Expanding grasslands? Structural biome shifts in the dryland rangelands of the eastern Karoo revealed through long-term observation of climate, vegetation and land use change

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Declaration

I, Gina Arena, hereby declare that the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. I grant the University permission to reproduce, in whole or in part, any portion of the thesis for the purpose of research in any manner whatsoever.

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Abstract

Biome shifts caused by climate and land use change threaten global dryland ecosystems and the provision of services needed to sustain human livelihoods. The overarching drivers of early 20th century dryland degradation in South Africa have been attributed to high stocking rates and overgrazing by domestic livestock. Predictions of an eastward encroachment of shrublands into the semiarid grasslands, and resultant declines in productivity, emerged in the 1950s based on concerns that livestock overgrazing would persist. In response to these concerns, appropriate research and government interventions were implemented to address rangeland and livestock mismanagement. However, the role of long-term climate as a driver of semiarid vegetation change was poorly understood, particularly for changes occurring at the interface of the Nama-Karoo and Grassland biomes where shrubland encroachment could be detected along a gradient of increasing annual rainfall. It is this gradient that controls the natural biome transition from shrub-dominance to grass-dominance. However, the prediction of shrubland encroachment was refuted when research in the early 1990s revealed that the vegetation of this region (known as the 'eastern Karoo') had undergone an increase in grass cover; a trend that persisted into the early 2000s. Questions around the influence of changing rainfall patterns on driving this increase in grassiness have since been investigated at a single location in the eastern Karoo. Findings indicated that an increase in annual rainfall drove the increase in grass cover, but the generality of this relationship across the broader rainfall gradient of the biome transition has not been examined. In addition to rainfall, grazing by domestic livestock has had a significant influence on the relative proportion of grasses and shrubs in the eastern Karoo. While other studies have alluded to changes in land use, few data have been presented and the relative influence of land use change has usually been under-estimated. The availability of historical data from past vegetation surveys, climate station records and magisterial district livestock censuses makes it possible to develop a more comprehensive synthesis of how vegetation has changed across the rainfall gradient in order to address questions around biome shifts. This thesis, therefore, aimed to determine whether a biome shift is related to a broader shift in the climate regime through the assessment of long-term vegetation change along the rainfall gradient, in relation to climate and land use change since the early 20th century.

Annual and seasonal trend analysis was applied to monthly rainfall, temperature, pan evaporation, evapotranspiration and wind speed data. Trends indicated that 32% of sites in the eastern Karoo showed an increase in annual rainfall between 1874 and 2019, which was also defined by a significant shift to increasing early summer rainfall. A concomitant trend of decreasing annual, and late summer rainfall, was detected at 32% of sites located on the mesic end of the rainfall gradient. Monthly maximum temperature between 1971 and 2019 also increased by 1.0 °C at a rate of 0.04 ± 0.06 °Cy^{-1} and monthly minimum temperature decreased by 0.3 °C at a rate of -0.03 ± 0.11 °Cy^{-1}. Wind speed, an important driver of evaporative processes, decreased at 44% of sites since 1971 and decreasing trends in A-Pan evaporation were found at all sites. No discernible trends in evapotranspiration were detected. Declines in wind speed and evaporation were suggested to promote an increase in vegetation cover which may restore ecosystem processes and improve rangeland productivity. An analysis of multi-decadal wet-dry phases in the climate record was also undertaken using the Standardised Precipitation Index. Through this, it was observed that the rainfall regime over the eastern Karoo is defined by three significant phases over the last century: an early wet phase (1886-1902), a 70-year long dry phase (1902-1970), followed by the recent wet phase (1970-2014) that commenced with heavy rains in the mid-1970s across the summer rainfall region of southern Africa.

Long-term changes in the cover and composition of plant species and growth forms were compared between 1962 and 2018 at 27 sites using the point intercept method. Changes in species composition were determined from Bray-Curtis similarity distances. The dominant growth forms were organised along a rainfall-edaphic gradient and plant communities were further defined by altitude. Hierarchical clustering of species cover per site recognised this underlying gradient. Thus, sites were categorised into three vegetation units: 'Karoo', 'Escarpment' and 'Grassland'. Results showed that vegetation cover increased, and bare ground cover decreased, significantly at all but one site. Perennial grasses increased by 20%, 24% and 35% at Karoo, Escarpment and Grassland sites, respectively. Palatable dwarf shrubs increased by 15% at Karoo sites. These growth form changes translated to a broader-scale shift in the relative dominance of dwarf shrubs to grasses at 59% of sites in the Nama-Karoo biome, coinciding with the spatial pattern of increasing early summer rainfall and temperature. However, a multivariate analysis provided minimal evidence of species shifts between vegetation units or biomes, suggesting that compositional stability was maintained across the rainfall gradient. Percent changes in the cover of grasses and dwarf shrubs were analysed in relation to the climatic and edaphic parameters using multiple regression analysis, but no significant linear relationships were found. However, summer rainfall and temperature combined explained 26% of the variation in the percent change in grass cover. The effect of these changes on rangeland grazing capacity (ha/Large Stock Unit) was also evaluated using the ecological index method of the assessment of veld condition. There was a fivefold improvement in grazing capacity at Karoo sites and a twofold improvement at Escarpment and Grassland sites. Changes in the cover of grasses, dwarf shrubs and trees were additionally determined through fixed-point repeat photography at 85 sites on two different landforms, plains and hillslopes. A shift towards grass dominance relative to dwarf shrubs was estimated at 90% of sites located on the plains and at 100% of sites located on the hillslopes in the Nama-Karoo. Variable trends were found at Grassland sites in both landforms. Tree cover remained unchanged in both biomes.

Agricultural livestock census data at the magisterial district-level showed a fivefold decrease in sheep numbers between 1911 and 2017 while the number of cattle and equine animals remained largely unchanged. Goat numbers fluctuated over time in response to the demands for Angora mohair. Supporting perceptions of significant reductions in livestock numbers since the 1960s were conveyed by 18 local landowners as derived from semi-structured interviews. The introduction of conservation-friendly grazing systems, seasonal rainfall shifts, and increased drought frequency were also perceived as important drivers of vegetation change. However, a number of socio-ecological challenges, for example, livestock losses to theft, vermin, or fire, emerged as having significantly influenced management decisions.

Therefore, the persistent structural shift in growth forms across the rainfall gradient since the 1960s has largely coincided with significant climatic shifts in rainfall and temperature. A secondary influence of long-term reductions in livestock numbers, and a change to conservation-friendly management practices, is suggested to have supported the recovery of vegetation, especially that of perennial grasses, and rangeland productivity.

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Chapter 1: General introduction

1.1. Problem statement

Global dryland ecosystems are vulnerable to land degradation that is mostly caused by a host of land use changes and by climate change (Burrell et al., 2020; Huang et al., 2016). In South Africa, semiarid and arid rangelands in the Karoo, which are used primarily for livestock agriculture, have undergone significant changes since the 19th and 20th centuries (Acocks, 1953; Hoffman et al., 1995; Keay-Bright & Boardman, 2009; Rutherford & Powrie, 2010; Tidmarsh, 1948). The western arid Karoo, which is dominated by dwarf shrubland vegetation, transitions into a mixture of shrublands and grasslands towards the central-eastern parts of South Africa as mean annual rainfall increases in an easterly direction. By the mid-1950s, dire concerns of shrubland expansion were conveyed after the negative effects of livestock overgrazing had been observed across the Karoo, particularly through the loss of perennial grass cover (Acocks, 1953). Shrubland expansion was thus predicted to have advanced eastwards into the mesic grasslands and would eventually lead to reduced rangeland productivity across the rainfall gradient (Acocks, 1953). Land degradation was tackled through various government, policy and management interventions and rangeland research (Roux & Vorster, 1983a). By the 1990s, however, in contradiction to Acocks' prediction of an expanding Karoo, an unexpected increase in grass cover was reported across the rainfall gradient between the Nama-Karoo and Grassland biomes of South Africa (Hoffman & Cowling, 1990). These findings raised questions regarding the drivers of these changes in vegetation, particularly within the context of global warming, and provided impetus for the continuation of tracking change along this biome transition. A decade later, repeated observation revealed that a trend of increasing grassiness across the rainfall gradient had persisted (Masubelele et al., 2014, 2015b). This increase in grass cover contradicted the global trend of change in similar semiarid biome boundaries (e.g., Bestelmeyer et al., 2018; Peters, 2002). Shortly thereafter, an analysis of long-term rainfall trends at a single location indicated that increasing annual rainfall and a shift in rainfall seasonality was predominantly responsible for the increase in grass cover (Du Toit & O'Connor, 2014). However, the spatial extent of these rainfall trends remains unclear for the broader rainfall gradient, as do the trends of other interacting climate variables, such as temperature and evaporation, that could enhance grass dominance. The state-subsidised livestock reduction programmes (Baard, 1978) and development of recommended grazing capacities (Du Toit et al., 1991) have often been referred to in the literature (Hoffman et al., 1999, 2018; Masubelele et al., 2014). However, the impact of these long-term land use changes in stocking density on rangeland condition has not been examined through an analysis of species compositional change.

This thesis, therefore, aims to examine the long-term changes in rangeland vegetation along the rainfall gradient of the Nama-Karoo-Grassland biome transition (also known as the 'eastern Karoo') within the context of regional long-term trends in climate and land use change. The long-term tracking of change using historical datasets is useful in addressing existing knowledge gaps and to gain a greater understanding of how ecosystems have been affected by past and present anthropogenic and climate change factors. This study makes a novel contribution to the existing literature on land degradation and biome boundary vegetation change in South Africa (Potts et al., 2015a, 2015b) and offers new insights into climate-driven growth form shifts in the eastern Karoo.

A number of historical vegetation surveys located along the biome transition, conducted by Dr. Piet Roux in the late 1950s to 1960s (Roux, 1969), have provided an opportunity to examine questions of the nature and extent of vegetation change. Accompanying historical landscape photographs capturing the visual conditions at many of these sites were also available for re-photographing, thus incorporating a second approach of comparison between past and present conditions at a coarser resolution of vegetation units across multiple landforms. Long-term climate and livestock census data, which have been recorded by government departments over the past century, were also used in the assessment of long-term change. The global vegetation changes of semiarid grassland-shrubland biome boundaries ascribe to ongoing woody plant encroachment, increasing dryland expansion and plant invasions (Bestelmeyer et al., 2018; Eldridge et al., 2011; Huang et al., 2017). The thesis, however, makes a significant contribution to this international literature by offering a uniquely different perspective of change in semiarid environments, with particular emphasis on the contrasting trend of expanding grasslands. The mechanisms behind these vegetation changes are investigated through a detailed climate trends analysis and are supported by land use information and livestock census data. The study is characterised by a combination of the following important considerations to assessing broad-scale vegetation change, i) it addresses vegetation change at multiple spatial scales and ii) over decadal timeframes, iii) it uses more than one methodological approach, and iv) it incorporates local knowledge. The study thus integrates diverse data and knowledge sources and uses interdisciplinary methods and approaches to understand long-term change in landscapes of the eastern Karoo (Sayre et al., 2012).

This introduction first outlines the problems facing global dryland rangelands, followed by a brief history of the global narrative of desertification, which was influenced by a dynamic evolution of rangeland ecological theories. After outlining the different rangeland theories and the debates that have emerged around each, it is proposed that the semiarid eastern Karoo is best described and understood as a dynamic and heterogeneous landscape transitioning between multiple stable vegetation states at multiple spatial scales varying significantly over several timeframes. This dynamic system is further influenced by the underlying environmental gradient that exists along a south-west to north-east biome transition. A review of the global dryland climate and land use trends and predictions, as well as those relevant to the South African context, is presented. In addition, a summary of the nature of vegetation change for semiarid biome boundaries is provided. The chapter concludes with an outline of the thesis aims and objectives and general structure of the thesis.

1.2. Dryland rangelands

1.2.1. Introduction

Global drylands, which occupy ~40% of the earth's land surface, support more than two billion people (Millennium Ecosystem Assessment, 2005). Drylands are defined by an Aridity Index of 0.65 or lower, which indicates that potential evapotranspiration is at least 50% greater than mean precipitation (Davies, 2017). Drylands are some of the most susceptible environments to degradation brought on by anthropogenic land use change and climate change (Burrell et al., 2020; Huang et al., 2016). Dryland degradation, unsurprisingly, has been an almost insurmountable challenge to understand and address in dryland research. Key to solving successful dryland conservation and sustainable use, is developing a sound understanding of the complex dynamics of dryland ecosystem processes and functions, as well as the most crucial drivers of change (IPBES, 2018; IPCC, 2019).

Drylands offer an important agricultural service to humans, mainly through providing rangeland forage to grazing livestock. Unfortunately, 19th and 20th century pastoralist practices drove many of these rangelands into severely degraded states (Call & Roundy, 1991; Milton & Dean, 1995; Oliva et al., 2016). Land degradation, which exists in all ecosystems around the world, refers generally to the long-term reduction or loss of ecological function, productivity and capacity to deliver services to people (IPBES, 2018). It is usually represented by losses in cover and biodiversity, changes in species composition, an increase in woody plants (bush encroachment), annual species and alien plants, and by severely eroded soils (Hoffman et al., 1999; Roux & Vorster, 1983b). It is also usually accompanied by an overall reduction in grazing capacity and animal production (Bestelmeyer et al., 2018; Pierce et al., 2019). Reduction or complete removal of livestock and active rehabilitation over varying timeframes has, in some cases, assisted rangeland recovery indicating that management-induced biotic change is reversible (Pérez et al., 2019). In regions where rainfall is erratic, and temperatures are extreme, rangeland recovery is usually much slower. However, management-induced changes of the abiotic environment are irreversible in such arid conditions (Call & Roundy, 1991). Ecosystems that enter 'alternate states' of either greater or lesser resilience caused by land management practices forces humans to adapt their management approaches to maintain some level of rangeland productivity. However, this is becoming increasingly difficult to achieve as drought frequency and severity increase (Falkenmark & Rockström, 2008). Therefore, it is important to address the existing knowledge gaps in dryland research in order to improve management and conservation practices to offer sustainable solutions that will support human wellbeing, livelihoods and resilience.

1.2.2. A brief history of desertification theory

Rangeland science was largely influenced by early European (western) scientific thinking in the 18th, 19th and 20th centuries. Early understanding of desertification, a term derived from desiccation theory, was widely accepted as a phenomenon where deforestation caused the climate to dry and rainfall to decrease (Davis, 2016). It was initially applied to semiarid desert environments that were created and further exacerbated by people (Behnke & Mortimore, 2016). The phrase 'encroaching Sahara', for example, was believed to describe an area that had become a desert created by the land use practices of pastoralists, which ultimately led to 'self-perpetuating droughts' such as that experienced in the Sahel in the 1970s (Behnke & Mortimore, 2016; Bovill, 1921; Giannini, 2016; Nicholson, 2000).

It became clear, however, that there was a considerable lack of understanding for the magnitude of the Sahel droughts, as well as for the processes by which land use change influenced local climate (Behnke & Mortimore, 2016; Giannini, 2016). Eventually, a greater understanding began to emerge that climate and land use systems are deeply connected. The development of dynamic predictive models, such as the El Niño-Southern Oscillation (ENSO) (Cane et al., 1986), were pivotal in broadening the scope of rangeland science. Palmer (1986) and Folland et al., (1986) found that stark contrasts in sea surface temperatures between the warmer tropical and the cooler north Atlantic oceans were the major factors in causing the Sahelian droughts. Although these droughts may, to some extent, be supressed or exacerbated by local land use changes, this new understanding and altitude of the role of climatic drivers encouraged greater distinction between local anthropogenic versus global anthropogenic influences in the literature (Nicholson, 2005).

Nevertheless, the mainstream desertification narrative became the basis for the United Nations Educational, Scientific and Cultural Organization's Arid Zone Program in the 1950s, and later for the United Nations Conference on Desertification in 1977, and the United Nations Convention to Combat Desertification in 1996 (Behnke & Mortimore, 2016). Land degradation and desertification have since been a major focus of dryland science at global, national and local scales and applied by policy and management (Briassoulis, 2019; Hoffman & Todd, 2000; Hoffman et al., 1999; Li et al., 2013; Reed et al., 2015).

