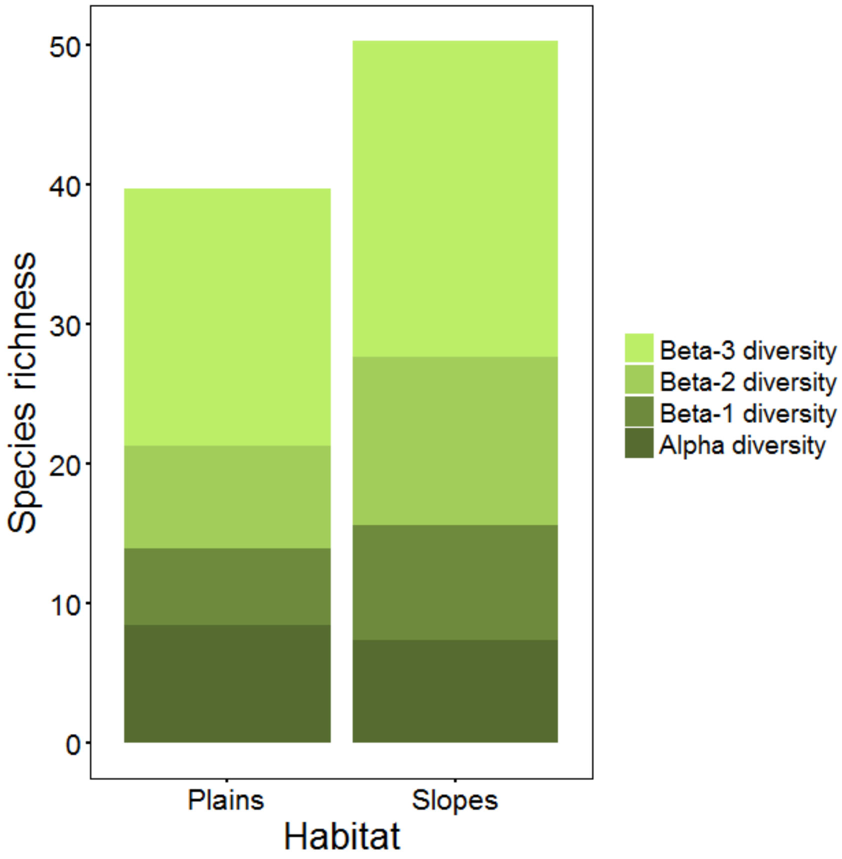

Figure 8: Additive diversity partitioning of species richness across five sampling scales.

3.1.4 Plant associations and their correspondence with the current vegetation map of South Africa

3.1.4.1 Plant associations on plains and slopes

The cluster analysis identified four clusters for plains habitats (P1, P2, P3 and P4), and three clusters for slope habitats (S1, S2 and S3). Clusters for plains habitats showed very little correspondence with their respective vegetation types, with considerable variation within and among the branches (Fig. 9A). Clusters for slope habitats, however, had less chaining and showed better correspondence with their respective vegetation types (Fig. 9B). Cluster S1 belonged largely to the Eastern Upper Karoo vegetation type, while cluster S2 belonged to the Western Upper Karoo vegetation type. Cluster S3, the outgroup, showed no clear correspondence with any one vegetation type (Fig. 9B).

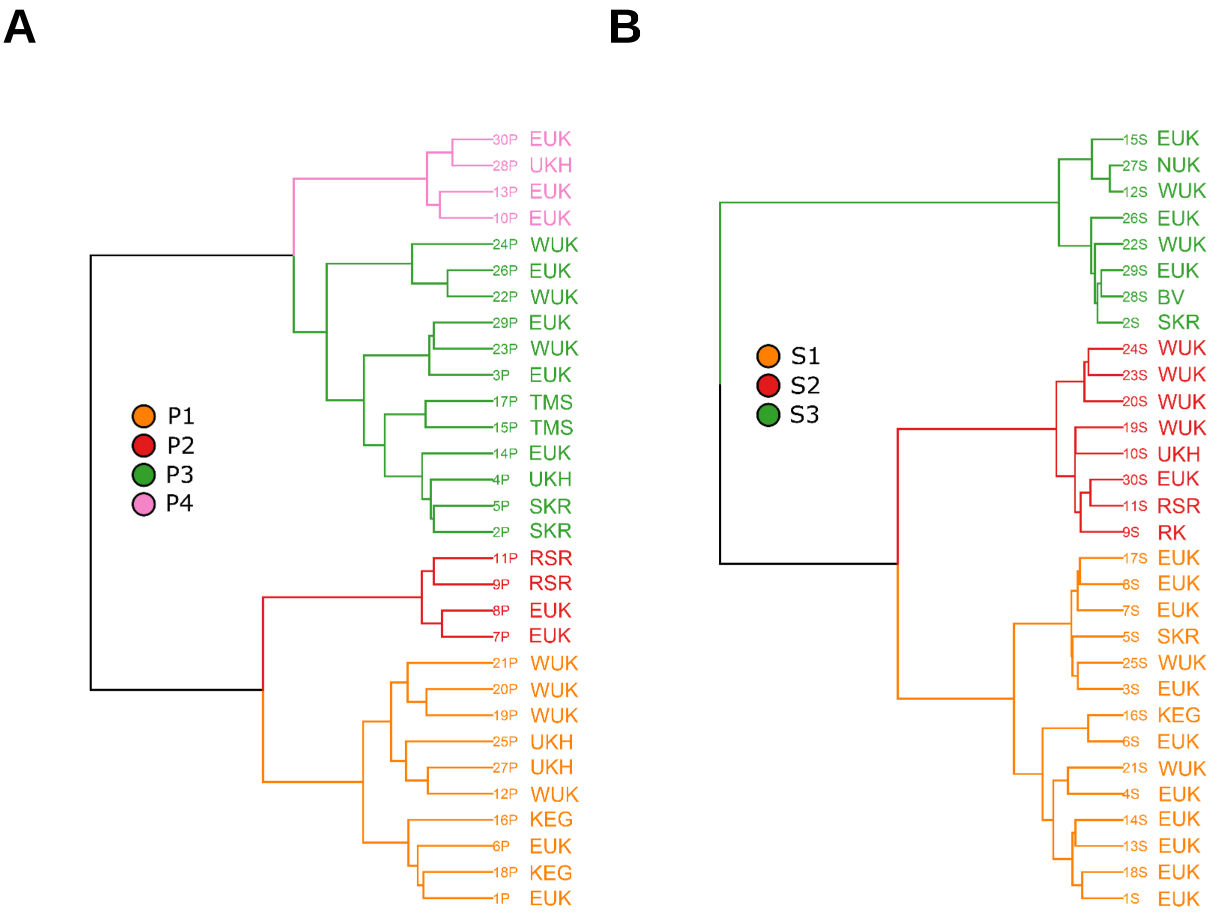

Figure 9: Cluster dendrograms showing cluster membership and vegetation type per sample site (1 m^2 scale) in **(A)** plains and **(B)** slope habitats. **BV** = Bushmanland Vloere, **EUK** = Eastern Upper Karoo, **KEG** = Karoo Escarpment Grassland, **NUK** = Northern Upper Karoo, **RK** = Roggeveld Karoo, **RSK** = Roggeveld Shale Renosterveld, **SKR** = Southern Karoo Riviere, **TMS** = Tarkastad Montane Shrubland, **UKH** = Upper Karoo Hardeveld, **WUK** = Western Upper Karoo.

At a larger scale, cluster correspondence improved when grouped by bioregion rather than vegetation type. Most sites, and therefore most clusters, fell within the Upper Karoo bioregion (Fig. 10). The remaining sites fell within one of Karoo Renosterveld, Dry Highveld Grassland, Sub-Escarpment Grassland, Inland Saline Vegetation or Trans-Escarpment Succulent Karoo. While clusters for plains appeared to be interspersed when plotted spatially (Fig. 10A), clusters for slopes appeared to aggregate according to their position along the longitudinal gradient. Cluster S2 comprised the far-west sites, S1 comprised the far-east sites, and S3 comprised the central sites (Fig. 10B).

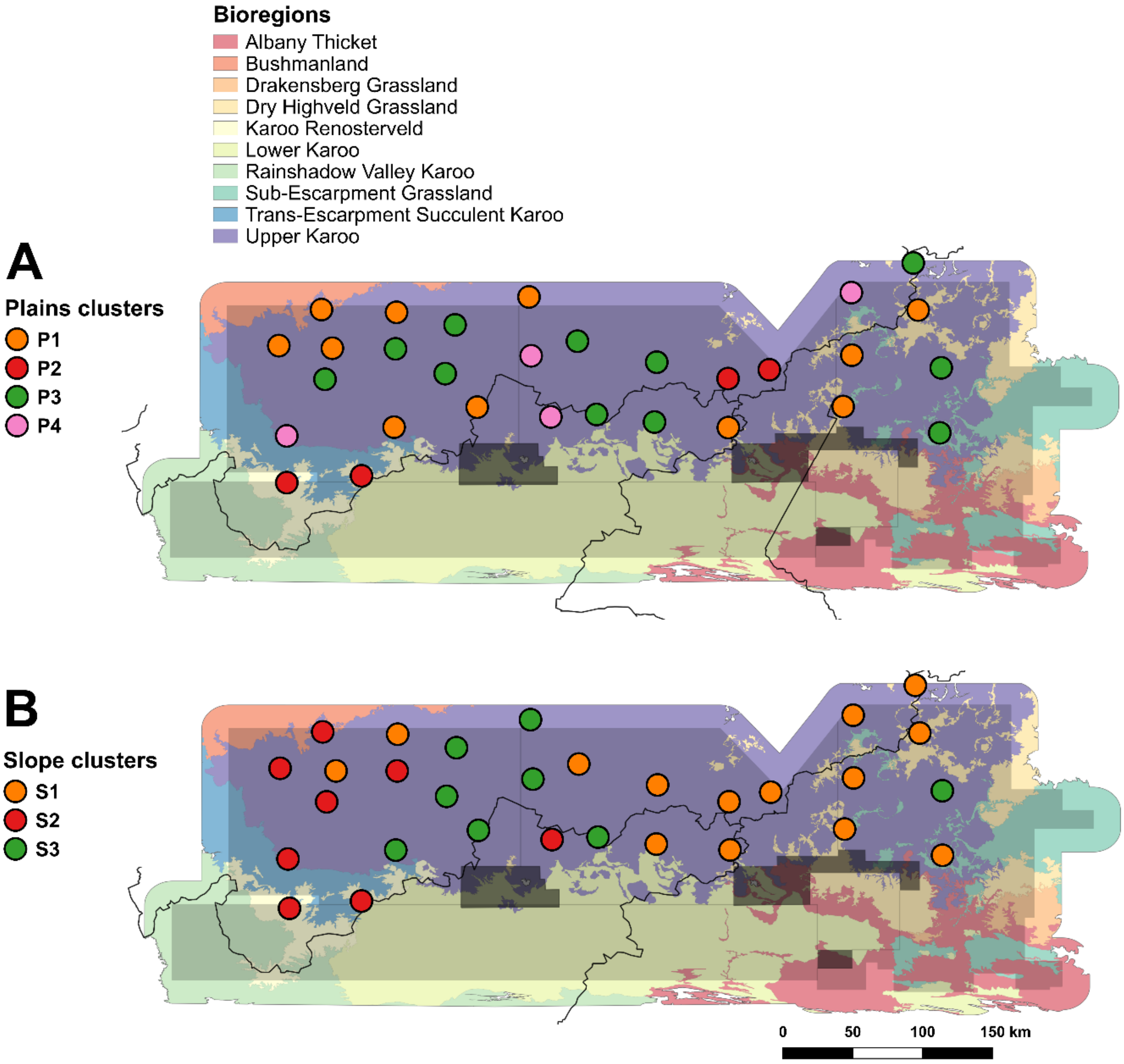

Figure 10: Map of the bioregions of South Africa, showing cluster membership as defined by agglomerative nesting and K-means clustering using Bray-Curtis distances for observed species in **(A)** plains habitats and **(B)** slope habitats (1 m^2 scale).

3.1.4.2 Growth form diversity patterns within clusters

Patterns of growth form diversity based on relative cover within clusters were mostly consistent with the general patterns observed within habitat types overall. Low woody shrubs contributed the most out of the five dominant growth forms to the total percent relative cover in all clusters for both plains and slope habitats. The relative cover of low woody shrubs was particularly high in cluster P2 (87%; Fig. 11A). Leaf-succulent shrubs were generally low in relative cover in all clusters for both plains and slope habitats, with the highest contribution being 16% in cluster P3, and the lowest contribution being < 1% in cluster P4 (Fig. 11A). Relative cover of perennial and annual grasses were higher in clusters for plains habitats (Fig. 11A), but was also comparatively high in clusters S1 and S3 for slope habitats (Fig. 11B). Perennial forbs, like leaf-succulent shrubs, were also generally low in relative cover in all clusters for both plains and slope habitats, except cluster S1 (15%; Fig. 11B).

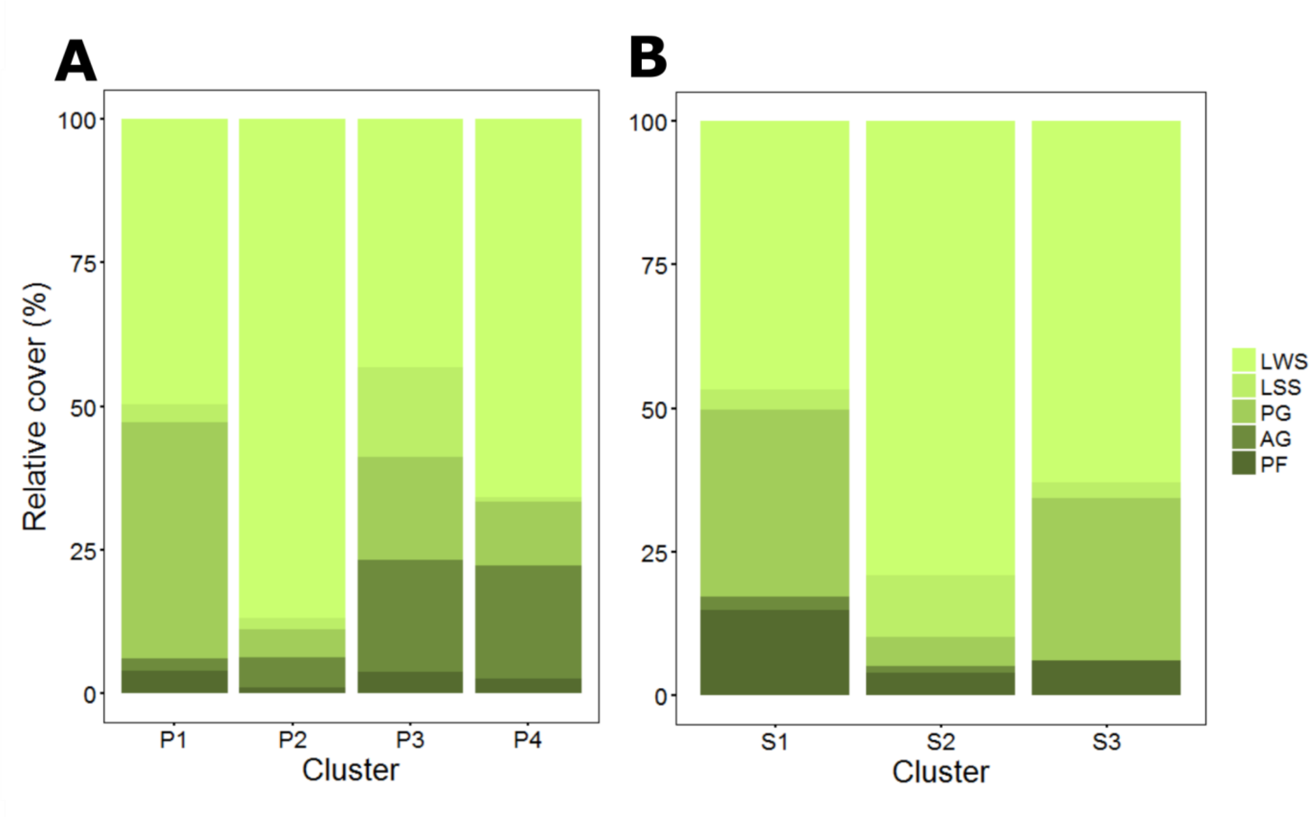

Figure 11: Relative percent cover of the five dominant growth forms in each cluster for **(A)** plains, and **(B)** slope habitats (1 m^2 scale). **LWS** = low woody shrub; **LSS** = leaf-succulent shrub; **PG** = perennial grass; **AG** = annual grass; **PF** = perennial forb.

3.2 Biophysical predictors of species richness and composition

3.2.1 Relating patterns of plant diversity and species composition to the environment

3.2.1.1 Plains habitats

NMDS ordination of 30 samples on plains (n = 181 species) showed some separation of plant associations when grouped by cluster membership (cluster P3; Fig. 12B, 12C). A biplot overlaid with environmental and climatic variables indicated a strong moisture and soil fertility gradient along Axis 1 (Fig. 12A). Mean annual precipitation (tau = 0.65) and soil fertility (tau = 0.58) appeared to strongly influence the ordination of sites, and had strong positive correlations with Axis 1, suggesting the moist end of the gradient. Percent NH_4 and soil texture also appeared to describe the moist end of the gradient, with intermediate Kendall correlation coefficient values for Axis 1 (Table 4). Water stress (tau = -0.65), mean annual A-pan evaporation (tau = -0.67) and, to a lesser extent, maximum temperature of the hottest month (tau = -0.52), were negatively correlated with Axis 1 and influenced the ordination in the opposite direction to the moist end, suggesting the arid end of the gradient (Table 4).

Axis 3 indicated a weak temperature gradient, with number of frost days and altitude influencing the ordination in one direction, and mean annual temperature and minimum temperature of the coldest month influencing it in the other direction (Fig. 12B, 12C). Cluster P3 appeared to separate from the other clusters along Axis 3, suggesting that P3 is more sensitive to variations in temperature than to variations in moisture (Fig. 12B, 12C). Axis 2 (Fig. 12A, 12C) appeared to have little effect on the ordination of sample sites in species space, which suggested that there may be some other variable unaccounted for.

3.2.1.2 Slope habitats

NMDS ordination of 30 samples on slopes (n = 225 species) showed some separation of plant associations when grouped by cluster membership (Fig. 12D-F). As observed in the biplots for plains, Axis 1 for slope habitats suggested a moisture and soil fertility gradient, with mean annual precipitation and soil fertility indicating the moist, fertile end of the gradient, and water stress, mean annual A-pan evaporation, and salinity (Na) indicating the arid, saline end of the gradient (Fig. 12D, 12E). The distinction between plant associations was clearest in a plot of Axis 1 vs Axis 3 (Fig. 12E), which showed a clear separation of cluster S1, S2 and S3 along the apparent moisture gradient.

Axis 2 suggests a clear temperature gradient, with mean annual temperature and maximum temperature of the hottest month influencing the ordination in one direction, and altitude and number of frost days influencing the ordination in the opposite direction (Fig. 12D, 12F). The correlations of climatic and biophysical variables with the axes were, however, not strong (Table 4). Axis 3 (Fig. 12E, 12F) appeared to have little effect on the ordination of sample sites in species space, which suggested that there may be some other unknown variable influencing community composition that has not been accounted for.