1.2.3. Theoretical framework applied to rangeland science

To address the prevailing threat of land degradation and desertification, rangeland theories have evolved in parallel over time. The theoretical framework developed for natural resource management has had varying levels of success and failure in application since the 1980s. The first model applied to rangeland systems, commonly known as equilibrium theory (also the range model or succession theory), was first developed by Clements (1916). Equilibrium theory relies on a simplistic and linear tight coupling between herbivore biomass and a vegetation resource base. When herbivore numbers exceed carrying capacity, livestock biomass is lowered thereby allowing the vegetation to recover through successional processes returning vegetation to a climax state (Clements, 1916; Vetter, 2005). Coupled consumer-resource dynamics have been experimentally examined in closely managed grazing systems in the past, having provided a mechanistic basis for understanding livestock biomass-vegetation relationships (e.g., Hempson et al., 2015; Roux, 1967). Equilibrium theory provided land managers with a way to calculate optimal stocking rates in order to regulate optimal primary productivity (Briske, 2017). In South Africa, this model remains present in the assessment of rangeland condition (Du Toit, 1995, 2003) and the 'expanding Karoo' hypothesis was partly influenced by this theory (Acocks, 1953). However, this theory assumes that degradation is reversible and can be applied to all rangeland contexts, but owing to the complex nature of vegetation dynamics that exists among all rangeland systems across all spatiotemporal scales, it eventually came under scrutiny (Briske, 2017; Briske et al., 2005). As a result of the growing criticism and failure in application, the non-equilibrium (Westoby et al., 1989) and ecological resilience theories (Holling, 1973) began to emerge in rangeland science.

A common understanding had begun to take shape, in that vegetation dynamics are complex and event-driven and are influenced by a variety of stochastic abiotic factors, and that herbivore density was only secondarily important in influencing vegetation (Westoby et al., 1989). The effect of rainfall variation on vegetation growth has been investigated under various systems of sheep grazing in the eastern Karoo providing further understanding of the influence of abiotic drivers on livestock-vegetation dynamics (O'Connor & Roux, 1995). The non-equilibrium theory broadened the framework to include various state-and-transition management models, as well as the threshold concept, which are still broadly applied in the rangeland profession today (Briske et al., 2005; Wessels et al., 2007). The efficacy of the adapted state-and-transition model for the eastern Karoo (Milton & Hoffman, 1994), which was informed by data and experimental grazing-rainfall-vegetation studies (Hoffman & Cowling, 1990; O'Connor & Roux, 1995; Roux, 1967; Roux, 1969), has been most evident in its application of range health assessments (e.g., Esler et al., 2006) as well as in contextualising circumstances under which active rehabilitation of a degraded site could potentially work (Milton & Dean, 2015; Pyke et al., 2002). The concept of resilience recognises that ecosystems that prescribe to non-equilibrium dynamics are able to retain their self-organised structures and functions, while experiencing a certain level of disturbance (Gunderson, 2000). It suggests that ecosystems can enter alternate stable states in instances where the resilience of the initial state has been exceeded due to a critical threshold being surpassed (Briske, 2017; Briske et al., 2005; Gunderson, 2000; Stringham et al., 2001). A common example would be that of fire suppression in a savanna which could tip the system into an alternate state dominated by woody plants. These ideas imply that rangeland systems are in a state of non-equilibrium that can undergo multiple stable states (Ellis & Swift, 1988; Holling, 1973).

While the non-equilibrium theory has grown in popularity, critiques on both theories (Hempson et al., 2015; Illius & O'Connor, 1999; Sullivan & Rohde, 2002; Vetter, 2005) have stimulated healthy debates in the literature and increased engagement with the theory and practice (Briske et al., 2005; Derry & Boone, 2010; Milton et al., 1994; Richardson et al., 2005; Stringham et al., 2001; Wessels et al., 2007). Briske et al., (2020) have recently provided a useful review on the lessons learned from the debate concluding that rangeland systems exhibit tremendous spatial and temporal vegetation dynamics. Therefore, prescribing a single model to a system is inadequate to capture such heterogeneity.

1.2.4. Contextualising the thesis

It is through this lens that understanding decadal vegetation change in the eastern Karoo is viewed. The thesis does not attempt to identify strongly with any particular ecological theory, in this case equilibrium or non-equilibrium. Instead, it attempts to examine the efficacy of the state-and-transition model (Milton & Hoffman, 1994) by identifying changes in the critical structural thresholds (e.g., shrubland or grassland dominance, species composition, rangeland condition, grazing capacity) that have determined past and present vegetation states across a broader range of environments than was previously assessed in the eastern Karoo. Significant changes in structural thresholds affect the functional thresholds (e.g., soil water infiltration, nutrient availability) that maintain ecosystem health, productivity and human wellbeing (Briske et al., 2005). Thus, cautious inferences are made regarding future trajectories of change that could trigger transitions to potentially irreversible alternate states. Therefore, the state-and-transition model is a valuable benchmark model upon which new data and insights can build and be refined. Furthermore, continued monitoring of long-term vegetation change within the context of global change is necessary for building our understanding of the current and predicted trajectories of change which could inform local and regional policies and management.

1.3. Global and local climate and land use trends and predictions

Climate trends and predictions

Observed land surface air temperature has risen by 1.5 ºC since the pre-industrial period (1850-1900) (IPCC, 2019). Ecologically, global climate zones have shifted in many arid regions thus affecting plant and animal species ranges, abundances and seasonal activities (IPCC, 2019). Global warming has led to an increased frequency, intensity and duration of heat waves, droughts and heavy rainfall events, all which have negatively impacted food systems and security, biodiversity, human and ecosystem health and infrastructure (IPCC, 2019). Drylands are particularly vulnerable to drying trends in the climate, increases in dust storms, air temperature, evapotranspiration, the conversion of natural lands for crop agriculture or for grazing lands, urban expansion and development, and are further expected to expand in area across the globe (Feng & Fu, 2013). Yet, an increase in vegetation greening over the last 30 years has been reported over parts of Asia, Europe, the Americas, and Australia due to changes in land use, increases in nitrogen deposition, CO_2 fertilisation, and longer growing seasons (IPCC, 2019). Changes in land cover further affects global and regional climate by reducing or exacerbating warming and extreme events (IPCC, 2019). These climate and land use changes each directly and indirectly cause a loss of ecosystem services by impacting species distributions, biodiversity, vegetation cover, soil and nutrients, and exacerbate the spread of alien plants and pest outbreaks (IPBES, 2018; Ratajczak et al., 2012; Roux & Vorster, 1983b).

South Africa is an arid country, with ~91% of the area categorised as sub-humid, semiarid and arid land which is vulnerable to desertification and land degradation (Von Maltitz et al., 2019). Although there are existing gaps in understanding the mechanisms that have driven historical climate patterns and how these have varied over different time scales, it is generally agreed that a complex interplay of solar radiation, sea surface temperature changes, sea ice changes, and shifts in the temperate and tropical systems drive the climatic patterns over southern Africa (Chase et al., 2020; Humphries et al., 2019; Washington & Todd, 1999). Hence, due to its geography, the surrounding oceanic-atmospheric dynamics and steep topography (Fauchereau et al., 2003; Richard et al., 2001), the country experiences high interannual rainfall variability which is heightened during ENSO events (Jury et al., 1997; Meadows & Hoffman, 2002). Drier areas, typically in the western half of the country, exhibit a coefficient of variation of greater than 40% of the annual rainfall which contributes to higher interannual rainfall variability compared to the wetter areas in the eastern half of the country that experience a relatively stable rainfall regime (Tyson, 1986; Vogel & Drummond, 1993). The eastern Karoo is situated in the middle of the country and is located within the summer rainfall zone. Because of this it experiences a gradient of semiarid to dry sub-humid climate conditions that are predominantly responsible for the biome transition.

Reconstructive projections of historical climate over southern Africa during the Last Glacial Maximum (19-23 cal ka BP) have indicated that temperatures were at least 5-7 °C cooler (Engelbrecht et al., 2019) and this period was also associated with generally much wetter conditions compared to present-day climate (Chase & Meadows, 2007; Mills et al., 2012, 2017; Scott, 1989). More recent paleoecological records of the Holocene (5700 cal ka BP) have revealed an unstable climate characterised by severe dry episodes showing linkages to the frequency of ENSO events (Humphries et al., 2019). However, under ongoing global warming, a prediction of increasing drought frequency and intensity, heightened magnitude of extreme weather events, and increasing wildfires in some parts, is expected to exacerbate dryland expansion in southern Africa, which would place further strain on natural water systems and the agricultural industry, threatening food security, human wellbeing and the economy (Gbetibouo & Hassan, 2005; IPBES, 2018; IPCC, 2019; Lindesay & Jury, 1991; Strydom et al., 2018; Wigley, 1985).

Land use trends and predictions

Livestock overgrazing during the 19th and 20th centuries, which has led to considerable land degradation, is evident on dryland rangelands in South America (e.g., Busso & Fernández, 2018; Oliva et al., 2016), North America (e.g., Bahre, 1991; Call & Roundy, 1991; Hastings & Turner, 1966), Africa (e.g., Bekele & Kebede, 2014; Dean et al., 1995), Asia (e.g., Han et al., 2008; Li et al., 2013) and Australia (e.g., Jackson & Prince, 2016). In South Africa, livestock farming accounts for the majority of agricultural practices on arid and semiarid rangelands of the Karoo. The deterioration of the veld in the first half of the 20th century was primarily a result of overgrazing by livestock and inappropriate management (Acocks, 1953; Tidmarsh, 1948). John Acocks was dedicated to raising awareness of the encroachment of the arid and semiarid Karoo shrublands into the mesic and grassier eastern part of the country (Acocks, 1953). He suggested that this degradation was exacerbated by a major expansion in the agricultural industry (particularly in the production of wool and ostrich feathers) in the first half of the 20th century when livestock densities exceeded carrying capacities on rangelands managed under a commercial farming system. Areas under the communal land tenure system have also suffered from the effects of livestock overgrazing but for reasons related to having been significantly under-resourced and containing high populations (Meadows & Hoffman, 2002). The unique political history that influenced land tenure and land use policies, as well as management practices, combined with erratic rainfall and devastating droughts of the 20th century are recognised factors that have contributed towards an increase in land degradation in South Africa (Meadows & Hoffman, 2002; Moyo et al., 2008; Roux & Vorster, 1983a; Tidmarsh, 1948).

A number of in-depth investigations by the government were conducted to address the threat of desertification, soil erosion, drought, and a loss in grazing capacity in South Africa (Roux & Vorster, 1983a). The 1923 Drought Investigation Commission, the 1951 Desert Encroachment Committee, and the 1980 Departmental Committee for Veld Deterioration each served its purpose which was to stimulate veld management research in the Karoo and provide recommendations to address land degradation. These investigations gave rise to research (reviewed in Roux & Vorster, 1983a), to determine the effectiveness of the rotational group-camp system in the Karoo (Roux & Skinner, 1970), or other management systems such as non-selective grazing (Acocks, 1966; McCabe, 1987; Roux, 1967; Savory, 1988). Government intervention schemes were also informed through these investigations. Such schemes included the 'betterment' schemes for communal areas (De Wet, 1995, 2012), the Stock Reduction Scheme of 1969-1978 for commercial lands (Baard, 1978), and the 1985 National Grazing Strategy (Du Toit et al., 1991). The Stock Reduction Scheme subsidised 4,905 commercial landowners to reduce their animal numbers by a third of the recommended number, as well as to rest a third of their grazing lands every year (Baard, 1978; Hoffman et al., 1999). Although the total reduction in small stock units during the five-year period was not reported, it cost nearly R48 million to subsidise reductions on participating farms (Baard, 1978). The National Grazing Strategy (1985) further promoted good veld conservation techniques via the provision of agricultural extension services and recommended stocking rates were determined by benchmarks of grazing capacity (Du Toit et al., 1991). Although the direct benefits of the Stock Reduction Scheme on rangeland condition were not realised within the set timeframe (Baard, 1978; Hoffman et al., 1999), a longer-term solution to promote broad-scale biodiversity, sustainability and to support communities stemmed from these initiatives (Bastin et al., 2012). For example, the value of the extension services is known to have had a longer-lasting positive influence on the overall improvement and implementation of more conservative veld management practices (Hoffman & Todd, 2000; Roux & Vorster, 1983a). The implementation of these schemes also coincided during an unusually wet period in the mid-1970s. It took another 20-30 years for the effect of both land use policies and changes in climate to be detected in the condition of commercial rangelands in the eastern Karoo (Hoffman & Cowling, 1990; Masubelele et al., 2014).

Other important discoveries were being made at the time in the realm of Karoo rangeland ecology. From as early as 1934, the Grootfontein College of Agriculture (now known as the Grootfontein Agricultural Development Institute, 'Grootfontein' is used hereon) played a leading role in agricultural and ecological research in South Africa. Most of their studies were of a short-term nature owing to the interannual variability of rainfall, which is a major driving factor of vegetation dynamics in arid regions (Roux & Vorster, 1983a). However, these studies provided impetus to develop relevant degradation models for the Karoo to assess rangeland condition (Milton & Hoffman, 1994; Roux & Vorster, 1983b). The linear 5-phase degradation model, for example, provides supporting evidence to identify the degradation phases in a tract of vegetation (Roux & Vorster, 1983b). The state-and-transition model of Milton & Hoffman (1994), however, acknowledged the dynamic, non-linear nature of changes in semiarid rangelands and how climate, land and plants interact to create reversible or irreversible transitions between states. These studies also led to the development and testing of the group-camp grazing management system (Roux & Skinner, 1970). Various other grazing management systems were also developed, such as non-selective grazing (NSG) or ultra-high-density grazing (Acocks, 1966; Roux, 1967; Skinner, 1976), but these were not tested as widely as the group-camp system. These systems advocated for higher density grazing over shorter durations followed by prolonged periods of rest to allow the vegetation to recover.

1.4. Semiarid biome boundaries

Understanding the dynamics and structure of biomes, and the physical factors that shape biome distributions, is key to interpreting long-term vegetation change, particularly occurring across biome boundaries (Potts et al., 2015a). A biome boundary, also referred to as a 'biome transition', is defined as a geographic zone where adjacent ecological systems join and the biotic communities within this zone are at their ecological limits along environmental gradients of soil, moisture, temperature, altitude or fire (Potts et al., 2015b; Strayer et al., 2003). Biotic communities fluctuate in response to changes in physical and land use conditions. As a result, biome boundaries are ideal regions from which to observe contracting or expanding biomes by examining the directional trends in species composition, dominance and distributions, growth form abundance, phenology, interactions and net primary productivity over space and time. The Nama-Karoo-Grassland biome boundary is largely determined by a gradient of increasing mean annual rainfall from south-west to north-east (Mucina & Rutherford, 2006), and thus changes detected in the rainfall regime and/or other climate factors are expected to influence the distribution of these biomes. Thus, the presence and location of critical shifts to alternate states can be detected at the same time. Abrupt transitions between biomes are easier to see along sharper, contrasting boundaries, such as at forest-grassland or forest-fynbos boundaries, where a treeline is easily detectable from satellite imagery or aerial photography (Danz et al., 2013). Less sharp biome boundaries where dominant growth forms naturally coexist in a heterogeneous vegetation matrix (e.g., mixed grassland-shrubland vegetation), however, benefit from frequent and long-term monitoring at multiple spatial scales to detect subtle shifts over time (Potts et al., 2015b).

Studies have found that shrub encroachment and dominance is a consequence of frequently occurring drought, increased microclimatic temperature, and is sustained by positive feedbacks or disturbances (Archer, 1994; D'Odorico et al., 2012; Du Toit & O'Connor, 2017; Duker et al., 2015; He et al., 2015; Muller et al., 2016). Furthermore, woody plant encroachment negatively impacts rangeland carrying capacity for grazing livestock, biodiversity, grass biomass, the water table and leads to erosion (Von Maltitz et al., 2019). Numerous studies assessing the historical climate trends in different parts of South Africa over the past century have shed some light on understanding the vegetation patterns and trends in those parts (Kruger & Shongwe, 2004; Malherbe et al., 2016; Vogel & Drummond, 1993). Rainfall seasonality and amount of rainfall are strong drivers of vegetation composition (O'Connor & Roux, 1995). Du Toit & O'Connor (2014, 2016), for example, have shown how a long-term trend of increasing summer rainfall in Middelburg in the Eastern Cape, is responsible for driving the increase in grass cover in that area. In order to understand the relative contributions of climate and land use change to driving vegetation change along biome boundaries, temporally long and spatially extensive records are needed.

Studies have predicted ongoing shrub encroachment across grassland-shrubland boundaries under rising global temperatures, CO_2 enrichment, aridity and extreme climate fluctuations (Archer et al., 2017; Bestelmeyer et al., 2018; Bond & Midgley, 2000; Liu et al., 2020). These feedbacks can be further complicated or masked by land use impacts (especially during dry spells), such as high stocking rates and prolonged grazing. Although there is growing evidence of an expansion of shrublands into semiarid grasslands around the world (Bestelmeyer et al., 2018; Cabral et al., 2003; Cipriotti & Aguiar, 2012; Eldridge et al., 2011; He et al., 2015; Peng et al., 2013), grassland expansion in South Africa across the Nama-Karoo-Grassland biome boundary has been reported offering an alternative hypothesis of global semiarid biome shifts (Masubelele et al., 2014).

Specific questions relating to directional changes in rainfall amount and seasonality should be examined along the rainfall gradient of the eastern Karoo. Masubelele et al., (2014), for example, could find no significant long-term trends in annual rainfall at both Karoo and Grassland sites. From the end of the 19^{th} century until the 1980s, rainfall was shown to be evenly distributed over the year but has since become less evenly distributed (Du Toit & O'Connor, 2014), providing explanation for the increasing grassiness in the area. Trends in other important climate variables should not be ignored either, as these also offer valuable insights into the vegetation feedbacks in the region. The functioning of land as a carbon source-sink is highly uncertain under ongoing climate change due to the role of natural fluxes in the system. However, on a global-scale, a vegetation 'greening' trend (increasing net primary productivity) has been observed from satellite data over an estimated 18 million km^2 of drylands including the Sahel, since the 1980s (Burrell et al., 2020; Donohue et al., 2013; Fensholt et al., 2012; Zhu et al., 2016). The drivers attributed to global dryland greening are CO_2 fertilization due to rising atmospheric CO_2 (Donohue et al., 2013; Zhu et al., 2016), increasing temperature and rainfall (Fensholt et al., 2012), and changing land uses (Burrell et al., 2020). Therefore, incorporating a variety of climate variables into a trends analysis would allow greater understanding of the potential links between interacting variables that are driving the vegetation patterns observed in the region.

1.5. Thesis overview

1.5.1. Research aims and objectives

The overarching aim of the thesis was to gain an understanding of the long-term vegetation changes that have occurred across the rainfall gradient of the Nama-Karoo-Grassland biome boundary since the 1960s. This assessment was carried out predominantly on privately-owned livestock farms in the region, however, commonage rangelands and informal protected areas represent a very small percentage of the sites. Two unique features of this study are i) a considerable increase in the number of study sites used to assess vegetation change than has previously been used (Hoffman & Cowling, 1990; Masubelele et al., 2014), and ii) an analysis of climate trends across the rainfall gradient, based on the initial analyses carried out in Middelburg-EC (Du Toit & O'Connor, 2014). The specific objectives of the study are described below.

1. To describe the physical environment, vegetation, climate, and agricultural practices of the study area using qualitative information and quantitative analyses of data.
2. To examine regional trends in livestock densities using magisterial district livestock census data.
3. To examine the local perceptions of past and present land use and change derived from semi-structured interviews.
4. To analyse the long-term annual and seasonal trends in rainfall, temperature, wind speed and evaporation in the study area from the 1870s to 2019.
5. To ascertain the spatial extent of these climate trends over the study area.
6. To assess the long-term changes in growth form cover and species composition since the 1960s using repeated point intercept transects carried out on the plains.
7. To describe species compositional shifts, and therefore plant community changes, over time.
8. To compare past and present-day rangeland condition as estimated from grazing capacity (ha/Large Stock Unit).
9. To assess the long-term changes in growth form covers on the plains and hillslopes using repeat photography.
10. To summarise the major vegetation shifts that have occurred along the rainfall gradient since the 1960s.
11. To discuss the findings within the broader contexts of climate, land use and vegetation trends and trajectories of change for the region and global semiarid rangelands, as well as to position the findings within the conceptual framework of biome boundary vegetation shifts.
12. To highlight some of the key implications, limitations and knowledge gaps in dryland research.

1.5.2. Thesis structure and outline

The thesis uses a traditional structure containing an Introduction (Chapter 1), Study area description (Chapter 2), three data chapters (Chapters 3, 4, 5) and a concluding synthesis of the study findings (Chapter 6).

Chapter 1 contains a review of the literature relevant to the study and lays the foundation for why the study was conducted and how the study contributes to the field by filling specific research or knowledge gaps. Chapter 2 provides a description of the biophysical, vegetation, and land cover, land tenure and land use characteristics of the study area. Various climate data (used for the analysis in Chapter 3) were also analysed to provide descriptive statistics of the climate of the study area. Semi-structured interview data were analysed to briefly synthesise the local perceptions of land use, climate, and vegetation change in the eastern Karoo. Chapter 3 is the first of three data chapters, which investigates the climate trends of the study area between 1870 and 2018. Chapter 4 provides an assessment of the vegetation changes that have occurred between the 1960s and 2017-18 derived from repeated point intercept vegetation surveys. Chapter 5 builds upon the assessment of vegetation change by examining the cover changes of grasses, dwarf shrubs and tall shrubs on plains and hillslopes as estimated from photograph comparisons. Chapter 6 synthesises the findings of the thesis. It also provides a summary of the limitations of the study and addresses the research gaps of the region that emerged out of the study. The literature cited throughout the thesis is contained in one bibliography. Various supporting graphical and tabular information for individual chapters are provided in Appendices A-D found at the end of the thesis. R code used for data analysis and visualisation is provided via the link in Appendix E.

Chapter 2: Description of the study area

The study area is situated in the central-eastern interior of South Africa at the interface between the Nama-Karoo and the Grassland biomes. The study area straddles the north-western parts of the Eastern Cape, the north-eastern tip of the Western Cape, the south-eastern side of the Northern Cape and southern Free State (**Figure 2.1**). Delineation of the study area boundary was derived using political boundaries at the level of magisterial districts and further guided by the location of relevant historical photographs, vegetation surveys and climate records. All relevant site information and district municipalities pertaining to the study area are detailed in Appendix C1. The total estimated area within the predefined bounds of the study area is approximately 19,500 km^2. The aim of this chapter is to provide qualitative and quantitative descriptions of the study area in terms of its biophysical features, climate and land uses. Species names used in the thesis have been updated to their most recent taxonomic nomenclatures according to the South African National Biodiversity Institute Plants of southern Africa checklist (South African National Biodiversity Institute, 2016).

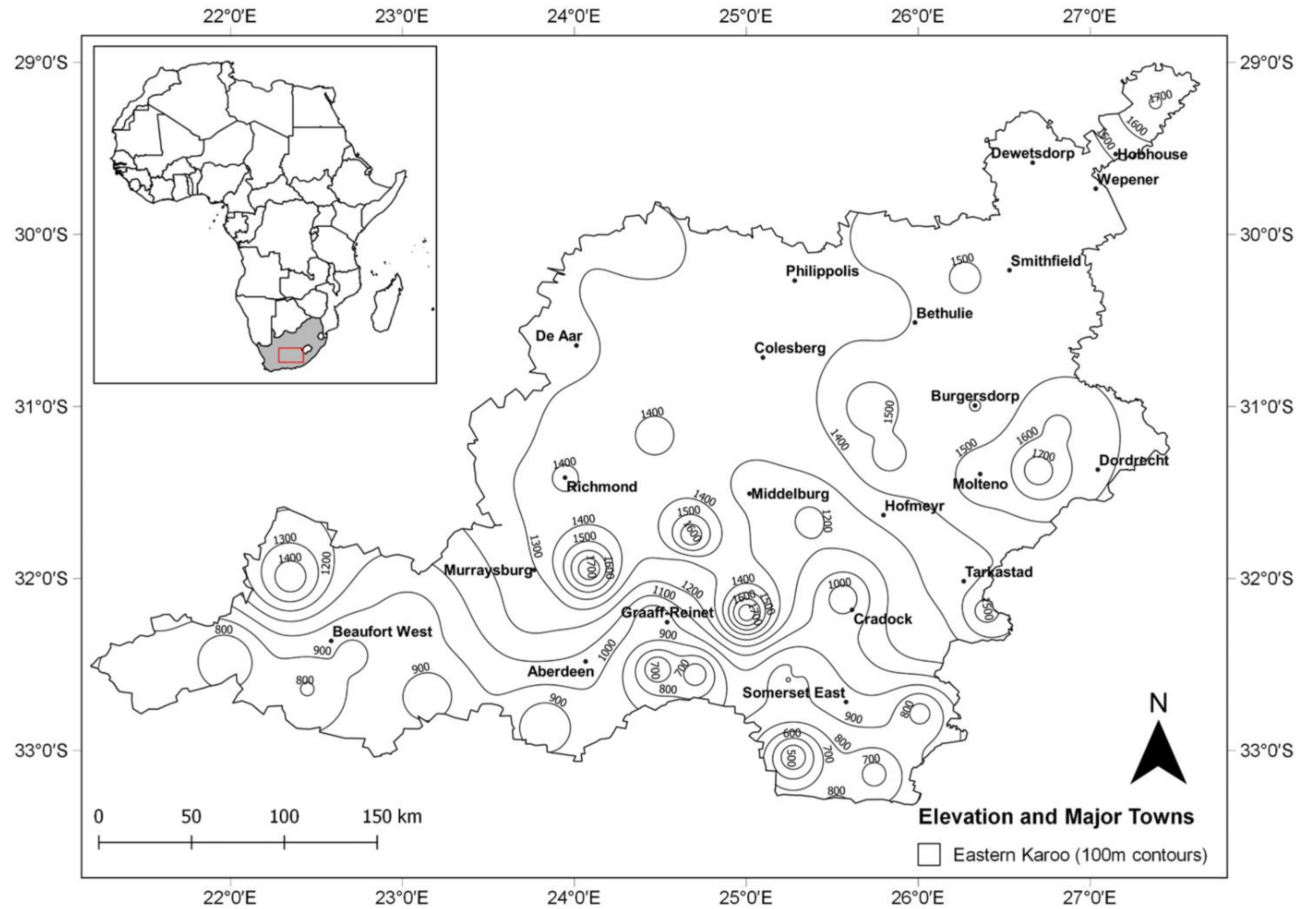

Figure 2.1 Elevation map of the study area located in central interior of South Africa, showing the names of major towns.

2.1. Physiography, topography, geology, and soils

The area consists of four physiographic regions, namely, i) the Great Karoo Escarpment extending from Beaufort West eastwards where it merges into the ii) Drakensberg in the east of the study area, iii) the Great Karoo south of the Escarpment between Beaufort West and Graaff-Reinet, and the iv) Inland Plateau, towards the north. The primary river catchments that drain the physiographic regions of the study area are the Caledon and Orange Rivers in the Drakensberg and Inland Plateau regions, the Sundays and Great Fish Rivers which flow through the Great Escarpment and Great Karoo regions, and the Sak and Kariega Rivers in the west of the study area. Topographically, the region is relatively heterogeneous along the Great Escarpment with flat plains broken by koppies, buttes and mesas, some becoming quite steep at the higher altitudes. Soils are typically shallow and stony in the western and southern regions becoming deeper and less stony towards the north-eastern dry Highveld grasslands.

2.1.1. Great Escarpment

The Great Escarpment consisting of mountains and hills with flats, lies above 1000 m above sea level. This area has an extensive network of dolerite and sill intrusions interrupting the plains (Sobczyk & Kirsten, 2006). The Great Escarpment is underlain by mudstone, siltstone, shale, and sandstone sediments of the Beaufort Group in the west of the study area and Stormberg Group towards the north-east. The mountains and hills are underlain by Beaufort sediments characterised by rock and lithosols, and to a lesser extent duplex and red apedal soils (Oosthuizen et al., 2003). The plains of the Great Escarpment are also predominantly Beaufort sediments consisting of lithosols, while the deeper deposits of colluvial and alluvial origin are found in the floodplains. The soils are typically shallow and stony, lightly leached and calcareous in the western and southern regions (Oosthuizen et al., 2003). Soils become deeper and less stony towards the north-eastern dry Highveld grasslands of the Stormberg Group. Soils here become more leached as rainfall increases, for example at higher elevations in the Stormberg Plateau (Mucina & Rutherford, 2006).

2.1.2. Drakensberg Escarpment

The Drakensberg Escarpment lies at an elevation above 1,500 m above sea level and consists of undulating hills and steep mountains. The Drakensberg portion of the Great Escarpment towards the east of the study area contains underlying Elliot and Molteno mudstones and sandstones belonging to the Stormberg Group. The Stormberg Group overlies the Beaufort Group (both forming part of the Karoo Supergroup). The soils in this region tend to be shallow duplex, coarse-grained containing lime, nutrient-poor due to leaching by the higher rainfall (Mucina & Rutherford, 2006; Sobczyk & Kirsten, 2006).

2.1.3. Great Karoo

The Great Karoo consisting mostly of flats with fewer dolerite intrusions than the northern physiographic regions, lies below 1000 m above sea level. The Great Karoo region is underlain by Beaufort sediments consisting of tillite, shale and sandstone of the Ecca Group, which are covered by alluvial slope deposits (Sobczyk & Kirsten, 2006).

2.1.4. Inland Plateau

The Inland Plateau lying between 1150 and 2500 m above sea level, comprises plains on each side of the escarpment (between De Aar, Philippolis and Colesberg and between Middelburg-EC, Hofmeyr and Cradock), as well as frequent dolerite intrusions that occur as isolated hills and plateaux that are encapsulated by the Sneeuberg, Agter-Renosterberg, Kikvorsberg and Suurberg mountains (Sobczyk et al., 2012). The inland plateau region is underlain by sandstone and mudstones of the Ecca Group, and mudstones of the Beaufort Group. Large areas are covered by aeolian deposits that have been carried by winds from the Kalahari (Sobczyk et al., 2012). The sandstones of the Ecca Group are mostly shallow, red apedal and eutrophic. Soils are fine sandy loams to sandy clay loams. The mudstones of the Beaufort Group are red and dominated by fine clay loam soils. The hills and plateaux are dominated by shallow soils and rocky outcrops. The plains are dominated by fine-grained sandstone and red and green-grey mudstone of the Katberg Formation (also Beaufort Group). Many places are overlain with alluvium, colluvium and calcrete (Sobczyk et al., 2012). The shallow, gravelly soils dominate the calcareous areas of these plains.

2.2. Climate

2.2.1. South Africa

South Africa is a semiarid country receiving an average of 450 mm of rain per year (King & Pienaar, 2011), which is a little more than half of the global average (860 mm/yr). It is geographically positioned within the subtropical high-pressure belt that extends from the Atlantic Ocean in the west to the Indian Ocean in the east (Dyer, 1979; Tyson, 1986). The high-pressure cells and migrations of easterlies, associated with the Intertropical Convergence Zone (ITCZ), strongly influences the climatic conditions in the north and eastern summer rainfall zone of South Africa. Climate in the winter rainfall zone is primarily driven by the temperate frontal systems associated with the westerlies (Tyson & Preston-Whyte, 2000). The origin of almost all of the rainfall that falls in the summer rainfall zone is convective in nature (Tyson, 1986). Severe storms, accompanied by hailfall, are most frequent and intense over these parts of the Highveld and eastern escarpment, and diminish in intensity and frequency towards the drier western and southern regions of the country (Carte & Held, 1978; Tyson, 1986).