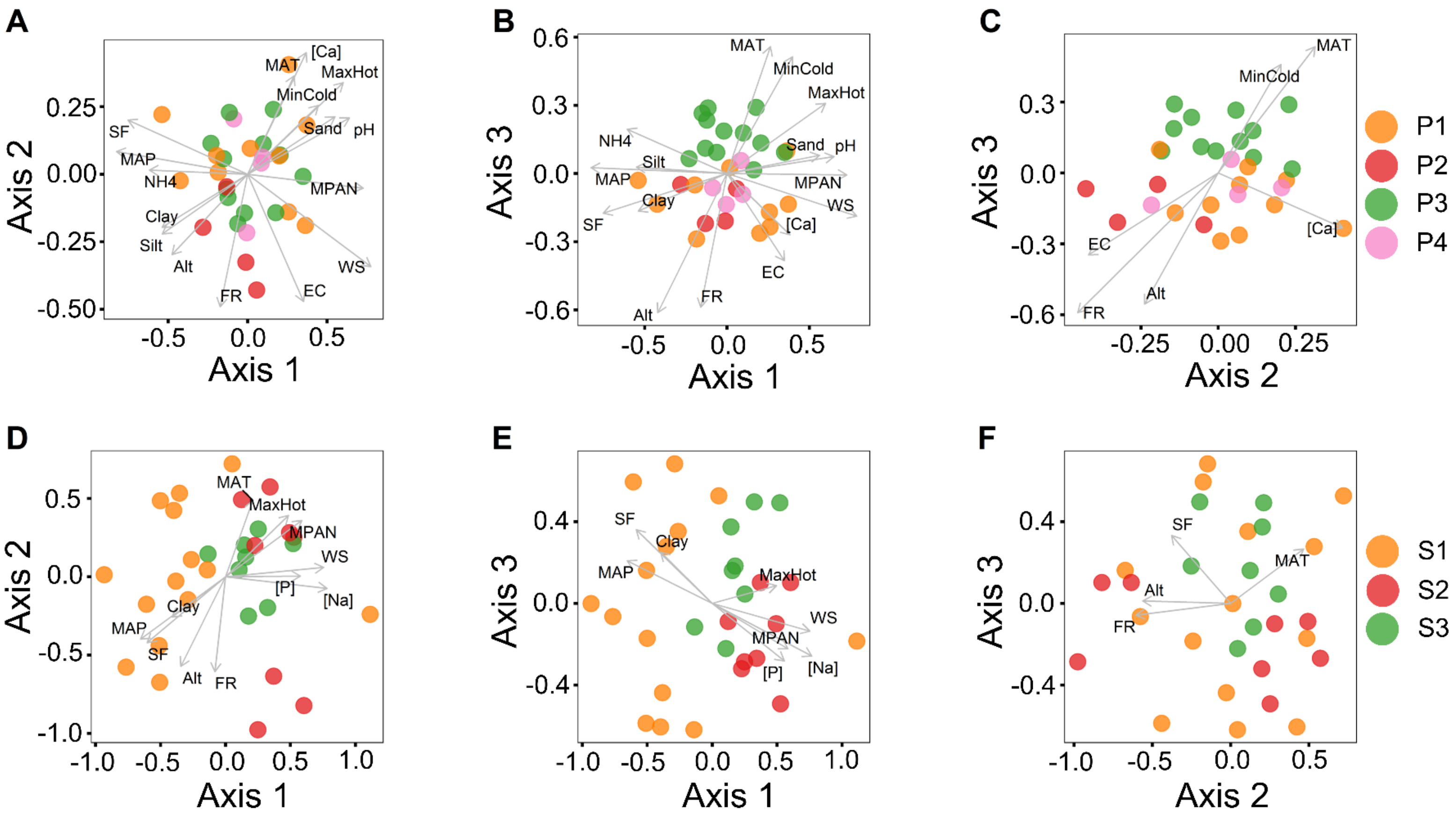

Figure 12: NMDS biplots of 30 sample sites (1 m^2 scale) in plains (**A - C**) and slope (**D - F**) habitats, grouped by cluster membership. Only vectors with $p < 0.05$ are shown. **MAP** = mean annual precipitation, **MPAN** = mean annual A-pan evaporation, **WS** = water stress during hottest month, **MAT** = mean annual temperature, **MaxHot** = maximum temperature during hottest month, **MinCold** = minimum temperature during coldest month, **FR** = mean annual number of days with heavy frost, **SF** = soil fertility, **Alt** = altitude, **Sand** = percent sand, **Silt** = percent silt, **Clay** = percent clay, **EC** = electroconductivity, **[Ca]** = calcium concentration, **[Mg]** = magnesium concentration**, [Na]** = sodium concentration, **[K]** = potassium concentration, **[P]** = phosphorus concentration, **NH4** = percent ammonium (NH_4).

Table 4: Kendall correlations (tau) of climatic and biophysical variables with the axes for plains and slope habitats. Correlation coefficients > 0.5 appear in bold font.

	Plains			***Slopes***		
Axis	**1**	**2**	**3**	**1**	**2**	**3**
Climatic						
Mean annual precipitation	**0.65**	0.01	0.03	0.39	0.11	0.33
Mean annual pan evaporation	**-0.67**	0.02	-0.01	-0.41	0.02	-0.35
Water stress during hottest month (January)	**-0.65**	-0.17	-0.02	**-0.53**	0.04	-0.14
Mean annual temperature	-0.25	0.30	-0.15	-0.18	0.08	**-0.53**
Maximum temperature of the hottest month (January)	-0.52	0.18	-0.01	-0.37	0.12	-0.43
Minimum temperature of the coldest month (July)	-0.23	0.21	-0.25	-0.23	0.00	-0.34
Mean annual number of days with heavy frost	0.08	-0.38	0.19	0.11	0.04	0.48
Biophysical						
Soil fertility	**0.58**	-0.08	0.20	0.35	0.14	0.38
Elevation	0.27	-0.26	0.26	0.27	0.09	0.38
Sand	**-0.55**	0.14	0.12	-0.30	-0.21	-0.24
Silt	**0.54**	-0.10	-0.15	0.16	0.15	0.25
Clay	**0.51**	-0.18	-0.08	0.32	0.23	0.24
Resistance (electroconductivity)	-0.38	-0.17	0.09	-0.16	0.05	-0.05
pH	-0.49	0.07	-0.12	-0.13	0.14	-0.23
[Ca]	-0.17	-0.08	0.03	0.22	0.21	0.08
[Mg]	-0.08	0.12	0.04	0.01	0.15	0.21
[Na]	-0.04	-0.01	-0.21	-0.49	-0.07	0.02
[K]	-0.17	-0.25	-0.01	0.26	0.37	-0.04
[P]	-0.25	-0.10	-0.18	-0.28	0.06	-0.13
Ammonium (NH_4)	**0.52**	-0.07	-0.06	0.39	0.18	0.03

3.2.2 Attributing drivers of species richness and growth form diversity

Multiple regression models with the lowest exact AIC values as determined by forward and backward stepwise selection were chosen as the final models (Appendix 1). The final models had varying numbers of predictor variables for each of the six response variables (Fig. 13).

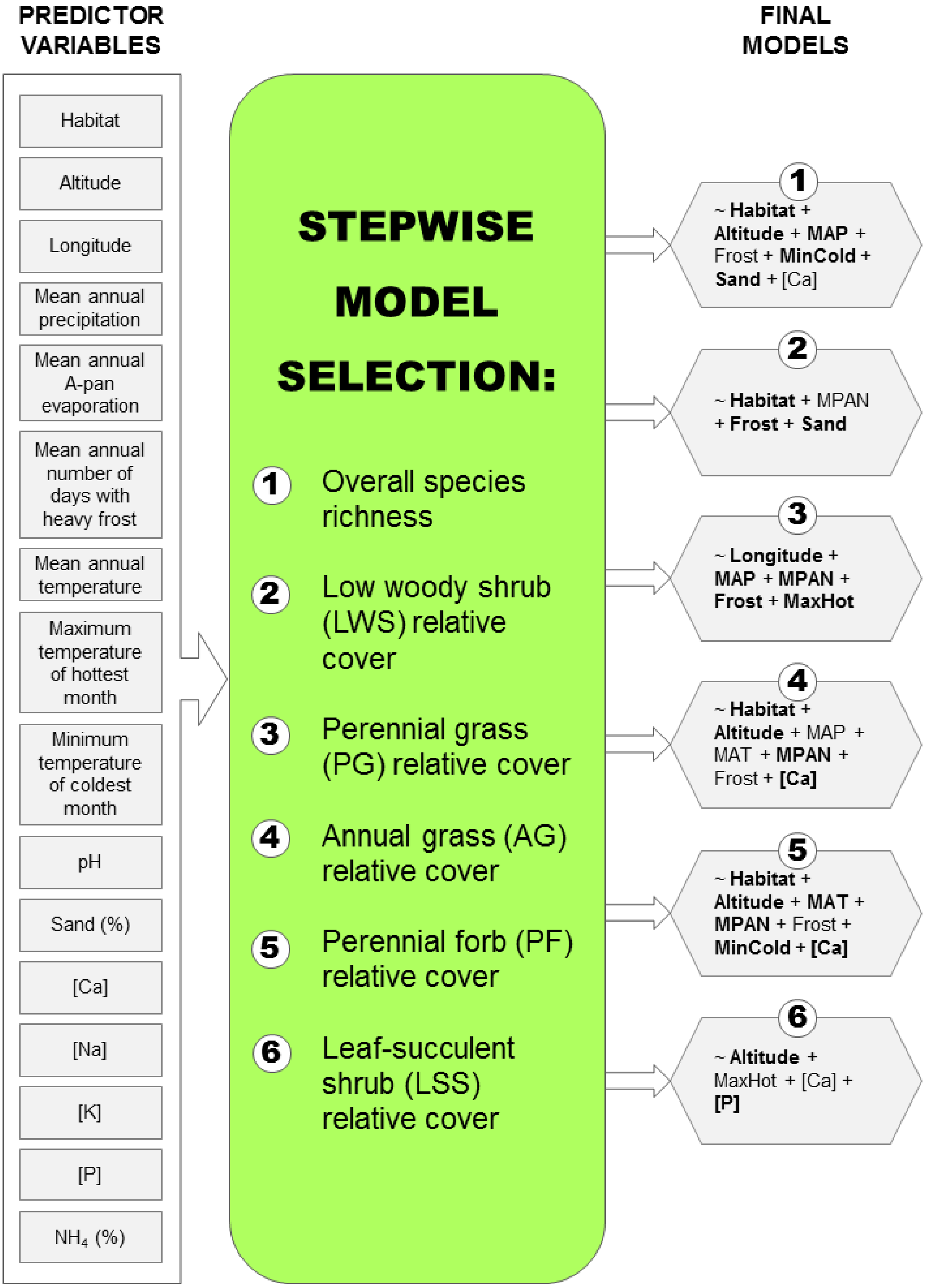

Figure 13: Final model selection for overall species richness and relative cover of the five dominant growth forms based on a maximal model including 16 potential predictor variables. Significant predictor variables for the final models appear in bold font.

3.2.2.1 Overall species richness

The final model for overall species richness included seven predictor variables ($F_{7, 52} = 10.27$, adjusted $R^2 = 0.52$) (Fig. 13). Overall species richness was significantly predicted by habitat type ($t = 4.70$, $p < 0.001$), altitude ($t = -3.42$, $p < 0.01$), MAP ($t = 7.00$, $p < 0.001$), minimum temperature of the coldest month ($t = -2.31$, $p < 0.05$), as well as percent sand of total soil texture ($t = 2.11$, $p < 0.05$) (Table 5). Overall species richness was positively correlated with MAP and percent sand, and negatively correlated with altitude and minimum temperature of the coldest month (Fig. 14).

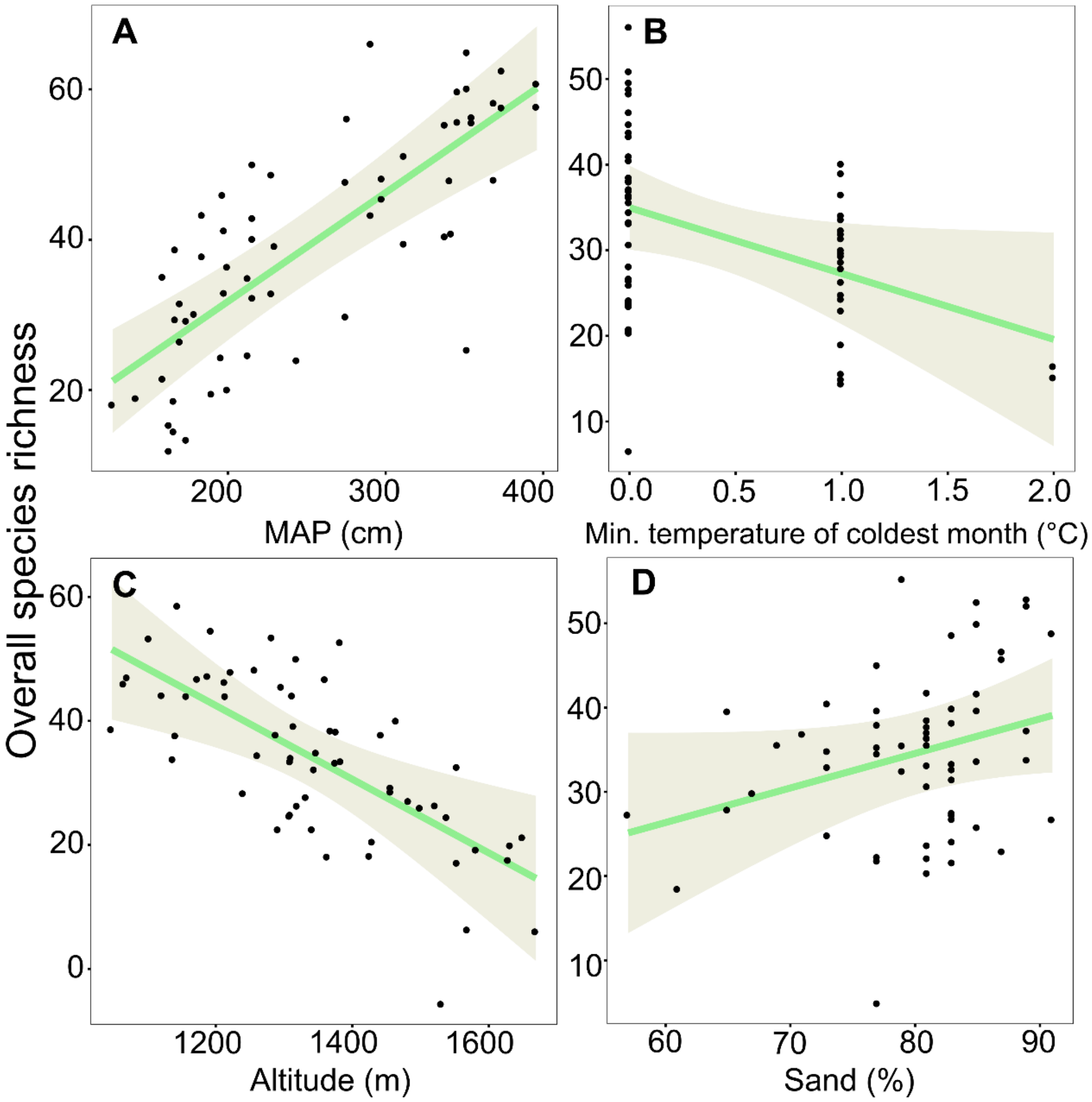

Figure 14: Scatterplots for multiple linear regression of **(A)** MAP, **(B)** minimum temperature of the coldest month, **(C)** altitude, and **(D)** percent sand, the four variables which significantly predicted overall species richness in plains and slope habitats (0.1 ha scale).

3.2.2.2 *Low woody shrubs*

The final model for relative cover of low woody shrubs included four predictor variables ($F_{4,\ 55}$ = 6.855, adjusted R^2 = 0.28) (Fig. 13). Low woody shrub relative cover was significantly predicted by habitat type (t = -2.31, $p < 0.05$), mean annual number of days with heavy frost (t = 3.72, $p < 0.001$), and percent sand of total soil texture (t = -2.31, $p < 0.05$) (Table 5). Low woody shrub relative cover was positively correlated with the mean annual number of frost days, and negatively correlated with percent sand (Fig. 15).

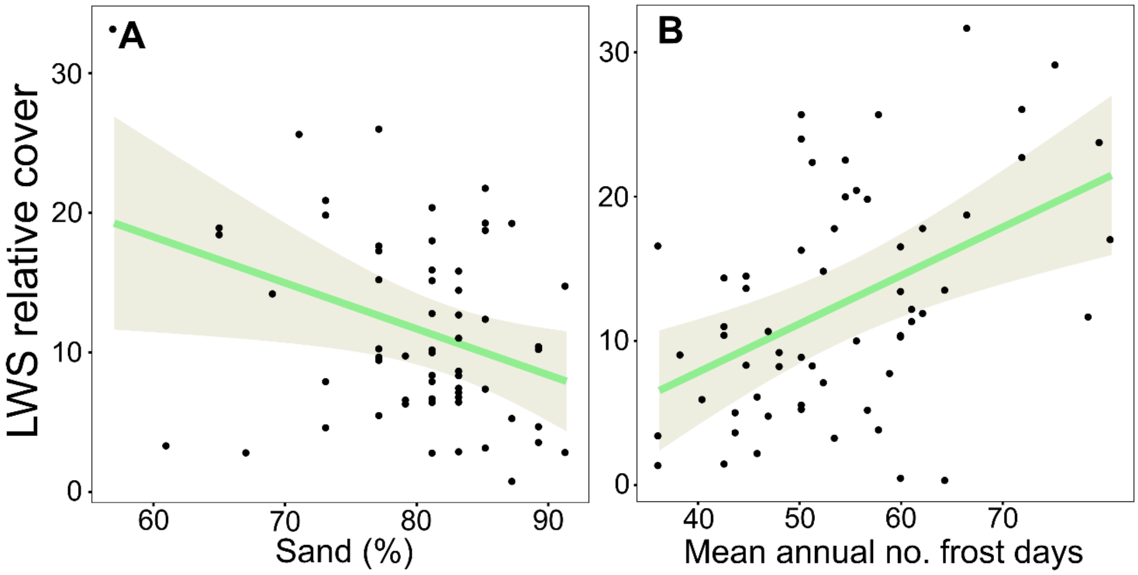

Figure 15: Scatterplots for multiple linear regression of **(A)** mean annual number of frost days, and **(B)** percent sand, the two variables which significantly predicted low woody shrub relative cover in plains and slope habitats (1 m^2 scale).

3.2.2.3 Perennial grasses

The final model for relative cover of perennial grasses included five predictor variables ($F_{5,\ 54}$ = 19.44, adjusted R^2 = 0.61) (Fig. 13). Longitude was a significant predictor of perennial grass abundance ($t = 5.71$, $p < 0.001$) exclusively (Table 5), and was not included in any other final models (Fig. 13). Perennial grass relative cover was also significantly predicted by MAP ($t = 3.51$, $p < 0.001$), MPAN ($t = 5.30$, $p < 0.001$), mean annual number of days with heavy frost ($t = 3.87$, $p < 0.001$), and maximum temperature of the hottest month ($t = 2.88$, $p < 0.01$) (Table 5). Perennial grass relative cover was positively correlated with all five predictor variables in the final model (Fig. 16).

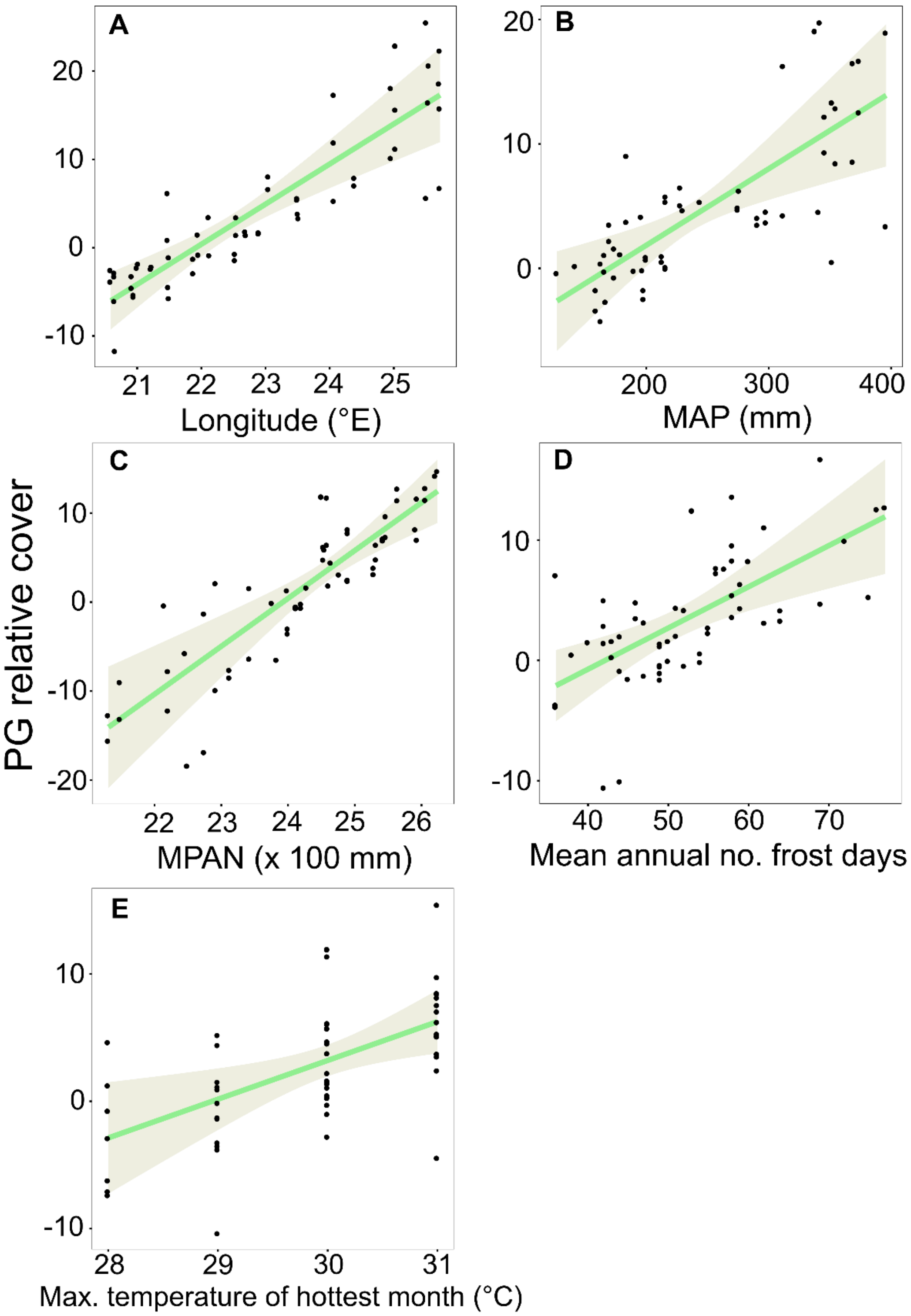

Figure 16: Scatterplots for multiple linear regression of **(A)** longitude, **(B)** MAP, **(C)** MPAN, **(D)** mean annual number of frost days, and **(E)** maximum temperature of the hottest month, the five variables which significantly predicted perennial grass relative cover in plains and slope habitats (1 m^2 scale).