2.2.2. Eastern Karoo

The climate of the eastern Karoo is characterised as semiarid in the south-west and dry sub-humid in the north-east with an Aridity Index range of 0.1 to 0.5 (Hoffman & Ashwell, 2001; Trabucco & Zomer, 2018). Spanning some 500 km, rainfall increases from the south-west to north-east ranging roughly from 250 mm near Beaufort West, and 540 mm in the central Stormberg Plateau between Molteno and Dordrecht, to 560 mm near Wepener and Dewetsdorp (**Figure 2.2A**). Rainfall over the eastern Karoo is seasonal, occurring almost entirely in the austral summer (Tyson, 1986). Towards the north-eastern part of the study area, rainfall tends to fall a little earlier (October-December) in the summer period compared to areas further west (Tyson, 1986). Mean annual air temperature varies between 16 °C in the south to 15 °C in the northern areas and reaches about 12 °C at the higher elevations interspersed along the Escarpment (**Figure 2.2B**). Frost incidence is relatively high throughout much of the region, particularly at the higher elevations of the Drakensberg escarpment region where temperatures are cooler and snowfall is relatively common compared to the lowest elevations of the study area where snowfall is absent (Mucina & Rutherford, 2006). Strong winds over the central-eastern interior during summer are generated mostly by thunderstorms caused by air movement from the Atlantic and Indian oceans (Kruger et al., 2010). To some extent, the passage of cold fronts originating from the westerlies in the south also contribute to the annual strong winds over the eastern Karoo (Kruger et al., 2010).

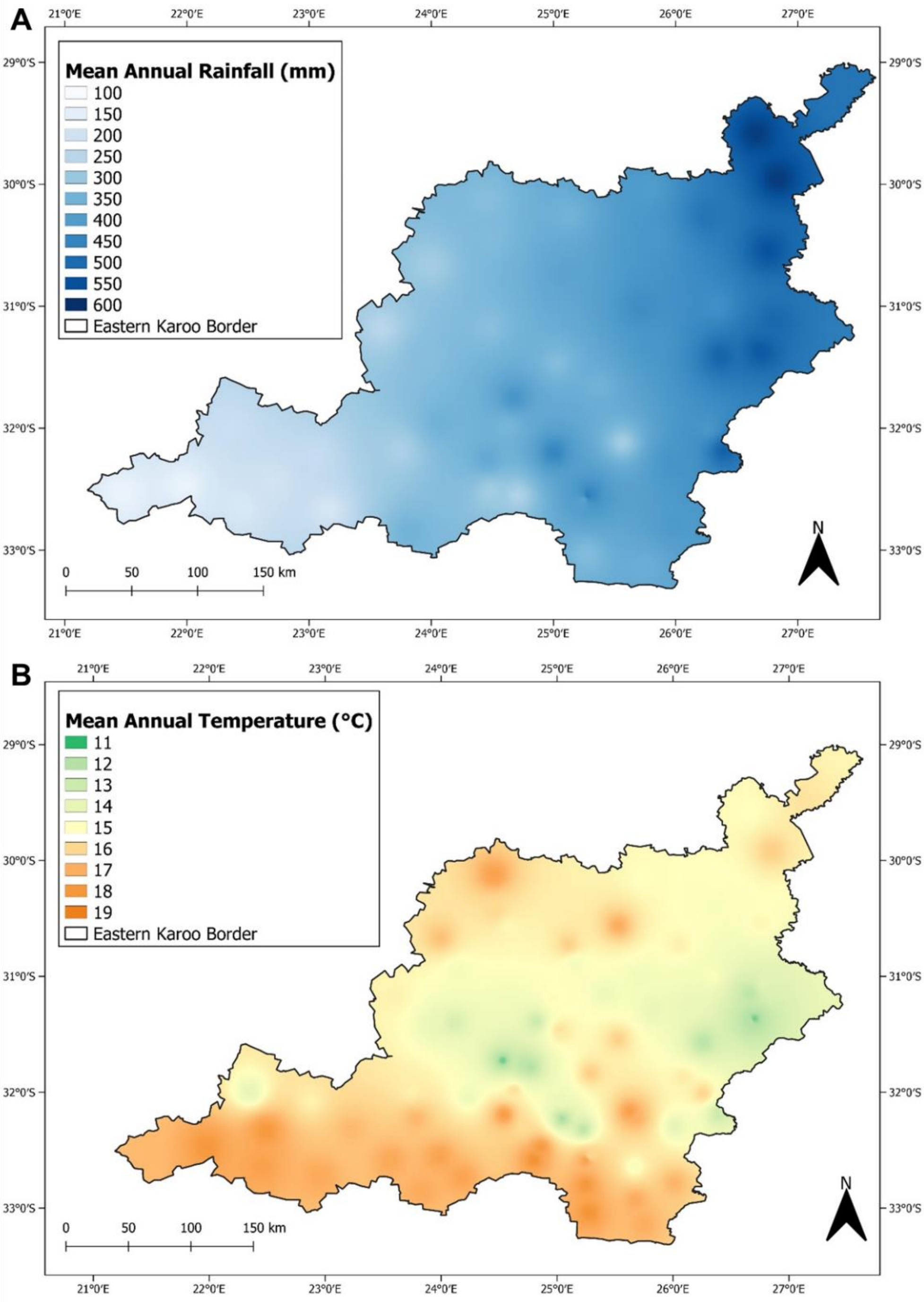

Figure 2.2 Gradients of A) mean annual rainfall mapped using gridded pentad data from the Climate Hazards Group InfraRed Precipitation with Station Data (Funk et al., 2015), and B) temperature mapped using TerraClimate, a high-resolution (1/24°, ~4 km) dataset of global monthly land surface climate and water balance (Abatzoglou et al., 2018).

A quantitative description of the climate of the study area has been provided below using the rainfall, temperature, A-Pan evaporation, and wind run records used in Chapter 3. The climate data used here were obtained from the South African Weather Service (SAWS), the Climate Systems Analysis Group (CSAG), the South African Agricultural Research Council's Institute for Soil, Climate and Water (ARC-ISCW), Lynch et al. (2004) and local farm records (**Figure 2.3**).

The long-term (145 years) annual rainfall mean for the study area was 390.5 mm (± 97.9 standard deviation) with a mean coefficient of variation of 25.1%. Individual long-term rainfall means per site are provided in ascending order of longitude (**Figure 2.4A**). In general, the start of the rainfall season in the study area begins in October contributing an average of 8.0% to the average annual total (31.2 ± 9.2 mm). The rainfall season peaks in March (61.2 ± 14.2 mm) contributing an average of 15.7% to the annual total (**Figure 2.4B**). Seventy percent of the total annual rainfall falls in summer (October-March; 272.3 ± 73.8 mm). Autumn (April-June; 70.8 ± 16.1 mm) and winter (July-September; 47.5 ± 14.9 mm) combined contributed 30.2% to the annual total. Summer rainfall was distributed more in the late summer months of January to March (41.6%; 162.4 ± 43.9 mm) compared to the early summer months of October to December (28.3%; 110.5 ± 32.3 mm). Mean annual maximum and minimum temperature for the study area was 23.8 ± 4.8 °C and 7.6 ± 5.1 °C, respectively. Mean maximum temperatures ranged from 16.6 °C in June to 29.9 °C in January (**Figure 2.4B**). Mean minimum temperatures ranged from 0.05 °C in July to 14.1 °C in January. The long-term (41-year) mean of total annual A-Pan evaporation in the study area was 1836.2 ± 119.5 mm/year. The long-term mean of total annual evapotranspiration (ET) was 1417.1 ± 89.5 mm/year. December had the highest monthly mean A-Pan (244.5 ± 19.6 mm) and ET (187.6 ± 13.5 mm) evaporation (**Figure 2.4C**). Overall, the summer months (October-March) contributed 64.7% (A-Pan) and 64.6% (ET) towards the total annual evaporation, while the combined autumn and winter months contributed 26.7% and 29.0%, respectively. The long-term mean for annual wind run was 202 km/day. The windiest month on record was November (241.7 ± 53.3 km/day) while April was the least windy month (160.5 ± 37.7 km/day). Wind run during the combined early and late summer months was higher (218.45 ± 47.0 km/day) than autumn and winter combined (185.9 ± 46.3 km/day; **Figure 2.4D**).

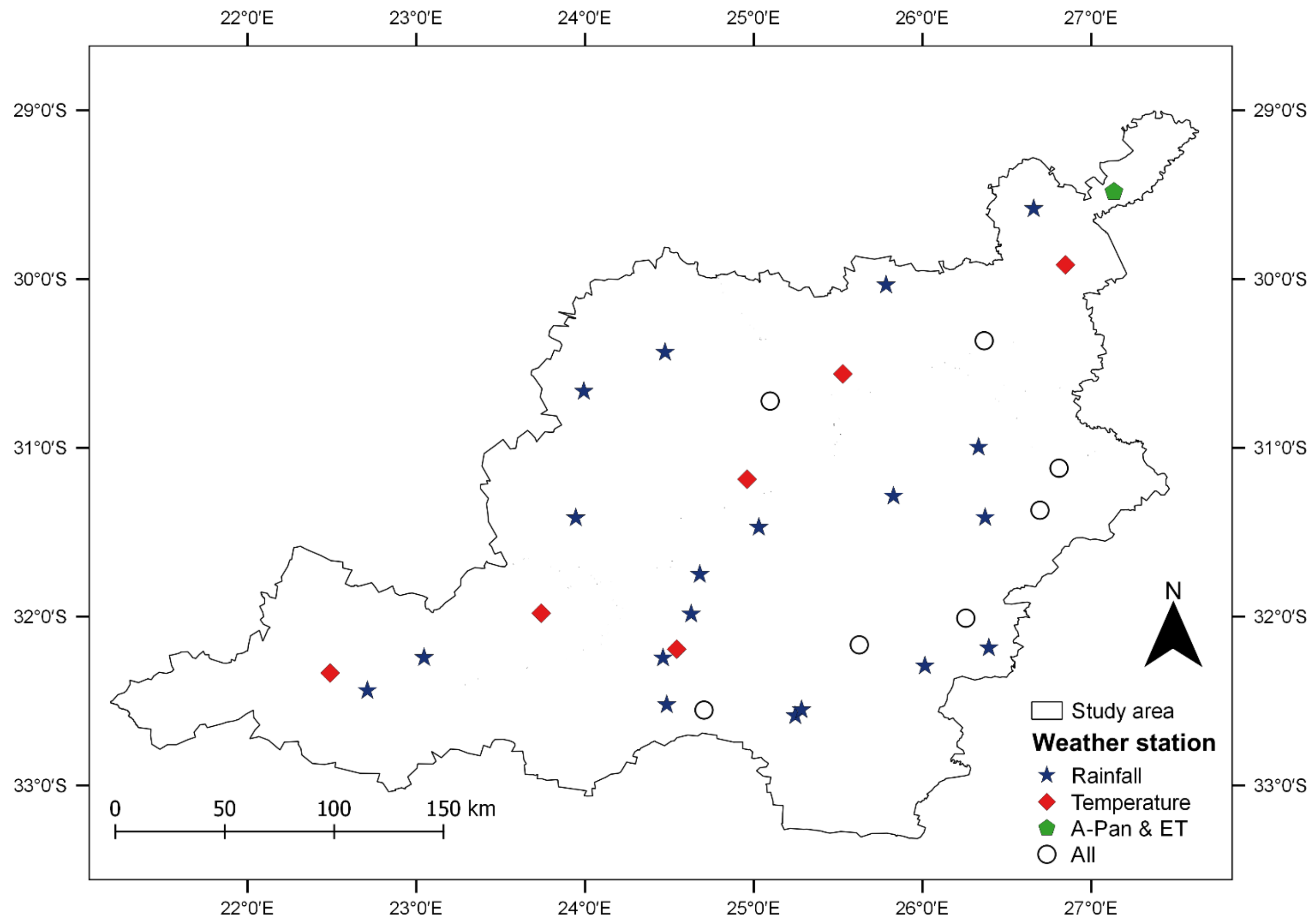

Figure 2.3 The location of climate records in the eastern Karoo used to quantify the climate of the eastern Karoo. The accompanying Figure 2.4 provides descriptive statistics derived from these weather station records.

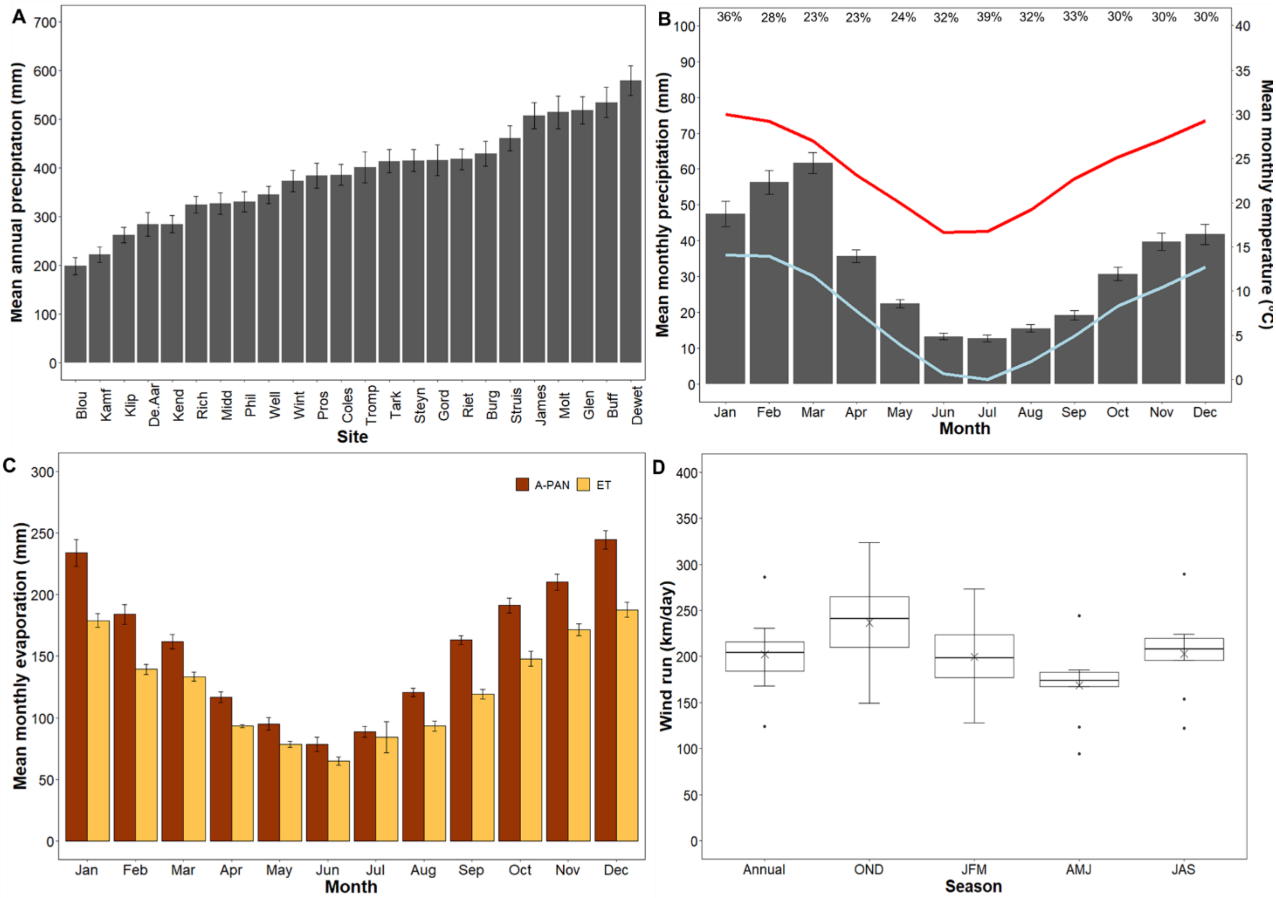

Figure 2.4 A quantitative description of the climate of the eastern Karoo based on long-term climate records. A) Long-term annual rainfall average per site representing the rainfall gradient of the region increasing in a south-west (Blou) to north-east (Dewet) direction. B) Average monthly rainfall (bars; n = 26), maximum (red line) and minimum (blue line) temperature (n = 17). Percent values are the coefficient of variation of monthly rainfall. C) Average monthly A-Pan evaporation (n = 7) and evapotranspiration (ET, n = 5). D) Wind run (n = 9) per season where X represents the mean and the whiskers are the inter-quartile ranges between the 25th and 75th percentiles. Error bars on bar plots are standard errors. OND = early summer; JFM = late summer; AMJ = autumn; JAS = winter.