3.2.2.4 Annual grasses

The final model for relative cover of annual grasses included seven predictor variables ($F_{7, 52} = 9.42$, adjusted $R^2 = 0.50$) (Fig. 13). Habitat type was a significant predictor of the relative cover of annual grasses ($t = -3.25$, $p < 0.01$), along with altitude ($t = -3.34$, $p < 0.01$), MPAN ($t = -4.62$, $p < 0.001$) and soil concentration of calcium ($t = -3.05$, $p < 0.01$) (Table 5). Annual grass relative cover was negatively correlated with all three significant predictor variables (Fig. 17).

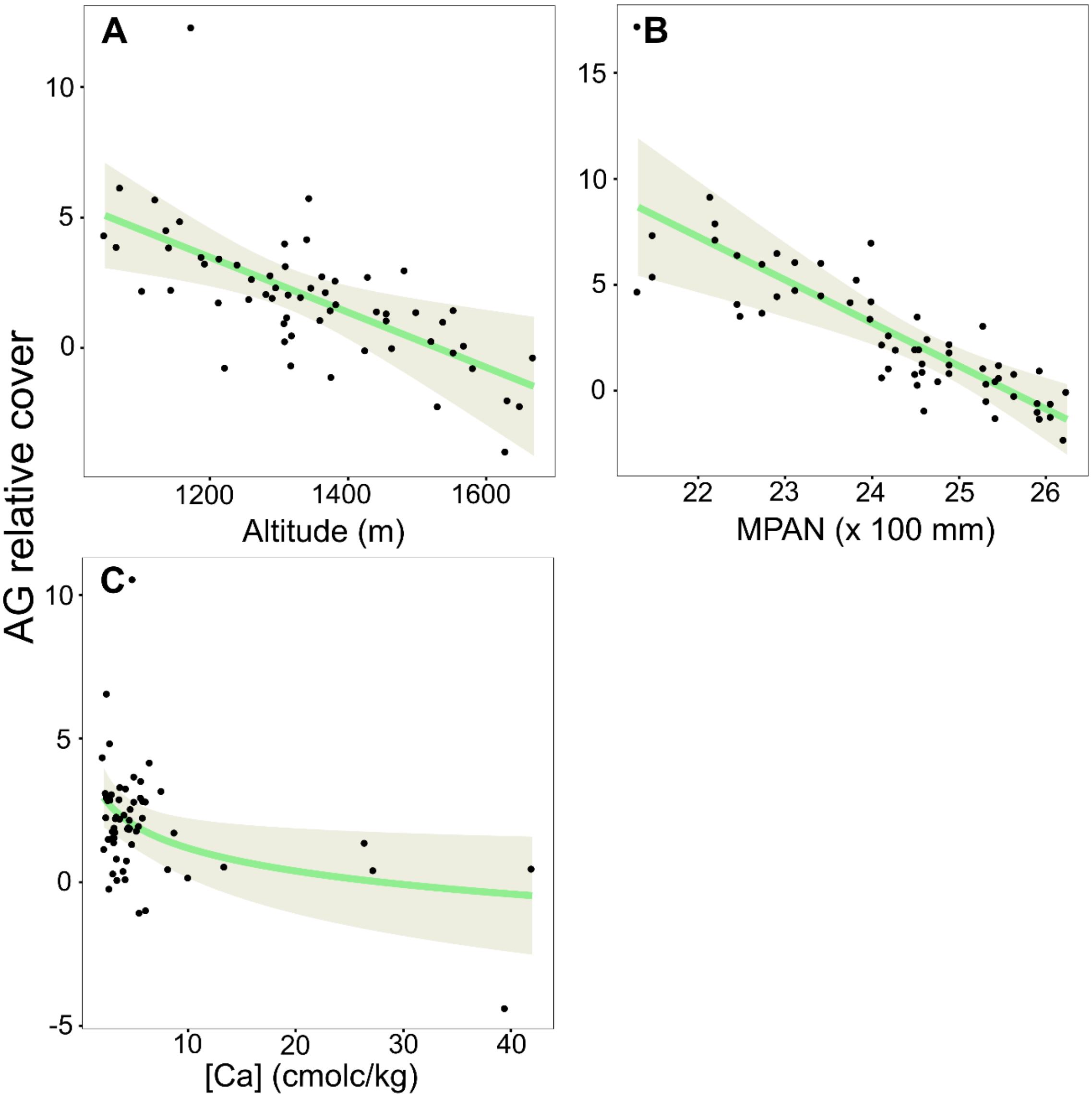

Figure 17: Scatterplots for multiple linear regression of **(A)** altitude, **(B)** MAN, and **(C)** calcium concentration, the three variables which significantly predicted annual grass relative cover in plains and slope habitats (1 m^2 scale).

3.2.2.5 Perennial forbs

The final model for relative cover of perennial forbs included seven predictor variables ($F_{7,\ 52}$ = 8.05, adjusted R^2 = 0.46) (Fig. 13). Perennial forb relative cover was significantly predicted by habitat type (t = 2.72, $p < 0.01$), altitude (t = -3.15, $p < 0.01$), MPAN (t = -5.37, $p < 0.001$), as well as soil concentration of calcium (t = 3.78, $p < 0.001$). Of the temperature-related variables, mean annual temperature and minimum temperature in the coldest month were both significant predictors of the relative cover of perennial forbs (MAT: t = 2.12, $p < 0.05$; MinCold: t = -3.19, $p < 0.01$) (Table 5). Perennial forb relative cover was positively correlated with MAT and soil calcium concentration, and negatively correlated with altitude, MPAN, and minimum temperature of the coldest month (Fig. 18).

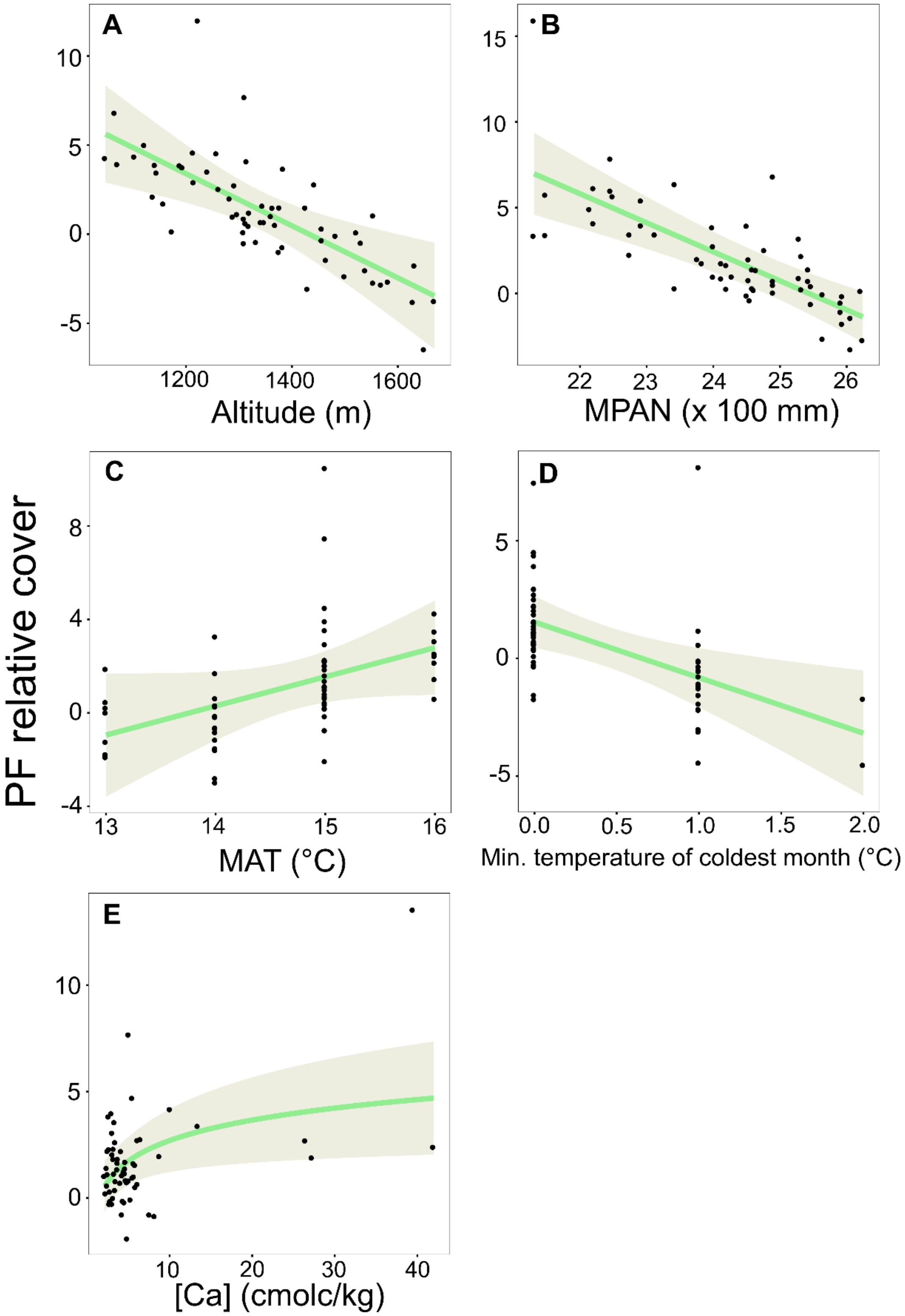

Figure 18: Scatterplots for multiple linear regression of **(A)** altitude, **(B)** MPAN, **(C)** MAT, **(D)** minimum temperature of the coldest month, and **(E)** calcium concentration, the five variables which significantly predicted perennial forb relative cover in plains and slope habitats (1 m^2 scale).

3.2.2.6 Leaf-succulent shrubs

The final model for relative cover of leaf-succulent shrubs included four predictor variables ($F_{4, 55}$ = 4.87, adjusted R^2 = 0.21) (Fig. 13). Of these four predictors, only two significantly predicted LSS abundance: altitude (t = -2.64, $p < 0.05$) and soil concentration of phosphorus (t = 3.33, $p < 0.01$), the latter of which was not included in any other final model (Table 5). Leaf-succulent shrub relative cover correlated negatively with altitude, but positively with soil phosphorus concentration (Fig. 19).

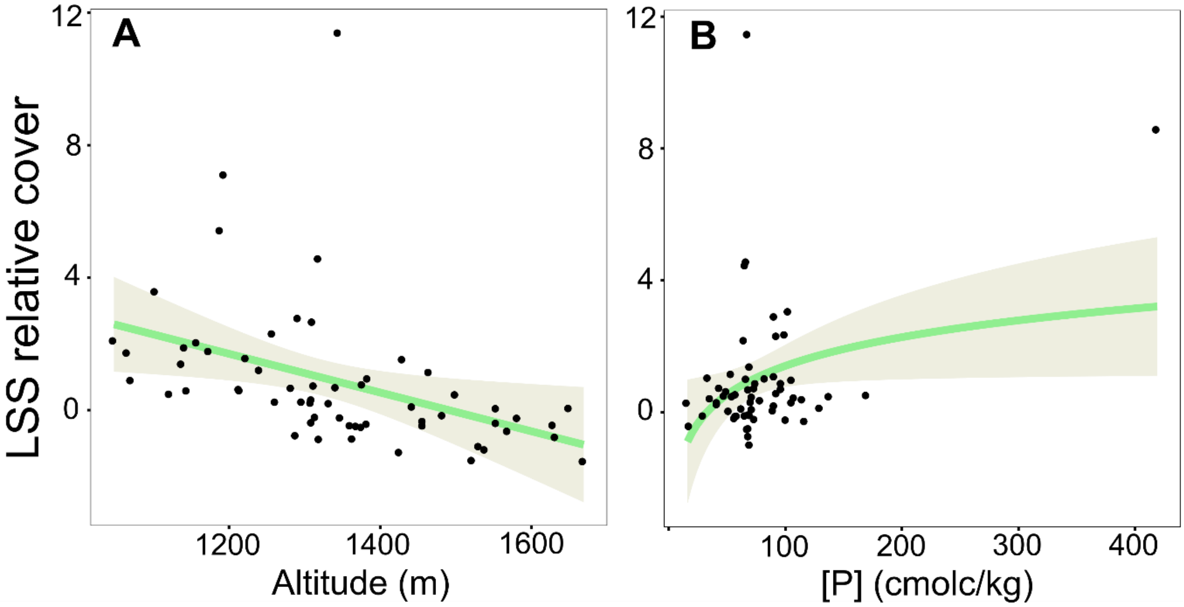

Figure 19: Scatterplots for multiple linear regression of **(A)** altitude, and **(B)** phosphorus concentrations, the two variables which significantly predicted leaf-succulent shrub relative cover in plains and slope habitats (1 m^2 scale).

Table 5: Significance of linear model outputs for overall species richness and relative cover of the five dominant growth forms (1 m^2 scale). Variables which were not included in the final models are marked by '*N/A*'.

*Significance levels: n.s. = not significant; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

	Overall species richness	**Low woody shrubs**	**Perennial grasses**	**Annual grasses**	**Perennial forbs**	**Leaf-succulent shrubs**
Habitat	***	*	N/A	**	**	N/A
Altitude	**	N/A	N/A	**	**	**
Longitude	N/A	N/A	***	N/A	N/A	N/A
Mean annual precipitation	***	N/A	**	n.s.	N/A	N/A
Mean annual A-pan evaporation	N/A	n.s.	***	***	***	N/A
Number of days with heavy frost	n.s.	***	***	n.s.	n.s.	N/A
Mean annual temperature	N/A	N/A	N/A	n.s.	*	N/A
Maximum temperature of hottest month	N/A	N/A	**	N/A	N/A	n.s.
Minimum temperature of coldest month	*	N/A	N/A	N/A	**	N/A
pH	N/A	N/A	N/A	N/A	N/A	N/A
Percent sand	*	*	N/A	N/A	N/A	N/A
[Ca]	n.s.	N/A	N/A	**	***	n.s.
[Na]	N/A	N/A	N/A	N/A	N/A	N/A
[K]	N/A	N/A	N/A	N/A	N/A	N/A
[P]	N/A	N/A	N/A	N/A	N/A	**
Percent NH_4	N/A	N/A	N/A	N/A	N/A	N/A

3.2.3 Relating differences in species richness and growth form diversity to habitat type

Multiple regression models with the lowest exact AIC values as determined by forward and backward stepwise selection were chosen as the final models (Appendix 2). As before, final models varied in the number of predictor variables for each of the six response variables (Fig. 20).

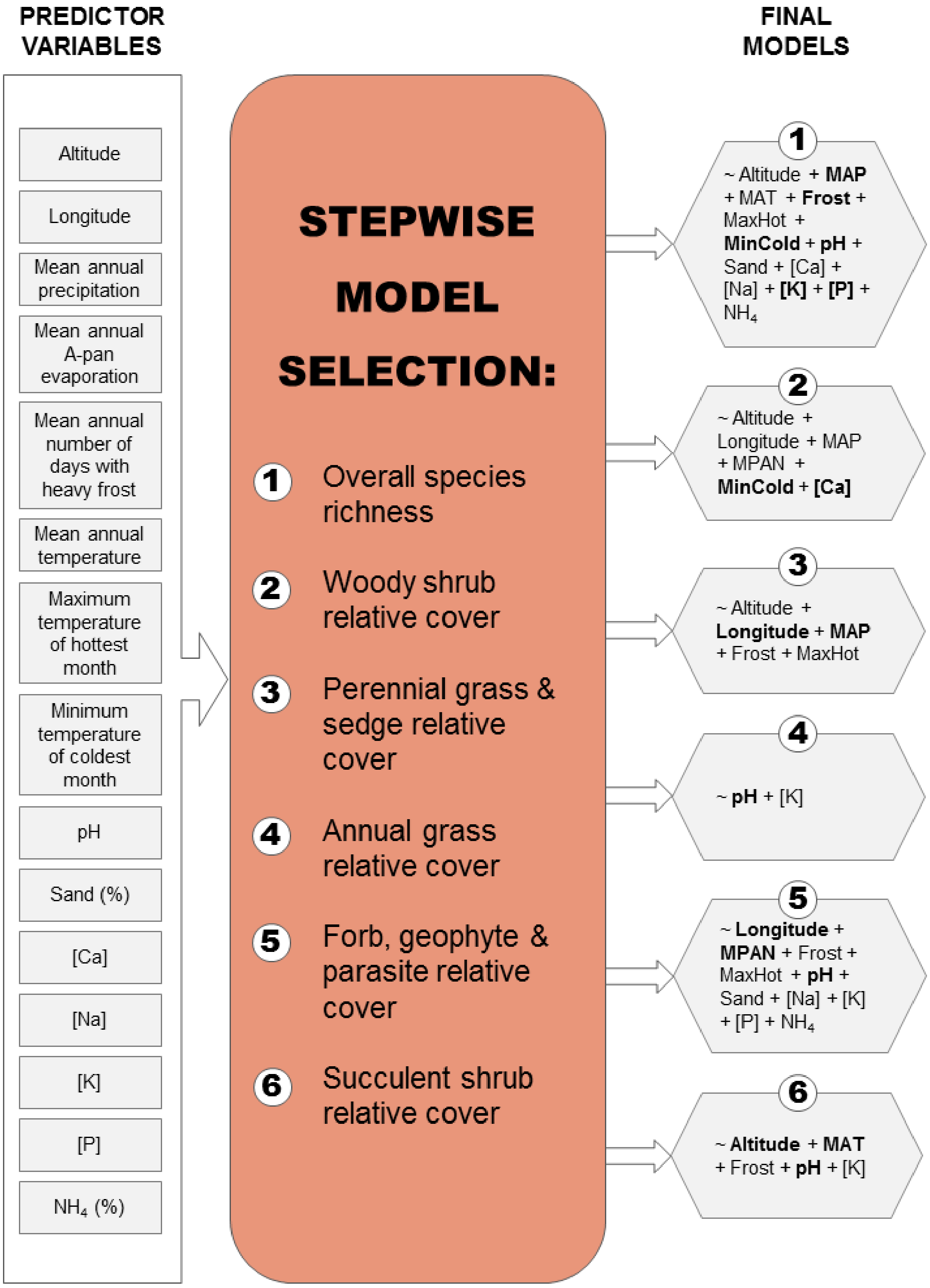

Figure 20: Final model selection for Bray-Curtis distances between plains and slopes overall and for five key plant functional types (PFTs) based on a maximal model including 15 potential predictor variables. Significant predictor variables for the final models appear in bold font.

3.2.3.1 Overall dissimilarity

The final model for overall dissimilarity between plains and slope habitats included 13 predictor variables ($F_{13, 16} = 3.493$, adjusted $R^2 = 0.53$) (Fig. 20). Of these, six variables significantly predicted overall dissimilarity. Among the climate-related predictor variables were MAP ($t = -3.87$, $p < 0.01$), mean annual number of frost days ($t = -3.27$, $p < 0.01$), and minimum temperature of the coldest month ($t = 2.27$, $p < 0.05$). Among the soil-related variables were pH ($t = -2.21$, $p < 0.05$), and soil concentrations of potassium ($t = 3.55$, $p < 0.01$) and phosphorus ($t = -3.05$, $p < 0.01$) (Table 6). Dissimilarity in overall species richness between plains and slope habitats was positively correlated with minimum temperature of the coldest month and soil concentration of potassium, and negatively correlated with MAP, mean annual number of frost days, pH, and soil concentration of phosphorus (Fig. 21).

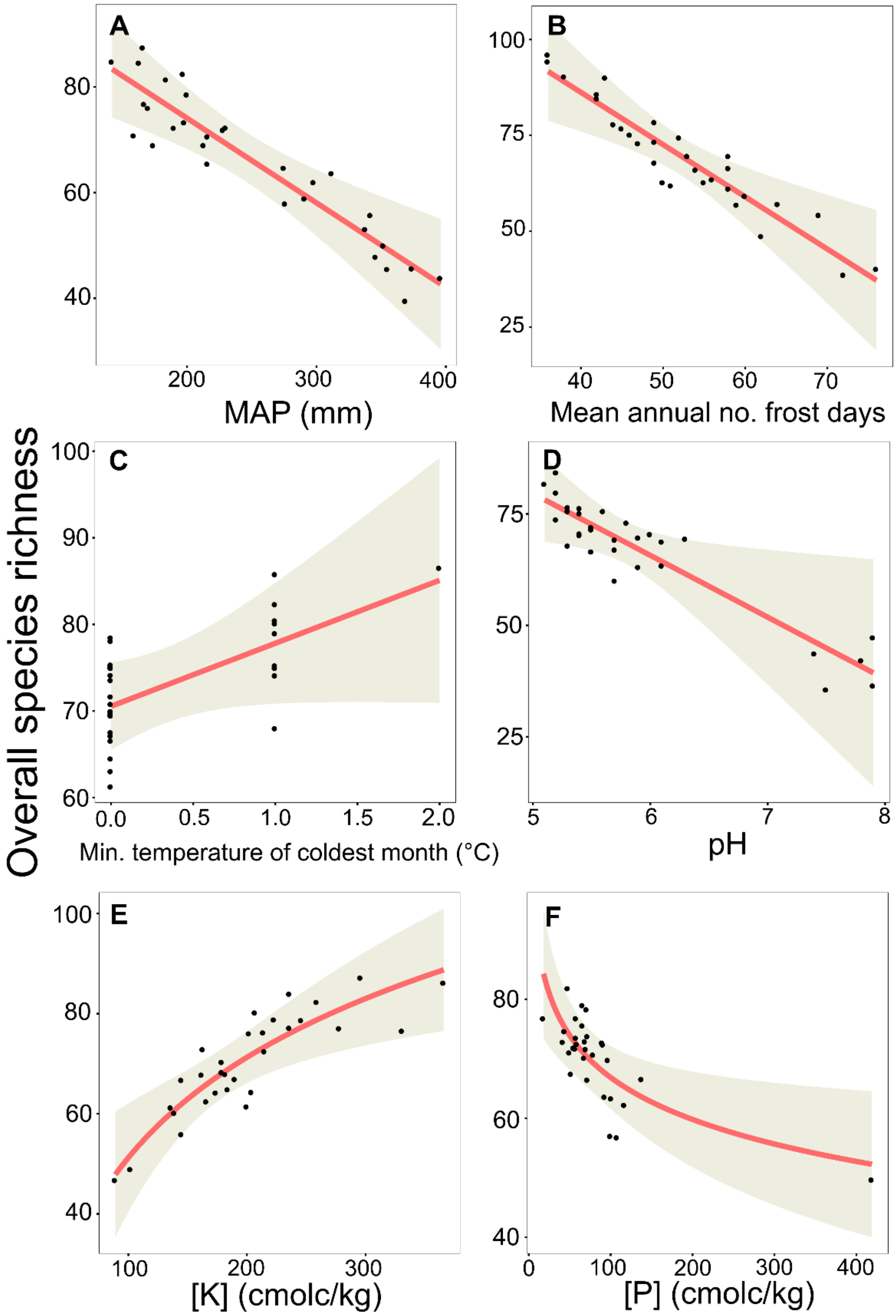

Figure 21: Scatterplots for multiple linear regression of **(A)** MAP, **(B)** mean annual number of frost days, **(C)** minimum temperature of the coldest month, **(D)** pH, and **(E)** potassium and **(F)** phosphorus concentrations, the six variables which significantly predicted Bray-Curtis distances in overall species richness between plains and slopes (0.1 ha scale).

3.2.3.2 Woody shrubs

The final model for dissimilarity in relative cover of woody shrubs (including lianas, low woody shrubs, tall woody shrubs, and trees) between plains and slope habitats included six predictor variables ($F_{6, 23} = 8.408$, adjusted $R^2 = 0.61$) (Fig. 20). Minimum temperature of the coldest month ($t = 2.87$, $p < 0.01$) and soil concentrations of calcium ($t = 2.65$, $p < 0.05$) were the only significant predictors (Table 6). Dissimilarity in woody shrub relative cover between plains and slope habitats was positively correlated with minimum temperature of the coldest month and soil concentration of calcium (Fig. 22).

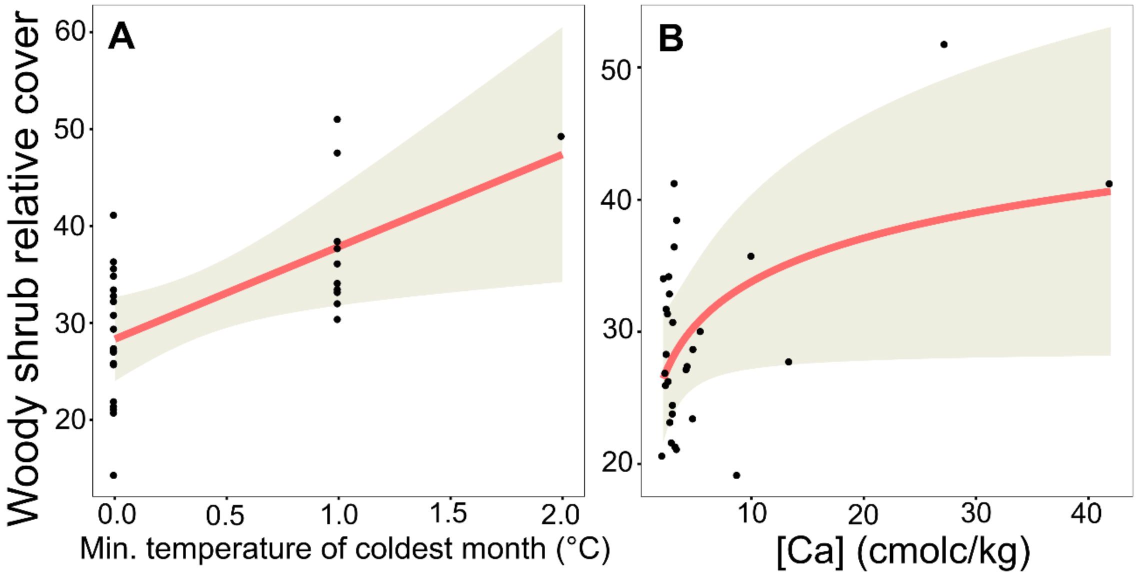

Figure 22: Scatterplots for multiple linear regression of **(A)** minimum temperature of the coldest month and **(B)** calcium concentration, the two variables which significantly predicted Bray-Curtis distances in woody shrub relative cover between plains and slopes (1 m^2 scale).

3.2.3.3 Perennial grasses and sedges

The final model for dissimilarity in perennial grass and sedge relative cover between plains and slope habitats included five predictor variables ($F_{5,\,24} = 5.431$, adjusted $R^2 = 0.43$) (Fig. 20). Longitude ($t = 2.99$, $p < 0.01$) and MAP ($t = -4.02$, $p < 0.001$) were the only significant predictors (Table 6). Dissimilarity in perennial grass and sedge relative cover between plains and slope habitats was positively correlated with longitude and negatively correlated with MAP (Fig. 23).

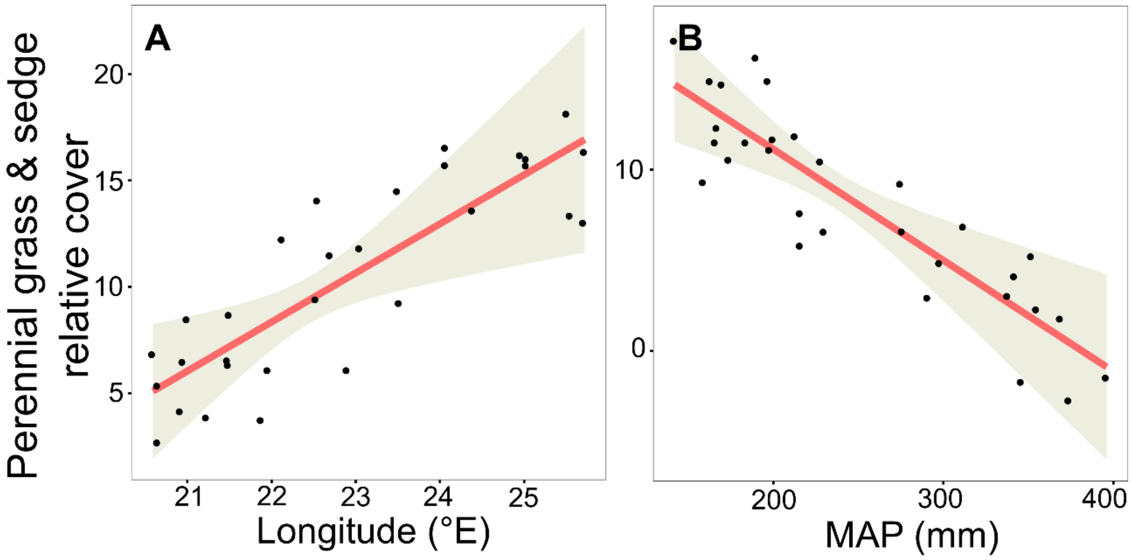

Figure 23: Scatterplots for multiple linear regression for **(A)** longitude and **(B)** MAP, the two variables which significantly predicted Bray-Curtis distances in perennial grass and sedge relative cover between plains and slopes (1 m^2 scale).

3.2.3.4 Annual grasses

The final model for dissimilarity in annual grass relative cover between plains and slope habitats included two predictor variables ($F_{2, 27} = 4.783$, adjusted $R^2 = 0.21$) (Fig. 20), of which only pH ($t = -3.09$, $p < 0.01$) was a significant predictor (Table 6), and correlated negatively with dissimilarity in annual grass relative cover between plains and slope habitats (Fig. 24).

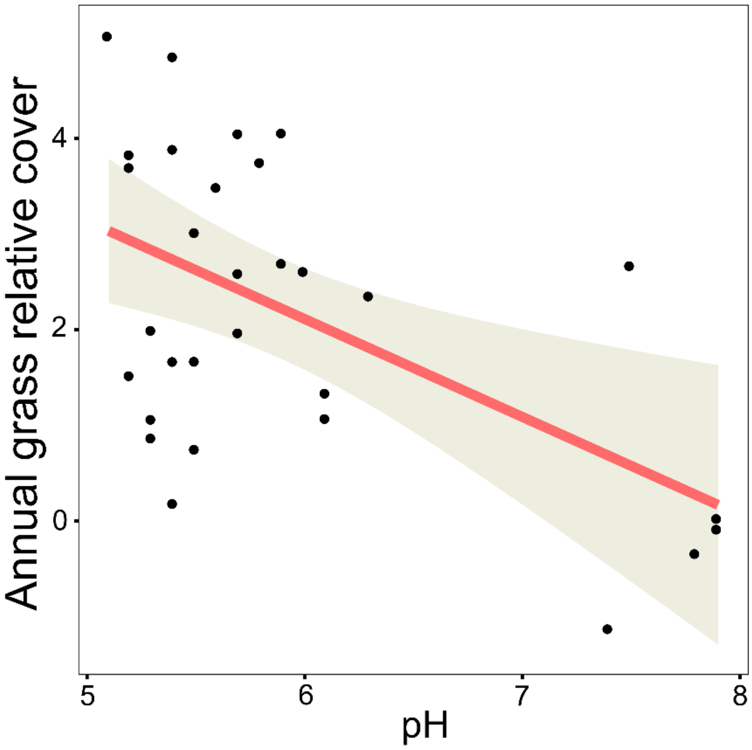

Figure 24: Scatterplots for multiple linear regression of pH, the variable which significantly predicted Bray-Curtis distances in annual grass relative cover between plains and slopes (1 m^2 scale).

3.2.3.5 *Forbs, geophytes and parasites*

The final model for dissimilarity in forb relative cover (including geophytes and parasitic plants) between plains and slope habitats included ten predictor variables ($F_{10,\ 19}$ = 2.970, adjusted R^2 = 0. 40) (Fig. 20). Longitude ($t = -3.44$, $p < 0.01$), MPAN ($t = -2.88$, $p < 0.01$), pH ($t = -3.66$, $p < 0.01$), and soil concentration of phosphorus ($t = -2.24$, $p < 0.05$) were the only significant predictors (Table 6). Dissimilarity in forb relative cover between plains and slope habitats was negatively correlated with longitude, MPAN, pH, and soil concentration of phosphorus (Fig. 25).

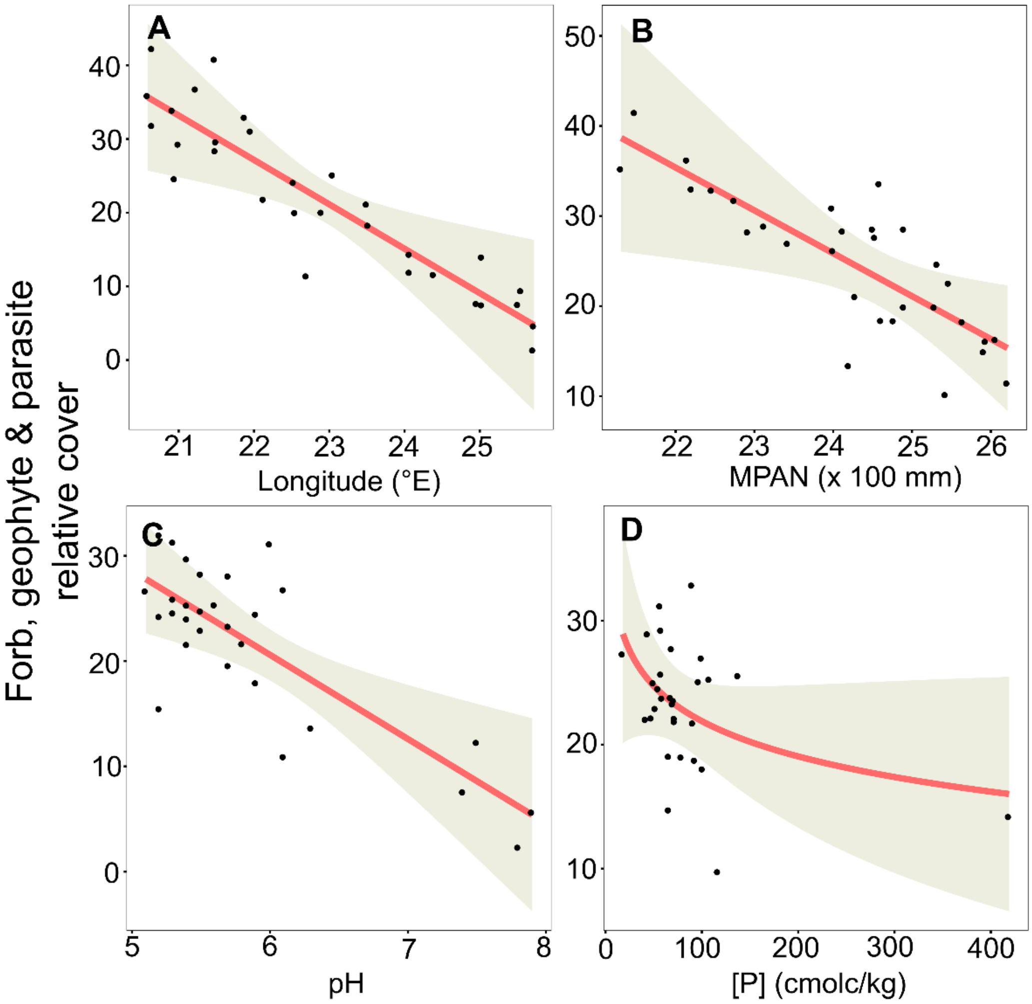

Figure 25: Scatterplots for multiple linear regression of **(A)** longitude, **(B)** MPAN, **(C)** pH, and **(D)** phosphorus concentration, the four variables which significantly predicted Bray-Curtis distances in forb, geophyte and parasite relative cover between plains and slopes (1 m^2 scale).

3.2.3.6 Succulent shrubs

The final model for dissimilarity in succulent shrub relative cover (including dwarf succulents, leaf-succulents, and stem-succulents) between plains and slope habitats included five predictor variables ($F_{10, 19} = 2.970$, adjusted $R^2 = 0.40$) (Fig. 20). Altitude ($t = -3.73$, $p < 0.01$), MAT ($t = -3.37$, $p < 0.01$), and pH ($t = 2.53$, $p < 0.05$) were significant predictors (Table 6). Dissimilarity in succulent shrub relative cover between plains and slope habitats was negatively correlated with altitude and MAT, and positively correlated with pH (Fig. 26).

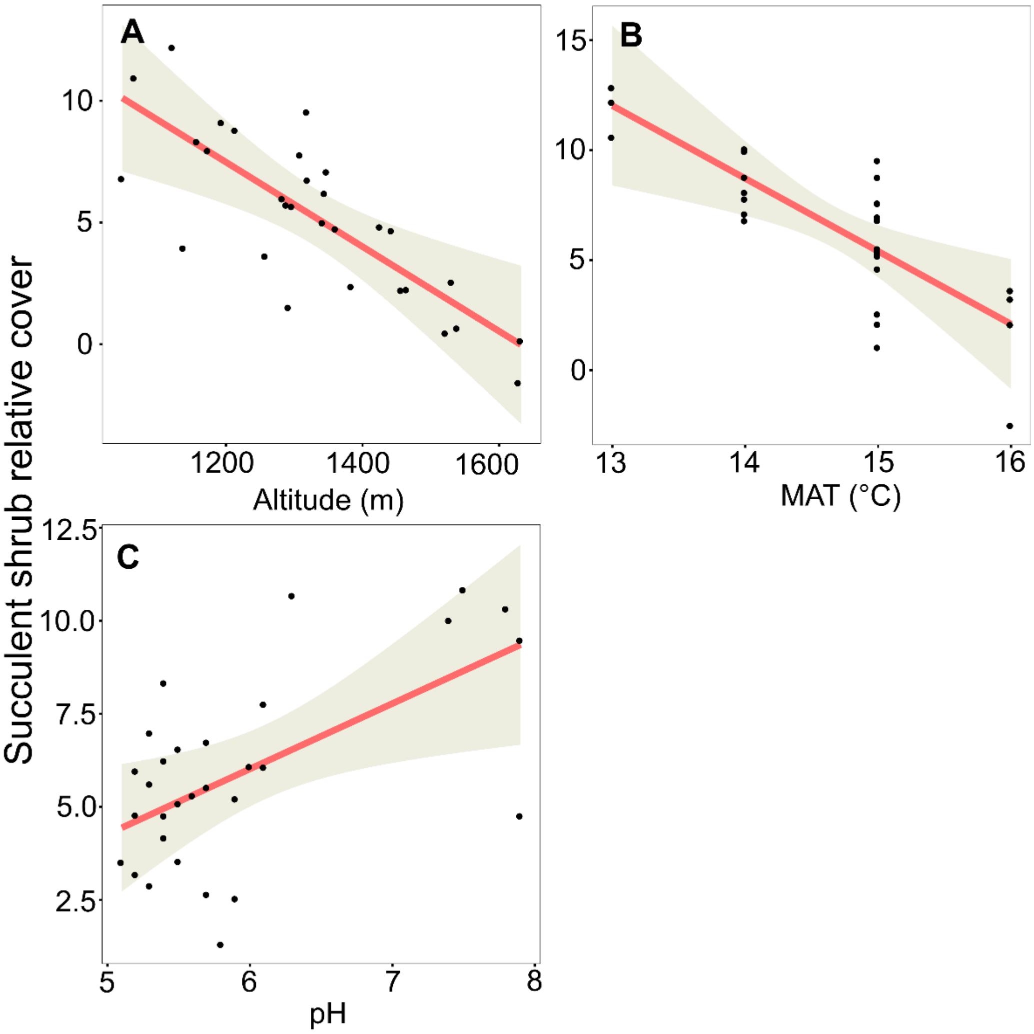

Figure 26: Scatterplots for multiple linear regression of **(A)** altitude, **(B)** MAT, and **(C)** pH, the three variables which significantly predicted Bray-Curtis distances in succulent shrub relative cover between plains and slopes (1 m^2 scale).