2.3. Vegetation structure and composition

The vegetation is complex as it transitions from arid dwarf shrublands in the south-west into grassy dwarf shrublands and montane shrublands at the higher elevations in the Great Escarpment to becoming almost dominated by grasses in the north-east (Mucina & Rutherford, 2006). While the Nama-Karoo and Grassland are the two dominant biomes of the area, the Albany Thicket biome and Inland Azonal Vegetation make up a smaller area (**Figure 2.5A**). Several vegetation types (**Table 2.1**) make up each of the bioregions that fall within the study area. A combination of rainfall amount and seasonality, temperature, soil type and soil depth contribute to shaping the vegetation structure and composition of the eastern Karoo. Other important drivers of eastern Karoo vegetation include grazing by livestock and wildlife, fire, soil erosion and episodic events such as hailstorms and locust outbreaks (Mucina & Rutherford, 2006). Sheet, rill and gully erosion are the more common forms of erosion in the study area. Although fire is uncommon in the semiarid Nama-Karoo, the vegetation of the higher elevation Escarpment possess relevant adaptations to fire (Kraaij et al., 2017; Roux & Vorster, 1983a).

2.3.1. Nama-Karoo Biome

The Nama-Karoo is not particularly rich in plant species, nor does it contain any centre of endemism (Mucina & Rutherford, 2006). Nonetheless, species richness has been found to be higher on the dolerite hillslopes (Petersen et al., 2020) and along drainage lines (Milton, 1991), compared with that of the bottom plains of the biome. Succulence is very low in the Nama-Karoo on account of the cold and wet winter season and dry summer and is mostly found along its boundaries to the Fynbos and Succulent Karoo biomes. Succulents are nearly absent towards the east (where the study is positioned) where Poaceae increases in dominance as rainfall increases and soil type changes (Mucina & Rutherford, 2006). Therefore, the major plant lifeforms contained within the study area are perennial and annual dwarf shrubs and grasses, as well as taller shrubs (> 1 m high), which more commonly grow on the dolerite slopes and in the riparian areas.

There are nine bioregions contained in the study area (**Figure 2.5B**). The Upper Karoo and Lower Karoo are the two dominant bioregions of the Nama-Karoo, the former occurring at the higher elevations where the vegetation comprises montane shrublands and grassy dwarf shrublands on the plains. The Lower Karoo, lying at the lower elevations of the Great Karoo region, is covered with dwarf microphyllous spiny shrubland and patches of grasses cover the sandy and silty bottomlands (Mucina & Rutherford, 2006). Leaf-succulent dwarf shrubs and scattered low trees (e.g., *Pappea capensis*, *Schotia afra*) also occur in these drier parts.

2.3.2. Grassland Biome

The Grassland biome, in contrast, has five centres of plant endemism within its borders. Within the study area, high concentrations of regional endemics have been found in the Sneeuberg Mountains (Clark et al., 2009) of the Karoo Escarpment Grassland vegetation type which occurs within the Drakensberg Alpine centre of endemism (Mucina & Rutherford, 2006).

The extent of the Grassland biome that covers the study area largely comprises the Dry Highveld Grassland bioregion. The Drakensberg Grassland, Mesic Highveld Grassland and Sub-Escarpment Grassland bioregions make up smaller areas of the study area. Dry Highveld Grassland, as indicated by its name, is the driest of the Grassland bioregions, receiving less than 600 mm of rainfall per annum (Mucina & Rutherford, 2006). However, within the context of the study area, this bioregion is located at the wettest extreme of the biome boundary. The vegetation of this bioregion is mostly ‘sweet’ grassland on the plains and ‘sour’ tussock grassland on the steep mountain slopes where *Tenaxia disticha* dominates (Mucina & Rutherford, 2006). The irregular plains also support patches of dwarf Karroid shrubs, which become more visible during years of below-average rainfall. The slopes support both dwarf Karroid shrubs and tall shrubs such as *Searsia erosa*, *Euclea undulata* and *Diospyros austro-africana* (Mucina & Rutherford, 2006) where these elements are also scattered in the Nama-Karoo biome embedded in patches of Besemkaree Koppies Shrubland. Drakensberg Grassland vegetation, occurring in the Stormberg Plateau, has a dwarf shrub component that is greater than in the other Grassland bioregions. The grassland is a mix of C_3 and C_4 grasses, the former becoming less abundant or absent at the warmer lower elevations of the region. The Mesic Highveld Grassland bioregion, which covers the north-eastern fringe of the study area (**Figure 2.4B**), contains undulating plains of patchy open 'sour' grassland, which in parts, has been heavily grazed (Mucina & Rutherford, 2006). Lastly, the vegetation of the Sub-Escarpment Grassland bioregion is low, semi-open mixed shrubland with grasses.

2.3.3. Albany Thicket Biome

The southern tip of the study area contains all three biomes, but Albany Thicket is the most dominant (**Figure 2.4A**). The vegetation comprises of drier shrubland, grassy scrub and riparian woodland found along the river basins (Mucina & Rutherford, 2006).

2.3.4. Inland Azonal Vegetation

Azonal vegetation is predominantly located towards the south and south-western extent of the study area (**Figure 2.4A**). It occurs along narrow riverine flats where soils are wetter, heavier and contain high concentrations of salt where *Salsola*-dominated shrubland can tolerate the salinity (Mucina & Rutherford, 2006). Common small tree or shrub species found in the woody thicket Southern Karoo Riviere vegetation are *Vachellia karroo*, *Leucosidea sericea*, *Tamarix usneoides*, and *Rhamnus prinoides.* Other common species found in the sandy drainage lines include the grass *Stipagrostis namaquensis*.

Table 2.1 A breakdown of the vegetation types that fall within the boundary of the study area according to Mucina and Rutherford (2006). Superscript letters indicated where vegetation transects[a] and repeat photographs[b] were sampled

Vegetation Types of the Eastern Karoo			
Nama-Karoo Biome		**Albany Thicket Biome**	
Upper Karoo		AT 17	Albany Mesic Thicket
NKu 1	Western Upper Karoo	AT 18	Albany Valley Thicket
NKu 2	Upper Karoo Hardeveld[ab]	AT 19	Baviaans Valley Thicket
NKu 3	Northern Upper Karoo	AT 24	Doubledrift Karroid Thicket
NKu 4	Eastern Upper Karoo[ab]	AT 25	Eastern Gwarrieveld
Lower Karoo		AT 27	Escarpment Arid Thicket
NKl 1	Gamka Karoo[b]	AT 28	Escarpment Mesic Thicket
NKl 2	Eastern Lower Karoo[ab]	AT 29	Escarpment Valley Thicket[ab]
NKl 4	Albany Broken Veld	AT 31	Fish Mesic Thicket
Grassland Biome		AT 32	Fish Valley Thicket
Drakensberg Grassland		AT 47	Saltaire Karroid Thicket
Gd 1	Amathole Montane Grassland	AT 49	Sundays Arid Thicket
Gd 2	Amathole Mistbelt Grassland	AT 54	Vanstadens Forest Thicket
Gd 3	Stormberg Plateau Grassland[ab]	**Inland Azonal Vegetation**	
Gd 4	Southern Drakensberg Highland Grassland[b]	*Alluvial Vegetation*	
Gd 8	Lesotho Highland Basalt Grassland	AZa 4	Upper Gariep Alluvial Vegetation
Dry Highveld Grassland		*Inland Saline Vegetation*	
Gh 1	Karoo Escarpment Grassland[ab]	AZi 5	Bushmanland Vloere
Gh 2	Aliwal North Dry Grassland[ab]	AZi 6	Southern Karoo Riviere[b]
Gh 3	Xhariep Karroid Grassland[ab]		
Gh 4	Besemkaroo Koppies Shrubland[ab]		
Gh 5	Bloemfontein Dry Grassland		
Gh 6	Central Free State Grassland[ab]		
Gh 7	Winburg Grassy Shrubland		
Mesic Highveld Grassland			
Gm 1	Zastron Moist Grassland		
Gm 3	Eastern Free State Clay Grassland		
Gm 4	Eastern Free State Sandy Grassland		
Gm 5	Basotho Montane Shrubland		
Sub-Escarpment Grassland			
Gs 15	Tsomo Grassland		
Gs 16	Queenstown Thornveld[b]		
Gs 17	Tarkastad Montane Shrubland		
Gs 18	Bedford Dry Grassland		

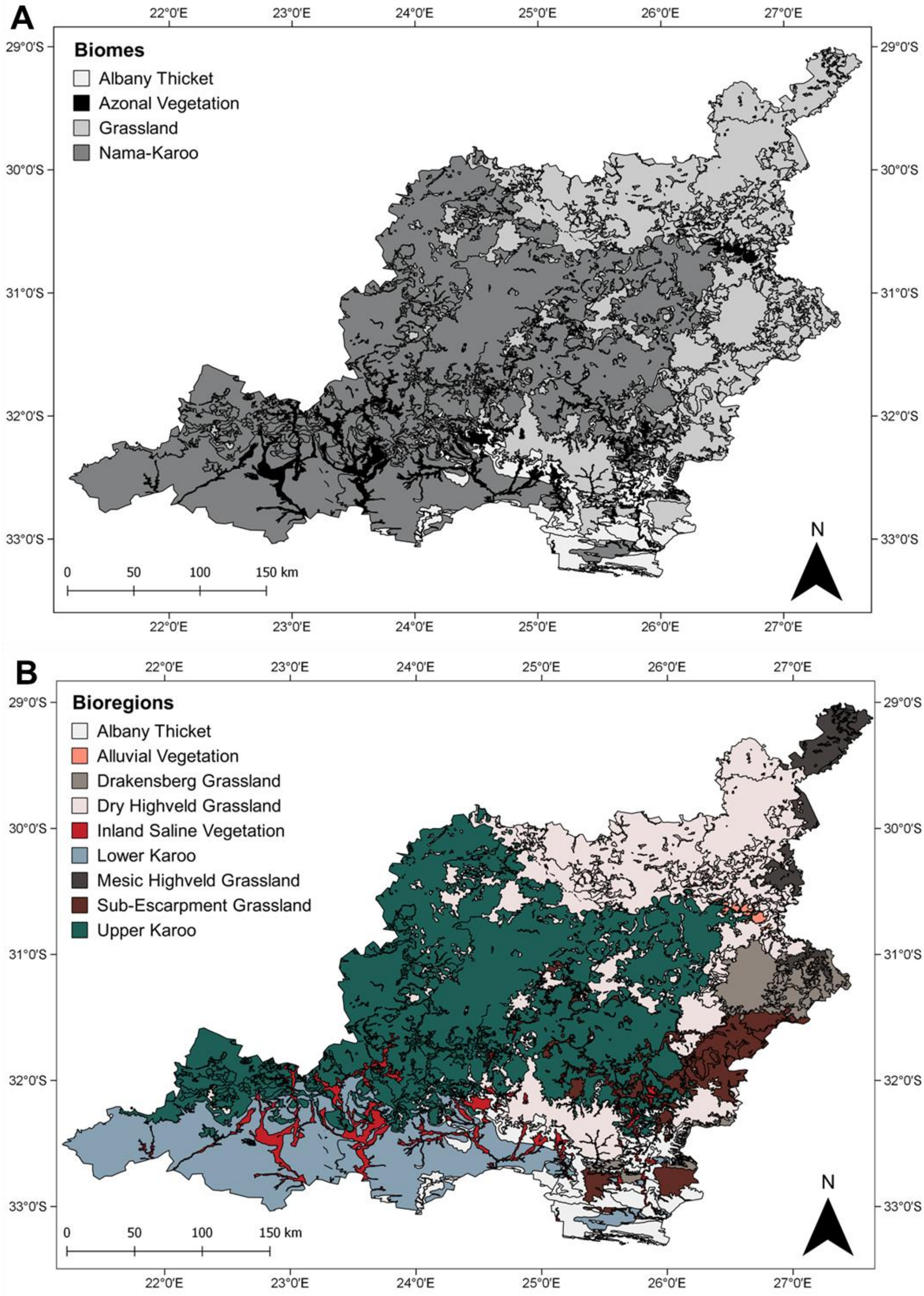

Figure 2.5 The eastern Karoo comprises three main biomes (A), divided into nine major bioregions (B). Significantly smaller bioregions are not included. Alluvial Vegetation and Inland Saline Vegetation form part of the Inland Azonal Vegetation classification.

2.4. Agricultural practices

2.4.1. Land cover, land tenure and land use

The majority of land cover, or the observed biophysical cover, of the study area comprises natural low shrubland and grassland rangeland according to the National Landcover map of South Africa created by the Department of Environmental Affairs (Department of Environmental Affairs, 2013). A smaller percentage of the area comprises open and wooded thicket and woodland, found mostly along the Sneeuberg and Lower Karoo riparian areas. The least amount of area is covered by bare ground, cultivated crops, pivot fields and dams (Department of Environmental Affairs, 2013). Most of the land tenure (land ownership) of the study area comprises privately-owned (commercial) rangeland, while state-owned land makes up the remainder of the area.

The dominant land use type has been commercial livestock farming since the early 20th century. Roughly 91% of the total area of the study region is natural rangeland used for grazing and browsing by livestock and wild game, and 8% of the study region is arable land used for irrigated and dry land field crops (maize, grass and lucerne) as well as horticulture crop products (Stats SA, 2017a, 2017b, 2017c, 2017d). Scattered across the region are a small number of formal protected areas comprising national parks (Karoo, Camdeboo and Mountain Zebra), nature reserves and aquatic protected areas (Gariep Dam and Caledon River). A growing cluster of informal protected areas mostly in the form of private (safari) game farms and private nature reserves are located between Graaff-Reinet, Middelburg-EC and Cradock (South African National Biodiversity Institute, 2011). The area of rangeland used for communal livestock farming is unknown but estimated to make up the smallest percentage of the total area of the study area and is predominantly concentrated near the main towns.

2.4.2. Trends in livestock numbers

Magisterial district-level livestock counts collected between 1911 and 2007, and district municipality livestock counts collected in 2017-18, indicated that sheep numbers have experienced the greatest decline by almost fivefold (**Figure 2.6**). The early 20th century wool boom drove sheep numbers in the study area to over 10.5 million, but these numbers have since declined to just over 2.5 million. The downward trend in sheep numbers was occasionally marked by increases in the 1930s, 40s, 50s and 80s coinciding with peaks in the wool industry (Nel et al., 2007), but overall the number of sheep has declined by 70% since 1939. The number of cattle and equine animals have remained comparatively stable over time. The number of goats has fluctuated over time with an initial decline from 2.5 million to 570 000 between 1911 and 1928 which thereafter remained relatively stable. Their numbers increased briefly in 1983 (> 1 million) when Angora goat mohair production rose but then decreased to just over 420 000 in recent decades (Hoffman et al., 2018). The trends in sheep and goat numbers mirror those reported for the greater Nama-Karoo biome (Hoffman et al., 2018). Others have suggested that while the number of farms in the eastern Karoo declined between 1928 and 2002, the area under agricultural production remained constant indicating that an overall increase in average farm size had taken place in this period (Nel et al., 2007; Nel & Hill, 2008). This phenomenon was made possible after the abandonment of land by the emigrating white populations (Atkinson, 2009). If combining sheep, cattle, goat and equine numbers, the effect of the Stock Reduction Scheme between 1969 and 1978 is estimated to have resulted in a 12% decrease in stock numbers during this five-year period. However, the long-term trend (**Figure 2.6**) indicates that sheep numbers had been in decline long before the scheme was implemented implying that other more important factors were responsible for this decline. The livestock trends, coupled with improved stocking techniques, resources and the rotational grazing management system are, however, suggested to have encouraged a large-scale movement towards a more effective sustainable agricultural system in the eastern Karoo (Nel & Hill, 2008).