Table 6: Significance of linear model outputs for Bray-Curtis distances between plains and slopes overall and for the five dominant growth forms (1 m^2 scale). Variables which were not included in the final models are marked by '*N/A*'.

*Significance levels: n.s. = not significant; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

	Overall dissimilarity	**Woody shrubs**	**Perennial grasses & sedges**	**Annual grasses**	**Forbs, geophytes & parasites**	**Succulent shrubs**
Altitude	n.s.	n.s.	n.s.	N/A	N/A	***
Longitude	N/A	n.s.	**	N/A	**	N/A
Mean annual precipitation	**	n.s.	***	N/A	N/A	N/A
Mean annual A-pan evaporation	N/A	n.s.	N/A	N/A	**	N/A
Number of days with heavy frost	**	N/A	n.s.	N/A	n.s.	n.s.
Mean annual temperature	n.s.	N/A	N/A	N/A	N/A	**
Maximum temperature of hottest month	n.s.	N/A	n.s.	N/A	n.s.	N/A
Minimum temperature of coldest month	*	**	N/A	N/A	N/A	N/A
pH	*	N/A	N/A	**	**	*
Percent sand	n.s.	N/A	N/A	N/A	n.s.	N/A
[Ca]	n.s.	*	N/A	N/A	N/A	N/A
[Na]	n.s.	N/A	N/A	N/A	n.s.	N/A
[K]	**	N/A	N/A	n.s.	n.s.	n.s.
[P]	**	N/A	N/A	N/A	*	N/A
Percent NH_4	n.s.	N/A	N/A	N/A	n.s.	N/A

CHAPTER 4: Discussion

This chapter discusses the implications of the observed patterns of plant species richness and relative cover of growth forms, and elaborates on the possible drivers thereof. Comment is made on how these patterns differ at various spatial scales, and the implications of these results for our current understanding of vegetation types in the Nama-Karoo. The observed patterns of plant species richness and diversity are discussed in the context of changing climate and land-use, with reference to the newly emerging threats to the region. Finally, the key findings and caveats of this study are summarised, and suggestions for continued research are proposed.

4.1 Plant diversity in the Upper Karoo

4.1.1 Local and regional patterns of biodiversity

4.1.1.1 Species richness and relative cover of growth forms at different scales

Overall species richness is higher in slope habitats than in plains habitats in the Upper Karoo. Differentiation diversity, the change in the composition of vegetation along habitat gradients (i.e. β-diversity) and geographic gradients (i.e. γ-diversity) (Cody, 1986; Cowling et al., 1996), in the Upper Karoo showed a similar pattern between habitat types within a site, and across the longitudinal environmental gradient. Local level species richness at the 0.1 ha scale was higher in slope habitats than in plains habitats. This is very similar to the results of a study by Cowling and Hilton-Taylor (1999), which reported a mean species richness of 47 species (range: 22 – 76 species, n = 21) for the Nama-Karoo biome at the 0.1 ha scale. The minimum number of species observed in plains habitats in the present study were, however, lower than those reported by Cowling and Hilton-Taylor (1999). Plains habitats in the western extent of the study area were particularly species-poor, with clear signs of overgrazing, soil erosion, and a clear lack of moisture input, likely due to the drought (pers. obs.).

On a regional scale, irrespective of habitat type, species richness was higher in the eastern reaches of the Upper Karoo than in the west, and showed little overlap in relative cover of growth forms. Low woody shrubs, typical of the shrubland of the

Nama-Karoo (Mucina et al., 2006), were predominant across the landscape. Slope habitats were dominated by low woody shrubs, perennial forbs and perennial grasses, while plains habitats were dominated largely by annual and perennial grasses. This trend is well established in literature arising from the Nama-Karoo biome (Acocks, 1988; Cowling and Hilton-Taylor, 1999, 1994; Kraaij and Milton, 2006). In a previous study, evergreen and deciduous shrubs were shown to have high relative abundances in plains habitats in the Nama-Karoo, but grasses also appeared to make up a large proportion of total abundance (Cowling et al., 1994a), particularly towards the east. Sampling near the Nama-Karoo/Grassland biome ecotone meant that topographic relief was lower, and grasses, typical of the Grassland biome, were more abundant across both habitat types. It is likely that the factors contributing to the observed vegetation patterns are less stable (spatially and temporally) at ecotonal boundaries between different biomes, particularly with regard to soil properties, soil carbon dynamics, and interspecies competition for resources (e.g. water) (Kieft et al., 1998; Milton and Dean, 1995; Shiponeni et al., 2011). This highlights the important influence that habitat has on vegetation patterns.

Habitat heterogeneity, particularly in arid and semi-arid regions, is one of the strongest predictors of species richness. The term ‘habitat’ can be defined as the “spatial extent of a resource for a particular species” (Bunce et al., 2013). Differences in habitats, such as soil texture and moisture availability, are postulated to be strong determinants of the diversity of species and functional type abundance (Shmida and Wilson, 1985; Whittaker, 1977). Heterogeneous moisture and temperature conditions, or ‘microsites’ (Whittaker, 1977; Whittaker and Levin, 1977), occur more often on rocky hills with sandy soils, than on plains with finer soils. There is typically higher species richness and growth form diversity on rocky hills than on plains (Cowling et al., 1994a; Whittaker, 1977; Whittaker and Levin, 1977), and the results of this study are consistent with this pattern.

4.1.1.2 The relevance of plot size in richness and cover sampling

Measuring richness and diversity in relation to microsites within habitats requires a high sampling resolution in both plot size and number of plots, which may in turn influence the patterns of richness and diversity that emerge. This study observed species richness at the 0.1 ha scale, but also on finer sampling scales. The multiple sampling scales associated with modified Whittaker plots allowed for insight into how species richness changed as plot size increased. Smaller plot sizes (1 m^2 – 10 m^2) exhibited a narrow range of species richness values, while larger plots (100 m^2 – 1000 m^2) had a wider range and higher maxima for species richness. Most diversity was found at the 0.1 ha scale for both habitat types, indicating that larger plots capture more diversity, regardless of habitat type. This effect is a well-established ecological law, stating that as the cumulative sampled area increases, new habitats and, therefore more species, are encountered (Connor and McCoy, 1979; Williams, 1964).At small plot sizes, diversity is limited by the size of the plants themselves which constrains the number of individuals observed in each plot, and therefore places a strong upper limit on the maximum diversity of small plots. With large plot sizes, there are many more individuals than species observed, so the effect of plant size on species richness is considerably reduced. This allows the effect of habitat heterogeneity to become more apparent.

In a study by Cowling et al. (1994), results showed that sampling at the 25 m^2 scale in the Nama-Karoo yielded an average of 7 species (n = 18), with no significant habitat effect. However, at the 0.1 ha scale, an average of 47 species were recorded (n = 21). Karoo vegetation consistently demonstrates high levels of spatial variability at scales between 0.01 and 0.1 ha (100 m^2 – 1000 m^2), owing to heterogeneity in soil moisture, depth (Cowling and Hilton-Taylor, 1999) and nutrient status (Kraaij and Milton, 2006; Palmer et al., 1999). The scale-dependent heterogeneity in the Karoo means that selecting the correct plot size for sampling in different habitats influences the emergent vegetation patterns. In this study, only one modified Whittaker plot was sampled per habitat type per site, with aspect kept constant. This meant that only a portion of the full habitat type was sampled, and therefore many patches containing microsite-sensitive species may have been overlooked. Furthermore, logistical constraints (e.g. access to both habitat types on a property) limited the overall sampling effort, while confounding factors (e.g. different grazing intensities on plains vs koppies) influenced the number of species recorded at a site. Despite these limitations, the sampling scale of the Whittaker plot (i.e. 0.1 ha) appeared to capture a representative sample of the biodiversity present within each habitat type.

4.1.1.3 Patterns of relative cover of growth forms along a longitudinal environmental gradient

Gradient analyses have been used by scientists for centuries to investigate large-scale ecosystem responses to different environmental and climatic drivers. Strong underlying gradients contribute to the shaping of terrestrial ecosystems. Hence, investigating ecosystem structure, function and composition along a defined gradient helps clarify how these ecosystems respond to the environment, as well as to future climate change (Dunne et al., 2004; Koch et al., 1995). The Upper Karoo bioregion occurs along a longitudinal environmental gradient which spans the 570 km length of the study area from west to east. A strong moisture gradient occurs from east to west, with low annual rainfall (as low as 127 mm MAP) in the west, and higher annual rainfall (up to 396 mm MAP) in the east.

From west to east along the abovementioned gradient, a decline in relative cover of low woody shrubs from approximately 75% to 50% was observed, with shrubs giving way to annual and perennial grasses. However, palatable perennial grasses were more abundant on slopes than on the more highly-utilised plains habitats. The complexity of the interaction between grazing/herbivory and climate in the region has been widely acknowledged (Hoffman and Cowling, 1990; Kraaij and Milton, 2006; O’Connor and Roux, 1995).

Considering the long history of grazing by a very narrow guild of domestic livestock in the Karoo, it is unsurprising that losses in productivity and diversity of rangelands have been observed (Hoffman, 1991; Milton et al., 1994). The continuous removal of young, palatable shrubs and grasses by domestic livestock has resulted in a shift towards unpalatable woody shrubs (Kraaij and Milton, 2006; Milton, 1994; Riginos and Hoffman, 2003). Studies have investigated these vegetation changes at different scales, including on and off termitaria (Rahlao et al., 2008), along fence-lines (Dreber et al., 2011; Hanke et al., 2014; Todd and Hoffman, 2009, 1999), and within different landform and habitat units (Masubelele et al., 2015). While the results varied depending on when and where the study was conducted, they have a common finding among them: vegetation responses to grazing pressure (including aboveground and seed-bank responses) are closely associated with growth form and/or plant functional type.

Apart from the marked decrease in relative cover of low woody shrubs and increase in relative cover of grasses eastward in the Upper Karoo, there also appeared to be a habitat effect on the relative cover of annual and perennial grasses. Studies investigating the differences in patterns of annual and perennial grass in the Nama-Karoo have shown that heavy or sustained grazing dramatically reduced the abundance and cover of palatable perennial grass species, and favoured the relatively unpalatable annual grasses (Dreber et al., 2011; O'Connor and Roux, 1995). When allowed to recover following a shift in land-use from livestock grazing to conservation, a significant increase in perennial grasses, corresponding to a significant decrease in annual grasses, was observed (Kraaij and Milton, 2006). This suggests that disturbances such as intensive grazing (Todd and Hoffman, 1999) are closely associated with unpalatable annual grass cover (Kraaij and Milton, 2006). Therefore, in the (eastern) Upper Karoo, it is likely that the plains habitats, having a higher relative cover of annual grasses, are more disturbed than the slope habitats. Although no measures of disturbance or indices of grazing were recorded at the sample sites in this study, that plains are more highly utilised in the Karoo in general, is well-evidenced (Anderson and Hoffman, 2007; Masubelele et al., 2015; Pienaar et al., 2004), and can therefore be extrapolated for this region. Understanding the community composition and cover within these critical habitat types is therefore an important step towards adequately conserving the baseline plant biodiversity in the Upper Karoo.

4.1.2 Correspondence with the current vegetation map of South Africa

4.1.2.1 Contemporary vegetation types versus Acocks' veld types

The Upper Karoo bioregion, according to the Vegetation Map of South Africa (Mucina et al., 2006) comprises four vegetation types: Western Upper Karoo (*NKu1*), Upper Karoo Hardeveld (*NKu2*), Northern Upper Karoo (*NKu3*), and Eastern Upper Karoo (*NKu4*). Based on Acocks' Veld Types of South Africa (1988), the area occupied by these four vegetation types had previously been differentiated into six different veld types (VT). These were (west to east): False Desert Grassveld (VT *33c*), Arid Karoo (VT *29*), Central Upper Karoo (VT *27*), Karroid Broken Veld (VT *26*), False Arid Karoo (VT *35*), and False Upper Karoo (VT *36*) (Acocks, 1988).

In a study by Rutherford et al. (2003) which revisited Acocks' veld types, it was found that the vegetation of the Nama-Karoo biome can be delineated into three main clusters by subdividing Acocks' original species data into 45 relatively homogenous sample groups. These clusters were most distinct in the arid north-western regions, and became less distinct along a longitudinal gradient east. In the present study, species data from slope habitats also separated relatively cleanly into three clusters (i.e. plant associations), with relatively good correspondence between the clusters and their respective vegetation types according to the current published vegetation map (Mucina and Rutherford, 2006). Plant community clusters from plains habitats, however, had a high degree of chaining and showed very little conformity to their respective vegetation types as defined by Mucina et al. (2006).

The similarity in plant associations in slope habitats could be attributed to the consistency in substrate of the habitat type. For this study, slope habitats were selected for their dolerite substrate, while the adjacent plains occurred on a range of different substrates. Soil on the plains habitats was derived from shale, dolerite, or, often, a mix of dolerite and shale. This, together with the relatively high grazing impact on the plains, could explain why clusters based on species data from plains habitats in the present study did not result in any clear longitudinal pattern. Interestingly, similar plant associations in plains habitats appeared widely scattered along the environmental gradient, instead of being confined to a discrete spatial area corresponding to a single vegetation unit. Acocks' research also suggested that certain veld types would appear in more localised and specific parts of any given landscape. For example, the Central Upper Karoo veld type was more prominent on hillslopes, when surrounded by False Arid Karoo in the western boundary of the latter veld type (Acocks, 1988). The vegetation types as described by Mucina and Rutherford (2006) consist of a broad range of different plant communities. This is supported by the findings of this study, with the four vegetation types encountered similarly consisting of a range of different plant associations, with complex underlying patterns and determinants that may repeat across the landscape.

4.1.2.2 The utility of vegetation types

Fine-resolution data are beneficial when considering pragmatic conservation strategies for complex landscapes. Habitat-level differences in plant community structure, richness, and diversity may be of greater importance than landscape-level differences when proposing areas for development. An important aspect of Acocks' veld types is that it provided detailed information and considered various habitat types as different enough to warrant their own denomination (in this case, veld type). While the current vegetation map of South Africa (Mucina and Rutherford, 2006) considers various representative plant communities, the resultant vegetation types for a bioregion as large as the Upper Karoo are coarse, and hence give the impression of homogeneity in a landscape that is, in reality, quite complex and heterogeneous. The potential impacts of fracking and uranium mining, as will be discussed later, are unlikely to act uniformly across the landscape (Todd et al., 2016), but may instead have habitat-specific impacts which can only be estimated and monitored if there exists a comprehensive understanding of the biodiversity at finer resolutions than is currently available. Additional robust and systematic sampling of the Upper Karoo bioregion, and indeed the Nama-Karoo biome, would improve the resolution of the vegetation map, and hence benefit conservation management prior to the impending disturbances in the Karoo region.

4.2 Drivers of species richness and growth form cover

4.2.1 Climatic variables versus biophysical variables

Determining the drivers of biodiversity in arid regions (or ‘drylands’) is a globally relevant exercise. Global drylands comprise approximately 41% of the Earth’s total land surface, and supports close to 38% of the global human population (Reynolds et al., 2007). Dryland ecosystems have been cited widely as being most vulnerable to climate change, to the effects of desertification (World Resources Institute, 2005), and to the over-use of productive land (Maestre et al., 2012; Reynolds et al., 2007). However, arguments have also been made against the institutional sensationalism of desertification, suggesting that the magnitude of the issue as portrayed by institutions remains unsupported by scientific case studies (Behnke and Mortimore, 2016). Despite the controversy surrounding the magnitude of climate change impacts, it remains a priority for governments to prepare for scenarios wherein socio-economically important drylands are at risk of being transformed beyond the point of rehabilitation.

Arid and semi-arid regions are characterised by their generally lower volume of available water relative to other regions (Noy-Meir, 1973). In plant ecology, available water is often the limiting factor for the establishment and growth of plants, and, along with a variety of other climatic variables, has been shown to influence vegetation structure and patterns on various scales. For example, a semi-arid grassland in Colorado experienced an increase in aboveground biomass, and a shift in the dominant plant functional type in response to higher moisture inputs (Lauenroth et al., 1978). However, available water is not only dependent on meteorological moisture inputs, but also on the environment that collects it. Biophysical variables such as soil texture and composition also play a role in regulating the processes of runoff and infiltration, which in turn influence plant access to moisture inputs by storing moisture temporarily (Chesson et al., 2004; Noy-Meir, 1973). Soils with high organic matter content (loamy soil) generally have a higher water-holding capacity than sandy soil (Hudson, 1994; Sala et al., 1988). However, sandy soil allows water to infiltrate more quickly, and is therefore able to retain more water (and have it available to plants) than loamy soils, particularly in drylands where most water loss occurs via evaporation from bare soil (Sala et al., 1988). It is therefore important to recognise the complexity of interactions between abiotic variables in determining patterns of plant community occurrence.

While the interactions between the climatic variables and biophysical variables included in the models in the present study were not investigated, the final model outputs suggested that climatic and biophysical variables both play an important role in determining overall species richness and growth form cover. The percent of sand in the total soil composition was important (but not significant) in predicting overall species richness, and was significant in predicting the relative cover of low woody shrubs, the overall most dominant growth form. In both cases, habitat type was also a significant predictor, indicating that soil physical properties differ between plains and slope habitats, due to their differing topography and underlying geology (Burke, 2002a). This is further supported by the finding that percent sand and silt differed significantly between the two habitat types. Apart from soil moisture, it has been shown that the Karoo has a heterogeneous spatial distribution of soil properties at scales of 0.1 ha and smaller, including soil depth (Cowling and Hilton-Taylor, 1999) and soil nutrient composition (Palmer et al., 1999). Soil depth was not measured in this study, but would most likely contribute to a better understanding of the differences in the biophysical processes (e.g. runoff, infiltration) that influence plant associations and communities in different habitat types.

The concentration of calcium in the soil emerged as a significant predictor of the relative cover of annual grasses and perennial forbs, while phosphorus concentrations significantly predicted the relative cover of leaf-succulent shrubs. Calcium, being a less stable nutrient (Burke, 2002a), is easily leached from the soil (e.g. Nyakairu and Koeberl, 2001) and is susceptible to fluctuations based on soil moisture regimes (Burke, 2002a). In the far-western, arid extent of the study area, plains habitats were sometimes observed to have visible calcrete (calcium carbonate) nearby river washes, and was almost always observed with arid- and saline-adapted plant species such as *Salsola tuberculata*. Similar soil patterns have been observed in the plains habitats of arid Namib inselberg landscapes (Burke, 2002b). The negative correlation of relative cover of annual grasses, and positive correlation of relative cover of perennial forbs with soil calcium concentration is indicative that annual grasses, which occurred more abundantly on plains than in slope habitats, are sensitive to salinity associated with the presence of calcium in the soil. Furthermore, relative cover of leaf-succulent shrubs was positively correlated with soil phosphorus concentrations. The incidence of succulence in plants is known to be positively correlated with soil salinity, as well as calcium and phosphorus concentrations (Barkman, 1979; Hoffman and Cowling, 1987; Van der Merwe and Van Rooyen, 2011). While leaf-succulents (and succulent shrubs in general) were poorly represented in the landscape, they showed higher relative cover on plains in the east, and in slope habitats in the west, again highlighting the importance of habitat type in determining plant species richness and growth form patterns across the landscape.