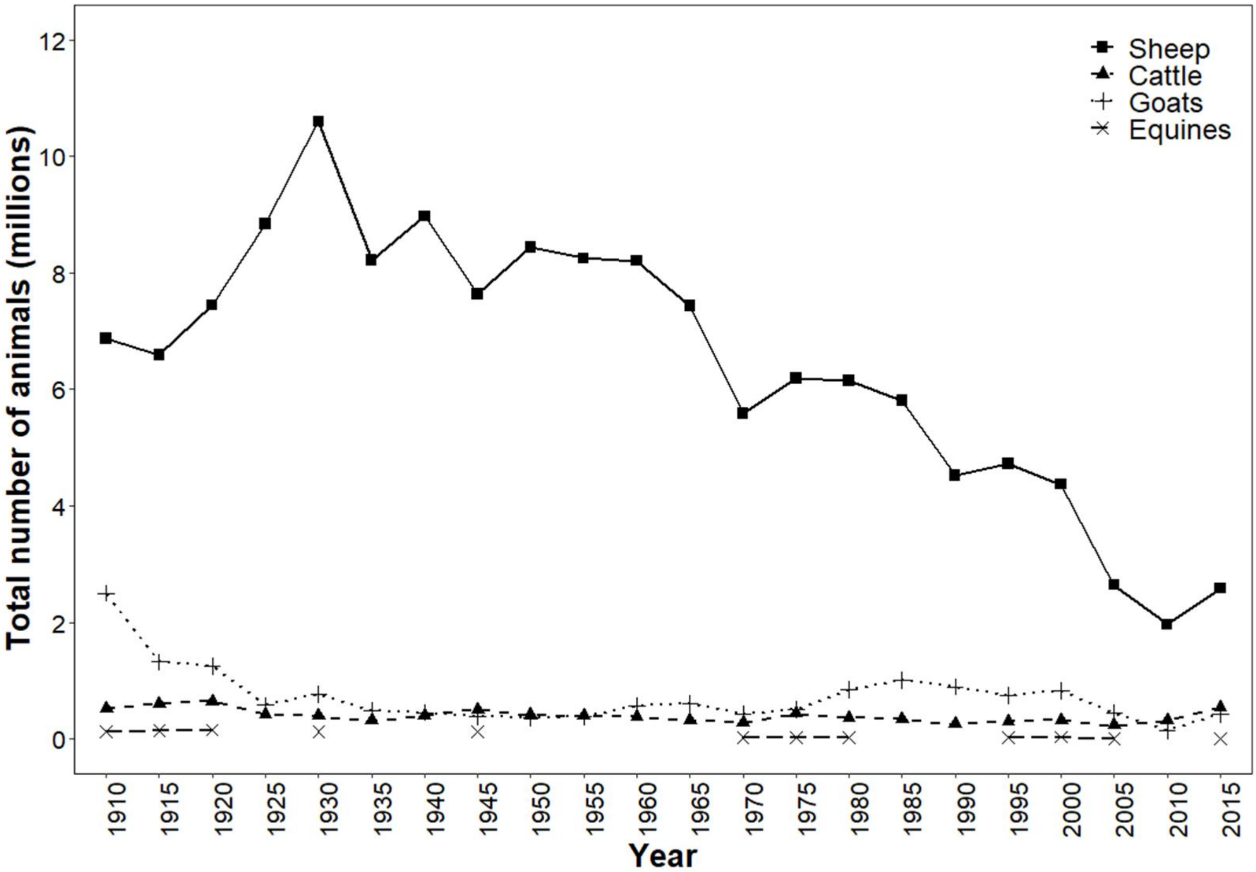

Figure 2.6 The total number of livestock animals between 1911 and 2017 in the study area.

2.4.3. Local perceptions

Semi-structured interviews containing open-ended questions (Appendix A) were carried out during the fieldwork collection of the thesis study (Ethics approval FSREC 48-2017). Sixteen landowners of commercial livestock farms and two private game reserve managers were interviewed. While this is based on a relatively small sample size (n = 18) relative to the size of the study area, an equal number of interviews were carried out in each of the Nama-Karoo and Grassland biomes. Anonymity of participants has been retained. The reason for conducting these interviews was to compile a database of information pertaining particularly to land use management practices (past and present) as well as to understand the local perceptions of long-term changes in the climate and vegetation of the region. This information has also been used to support and inform the findings of the detailed climate and vegetation analyses of Chapters 3, 4 and 5.

The interview data were analysed using a well-known method of text mining following Silge & Robinson (2017) using R version 3.5.2. (R Core Team, 2018). The information provided for each question was placed into broad themes of i) past and present management practices, ii) past and present animal types, iii) feed and nutrient supplementation, iv) climatic and vegetation changes, v) natural disturbances and vi) other challenges. The documents were tidied and formatted before being subjected to the analysis. Words that were not useful, known as *stop-words* (typically prepositions, numbers, articles, etc.) were removed from the text to produce a standardised body of text across documents. Word clouds were generated to identify the most frequently used words in each theme (**Figure 2.7**).

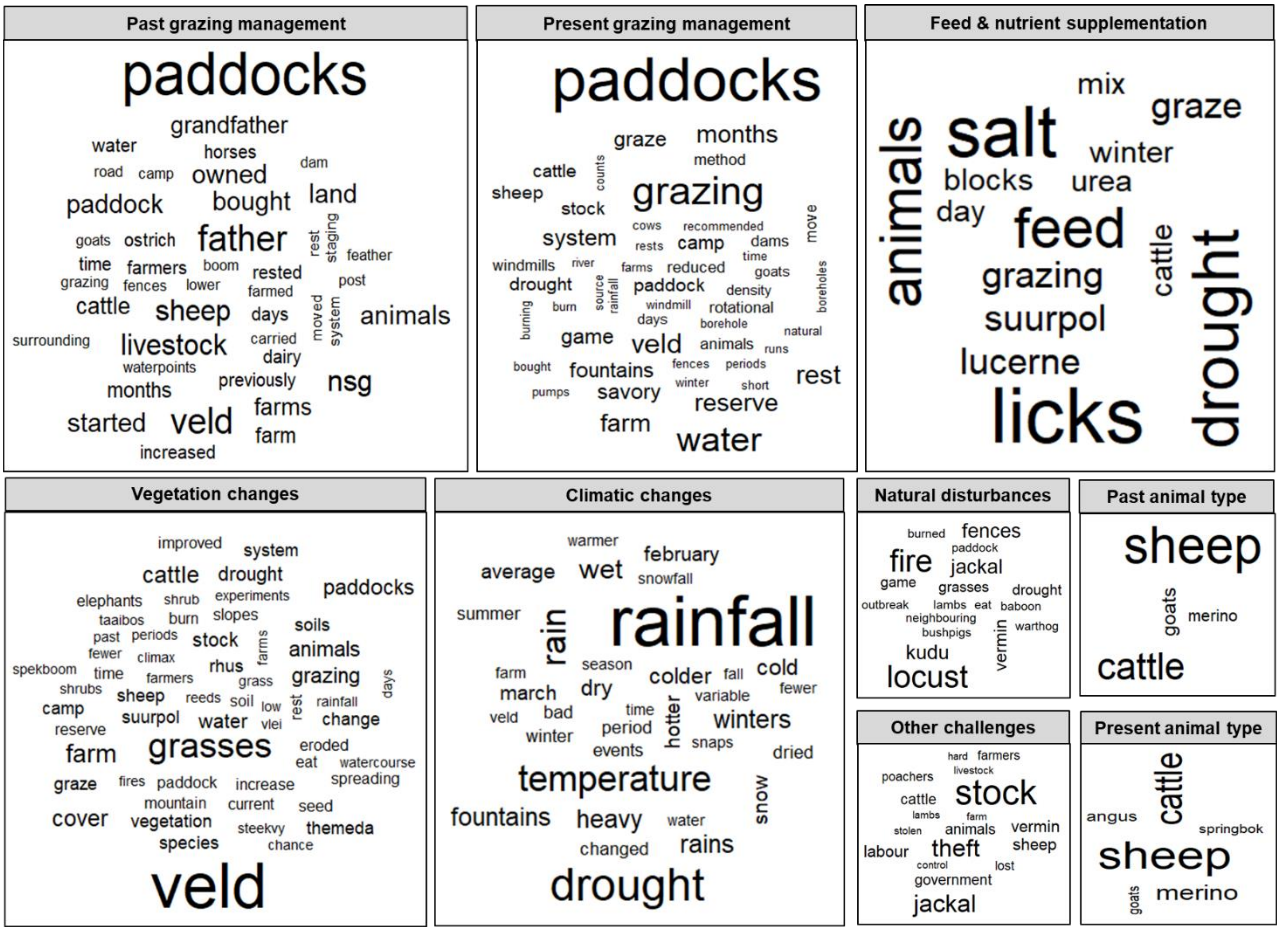

Figure 2.7 Word clouds per theme derived from semi-structured interviews conducted with landowners and managers (n = 18) in the study area between 2017 and 2018. The size of words indicates the relative frequency of use by interviewees. Larger words, therefore, were those used most frequently and smaller words used most rarely.

The body of text per theme was further analysed by determining how important some of these words are across all interviewees, known as *term frequency* (Silge & Robinson, 2017). This is simply the number of times a word occurred in a theme (n) divided by the total number of words contained in that specific theme (n/total) or document of text (Silge & Robinson, 2017). This same approach can be used to calculate term frequencies of more useful words, such as co-occurring double-words (*bigrams*) as shown in **Figure 2.8**.

Another approach to finding important words is by decreasing the weight for commonly used words and increasing the weight for rarely used words, known as *inverse document frequency*, which is then multiplied by the term frequency (Silge & Robinson, 2017). This statistic is widely used in natural language processing and is known as *term frequency-inverse document frequency*, or tf-idf. The tf-idf was determined for each term in each theme in the collection of interview documents and the ten highest tf-idf values per theme were plotted (**Figure 2.8**). The x-axis scales have not been standardised across themes because the aim of the analysis was to determine important words in each theme, but not among themes.

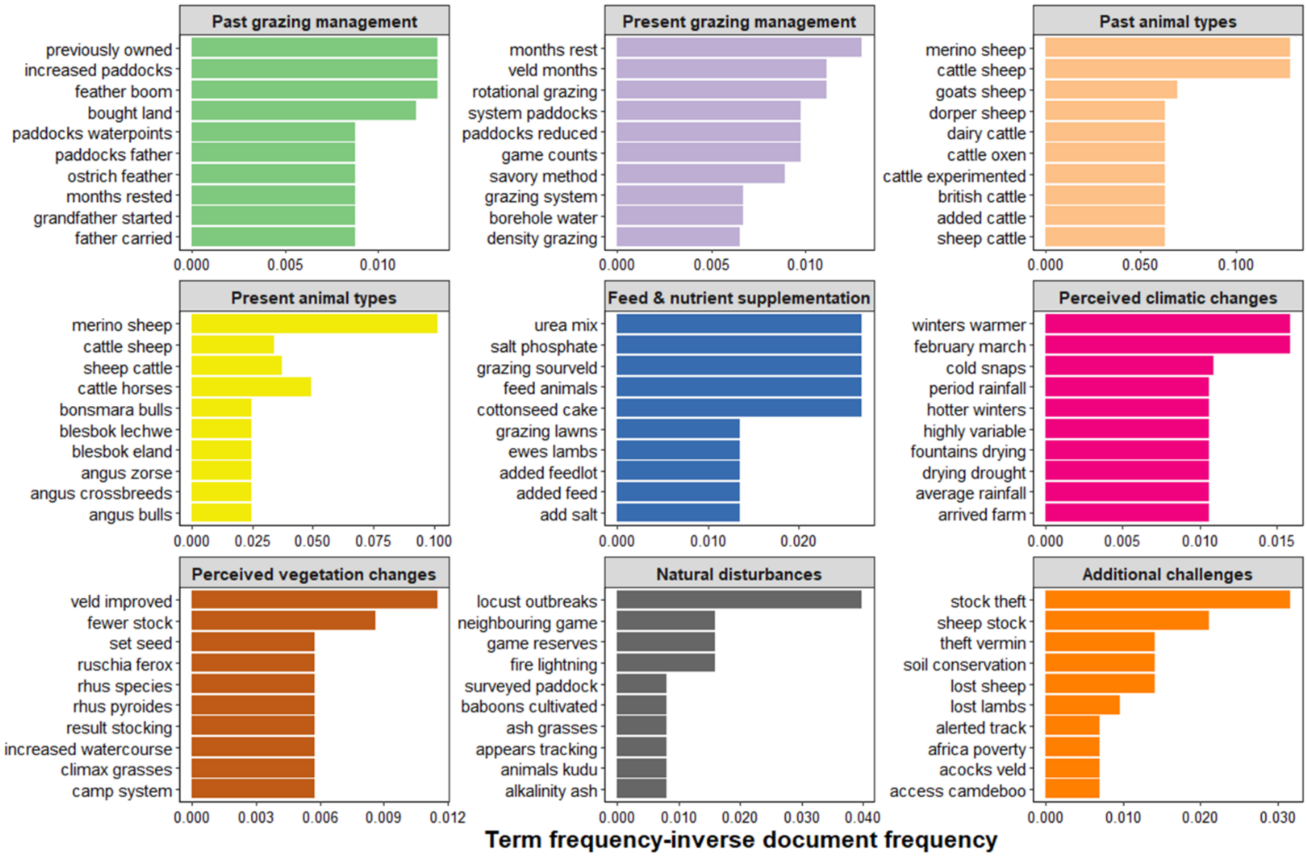

Figure 2.8 The co-occurring (bigram) terms identified per land use-related theme derived from semi-structured interviews conducted with landowners (n = 18) in the study area between 2017 and 2018.

Grazing management systems

Grazing management (past and present) contained the words ‘paddocks’, ‘livestock’, ‘father’, ‘grazing’, ‘veld’, ‘water’, and ‘rest’ most frequently (**Figure 2.7**). There were indications that ownership of land had changed hands in the past, that the ostrich feather booms were major economic events of the past, and that increasing the number of paddocks on farms started with previous generations. A large emphasis on the type of system employed by landowners in the region emerged in the present grazing management theme (**Figure 2.8**). The rotational grazing system appears to have been adopted by most farms within the last 50 years and is still currently used by most. In many instances, grazing management practices have also been further influenced by the principles of holistic management (Savory, 1988). Other key aspects of management today included emphasis on the time spent grazing versus the time spent resting veld ('months rest'), as well as water and livestock densities in paddocks.

Past and present animal types

Animal types used by landowners in the past consisted of sheep, cattle and goats with little change identified in the types of animals used in the present (**Figure 2.7**). However, the tf-idf statistic pulled out some key differences between past and present animal types used by landowners (**Figure 2.8**). Land uses today indicate the incorporation of, and in some cases a shift towards, game ranching. Historically, livestock agriculture was the prevailing land use in the region with sheep, goats and cattle of various breeds utilised across farms. Currently, while sheep and cattle farming are the main sources of income for these farms, many more have started carrying wild game for hunting as an additional source of income. Some livestock farms were sold and transitioned to informal protected areas, or game ranches, that only carry wild game species.

Feed and nutrient supplementation

All landowners and managers mentioned the regular use of additional feed and nutrient supplementation as part of their livestock management, which often coincides with the onset of drought conditions and decreasing available forage in the veld. 'Salt licks' or 'urea mixes' are the most common forms of nutrient supplementation used to stimulate gut digestion of the less palatable veld species such as 'suurpol' or *Tenaxia disticha*, a grass species that occurs in sour grassveld. Additional feed types mentioned also included maize, cottonseed and lucerne.

Perceived climate change

Landowners spoke most often about drought events and the effect drought had on natural water sources, mainly fountains. 'Drought' and 'wet' or 'heavy' were commonly used words when describing changes in rainfall (**Figure 2.7**). While all agreed that the majority of rainfall usually occurs in February and March, landowners indicated that the timing of the first rains had changed. They described rainfall as highly variable and arriving at unpredictable times. Changes in seasonal temperature was also mentioned often, particularly that temperatures were becoming 'hotter' or 'warmer'. They also identified that winters are becoming warmer.

Perceived vegetation changes

This theme captured a diversity of perceptions of vegetation change as depicted by the large number of words in the word cloud (**Figure 2.7**). Landowners mentioned that the biggest changes in the vegetation that they had noticed over the years has been an improvement in veld and this they owed to there being fewer numbers of livestock on their farms, and perhaps to a lesser extent, the introduction of the group-camp system. The term 'set seed' implies that the veld has had time to recover from past overgrazing, but landowners also emphasised the value of adequate resting of the veld from grazing to allow vegetation to set seed. Climax grasses have increased on their farms but so have various taller shrub species (e.g., *Searsia* species) along the watercourses.

Natural disturbances

The words 'fire', 'jackal' or 'vermin', 'locust', and 'fences' were used frequently when discussing natural disturbances that affected landowner management decisions (**Figure 2.7**). While locust outbreaks have not occurred in recent years, landowners displayed an intuitive understanding that these outbreaks often followed a very intense drought, which had been broken by the first very wet season (**Figure 2.8**). Locust, or other insect, outbreaks occur in response to post-drought regrowth, flowering and seeding of plants (Todd et al., 2002). In the context of neighbouring game ranches, antelope jumping over fences into livestock farms often causes damage to fences. Perceptions that an increase in game ranching in the region has caused an increase in the numbers of jackal, bushpig and warthog, which is problematic for livestock farmers who regularly lose lambs to vermin or find overgrazed areas of veld caused by wildlife. While some might utilise burning to manage their veld, landowners emphasised that natural fires were becoming more frequent causing damage to their infrastructure and veld, especially if fire precedes a spout of heavy rains and flooding.

Other challenges

Lastly, 'stock', 'theft', 'labour', and 'jackal' were the most important words identified as other challenges that landowners face on a regular basis (**Figure 2.7**). Livestock losses to theft and vermin were the most frequently mentioned challenges, particularly affecting farms located closer to towns and along, or close to, public roads (**Figure 2.8**). Landowners have resorted to keeping sheep away from certain paddocks that have been targeted in the past by livestock thieves during the festive seasons. They also kraal pregnant and lambing ewes where they can be protected from vermin. Some also mentioned that conserving soil is an ongoing challenge and one which is often interrupted or halted during drought, fire, and other financially draining circumstances.

Chapter 3: Climate trends in the eastern Karoo (1870-2019)

3.1. Introduction

In recent decades a number of studies have analysed historical climate trends in South Africa (Kruger & Shongwe, 2004; Malherbe et al., 2016; Muthoni et al., 2019; Ndiritu, 2005; Reason & Rouault, 2002; Richard et al., 2001; Van Wilgen et al., 2016; Vogel & Drummond, 1993). These studies have utilised meteorological observations collected from manual and automatic weather stations and are instrumental in understanding past climate patterns and for modelling future climate projections (Joubert et al., 1996; Kruger et al., 2019; MacKellar et al., 2014). Despite the relatively large number of studies, however, they poorly represent the historical climate trends over certain regions of South Africa, such as the eastern Karoo.

The eastern Karoo has been the focus of several studies that have examined changes in vegetation in response to grazing and climate (Acocks, 1953; Du Toit et al., 2018; Hoffman & Cowling, 1990; Masubelele et al., 2014). An observed increase in grass cover across the biome boundary, for example, has led to an investigation of the drivers of these changes. Of particular relevance to this chapter were two studies by Du Toit & O'Connor (2014, 2016), which examined a 123-year rainfall record collected at Grootfontein in Middelburg-EC. These analyses reported a significant increase in annual and summer rainfall since 1988 (Du Toit & O'Connor, 2014). Later, findings were published from the same record showing that this increase was further characterised by a shift in rainfall distribution from March to January (Du Toit & O'Connor, 2016). Total annual rainfall, and hence soil moisture availability, is a reliable predictor of seasonal vegetation growth and production in arid environments (Van den Hoof et al., 2018). This correlation has also been illustrated for large regions through satellite-derived indices and models (Le Houérou et al., 1988; Zeng et al., 2008). Having identified these rainfall trends at Grootfontein, and understanding that the main growth season of native grasses is summer (Milton & Hoffman, 1994), the increase in grassiness in the eastern Karoo was, thus, explained predominantly by a directional increase and seasonal shift in rainfall (Du Toit et al., 2018). However, the extent of this association is yet to be investigated at other locations along the east-west rainfall gradient.

Beyond the eastern Karoo, annual rainfall trends have been highly variable over South Africa. In the south-western winter rainfall region rainfall is shown to have declined (Ndebele et al., 2020). In the north-west Namaqualand region, no discernible trends have been detected (Davis et al., 2016), apart from being characterised by strong interannual variability and spatial seasonal variation (Davis et al., 2016; MacKellar et al., 2007). Declines in rainfall since 1985 in the north-central interior have been reported by Botai et al. (2016). Trends over the northern and eastern parts, although temporally quite variable, indicate that a greater concentration of rainfall during December to January has occurred, as well as an increase in daily rainfall intensity and the length of dry spells (Kruger & Nxumalo, 2017), which are in agreement with the global trends (Donat et al., 2013).

While rainfall is a major driver of Karoo vegetation, other climate variables also have an influence, for example, temperature and wind influence photosynthesis and evaporative processes respectively, which are all necessary for vegetation production and ecosystem functioning. African studies have indicated that temperature has increased during the last century over the continent (Hulme et al., 2001; Nicholson, 2000), but also regionally in South Africa (Kruger & Shongwe, 2004; Kruger et al., 2019) and locally in the arid western Karoo (Davis et al., 2016; Strydom et al., 2018). Temperatures are predicted to continue to increase over Africa with projected increases of 4-6 °C in the subtropics under a low mitigation climate change scenario (Engelbrecht et al., 2015; Kruger et al., 2019). Along with increasing global temperatures, a phenomenon known as global terrestrial 'stilling' (a decline in wind speeds over time) has more recently occurred since the 1980s (McVicar et al., 2012; Zeng et al., 2019). Regional declines in wind speeds have also been found over the south-western and central parts of South Africa (Eamus & Palmer, 2008; Hoffman et al., 2011). The causes of stilling are highly contested but the most common suggestions are increased land surface roughness due to increased vegetation, urbanisation, or changes in agricultural practices, and large-scale changes in atmospheric circulation (McVicar et al., 2012; Vautard et al., 2010). A recent study of historical wind speed data in the northern hemisphere, however, has since revealed that a large-scale reversal in the trend of wind speeds took place in the 2010s and which was more likely a response to decadal variability in ocean-atmosphere oscillations (Zeng et al., 2019). Based on the findings from the latter study, therefore, the current predictions for global wind speed trends anticipate a returning decline in the near-future associated with oscillation patterns (Zeng et al., 2019). Wind speed, in addition to humidity, air temperature and solar radiation, is also one of the primary climate variables that influences evaporation rates. Widespread declines in pan evaporation have been reported globally (Roderick et al., 2009) and in South Africa (Eamus & Palmer, 2008; Hoffman et al., 2011). Therefore, the predicted declines in wind speed are, in turn, expected to reduce surface evaporation and evapotranspiration rates over time (McVicar et al., 2012).

3.2. Aims and objectives

Based on these predictions of climate change, the aim of this chapter was twofold, i) to examine hypotheses of climate change by investigating spatial patterns and directional changes in rainfall, temperature, evaporation and wind run, and ii) to determine whether the historical trends provide reasonable explanations for the observed vegetation responses that have occurred across the rainfall gradient of the study area (Hoffman & Cowling, 1990; Masubelele et al., 2014). The study identifies a regional climate response over the past 149 years by studying trends at individual locations across the rainfall gradient to determine their spatial variability. First, the hypothesis that a directional increase in annual rainfall, and a shift in rainfall season, across the rainfall gradient in a westward direction was tested (Du Toit & O'Connor, 2014), and that this trend would result in a westward increase in grass cover. Likewise, a decline in rainfall at any point along the rainfall gradient would manifest as a decrease in grass cover. If supported by the findings, this would provide reasonable evidence for a rainfall-driven westward expansion of the Grassland biome. Second, the hypothesis that a directional increase in annual and seasonal maximum and minimum temperatures has occurred in the study area was tested, as has been found at several locations in South Africa (Kruger et al., 2019). Lastly, based on the stilling trend over the Cape Floristic Region (Hoffman et al., 2011), and other locations in the Karoo (Eamus & Palmer, 2008), as well as associated declines in pan evaporation, the hypothesis that directional decreases in wind run, pan evaporation and evapotranspiration have occurred in the eastern Karoo were examined.

3.3. Methods

The study area is situated in the central-eastern interior of South Africa at the interface of the Nama-Karoo and Grassland biomes (**Figure 3.1**, see Chapter 2 for a more detailed description of the study area). The climate data were obtained from the South African Weather Service (SAWS), the Climate Systems Analysis Group (CSAG), the South African Agricultural Research Council's Institute for Soil, Climate and Water (ARC-ISCW), Lynch et al. (2004) and local farm records.

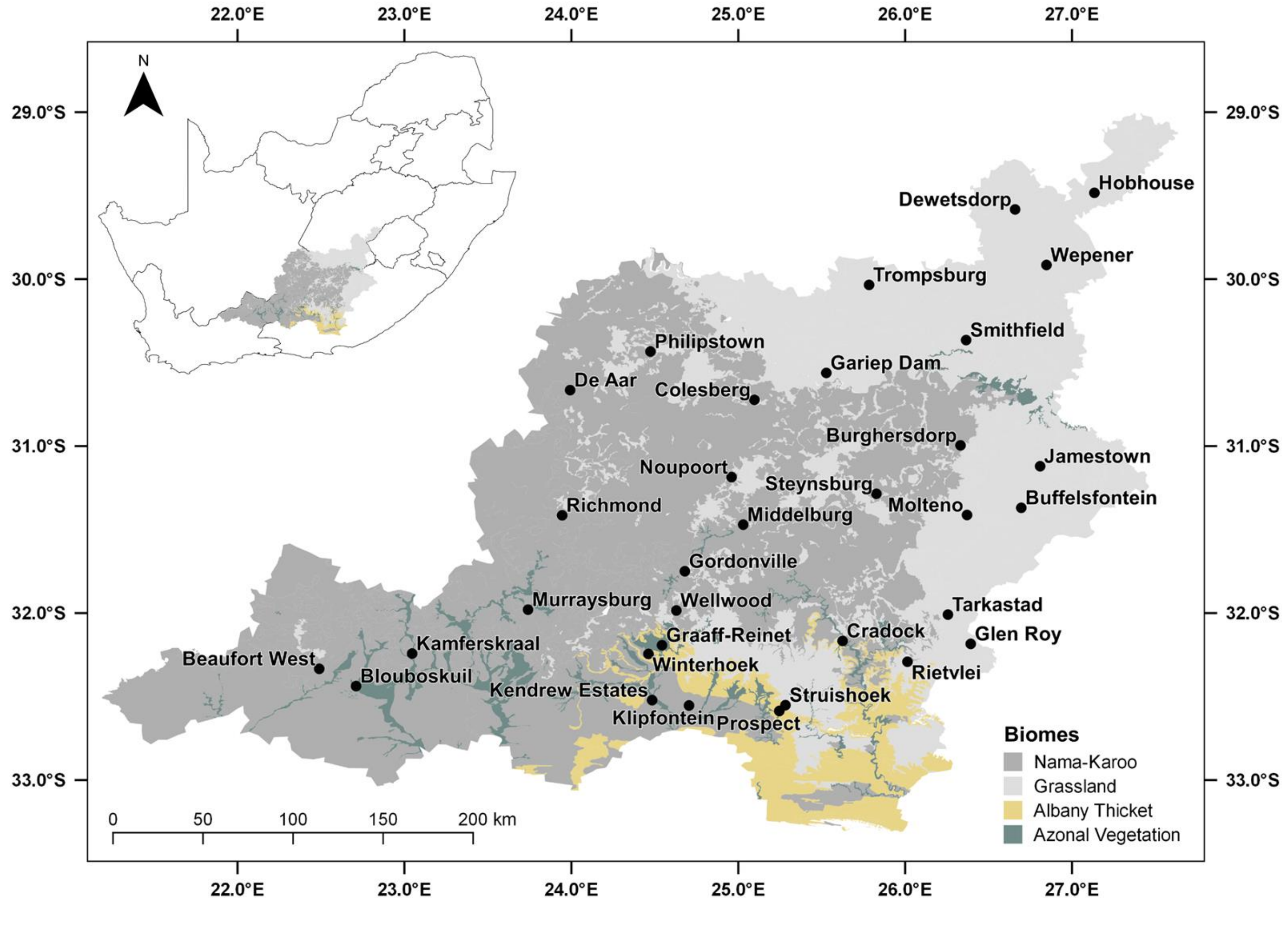

Figure 3.1 The location of historical climate records in the eastern Karoo used in the study. The accompanying Table 3.1 indicates the type of record available at each site. Tables 3.2 to 3.5 provide further details of each climate variable and station.

Table 3.1 The type and number of historical climate records analysed in the study

Site name	Rainfall	Temperature	A-Pan evaporation	Evapotranspiration	Wind speed
Beaufort West		1			
Blouboskuil	1				
Buffelsfontein	1	1	1		1
Burghersdorp	1				
Colesberg	1	1	1		1
Cradock		2	1		1
De Aar	1				
Dewetsdorp	1				
Gariep Dam		1			
Graaff-Reinet		1			
Glen Roy	1				
Gordonville	1				
Hobhouse		1	1	1	
Jamestown	1	2	1		1
Kamferskraal	1				
Kendrew Estates	1				
Klipfontein	1				
Middelburg	1	2		1	1
Molteno	1				
Murraysburg		1		1	1
Noupoort		1			
Philipstown	1				
Prospect	1				
Richmond	1				
Rietvlei	1				
Smithfield		1	1	1	1
Steynsburg	1				
Struishoek	1				
Tarkastad	1	1	1		1
Trompsburg	1			1	1
Wellwood	1				
Wepener		1			
Winterhoek	1				
	24	**17**	**7**	**5**	**9**

Rainfall records

Vegetation monitoring has been carried out within the study area since the early 1960s (Chapter 4). Therefore, the proximity of climate stations to these vegetation sites as well as the availability and quality of rainfall data were important criteria in selecting the records to be used in this analysis. The data also had to meet two additional criteria, i) length of the record (≥ 90 years), and ii) completeness, that is, datasets with less than 10% of the data missing. Based on these criteria, 25 rainfall stations were selected. They ranged in altitude from 612 m (Kendrew Estates) to 1765 m

(Buffelsfontein) above sea level (**Table 3.2, Figure 3.1**). Monthly rainfall totals were available for each station. The annual rainfall period in this analysis was calculated from July in the current year to June the following year. Seasons are represented as 'early summer' (OND), 'late summer' (JFM), 'autumn' (AMJ) and 'winter' (JAS).

Table 3.2 Climate stations for which monthly rainfall data (n = 25) were available. The number of months of missing data are reflected as a percentage of the total months of individual records

Climate station	**Location**		**Altitude (masl)**	**Years**	**Length (years)**	**Mean (mm)**	**% Missing data**
Blouboskuil	-32.438 S	22.710 E	877	1919-2017	99	199	6.6
Buffelsfontein	-31.370 S	26.696 E	1765	1885-2012	128	535	4.4
Burghersdorp	-30.996 S	26.332 E	1397	1887-2001	115	430	4.8
Colesberg	-30.723 S	25.097 E	1387	1878-2004	126	386	0.5
De Aar	-30.665 S	23.992 E	1286	1888-1992	104	287	9.9
Dewetsdorp	-29.583 S	26.659 E	1439	1906-2013	107	580	1.4
Glen Roy	-32.185 S	26.393 E	1548	1923-2018	95	519	1.1
Gordonville	-31.750 S	24.680 E	1676	1907-2005	98	416	2.7
Jamestown 1	-31.121 S	26.809 E	1617	1879-2008	129	508	2.9
Kamferskraal	-32.243 S	23.046 E	941	1900-2019	120	223	0.1
Kendrew Estates	-32.522 S	24.484 E	612	1890-2017	127	285	2.5
Klipfontein	-32.554 S	24.705 E	636	1892-2018	126	263	0.9
Leliekloof	-32.293 S	26.014 E	1272	1914-2018	104	421	0.6
Middelburg 1*	-31.471 S	25.029 E	1277	1878-2019	142	328	1.9
Molteno 1	-31.413 S	26.371 E	1580	1889-2001	113	515	7.2
Philipstown	-30.434 S	24.474 E	1359	1878-2002	124	332	1.6
Prospect	-32.587 S	25.246 E	792	1926-2018	92	384	1.6
Richmond	-31.415 S	23.945 E	1419	1878-2013	135	325	1.0
Rietvlei	-32.292 S	26.014 E	1279	1914-2019	105	418	0.1
Steynsburg	-31.286 S	25.828 E	1541	1878-2002	124	416	2.8
Struishoek	-32.552 S	25.283 E	920	1928-2018	90	462	0.6
Tarkastad	-32.009 S	26.256 E	1394	1878-2005	142	418	3.7
Trompsburg 1	-30.035 S	25.784 E	1416	1913-2018	105	402	0.5
Wellwood	-31.985 S	24.629 E	1205	1874-2017	143	345	0.9
Winterhoek	-32.245 S	24.462 E	905	1900-2015	116	373	1.5

* Dataset was extended using data from three other stations situated within a 20 km radius including Grootfontein II 145059 (Lynch) for the period 1974-1992, Middelburg 12378 (ARC) for the period 1993-2001, and Grootfontein 30097 (ARC) between 2001 and 2019.