Related to habitat type are the combined effects of altitude and temperature. Air temperature is estimated to decrease on average by 9.8°C with every 1 km increase in altitude. However, the difference in altitude between plains and slope habitats in the Karoo was too small (< 100 m) to experience a significant difference in ambient temperature. However, rocky hills have been shown to represent thermal refuge areas because of the heat retention capacity of the rocks, as well as being warmer than valleys in which frost accumulates (Muller et al., 2016). For all models in which altitude emerged as an important predictor of species richness and relative cover of growth forms, some measure of temperature was also present. Interesting comparisons can be made of maximum and minimum temperatures of the hottest and coldest months respectively, in the context of physiological stress (Körner, 2007). It is often not the decrease in temperature with altitude that is of importance, but instead the buffering effect of microsites in rocky habitats from extremes in temperature. Temperature inversion, also called ‘cold air damming’ (Bell and Bosart, 1988; Richwien, 1977), where cold air settles in low-lying areas, is common in landscapes with varied topography. It is within these relatively low-lying areas, usually plains habitats, that frost occurs. The mean annual number of days with heavy frost emerged as an important predictor in all the final models, except when predicting the relative cover of leaf-succulent shrubs, which is somewhat surprising. Among the many plant functional types, succulents are widely known to be vulnerable to frost, as cellular damage may result from the freezing of water within water-containing cells (Box, 1981). For example, in the Sonoran Desert, the distribution of the giant saguaro cactus is suggested to be limited by freezing winter temperatures at certain altitudes and latitudes (Osmond et al., 1987; Shreve, 1911). However, instead of mean annual number of frost days, relative cover of leaf-succulent shrubs in this study was significantly predicted by and negatively correlated with altitude. This suggests that at low altitudes, plants are less buffered against cold air damming, and are therefore vulnerable to die-off by frost. It is likely then that the leaf-succulent plant associations in slope habitats in the west are more stable and protected than those in the east, where frost is more common. Temperature likely plays an important role, but the relatively coarse modeled temperature data used in this study does not adequately capture the local temperature dynamics.

Patterns of relative cover of growth forms showed different trends across the longitudinal gradient. Longitude was included as a predictor variable in the overall model and represented a proxy for the general environmental gradient which spans the study area, comprising numerous interacting variables. In the final models, longitude was retained as a significant predictor of relative cover of perennial grasses. A strong positive correlation exists between relative cover of perennial grasses and longitude, indicating that relative cover increases eastward, from arid Nama-Karoo grassy shrubland to more mesic shrubby grassland near the Nama-Karoo-Grassland ecotone. Furthermore, the relative cover of perennial grasses in slope habitats decreased abruptly closer to the ecotone, switching instead to greater relative cover of low woody shrubs on slopes.

Habitat type was not a significant predictor of relative cover of perennial grasses, which contradicts some previous studies from the Karoo. South-facing slopes are wetter and cooler than north-facing slopes, and at higher rainfall as occurs in the east, can be observed to be dominated by large woody species in the genera *Celtis*, *Searsia*, *Cussonia*, and *Colpoon*, among others. This effect is described in The Vegetation of South Africa, Lesotho and Swaziland (Mucina et al., 2006b), whereby the Upper Karoo Hardeveld vegetation type, which is dominated by grasses, gives way to the Besemkaree Koppies Shrubland vegetation type, which is dominated by tall woody shrubs and trees, as one moves east or to areas of higher rainfall. In the arid west, however, the moister south-facing slopes are still too dry to support large woody components, so the effect is less prominent.

4.2.2 Dissimilarities between plains and slope habitat types

The results of a gap analysis in global arid land ecology revealed that habitat and spatial research were relatively understudied research topics (Greenville et al., 2017). This suggests that research focusing on the various spatial scales at which ecosystems function and ecological patterns emerge (Chave, 2013; Levin, 1992) is generally lacking in the existing drylands literature. Studying systems at the appropriate spatial scale, and developing models to interpolate across a range of scales, remains a challenge in modern ecological research (Chave, 2013; Greenville et al., 2017). It has been demonstrated that different habitat types are uniquely suited to support specific species (e.g. heuweltjies; Yeaton and Esler, 1990; Esler and Cowling, 1995), plant associations/communities and functional type assemblages (e.g. quartz patches; Schmiedel and Jürgens, 1999). This notion is reinforced by the discontinuity in vegetation type (Mucina and Rutherford, 2006) between plains and slope habitats within a single sample site in this study, often less than 1 km apart. Investigating the dissimilarities between various habitat types, and the drivers thereof, may therefore highlight potential priority areas for conservation in terms of sensitivity to broad-scale disturbances.

A combination of both climatic and biophysical variables emerged as significant predictors of the dissimilarity in overall species richness (based on species presence) between plains and slope habitats in the Upper Karoo. The dissimilarities between plant functional types within the two different habitat types also displayed a range of different predictors. This was to be expected, since different plant functional types may respond differently to climatic and biophysical variables, due to differing functional strategies (Cody, 1991; Schimper, 1903). The prevailing set of climatic and biophysical habitat conditions would therefore determine the functional type assemblages present in each habitat. Furthermore, habitats with greater heterogeneity in local conditions may support a more diverse assemblage of functional types. This has some implications for climate change and suggests that outcomes are likely to vary significantly between functional types and cannot be generalised through broad-scale vegetation modelling.

Fine-scale sampling of functional types at the habitat level may inform predictive models for vegetation dynamics within the Nama-Karoo and Grassland biomes. Dynamic vegetation models (DVMs) currently do not include four of the common functional types present in the Nama-Karoo: geophytes, annual forbs/grasses, succulent shrubs, and woody shrubs (Moncrieff et al., 2015). Not much is known about the differences in ecology between shrubs and trees, which makes it difficult to define a shrub plant functional type to be used in DVMs (Moncrieff et al., 2015). Moreover, the influence of land-use and grazing, particularly in these biomes, are often based on assumptions (Moncrieff et al., 2015) rather than fine-scale empirical data, which weakens the predictive power of DVMs. The utility of DVMs in predicting potential future changes in vegetation structure has been demonstrated for different ecosystems, for example, predicting Amazon forest dieback under projected climate conditions of lower precipitation (Scheiter et al., 2013). A tool which allows forecasting of changes in vegetation structure for the Karoo region would not only be of importance for conservation purposes in the face of a changing global climate, but may also have implications for farmers and landowners in terms of policy that informs recommended stocking rates and stewardship opportunities.

4.3 Future changes in the Upper Karoo

4.3.1 Climate and land-use change

Given that different habitat types in the Upper Karoo have been demonstrated to support different plant associations, understanding the possible future changes the Karoo may experience should be a priority. The level of habitat heterogeneity afforded by the matrix of plains interspersed with rocky dolerite hills in the Nama-Karoo biome means that any future changes in the region are unlikely to have a uniform effect across the landscape (Todd et al., 2016). This holds true for both climatic and land-use changes.

4.3.1.1 Climate change in the Karoo

Climate change acts over not only broad spatial scales, but also over long temporal scales. The assumption that spatial and temporal variation in ecosystems are equivalent is called ‘space-for-time substitution’ (Pickett, 1989), and is often implied by studies using natural spatial gradients (Dunne et al., 2004), such as the longitudinal environmental gradient observed in the present study. As such, the results of many spatial gradient studies may be misinterpreted in that ecosystems might not necessarily track climatic change as readily or as uniformly over time as they might across space. Furthermore, uncontrollable factors (e.g. historical land-use (Acocks, 1953; Dean and Milton, 2003; Talbot, 1961)) or stochastic events (e.g. severe or extended periods of drought (Hoffman et al., 2009; O’Connor and Pickett, 1992)) may also have unpredictable effects on an ecosystem (Pickett, 1989). This highlights the value and utility in collecting and analysing long-term climate data to quantify both the spatial and temporal variation in the variables that may affect vegetation dynamics and patterns of a region.

The present study was conducted during the second and third years (2016 – 2017) of an ongoing meteorological drought in the region. South Africa has experienced at least four major drought events (1919, 1933, 1965, 1991) over the last century (Donaldson, 1967; Laing, 1994). While some of the country’s most severe drought events have been recorded and monitored meticulously (Laing, 1994), research on the impacts of drought on the natural environment (rather than on agricultural practices) is still lacking. The Karoo is projected to experience longer dry spells (Hewitson, 1996), as well as rainfall events of greater magnitude (Hewitson and Crane, 2006) and variability (Mason et al., 1999). The variability in rainfall as a consequence of El Niño (Desmet and Cowling, 1999; Rouault and Richard, 2005) may result in summer rainfall becoming even less reliable in the Nama-Karoo biome. The consequences of this for the vegetation of the region will depend on the interaction between climate and other environmental variables. The Nama-Karoo biome is projected to shift spatially from west to east into the Grassland biome, in response to hotter, drier conditions, and higher CO_2 concentrations (Ellery et al., 1991; Midgley et al., 2008, 2002; Rutherford et al., 1996). Acocks (1953) predicted the directional expansion of the Karoo eastward, accompanied by a retreat by the Grasslands as a result of overgrazing and poor land management. The current projections for the region are very similar, despite the underlying mechanism for the shift being different. The interaction between climate and land-use in determining vegetation patterns is noteworthy, particularly in the Nama-Karoo.

4.3.1.2 Changes in land-use

While the naturally-occurring vegetation of an area is assumed to be adapted to the typical prevailing climatic variability (Du Pisani et al., 1998), the interactions between variable rainfall and land-use (e.g. high grazing intensities) may substantially influence the structure and composition of plant associations and communities. Milchunas et al. (1994) suggested that plant communities in shortgrass steppe systems in Colorado are more sensitive to rainfall variability than to changes in long-term grazing intensities, despite acknowledging the potential interactions between the climatic and land-use variables. A similar finding was reported by O’Connor and Roux (1995), wherein changes in plant communities were driven largely by variation in rainfall, but the effects of grazing on longer-lived plants became more pronounced in the long term. As proposed by Acocks’ (1953) expanding Karoo concept, selective grazing and poor land-use practice is likely to drive broad-scale changes in vegetation structure, notably an increase in woody shrub cover in traditionally grassland areas (Hoffman et al., 1999; Meadows, 2003). Additionally, the interaction between rainfall variability and increasing levels of carbon dioxide in the atmosphere may variably facilitate changes in cover of grasses and woody shrubs. More recent research based on repeat photo-monitoring suggests that dwarf shrub cover has declined significantly at several sites in the south-eastern interior of South Africa over time (Masubelele et al., 2015). The former study also suggested that privately-owned farm lands in the Nama-Karoo biome are less degraded with regard to vegetation cover and plant species composition than many other sites in South Africa (Hoffman and Ashwell, 2001; Masubelele et al., 2015). Numerous studies have shown that the vegetation in the Nama-Karoo biome changes readily between palatable perennial species and unpalatable perennial and annual species in response to overgrazing by livestock (Kraaij and Milton, 2006; O'Connor and Roux, 1995; Wiegand et al., 1995). Improvements to land-use practice could include halving the agricultural stocking rates in national parks to make allowances for rainfall variability (Kraaij and Milton, 2006; Novellie, 1989). While improvements to land-use practices can be made, it appears that the vegetation of the Nama-Karoo is intrinsically resilient to reasonable change, owing to the number of different habitat types and plant functional types it hosts. Nevertheless, efforts should be made to prevent the vegetation reaching a point at which potentially negative changes become permanent.

4.3.2 Shale gas exploration

When examining the viability of fracking in the Karoo, among the costs to consider are those associated with mitigating the impacts of disturbance on the environment (Fakir and Davies, 2016). Plains habitats are likely to experience the greatest level of disturbance by shale gas exploration and fracking activities, not only in terms of mining, but also in terms of the infrastructure required. Among the greatest threats arising from potential fracking activities are habitat fragmentation and loss of landscape connectivity resulting from the construction of roads and other infrastructure across the landscape (Todd et al., 2016). Plains habitats in the Upper Karoo are considered to be less sensitive to disturbance spatially, because of the recurring pattern of plant associations in plains habitats across the entire study area. While areas of higher elevation and ruggedness, such as the rocky dolerite slope habitats in this study, are considered to be more sensitive to disturbance due to their ability to support higher species richness and abundance (Todd et al., 2016), these rocky hills are already fragmented in the landscape. It is therefore the plains habitats that exist between the slope habitats which should be of higher conservation priority, to preserve connectivity between them.

Theories of island biogeography have been tested in Namibia and the Nama-Karoo of South Africa, regarding the potential of mesas and inselbergs to act as refugia for vulnerable species and azonal vegetation (Burke, 2002b, 2001; Burke et al., 2003), and as sources which are able to populate the surrounding matrix (Burke, 2002c). While the buffering effect of habitats with higher elevations on extreme conditions is widely accepted (Bond and Richardson, 1990; Skowno et al., 2009), the dynamics behind rehabilitating denuded landscapes is less commonly understood. Research into the life histories, reproductive strategies, pollination agents, and dispersal mechanisms of the relevant species is required to fully understand the consequences of habitat fragmentation by disturbance. Passive repopulation of denuded plains habitats by species-rich slope habitats is unlikely if the disturbance has resulted in the migration of potential pollinators and/or dispersers from the general vicinity, or if the matrix has been eroded to a state unfit for re-establishment. Active rehabilitation would be necessary to return the vegetation to its original structure. However, this is a costly venture for an arid region, where rehabilitation is notoriously challenging (Todd et al., 2016).

The Nama-Karoo biome is relatively under-studied and under-sampled, and the true diversity that exists in the region is therefore, not well understood. The habitat-specific impacts that are likely to arise from exploratory fracking can only be monitored if an adequate baseline inventory of biodiversity is available. Therefore, sampling habitats in the Nama-Karoo at a high spatial resolution is an essential exercise prior to the impending shale gas exploration. Spatial considerations must be made to preserve the ecological processes between plains and slope habitats. Ecological sensitivity models and maps (Oberholzer et al., 2016; Todd et al., 2016) offer a spatial context for the potential impacts of fracking on biodiversity in the Karoo basin, and provide an important first step towards understanding which areas are of greatest conservation concern. Broad-scale vegetation and physical data were used to generate the sensitivity map contained in Todd et al. (2016), suggesting that the resolution of the map could be enhanced by improved ground-truthing and habitat modelling.

4.4 Summary and general conclusions

This study determined the species richness, relative cover and growth form diversity of the vegetation of two key habitats of the Upper Karoo bioregion, and investigated the plant community patterns that emerged in relation to the current mapped vegetation types for the region. It also investigated the role that biophysical and climatic variables might play in determining species richness and relative cover of growth forms within plains and slope habitats. The key findings of this study are summarised below.

4.4.1 Species richness in the Upper Karoo is higher in slope habitats than in plains habitats

The results indicated that mean species richness was higher in slope habitats than in plains habitats. This trend persisted across the longitudinal environmental gradient, with higher overall species richness found at the wetter eastern end of the gradient. These results expand on what was previously found by Cowling et al. (1994a), who showed that species richness was significantly different at both the habitat and site level. It also expands on their description of the relative abundances of growth forms on plains by providing trends of relative cover of growth forms observed at many more locations in both plains and slope habitats in the Upper Karoo and across a longitudinal environmental gradient.

4.4.2 Plant associations in slope habitats have closer correspondence to the current vegetation map of South Africa than those in plains habitats

Plant associations in plains habitats exhibited a recurring pattern across the study area, and showed poor correspondence with current mapped vegetation types (Mucina et al., 2006b). Plant associations in slope habitats, however, appeared to cluster into three main groups, with good correspondence between the observed groups and the current mapped vegetation types. Sampling more than one 0.1 ha plot per habitat type per site may improve the correspondence with the vegetation map for slope habitats. A large volume of floristic research has been done which focuses on slope habitats as islands of higher species richness (Burke, 2004, 2002c, 2001; Burke et al., 1998), but not much research has focused on the basic floristic patterns in plains habitats (Cowling et al., 1994a; Cowling and Hilton-Taylor, 1999). Therefore, to understand the recurring pattern of plant associations in plains habitats across broad spatial scales in the study area, future floristic research should investigate the underlying determinants of vegetation patterns in plains habitats.

Compared to the numerous vegetation types recognised in the adjacent biomes, the vegetation types of the Nama-Karoo biome as defined by Mucina et al. (2006) are currently very broadly conceived, giving the impression of homogeneity in a region which contains a great deal of habitat heterogeneity and under-studied biodiversity. The entire Nama-Karoo biome is currently considered to consist of only 14 vegetation types, each with numerous plant associations as clearly demonstrated in the present study. Key research questions going forward should address which of these plant associations can be consistently recognised across the Nama-Karoo biome, and whether these plant associations could and/or should be recognised as distinct vegetation types.

4.4.3 Predictors of overall species richness and relative cover of growth forms are a complex mix of climatic, biophysical, and land-use-related variables

Traditionally, moisture-related climate variables have emerged as the most significant predictors of species richness and abundance in arid regions due to plant water availability being the limiting factor for growth (Noy-Meir, 1973). The results of this study suggest a similar pattern, with mean annual precipitation being a significant predictor of overall species richness. Furthermore, percent sand, which influences plant water availability (Hudson, 1994; Noy-Meir, 1973; Sala et al., 1988), also emerged as a significant predictor for the relative cover of low woody shrubs, the most dominant growth form across the study area. However, habitat and altitude were also important as significant predictors of overall species richness, as well as of the relative cover of low woody shrubs, annual grasses, and perennial forbs. An interesting finding was that relative cover of perennial grass was significantly predicted by, and strongly positively correlated with longitude. This, in addition to mean annual precipitation and various temperature-related variables also emerging as significant predictors, suggests a strong geographic influence of moisture and temperatures in driving perennial grass abundance across the landscape. This is of importance in the context of the Karoo, a region with a long history of livestock farming, where palatable perennial grasses are favoured by livestock in the landscape.

No indicators of grazing intensity, land-use and/or degradation were included in this study. The broad-scale approach employed in this study did not allow for the inclusion of interaction terms between climate, biophysical, and land-use variables which would probably better explain the relative importance of the potential drivers of species richness and growth form cover. However, the interaction terms were excluded because the large number of potential explanatory variables (and therefore large number of potential interaction terms) would have resulted in overfitting of the explanatory models. One approach which might address this shortcoming would be to conduct the study using a stratified sampling approach along local (smaller scale) environmental gradients, to constrain the potential number of variables influencing the plant community patterns that emerge.

4.4.4 Further research

While a great deal of research has been done on a diversity of topics in the Karoo, much of this has had an applied purpose and therefore has not focused on gathering baseline data across broad spatial scales. Further research is necessary to improve our current understanding of the baseline biodiversity in the region. High-resolution sampling within each habitat type present in the landscape (e.g. plains, slopes, riverine areas) provides a more complete representation of the total biodiversity, and is necessary to document baseline conditions. This would also improve the current mapped vegetation types of the region, which are essential in informing spatial planning for conservation. Furthermore, combining plant biodiversity datasets with data for other important taxa in the region, as is being undertaken by the Karoo BioGaps project, would undoubtedly provide a robust representation of the overall biodiversity of the Nama-Karoo biome, prior to future developments in the region.

Literature cited

Aarssen, L.W., 1984. On the distinction between niche and competitive ability: implications for coexistence theory. Acta Biotheoretica 33, 67–83.

Acocks, J.P.H., 1953. Veld Types of South Africa, 1st ed, Memoirs of the Botanical Survey of South Africa.

Acocks, J.P.H., 1988. Veld Types of South Africa, 3rd ed, Memoirs of the Botanical Survey of South Africa.

Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution 14, 273–277.

Amundson, R.G., Chadwick, O.A., Sowers, J.M., 1989. A comparison of soil climate and biological activity along an elevation gradient in the eastern Mojave Desert. Oecologia 80, 395–400.

Anderson, P.M.L., Hoffman, M.T., 2007. The impacts of sustained heavy grazing on plant diversity and composition in lowland and upland habitats across the Kamiesberg mountain range in the Succulent Karoo, South Africa. Journal of Arid Environments 70, 686–700.

Archer, E.R.M., 2004. Beyond the "climate versus grazing" impasse: Using remote sensing to investigate the effects of grazing system choice on vegetation cover in the eastern Karoo. Journal of Arid Environments 57, 381–408.

Armas, C., Pugnaire, F.I., 2005. Plant interactions govern population dynamics in a semi-arid plant community. Journal of Ecology 93, 978–989.

Austin, A.T., 2002. Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. Ecology 83, 328–338.

Austin, A.T., Sala, O.E., 2002. Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. Journal of Vegetation Science 13, 351–360.

Austin, A.T., Vitousek, P.M., 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. Oecologia 113, 519–529.

Barkman, J.J., 1979. The investigation of vegetation texture and structure. In: Werger, M.J.A. (Ed.), The Study of Vegetation. Junk, London, pp. 125–160.

Bassi, R., Prasher, S.O., Simpson, B.K., 2000. Extraction of metals from a contaminated sandy soil using citric acid. Environmental Progress 19, 275–282.

Becking, R.W., 1957. The Zürich-Montpellier School of Phytosociology. Botanical Review 23, 411–488.

Behnke, R., Mortimore, M., 2016. Introduction: The End of Desertification? In: Behnke, R., Mortimore, M. (Eds.), The End of Desertification? Disputing Environmental Change in the Drylands. Springer-Verlag, Berlin Heidelberg, pp. 1–34.

Bell, G.D., Bosart, L.F., 1988. Appalachian Cold-Air Damming. American Meteorological Society 116, 137–161.

Bond, W.J., Richardson, D.M., 1990. What can we learn from extinctions and invasions about the effects of climate change? South African Journal of Science 86, 429–433.

Bossdorf, O., Schurr, F., Schumacher, J., 2000. Spatial patterns of plant association in grazed and ungrazed shrublands in the semi-arid Karoo, South Africa. Journal of Vegetation Science 11, 253–258.

Box, E.O., 1981. Predicting physiognomic vegetation types with climate variables. Vegetatio 45, 127–139.

Bragazza, L., Parisod, J., Buttler, A., Bardgett, R.D., 2013. Biogeochemical plant-soil microbe feedback in response to climate warming in peatlands. Nature Climate Change 3, 273–277.

Breshears, D.D., Huxman, T.E., Adams, H.D., Zou, C.B., Davison, J.E., 2008. Vegetation synchronously leans upslope as climate warms. Proceedings of the National Academy of Sciences of the United States of America 105, 11591–11592.

Bunce, R.G.H., Bogers, M.M.B., Evans, D., Halada, L., Jongman, R.H.G., Mucher, C.A., Bauch, B., De Blust, G., Parr, T.W., Olsvig-Whittaker, L., 2013. The significance of habitats as indicators of biodiversity and their links to species. Ecological Indicators 33, 19–25.

Burke, A., 2001. Determinants of inselberg floras in arid Nama Karoo landscapes. Journal of Biogeography 28, 1211–1220.

Burke, A., 2002a. Properties of soil pockets on arid Nama Karoo inselbergs – the effect of geology and derived landforms. Journal of Arid Environments 50, 219–234.

Burke, A., 2002b. Plant communities of a Central Namib inselberg landscape. Journal of Vegetation Science 13, 483–492.

Burke, A., 2002c. Island-matrix relationships in Nama Karoo inselberg landscapes. Part I: do inselbergs provide a refuge for matrix species? Plant Ecology 160, 79–90.

Burke, A., 2004. From plains to inselbergs: species in special habitats as indicators for climate change? Journal of Biogeography 31, 831–841.

Burke, A., 2007. How sampling effort affects biodiversity measures in an arid succulent karoo biodiversity hotspot. African Journal of Ecology 46, 488–499.

Burke, A., Esler, K.J., Pienaar, E., Barnard, P., 2003. Species richness and floristic relationships between mesas and their surroundings in southern African Nama Karoo. Diversity and Distributions 9, 43–53.

Burke, A., Jürgens, N., Seely, M.K., 1998. Floristic affinities of an inselberg archipelago in the southern Namib desert - relic of the past, centre of endemism or nothing special? Journal of Biogeography 25, 311–317.

Chave, J., 2013. The problem of pattern and scale in ecology: What have we learned in 20 years? Ecology Letters 16, 4–16.

Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A., Weltzin, J.W., 2004. Resource pulse, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141, 236–253.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117–143.

Cody, M.L., 1986. Diversity, rarity, and conservation in meditarranean-climate regions. In: Conservation Biology: The Science of Scarcity and Diversity. pp. 123–152.

Cody, M.L., 1991. Niche theory and plant growth form. Vegetatio 97, 39–55.

Connor, E.F., McCoy, E.D., 1979. The Statistics and Biology of the Species-Area Relationship. The American Naturalist 113, 791–833.

Cowling, R.M., Esler, K.J., Midgley, G.F., Honig, M.A., 1994a. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. Journal of Arid Environments 27, 141–158.

Cowling, R.M., Esler, K.J., Midgley, G.F., Honig, M.A., 1994b. Patterns of plant species diversity in southern Africa. Journal of Arid Environments 27, 141–158.

Cowling, R.M., Hilton-Taylor, C., 1994. Patterns of plant diversity and endemism in southern Africa: an overview. In: Huntley, B.J. (Ed.), Botanical Diversity in Southern Africa. National Botanical Institute, Pretoria, pp. 31–52.

Cowling, R.M., Hilton-Taylor, C., 1999. Plant biogeography, endemism and diversity. In: Dean, W.R.J., Milton, S.J. (Eds.), The Karoo: Ecological Patterns and Processes. Cambridge University Press, Cambridge, pp. 42–56.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., Arianoutsou, M., 1996. Plant diversity in Mediterranean-climate regions. Trends in Ecology & Evolution 11, 362–366.

Crist, T.O., Veech, J.A., Gering, J.C., Summerville, K.S., 2003. Partitioning Species Diversity across Landscapes and Regions: A Hierarchical Analysis of α, β, and γ Diversity. The American Naturalist 162, 734–743.

CSIR, 2015. Strategic Environmental Assessment (SEA) for Shale Gas Development in South Africa [WWW Document]. URL http://seasgd.csir.co.za/#anchor3 (accessed 2.5.18).

de Sassi, C., Tylianakis, J.M., 2012. Climate change disproportionately increases herbivore over plant or parasitoid biomass. PLoS ONE 7, 1–8.

Dean, W.J., Milton, S.J., 1999. The Karoo: ecological patterns and processes. Cambridge University Press, Cambridge.

Dean, W.R.J., Milton, S.J., 2003. Did the flora match the fauna? Acocks and historical changes in Karoo biota. South African Journal of Botany 69, 68–78.

Desmet, P.G., Cowling, R.M., 1999. The climate of the Karoo - a functional approach. In: The Karoo: Ecological Patterns and Processes. Cambridge University Press, Cambridge, pp. 3–16.

Desmet, P.G., Rutherford, M.C., Mucina, L., Ward, R.A., 2006. Desert Biome. The Vegetation of South Africa, Lesotho and Swaziland.

Dewdney, P.E., Hall, P.J., Schilizzi, R.T., Lazio, T.J.L.W., 2009. The Square Kilometre Array. Proceedings of the IEEE 97, 1482–1496.

Díaz, S., Cabido, M., 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16, 646–655.

Donaldson, C.H., 1967. The immediate effects of the 1964/66 drought on the vegetation of specific study areas in the Vryburg district. Proceedings of the Annual Congresses of the Grassland Society of Southern Africa 2, 137–141.

Dreber, N., Oldeland, J., van Rooyen, G.M.W., 2011. Species, functional groups and community structure in seed banks of the arid Nama Karoo: Grazing impacts and implications for rangeland restoration. Agriculture, Ecosystems and Environment 141, 399–409.

Du Pisani, L.G., Fouché, H.J., Venter, J.C., 1998. Assessing rangeland drought in South Africa. Agricultural Systems 57, 367–380.

Du Toit, G.V.N., Snyman, H.A., Malan, P.J., 2006. Physical impact of sheep grazing on the arid Nama Karoo rangeland in South Africa. Journal of Animal Science 41, 9300.

Du Toit, J.C.O., O’Connor, T.G., Van den Berg, L., 2015. Photographic evidence of fire-induced shifts from dwarf-shrub- to grass-dominated vegetation in Nama-Karoo. South

African Journal of Botany 101, 148–152.

Du Toit, J.C.O., Van den Berg, L., O’Connor, T.G., 2014. Fire effects on vegetation in a grassy dwarf shrubland at a site in the eastern Karoo, South Africa. African Journal of Range & Forage Science 1–8.

Du Toit, L., 2016. Experiences from other jurisdictions. In: Glazewski, J., Esterhuyse, S. (Eds.), Hydraulic Fracturing in the Karoo: Critical Legal and Environmental Perspectives. Juta Publishers, Cape Town, pp. 16–33.

Du Toit, P.C. V, 1995. The grazing index method of range condition assessment. African Journal of Range and Forage Science 12, 61–67.

Du Toit, P.C. V, 1996. Karoobush Defoliation in the Arid Karoo. Journal of Range Management 49, 105–111.

Du Toit, P.C. V, Botha, W.V.D., Olivier, D.J., Blom, C.D., Meyer, E.M., Becker, H.R., Barnard, G.Z.J., 1995. Estimating grazing-index values for Karoo plants (South Africa).

Dunne, J.A., Saleska, S.R., Fischer, M.L., Harte, J., 2004. Integrating experimental and gradient methods in ecological climate change research. Ecology 85, 904–916.

Ellery, W.N., Scholes, R.J., Mentis, M.T., 1991. An initial approach to predicting the sensitivity of the South African grassland biome to climate change. South African Journal of Science 87, 499–503.

Erschbamer, B., Kiebacher, T., Mallaun, M., Unterluggauer, P., 2009. Short-term signals of climate change along an altitudinal gradient in the South Alps. Plant Ecology 202, 79–89.

Esler, K.J., Cowling, R.M., 1995. The comparison of selected life-history characteristics of Mesembryanthema species occurring on and off Mima-like mounds (heuweltjies) in semi arid southern Africa. Vegetatio 116, 41–50.

Fakir, S., Davies, E., 2016. The Economics of Shale Gas Fracking in the Karoo: What Can the American Experience Teach Us? In: Glazewski, J., Esterhuyse, S. (Eds.), Hydraulic Fracturing in the Karoo: Critical Legal and Environmental Perspectives. Juta Publishers, Cape Town, pp. 164–175.

Flahault, C., Schröter, C., 1910. Phytogeographische Nomenklatur. Berichte und Vorschläge. III. In: Congrés International de Botanique. Bruxelles, Zürich.

Glazewski, J., Esterhuyse, S., 2016. Introduction: Setting the Scene. In: Glazewski, J., Esterhuyse, S. (Eds.), Hydraulic Fracturing in the Karoo: Critical Legal and Environmental Perspectives. Juta Publishers, Cape Town, pp. 1–13.

Grace, J.B., 1987. Climatic tolerance and the distribution of plants. New Phytologist 106, 113–130.

Greenville, A.C., Dickman, C.R., Wardle, G.M., 2017. 75 years of dryland science: Trends and gaps in arid ecology literature. PLoS ONE 12, 1–10.

Hanke, W., Böhner, J., Dreber, N., Jürgens, N., Schmiedel, U., Wesuls, D., Dengler, J., 2014. The impact of livestock grazing on plant diversity: An analysis across dryland ecosystems and scales in southern Africa. Ecological Applications 24, 1188–1203.

Harrell, F.E., 2018. R Package “Hmisc.”

Hewitson, B.C., 1996. Analysis of Regional Precipitation Impacts from GCM-derived Regional Climate Change Scenarios. Unpublished progress report for the Climate Systems and Analysis Group, University of Cape Town.

Hewitson, B.C., Crane, R.G., 2006. Consensus between GCM climate change projections with empirical downscaling: Precipitation downscaling over South Africa. International Journal of Climatology 26, 1315–1337.

Hilton-Taylor, C., 1987. Phytogeography and origins of the Karoo flora. In: Cowling, R.M., Roux, P.W. (Eds.), The Karoo Biome: A Preliminary Synthesis. Part 2 - Vegetation and History. Foundation for Research Development, Pretoria, pp. 70–95.

Hoffman, M.T., 1991. Is the Karoo spreading? Veld & Flora 5–7.

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

Hoffman, M.T., Carrick, P.J., Gillson, L., West, A.G., 2009. Drought, climate change and vegetation response in the succulent karoo, South Africa. South African Journal of Science 105, 54–60.

Hoffman, M.T., Cousins, B., Meyer, T., Petersen, A., Hendricks, H., 1999. Historical and contemporary land use and the desertification of the Karoo. In: Dean, W.R.J., Milton, S.J. (Eds.), The Karoo: Ecological Patterns and Processes. Cambridge University Press, London, pp. 257–273.

Hoffman, M.T., Cowling, R.M., 1987. Plant physiognomy, phenology and demography. The Karoo Biome: a preliminary synthesis. Part 2 – Vegetation and history.

Hoffman, M.T., Cowling, R.M., 1990. Vegetation change in the semi-arid eastern Karoo over the last 200 years: an expanding Karoo - fact or fiction? South African Journal of Science 86, 286–294.

Hudson, B.D., 1994. Soil organic matter and available water capacity. Journal of Soil and Water Conservation 49, 189–194.

Illius, A., 2000. Another two unique biomes? Trends in Ecology & Evolution 15, 124.

Jonas, J.L., 2009. MeerKAT - The South African array with composite dishes and wide-band single pixel feeds. Proceedings of the IEEE 97, 1522–1530.

Kieft, T.L., White, C.S., Loftin, S.R., Aguilar, R., Craig, J.A., Skaar, D.A., 1998. Temporal Dynamics in Soil Carbon and Nitrogen Resources at a Grassland-Shrubland Ecotone. Ecology 79, 671–683.

Koch, G.W., Vitousek, P.M., Steffen, W.L., Walker, B.H., 1995. Terrestrial transects for global change research. Vegetatio 121, 53–65.

Körner, C., 2007. The use of “altitude” in ecological research. Trends in Ecology & Evolution 22, 569–574.

Kraaij, T., Milton, S.J., 2006. Vegetation changes (1995–2004) in semi-arid Karoo shrubland, South Africa: effects of rainfall, wild herbivores and change in land use. Journal of Arid Environments 64, 174–192.

Kruskal, J.B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29, 1–27.

Laing, M. V, 1994. Drought Monitoring and Advisory Services in South Africa. Drought Network News.

Lauenroth, W.K., Dodd, J.L., Sims, P.L., 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36, 211–222.

Levin, S.A., 1992. The Problem of Pattern and Scale in Ecology. Ecology 73, 1943–1967.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., Garcia-Gomez, M., Bowker, M.A., Soliveres, S., Escolar, C., Garcia-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceicao, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitan, J., Gatica, M.G., Ghiloufi, W., Gomez-Gonzalez, S., Gutierrez, J.R., Hernandez, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramirez-Collantes, D.A., Romao, R., Tighe, M., Torres-Diaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012. Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. Science 335, 214–218.

Mason, S., Waylen, P.R., Mimmack, G.M., Rajaratnam, B., Harrison, J.M., 1999. Change in extreme rainfall events in South Africa. Climatic Change 41, 249–257.

Masubelele, M.L., Hoffman, M.T., Bond, W.J., 2015. Biome stability and long-term vegetation change in the semi-arid, south-eastern interior of South Africa: A synthesis of repeat photo-monitoring studies. South African Journal of Botany 101, 1–9.

McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.

Meadows, M.E., 2003. John Acocks and the expanding Karoo hypothesis. South African Journal of Botany 69, 62–67.

Medinski, T. V, Mills, A.J., Esler, K.J., Schmiedel, U., Jurgens, N., 2010. Do soil properties constrain species richness? Insights from boundary line analysis across several biomes in south western Africa. Journal of Arid Environments 74, 1052–1060.

Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C., Powrie, L.W., 2002. Assessing the Vulnerability of Species Richness to Anthropogenic Climate Change in a Biodiversity Hotspot. Global Ecology and Biogeography 11, 445–451.

Midgley, G.F., Rutherford, M.C., Bond, W.J., Barnard, P., 2008. The heat is on... Impacts of climate change on plant diversity in South Africa.

Milchunas, D.G., Forwood, J.R., Lauenroth, W.K., 1994. Productivity of Long-Term Grazing Treatments in Response to Seasonal Precipitation. Journal of Range Management 47, 133–139.

Milton, S.J., 1994. Growth , flowering and recruitment of shrubs in grazed and in protected rangeland in the arid Karoo , South Africa. Vegetatio 17–27.

Milton, S.J., Dean, W.R.J., 1995. South Africa’s arid and semiarid rangelands: why are they changing and can they be restored? Environmental Monitoring and Assessment 37, 245–264.

Milton, S.J., Dean, W.R.J., Du Plessis, M.A., Roy, W., 1994. A Conceptual Model of Arid Rangeland Degradation. BioScience 44, 70–76.

Milton, S.J., Yeaton, R.I., Dean, W.R.J., Vlok, J.H.J., 1997. Succulent Karoo. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Ed.), Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 99–129.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global Biodiversity Conservation: The Critical Role of Hotspots. In: Zachos, F.E., Habe, J.C. (Eds.), Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas. Springer-Verlag Berlin Heidelberg, pp. 3–22.

Moncrieff, G.R., Scheiter, S., Slingsby, J.A., Higgins, S.I., 2015. Understanding global change impacts on South African biomes using Dynamic Vegetation Models. South African

Journal of Botany 101, 16–23.

Mucina, L., Jürgens, N., Le Roux, A., Rutherford, M.C., Schmiedel, U., Esler, K.J., Powrie, L.W., Desmet, P.G., Milton, S.J., 2006a. Succulent Karoo Biome. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, pp. 220–299.

Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Mucina, L., Rutherford, M.C., Palmer, A.R., Milton, S.J., Scott, L., Lloyd, J.W., van der Merwe, B., Hoare, D.B., Bezuidenhout, H., Vlok, J.H.J., Euston-Brown, D.I.W., Powrie, L.W., Dold, A.P., 2006b. Nama-Karoo Biome. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, pp. 325–347.

Muller, K., O’Connor, T.G., Henschel, J.R., 2016. Impact of a severe frost event in 2014 on woody vegetation within the Nama-Karoo and semi-arid savanna biomes of South Africa. Journal of Arid Environments 133, 112–121.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nakazawa, M., 2018. R Package “fmsb.”

Novellie, P., 1989. Recommended stocking rates for large herbivores in the Karoo National Park. Internal Report.

Noy-Meir, I., 1973. Desert Ecosystems: Environment and Producers. Annual Review of Ecology and Systematics 4, 25–51.

Nyakairu, G.W.A., Koeberl, C., 2001. Mineralogical and chemical composition and distribution of rare earth elements in clay-rich sediments from central Uganda. Geochemical Journal 35, 13–28.

O’Connor, T.G., Pickett, G.A., 1992. The Influence of Grazing on Seed Production and Seed Banks of Some African Savanna Grasslands. Journal of Applied Ecology 29, 247–260.

O’Connor, T.G., Roux, P.W., 1995. Vegetation changes (1949-71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. Journal of Applied Ecology 32, 612–626.

Oberholzer, B., Lawson, Q., Klapwijk, M., Young, G., Anderson, M., Orton, J., 2016. Visual, Aesthetic and Scenic Resources. In: Scholes, R., Lochner, P., Schreiner, G., Snyman-Van der Walt, L., de Jager, M. (Eds.), Shale Gas Development in the Central Karoo: A Scientific

Assessment of the Opportunities and Risks. CSIR, Pretoria.

Oksanen, J., Kindt, R., Guillaume Blanchet, F., Legendre, P., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. R Package “vegan.”

Ooi, M.K.J., Auld, T.D., Denham, A.J., 2012. Projected soil temperature increase and seed dormancy response along an altitudinal gradient: Implications for seed bank persistence under climate change. Plant and Soil 353, 289–303.

Osmond, C.B., Austin, M.P., Berry, J.A., Billings, W.D., Boyer, J.S., Dacey, J.W.H., Nobel, P.S., Smith, S.D., Winner, W.E., 1987. Stress Physiology and the Distribution of Plants. BioScience 37, 38–48.

Palmer, A.R., 1989. The vegetation of the karoo nature reserve, Cape Province. I: A phytosociological reconnaissance. South African Journal of Botany 55, 215–230.

Palmer, A.R., Cowling, R.M., 1994. An investigation of topo-moisture gradients in the eastern Karoo, South Africa, and the identification of factors responsible for species turnover. Journal of Arid Environments 26, 135–147.

Palmer, A.R., Hoffman, M.T., 1997. Nama-Karoo. In: Cowling, R.M., Richardson, D.M., Pierce, S.E. (Eds.), Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 167–188.

Palmer, A.R., Novellie, P.A., Lloyd, J.W., 1999. Community patterns and dynamics. In: Dean, W.R.J., Milton, S.J. (Eds.), The Karoo: Ecological Patterns and Processes. Cambridge University Press, Cambridge, pp. 208–223.

Partridge, T.C., 1997. Evolution of landscapes. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 5–20.

Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), Long-Term Studies in Ecology: Approaches and Alternatives. Springer-Verlag, New York, pp. 110–135.

Pickett, S.T.A., Cadenasso, M.L., 1995. Landscape Ecology: Spatial Heterogeneity in Ecological Systems. Science 269, 331–334.

Pienaar, E., Esler, K.J., Mucina, L., 2004. Vegetation of mesas and surrounding plains in the southeastern Nama Karoo, South Africa. South African Journal of Botany 70, 540–558.

Podani, J., Czárán, T., Bartha, S., 1993. Pattern, area and diversity: the importance of spatial scale in species assemblages. Abstracta Botanica 17, 37–51.

R Development Core Team, 2011. R: A Language and Environment for Statistical

Computing.

Rahlao, S.J., Hoffman, M.T., Todd, S.W., McGrath, K., 2008. Long-term vegetation change in the Succulent Karoo, South Africa following 67 years of rest from grazing. Journal of Arid Environments 72, 808–819.

Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz, P., Thuiller, W., Guisan, A., 2009. Climate change and plant distribution: Local models predict high-elevation persistence. Global Change Biology 15, 1557–1569.

Retuerto, R., Carballeira, A., 2004. Estimating plant responses to climate by direct gradient analysis and geographic distribution analysis. Plant Ecology 170, 185–202.

Reynolds, J.F., Stafford Smith, D.M., Lambin, E.F., Turner II, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. Science 316, 847–51.

Richwien, B.A., 1977. The damming effect of the southern Appalachians. University of Wisconsin.

Riginos, C., Hoffman, M.T., 2003. Changes in population biology of two succulent shrubs along a grazing gradient. Journal of Applied Ecology 40, 615–625.

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., 2017. Package “MASS.”

Rouault, M., Richard, Y., 2005. Intensity and spatial extent of droughts in southern Africa. Geophysical Research Letters 32, 2–5.

Rubin, F., Palmer, A.R., 1996. The physical environment and major plant communities of the Karoo National Park, South Africa. Koedoe 39, 25–52.

Rutherford, M., Mucina, L., Powrie, L., 2006. Biomes. In: Biomes and Bioregions of Southern Africa. pp. 31–51.

Rutherford, M.C., Midgley, G.F., Bond, W.J., Powrie, L.W., Musil, C.F., Roberts, R., Allsopp, J., 1999. South African country study on climate change.

Rutherford, M.C., Mucina, L., Powrie, L.W., 2003. Nama-karoo veld types revisited: a numerical analysis of original Acocks’ field data. South African Journal of Botany 69, 52–61.

Rutherford, M.C., O’Callaghan, M., Powrie, L.W., Hurford, J.L., Schulze, R.E., 1996. Predicting survival in new environments through analytical GIS application. Environmental Software 11, 113–121.

Rutherford, M.C., Westfall, R.H., 1994. Biomes of Southern Africa. An objective characterisation. Memoirs of the Botanical Survey of South Africa 63, 1–94.

Sala, O.E., Parton, W.J., Joyce, L.A., Lauenroth, W.K., 1988. Primary production of the central grassland region of the United States. Ecology 69, 40–45.

Scheiter, S., Langan, L., Higgins, S., 2013. Next generation dynamic global vegetation models: learning from community ecology. New Phytologist 198, 957–969.

Schimper, A.F.W., 1903. Plant Geography upon a Physiological Basis. Oxford University Press, Oxford.

Schmiedel, U., Jürgens, N., 1999. Community structure on unusual habitat islands: quartz-fields in the Succulent Karoo, South Africa. Plant Ecology 142, 57–69.

Schmiedel, U., Kühne, N., Twerski, A., Oldeland, J., 2015. Small-scale soil patterns drive sharp boundaries between succulent “dwarf” biomes (or habitats) in the arid Succulent Karoo, South Africa. South African Journal of Botany 101, 129–138.

Shiponeni, N., Allsopp, N., Carrick, P.J., Hoffman, M.T., 2011. Competitive interactions between grass and succulent shrubs at the ecotone between an arid grassland and succulent shrubland in the Karoo. Plant Ecology 212, 795–808.

Shmida, A., 1984. Whittaker’s plant diversity sampling method. Israel Journal of Botany 33, 41–46.

Shmida, A., Wilson, M. V, 1985. Biological Determinants of Species Diversity. Journal of Biogeography 12, 1–20.

Shreve, F., 1911. The influence of low temperatures on the distribution of the giant cactus. The Plant World 14, 136–146.

Silvertown, J., 2004. Plant coexistence and the niche. Trends in Ecology and Evolution 19, 605–611.

Silvertown, J., Araya, Y., Gowing, D., 2015. Hydrological niches in terrestrial plant communities: A review. Journal of Ecology 103, 93–108.

Skowno, A., Holness, S., Desmet, P.G., 2009. Biodiversity Assessment of the Central Karoo District Municipality - Final Report.

Smith, A.B., 1999. Hunters and herders in the karoo landscape. In: Dean, W.R.J., Milton, S.J. (Eds.), The Karoo: Ecological Patterns and Processes. Cambridge University Press, Cambridge, pp. 243–256.

Stanton, M.L., Rejmánek, M., Galen, C., 1994. Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorada, U.S.A. Arctic and Alpine Research 26, 364–374.

Stohlgren, T.J., Falkner, M.B., Schell, L.D., 1995. A Modified-Whittaker nested vegetation sampling method. Vegetatio 117, 113–121.

Talbot, W.J., 1961. Land utilization in the arid regions of southern Africa. Part I. South Africa: A history of land use in arid regions. Arid Zones Research 17, 299–338.

Tilman, D., 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, New Jersey.

Tilman, D., 2001. Functional Diversity. In: Encyclopedia of Biodiversity. Academic Press, pp. 587–596.

Todd, S.W., Hoffman, M.T., 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecology 142, 169–178.

Todd, S.W., Hoffman, M.T., 2009. A fence line in time demonstrates grazing-induced vegetation shifts and dynamics in the semiarid Succulent Karoo. Ecological Applications 19, 1897–1908.

Todd, S.W., Hoffman, M.T., Henschel, J.R., Cardoso, A.W., Brooks, M., Underhill, L.G., 2016. The potential impacts of fracking on biodiversity of the Karoo Basin, South Africa. In: Esterhuyse, S., Glazeweski, J. (Eds.), Hydraulic Fracturing in the Karoo: Critical Legal and Environmental Perspectives. Juta Publishers, Cape Town, pp. 278–301.

Townsend, A.R., Vitousek, P.M., Trumbore, S.E., 1995. Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. Ecology 76, 721–733.

Van der Merwe, H., Van Rooyen, M.W., 2011. Life form spectra in the Hantam-Tanqua-Roggeveld, South Africa. South African Journal of Botany 77, 371–380.

van der Walt, P.T., 1980. A phytosociological reconnaissance of the Mountain Zebra National Park. Koedoe 23, 1–32.

van N. du Toit, G., Snyman, H.A., Malan, P.J., 2009. Physical impact of grazing by sheep on soil parameters in the Nama Karoo subshrub/grass rangeland of South Africa. Journal of Arid Environments 73, 804–810.

Van Rooyen, M.W., Theron, G.K., Grobbelaar, N., 1990. Life form and dispersal spectra of the flora of Namaqualand, South Africa. Journal of Arid Environments 19, 133–145.

Van Wyk, A.E., Smith, G.F., 2001. Regions of floristic endemism in southern Africa: a review with emphasis on succulents. Umdaus Press, Pretoria.

Veech, J.A., Summerville, K.S., Crist, T., Gering, J.C., 2002. The Additive Partitioning of Species Diversity: Recent Revival of an Old Idea. Oikos 99, 3–9.

Vorster, M., Botha, P., Hobson, F.O., 1983. The Utilization of Karoo Veld by Livestock. In: Proceedings of the Grassland Society of South Africa. pp. 35–39.

Wagner, H.H., Wildi, O., Ewald, K.C., 2000. Additive portioning of plant species diversity in an agricultural mosaic landscape. Landscape Ecology 15, 219–227.

Webb, W., Szarek, S., Lauenroth, W.K., Kinerson, R., Smith, M., 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. Ecology 59, 1239–1247.

Werger, M.J.A., 1986. The Karoo and southern Kalahari. In: Evenari, M., Noy- Meir, I., Goodall, D.W. (Eds.), Hot Deserts and Arid Shrublands. Elsevier, Amsterdam, pp. 283–359.

Westoby, M., 1980. Elements of a theory of vegetation dynamics in arid rangelands. Israel Journal of Botany 28, 169–194.

Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic Management for Rangelands Not at Equilibrium. Journal of Range Management 42, 266–274.

Whittaker, R.H., 1977. Evolution of species diversity on land communities. In: Evolutionary Biology. pp. 1–67.

Whittaker, R.H., Levin, S.A., 1977. The Role of Mosaic Phenomena in Natural Communities. Theoretical Population Biology 39, 117–139.

Wickham, H., 2016. R Package ‘ggplot2.’

Wiegand, T., Milton, S.J., Wissel, C., 1995. A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. Ecology 76, 2205–2221.

Williams, C.B., 1964. Patterns in the balance of nature. Academic Press, London.

Williams, S.E., Bolitho, E.E., Fox, S., 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. Proceedings of the Royal Society: Biological Sciences 270, 1887–92.

World Resources Institute, 2005. Millennium Ecosystem Assessment, Ecosystems and Human Well-Being: Desertification Synthesis. Washington, DC.

Yeaton, R.I., Esler, K.J., 1990. The dynamics of a succulent karoo vegetation - A study of species association and recruitment. Vegetatio 88, 103–113.

Ziervogel, G., New, M., Archer, E.R.M., Midgley, G., Taylor, A., Hamann, R., Stuart-Hill, S., Myers, J., Warburton, M., 2014. Climate change impacts and adaptation in South Africa. Wiley Interdisciplinary Reviews: Climate Change 5, 605–620.

Appendix

Appendix 1: Results of forward and backward stepwise model selection based on exact Akaike information criterion (AIC) for overall species richness, and relative cover for the five dominant growth forms. Models with the lowest exact AIC values were selected as the final models (see Fig. 13).

Model run	Predictor variables	Model AIC
Response variable: Overall species richness		
1	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	294.77
2	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [K] + [P] + NH_4	292.8
3	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [K] + [P] + NH_4	290.85
4	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [K] + NH_4	288.99
5	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + NH_4	287.61
6	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MinCold + Sand + [Ca] + NH_4	286.8
7	Habitat + Altitude + Longitude + MAP + MPAN + Frost + MinCold + Sand + [Ca] + NH_4	285.35
8	Habitat + Altitude + MAP + MPAN + Frost + MinCold + Sand + [Ca] + NH_4	284.06
9	Habitat + Altitude + MAP + MPAN + Frost + MinCold + Sand + [Ca]	283.69
10	Habitat + Altitude + MAP + Frost + MinCold + Sand + [Ca]	283.23

Response variable: LWS relative cover		
1	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	248.89
2	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [K] + [P] + NH_4	246.93
3	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [K] + [P]	244.97
4	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [P]	243.03
5	Habitat + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [P]	241.08
6	Habitat + Longitude + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [P]	239.25
7	Habitat + Longitude + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [P]	237.55
8	Habitat + Longitude + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca]	236.01
9	Habitat + Longitude + MAT + MPAN + Frost + MaxHot + Sand + [Ca]	234.57
10	Habitat + MAT + MPAN + Frost + MaxHot + Sand + [Ca]	232.91
11	Habitat + MAT + MPAN + Frost + MaxHot + Sand	232.04
12	Habitat + MAT + MPAN + Frost + Sand	231.86
13	Habitat + MPAN + Frost + Sand	230.82
Response variable: PG relative cover		
1	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	193.46
2	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [K] + [P] + NH_4	191.55

3	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [P] + NH_4	189.7
4	Habitat + Altitude + Longitude + MAP + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + [P] + NH_4	188.08
5	Habitat + Altitude + Longitude + MAP + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na] + NH_4	186.5
6	Habitat + Altitude + Longitude + MAP + MPAN + Frost + MaxHot + MinCold + Sand + [Ca] + [Na]	184.91
7	Habitat + Altitude + Longitude + MAP + MPAN + Frost + MaxHot + MinCold + [Ca] + [Na]	183.25
8	Habitat + Longitude + MAP + MPAN + Frost + MaxHot + MinCold + [Ca] + [Na]	182.24
9	Habitat + Longitude + MAP + MPAN + Frost + MaxHot + MinCold + [Na]	181.52
10	Longitude + MAP + MPAN + Frost + MaxHot + MinCold + [Na]	180.81
11	Longitude + MAP + MPAN + Frost + MaxHot + MinCold	179.86
12	Longitude + MAP + MPAN + Frost + MaxHot	178.97
Response variable: AG relative cover		
1	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	98.52
2	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	96.52
3	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MinCold + pH + [Ca] + [Na] + [K] + [P] + NH_4	94.77
4	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MinCold + pH + [Ca] + [Na] + [K] + [P]	93.01
5	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MinCold + pH + [Ca] + [Na] + [K]	91.24
6	Habitat + Altitude + MAP + MAT + MPAN + Frost + MinCold + pH + [Ca] + [Na] + [K]	89.52

7	Habitat + Altitude + MAP + MAT + MPAN + Frost + MinCold + pH + [Ca] + [Na]	87.83
8	Habitat + Altitude + MAP + MAT + MPAN + Frost + MinCold + [Ca] + [Na]	86.13
9	Habitat + Altitude + MAP + MAT + MPAN + Frost + [Ca] + [Na]	84.99
10	Habitat + Altitude + MAP + MAT + MPAN + Frost + [Ca]	84.31
Response variable: PF relative cover		
1	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	105.38
2	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + NH_4	103.46
3	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MinCold + pH + Sand + [Ca] + [Na] + [K] + NH_4	101.58
4	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MinCold + pH + [Ca] + [Na] + [K] + NH_4	99.67
5	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MinCold + [Ca] + [Na] + [K] + NH_4	98.19
6	Habitat + Altitude + Longitude + MAT + MPAN + Frost + MinCold + [Ca] + [Na] + [K] + NH_4	97.54
7	Habitat + Altitude + MAT + MPAN + Frost + MinCold + [Ca] + [Na] + [K] + NH_4	96.3
8	Habitat + Altitude + MAT + MPAN + Frost + MinCold + [Ca] + [Na] + [K]	95.36
9	Habitat + Altitude + MAT + MPAN + Frost + MinCold + [Ca] + [Na]	94.29
10	Habitat + Altitude + MAT + MPAN + Frost + MinCold + [Ca]	93.31
Response variable: LSS relative cover		
1	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	100.11

2	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P]	98.11
3	Habitat + Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [K] + [P]	96.11
4	Habitat + Altitude + Longitude + MAP + MAT + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [K] + [P]	94.17
5	Altitude + Longitude + MAP + MAT + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [K] + [P]	92.28
6	Altitude + Longitude + MAP + MAT + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [P]	90.61
7	Altitude + Longitude + MAP + MAT + Frost + MaxHot + MinCold + pH + [Ca] + [P]	88.91
8	Altitude + Longitude + MAP + Frost + MaxHot + MinCold + pH + [Ca] + [P]	87.5
9	Altitude + Longitude + MAP + Frost + MaxHot + MinCold + [Ca] + [P]	86.4
10	Altitude + Longitude + Frost + MaxHot + MinCold + [Ca] + [P]	85.87
11	Altitude + Frost + MaxHot + MinCold + [Ca] + [P]	84.36
12	Altitude + MaxHot + MinCold + [Ca] + [P]	82.75
13	Altitude + MaxHot + [Ca] + [P]	81.48

Appendix 2: Results of forward and backward stepwise model selection based on exact Akaike information criterion (AIC) for overall Bray-Curtis dissimilarity between plains and slope habitats with respect to species richness, and relative cover for five key plant functional types (PFTs). Models with the lowest exact AIC values were selected as the final models (see Fig. 20).

Model run	Predictor variables	Model AIC
Response variable: Overall species richness		
1	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	128.01
2	Altitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	126.01
3	Altitude + MAP + MAT + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	124.06
Response variable: Woody shrub relative cover		
1	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	135.76
2	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [K] + [P] + NH_4	133.77
3	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [K] + [P]	131.83
4	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + [Ca] + [K] + [P]	129.86
5	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + [Ca] + [K] + [P]	127.96
6	Altitude + Longitude + MAP + MAT + MPAN + MaxHot + MinCold + [Ca] + [K] + [P]	126.10
7	Altitude + Longitude + MAP + MAT + MPAN + MaxHot + MinCold + [Ca] + [P]	124.93
8	Altitude + Longitude + MAP + MPAN + MaxHot + MinCold + [Ca] + [P]	124.00
9	Altitude + Longitude + MAP + MPAN + MinCold + [Ca] + [P]	123.37
10	Altitude + Longitude + MAP + MPAN + MinCold + [Ca]	122.66

Response variable: Perennial grass & sedge relative cover		
1	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	76.38
2	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	74.45
3	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + pH + Sand + [Ca] + [Na] + [K] + [P]	72.62
4	Altitude + Longitude + MAP + MAT + Frost + MaxHot + pH + Sand + [Ca] + [Na] + [K] + [P]	71.48
5	Altitude + Longitude + MAP + Frost + MaxHot + pH + Sand + [Ca] + [Na] + [K] + [P]	70.44
6	Altitude + Longitude + MAP + Frost + MaxHot + pH + Sand + [Ca] + [Na] + [K]	69.80
7	Altitude + Longitude + MAP + Frost + MaxHot + pH + Sand + [Ca] + [K]	68.80
8	Altitude + Longitude + MAP + Frost + MaxHot + pH + Sand + [K]	67.38
9	Altitude + Longitude + MAP + Frost + MaxHot + Sand + [K]	65.81
10	Altitude + Longitude + MAP + Frost + MaxHot + Sand	65.42
11	Altitude + Longitude + MAP + Frost + MaxHot	64.08
Response variable: Annual grass relative cover		
1	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	39.62
2	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Na] + [K] + [P] + NH_4	37.62
3	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Na] + [K] + NH_4	35.88
4	Altitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Na] + [K] + NH_4	34.39
5	Altitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + [Na] + [K] + NH_4	32.94

6	Altitude + MAP + MAT + MPAN + MaxHot + MinCold + pH + [Na] + [K] + NH_4	31.32
7	Altitude + MAP + MAT + MPAN + MaxHot + MinCold + pH + [K] + NH_4	29.74
8	Altitude + MAP + MAT + MaxHot + MinCold + pH + [K] + NH4	28.52
9	Altitude + MAT + MaxHot + MinCold + pH + [K] + NH_4	26.70
10	Altitude + MAT + MaxHot + pH + [K] + NH_4	25.56
11	Altitude + MaxHot + pH + [K] + NH_4	24.96
12	Altitude + pH + [K] + NH_4	24.12
13	Altitude + pH + [K]	23.44
14	pH + [K]	22.95
Response variable: Forb, geophyte & parasite relative cover		
1	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	116.49
2	Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	114.64
3	Longitude + MAP + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	113.03
4	Longitude + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	111.59
5	Longitude + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Na] + [K] + P + NH_4	110.36
6	Longitude + MPAN + Frost + MaxHot + pH + Sand + [Na] + [K] + [P] + NH_4	109.10
Response variable: Succulent shrub relative cover		
1	Altitude + Longitude + MAP + MAT + MPAN + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	66.49
2	Altitude + Longitude + MAP + MAT + Frost + MaxHot + MinCold + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	64.49
3	Altitude + Longitude + MAP + MAT + Frost + MaxHot + pH + Sand + [Ca] + [Na] + [K] + [P] + NH_4	62.51

4	Altitude + Longitude + MAP + MAT + Frost + MaxHot + pH + Sand + [Na] + [K] + [P] + NH_4	60.62
5	Altitude + MAP + MAT + Frost + MaxHot + pH + Sand + [Na] + [K] + [P] + NH_4	58.95
6	Altitude + MAP + MAT + Frost + MaxHot + pH + Sand + [Na] + [K] + NH_4	57.63
7	Altitude + MAT + Frost + MaxHot + pH + Sand + [Na] + [K] + NH_4	57.16
8	Altitude + MAT + Frost + pH + Sand + [Na] + [K] + NH_4	55.69
9	Altitude + MAT + Frost + pH + [Na] + [K] + NH_4	55.51
10	Altitude + MAT + Frost + pH + [Na] + [K]	54.59
11	Altitude + MAT + Frost + pH + [K]	53.31