Temperature records

Du Toit & O'Connor (2017) suggest that temperature datasets of less than 50 years may provide misleading indications of trends and that long-term datasets of at least 100 years are needed. However, although the majority of currently available historical temperature records in South Africa only begin around the 1970s or later, this timeframe appropriately captures the period of vegetation change examined in the thesis (Chapters 4 and 5). Seventeen stations were chosen, which collectively span the period 1971-2019 (**Table 3.3**). Mean monthly minimum (TMIN) and mean monthly maximum (TMAX) temperature was provided at each station. Mean annual temperature (MAT) was calculated by averaging mean monthly minimum and maximum values per year.

Table 3.3 Climate stations for which mean monthly minimum and maximum temperature data were available (n = 17)

Climate station	**Location**		**Altitude (masl)**	**Years**	**Length (years)**	**Mean (ºC)**	**% Missing data**
Beaufort West	-32.334 S	22.489 E	919	1990-2019	30	17.9	0
Buffelsfontein	-31.369 S	26.697 E	1763	1979-2017	39	11.5	2.1
Colesberg	-30.700 S	25.100 E	1328	1984-2003	21	16.2	3.7
Cradock 1	-32.168 S	25.625 E	931	1986-2017	32	17.6	1.3
Cradock 2	-32.217 S	25.683 E	846	1972-2002	31	16.9	3.8
Gariep Dam	-30.562 S	25.528 E	1281	2004-2017	14	17.2	3.0
Graaff-Reinet	-32.193 S	24.543 E	795	1993-2017	25	17.7	1.3
Hobhouse	-29.483 S	27.135 E	1500	1998-2019	22	15.7	0.7
Jamestown 1	-31.121 S	26.809 E	1612	1991-2017	27	13.6	1.5
Jamestown 2	-31.067 S	26.783 E	1650	1985-2007	23	14.0	1.6
Middelburg 1	-31.471 S	25.029 E	1277	1999-2019	20	15.9	8.3
Middelburg 2	-31.480 S	25.030 E	1262	1980-1992	13	15.3	0.6
Murraysburg	-31.980 S	23.740 E	1193	2005-2019	15	15.5	2.2
Noupoort	-31.186 S	24.960 E	1509	1994-2017	24	15.1	0.3
Smithfield 3	-30.365 S	26.365 E	1518	2002-2012	11	14.6	6.7
Tarkastad	-32.009 S	26.256 E	1315	1987-2019	33	16.0	6.9
Wepener	-29.916 S	26.847 E	1411	2000-2017	18	16.2	3.5

Evaporation and wind run records

The South African Weather Bureau traditionally measured evaporation from US Weather Bureau Class A-Pans and sunken Symon's pans, which had been installed sparsely across South Africa (Bosman, 1987; Clemence, 1987). The pans, containing water exposed to the atmosphere, were measured for daily evaporation by subtracting the observed water levels before and after precipitation had occurred (Rodda et al., 1976). Due to the high maintenance costs incurred from servicing the pans, they were eventually replaced by automated weather stations towards the end of the 1980s (Clemence, 1987). The automatic stations are designed to estimate daily relative evapotranspiration (ET), which is the sum of all water losses to the atmosphere through the co-occurring processes of evaporation and transpiration. Evapotranspiration is calculated using the

Penman-Monteith equation (Allen et al., 1998), which has been adapted to suit South African conditions. The algorithm indicates water loss from the soil on a lawn of short grass (C. Henningse, ARC-ISCW, *pers. comm.*). Total daily Class A-Pan evaporation (mm/day) and average total daily relative ET (mm calculated from hourly data) were provided by the ARC-ISCW (**Table 3.4**). These two variables were treated independently in the analyses due to their inherent differences. Wind run (km/day) data were also provided by the ARC-ISCW (**Table 3.5**). Wind run is a measure of the total distance (km) of passing wind at a given point in a period (24 h) and is measured using an anemometer that is fixed at a height of approximately 2 m above the ground.

Table 3.4 Climate stations for which total daily A-Pan evaporation (n = 7) and average total relative evapotranspiration (ET) data (n = 5) data were available

Climate station	Location		Altitude (masl)	Years	Length	Mean (mm)	% Missing data
A-Pan							
Buffelsfontein	-31.369 S	26.697 E	1763	1984-1997	14	146.1	0
Colesberg	-30.700 S	25.100 E	1328	1984-2003	20	165.5	1.3
Cradock 2	-32.217 S	25.683 E	846	1972-2002	31	168.9	4.5
Hobhouse 1	-29.484 S	27.134 E	1525	1998-2004	7	148.3	5.5
Jamestown 2	-31.067 S	26.783 E	1650	1985-2007	24	143.6	2.6
Smithfield 2	-30.217 S	26.365 E	1518	2002-2012	12	152.9	0.7
Tarkastad	-32.009 S	26.250 E	1274	1987-2005	19	178.2	2.7
ET							
Hobhouse 2	-29.482 S	27.134 E	1500	2005-2019	15	117.7	2.8
Middelburg 1	-31.471 S	25.029 E	1277	2002-2019	18	113.9	5.7
Murraysburg	-31.980 S	23.740 E	1193	2005-2019	15	121.5	2.2
Smithfield 1	-30.080 S	26.344 E	1554	2012-2019	8	136.6	3.0
Trompsburg 2	-30.338 S	25.810 E	1494	2010-2019	10	130.4	0

Table 3.5 Climate stations for which wind run (n = 9) data were available

Climate station	Location		Altitude (masl)	Years	Length	Mean (km/day)	% Missing data
Buffelsfontein	-31.369 S	26.697 E	1763	1984-1997	14	187.2	2.3
Colesberg	-30.700 S	25.100 E	1328	1984-2003	20	123.9	4.6
Cradock 2	-32.217 S	25.683 E	846	1977-2002	26	170.8	1.6
Jamestown 2	-31.067 S	26.783 E	1650	1985-2007	23	204.9	1.5
Middelburg 1	-31.471 S	25.029 E	1277	2002-2019	18	195.5	5.7
Murraysburg	-31.980 S	23.740 E	1193	2005-2019	15	214.5	2.2
Smithfield 1	-30.080 S	26.344 E	1554	2012-2019	8	230.8	3.0
Tarkastad	-32.009 S	26.250 E	1274	1987-2005	19	213.6	2.7
Trompsburg 2	-30.338 S	25.810 E	1494	2010-2019	10	285.8	0

3.4. Statistical analysis

Prior to the analyses, data were checked for errors, such as for negative monthly totals or missing data. Gaps in time series, i.e., months that had no recorded value, were removed prior to analysing trends. Where climate records have been merged for the drought analysis to produce a summary of wet and dry phases for the study area, individual analyses have also been provided in Appendix B to accompany the summary. Merging of datasets was only applied to the temperature variables when summarising the monthly and seasonal trends between 1971 and 2019 due to the general incompleteness and lack of temperature records available in South Africa. Otherwise in general, datasets of all climate variables have been analysed individually to examine the nature and spatial distribution of trends across the study area. The data analyses were divided into two main steps, a drought analysis based on the rainfall records and a trend analysis of the rainfall, temperature, wind run and evaporation records. The mathematical details of the trend tests are provided in Appendix B. All statistical analyses and plotting were carried out in R version 3.5.2. (R Core Team, 2018). Data manipulation, functional processing and plotting were performed using the packages broom (Robinson et al., 2021), tidyverse (Wickham et al., 2019), lubridate (Grolemund & Wickham, 2011), ggplot2 (Wickham, 2016) and gridExtra (Auguie, 2017). Packages specific to each analysis are mentioned below.

3.4.1 Drought analysis

The Standardised Precipitation Index (SPI) was used to assess drought frequency, intensity using monthly rainfall totals recorded in the study area (**Table 3.2**). This method has been applied broadly around the world to quantify droughts over different time scales relevant to the useable water source in question, be it streamflow, soil moisture or groundwater (McKee et al., 1993). The SPI, represented as a *z* score, is defined as the number of standard deviations from the long-term mean at which a random event (either negative or positive) occurs (Guenang & Kamga, 2014; McKee et al., 1993). Therefore, each SPI value provides a comparison of the accumulated rainfall in a period of *n*-months to the long-term mean (Guenang & Kamga, 2014). The precipitation rate (mm/month) is fitted to a gamma distribution for *n*-months. From the perspective of the ecological responses of semiarid Karoo vegetation to soil moisture and groundwater, a 24-month time scale was sufficient for examining droughts in the study area. The SPI responds more slowly to changes in rainfall at this time scale than at shorter time scales. Above- and below-zero events become fewer in number but longer in duration (McKee et al., 1993), thus aiding the interpretation of rainfall-driven vegetation shifts. The drought intensity categories as defined by McKee et al. (1993) have been used in this study to assess the frequency of events within each category over the entire time series (**Table 3.6**).

After removing gaps in each of the rainfall datasets to create a continuous time series of mean annual rainfall per sites, individual SPI analyses were run on each time series and the resultant patterns were visually compared among sites (Appendix B2). Based on the spatial and temporal variability of wet and dry phases among sites, a novel approach was adopted to aggregate the individual time series by averaging the total annual rainfall per year across all sites. This produced a single time series of average rainfall per year over time for the study area. The SPI analysis was then run on this time series of average rainfall values to provide a broad estimate of the wet and dry patterns for the whole area. While this is not a common approach it can be studied alongside the individual SPI graphs (Appendix B2). The R package spi (Neves, 2012) was used to run the analysis.

Table 3.6 Drought categories defined by McKee et al. (1993) based on the SPI values calculated from a monthly rainfall dataset for a period of 3, 6, 12, 24 or 48 months

SPI Values	**Drought category**
2.00 or more	Extremely wet
1.50 to 1.99	Severely wet
1.00 to 1.49	Moderately wet
0.99 to 0	Mildly wet
0 to -0.99	Mildly dry
-1.00 to -1.49	Moderately dry
-1.50 to -1.99	Severely dry
≤ -2.00	Extremely dry

3.4.2. Trend analysis

Monotonic, or fluctuating, annual and seasonal trends over the full length of each time series were assessed for rainfall, temperature, evaporation, and wind run. The variance corrected Mann-Kendall for lag-1 serial correlation (MKVC1) trend test was used to identify monotonic trends at significance levels of 0.01 and 0.05 (Hamed & Rao, 1998; Kendall, 1975). The MKVC1 test requires no distributional assumptions and reduces the occurrence of a Type I error (i.e., a trend is detected when in reality there is none) by correcting the variance of the test statistic if significant serial autocorrelation is detected in the first lag (Muthoni et al., 2019). The null hypothesis for the test statistic assumes that there is no monotonic trend in a given time series. Sen's slope estimator was also used to examine the magnitude of the trend determined by the slope and the intercept (Sen, 1968). **Figure 3.2** illustrates examples of two separate time series of total annual rainfall and total rainfall in early summer at Buffelsfontein (1885-2012). The MKVC1 tests were applied to the total rainfall time series (grey lines) for each season, as well as to total annual rainfall, at each site. This was repeated for each climate variable.

The nonparametric approach by Pettitt (1979) for change point detection was used to identify points in each annual and seasonal rainfall time series where a significant change in the direction of a trend took place. The frequency of change points for each decade was then obtained in order to determine where the highest occurrence of shifts in trends took place (Appendix B3). The packages used for the time series analyses included hydroTSM (Zambrano-Bigiarini, 2020) and forecast (Hyndman et al., 2020; Hyndman & Khandakar, 2008). Those used for the statistical testing of significant trends included Kendall (McLeod, 2011), modifiedmk (Patakamuri & O'Brien, 2020), trend (Pohlert, 2020) and zoo (Zeileis & Grothendieck, 2005).

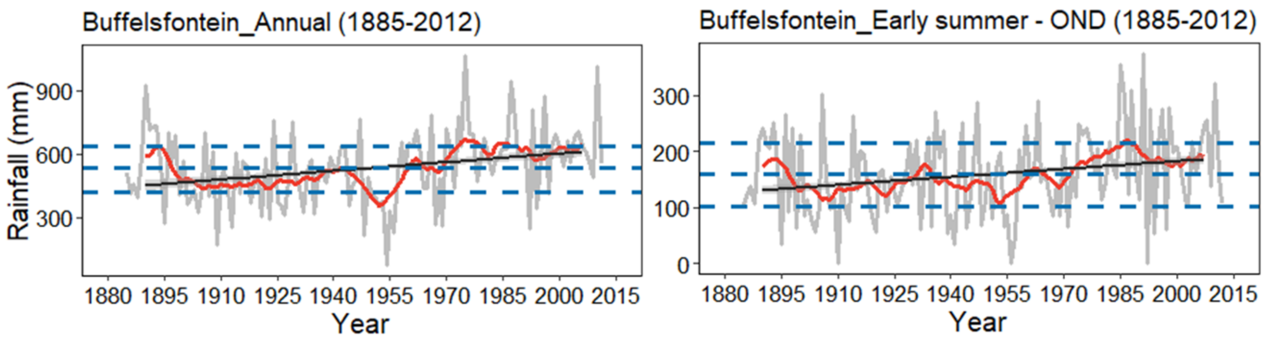

Figure 3.2 Examples of total annual rainfall (left) and total rainfall in the early summer months (right) at the Buffelsfontein weather station. The grey line is the time series of total rainfall; the red line is the 10-year moving average. The horizontal blue dashed lines are the positions of the upper quartile, mean and the lower quartile.

3.5. Results

3.5.1. Wet-dry phases (1875-2019)

The 24-month SPI analysis averaged across all 25 annual rainfall time series can be described by three major periods of i) above-average annual rainfall from 1886 to 1902, ii) prolonged below-average rainfall from 1902 to 1970, and iii) a recovery of above-average rainfall from 1970 to 2014 (**Figure 3.3A**). Most of the SPI events occurring in the second of these periods were categorised as ‘mildly dry’ events between 1911 and 1959 (**Table 3.7**). This long dry phase was occasionally interrupted by brief ‘mildly wet’ SPI events. One ‘extremely wet’ SPI event occurred between 1974 and 1975. During the recent wet recovery phase from 1970 to 2019, two shorter runs of below-average SPI events occurred between 1990 and 1999, and 2014 and 2019 (**Figure 3.3A**). The historical time series of 141 years was characterised by a high frequency of ‘mildly wet’ (729) and ‘mildly dry’ (855) SPI events (**Figure 3.3B**), the latter having lasted longer in duration.

Table 3.7 Number of wet and dry events from 1878 to 2019 categorised into eight drought categories (McKee et al., 1993), calculated using a 24-month SPI

SPI Values	Drought category	Frequency of SPI events	Notable periods
≤ -2.00	Extremely dry	6	1877
-1.50 to -1.99	Severely dry	4	1877-1878
-1.00 to -1.49	Moderately dry	46	1902-1904 1945-1946 2017
0 to -0.99	Mildly dry	855	1877-1886 1911-1959 1963-1970 1990-1999 2014-2019
0 to 0.99	Mildly wet	729	1886-1889 1894-1902 1954-1963 1970-1973 1977-1990 1996-2015
1.00 to 1.49	Moderately wet	45	1889-1890 1892-1894 1973-1976
1.50 to 1.99	Severely wet	38	1890-1892 1974-1975
≥ 2.00	Extremely wet	8	1891

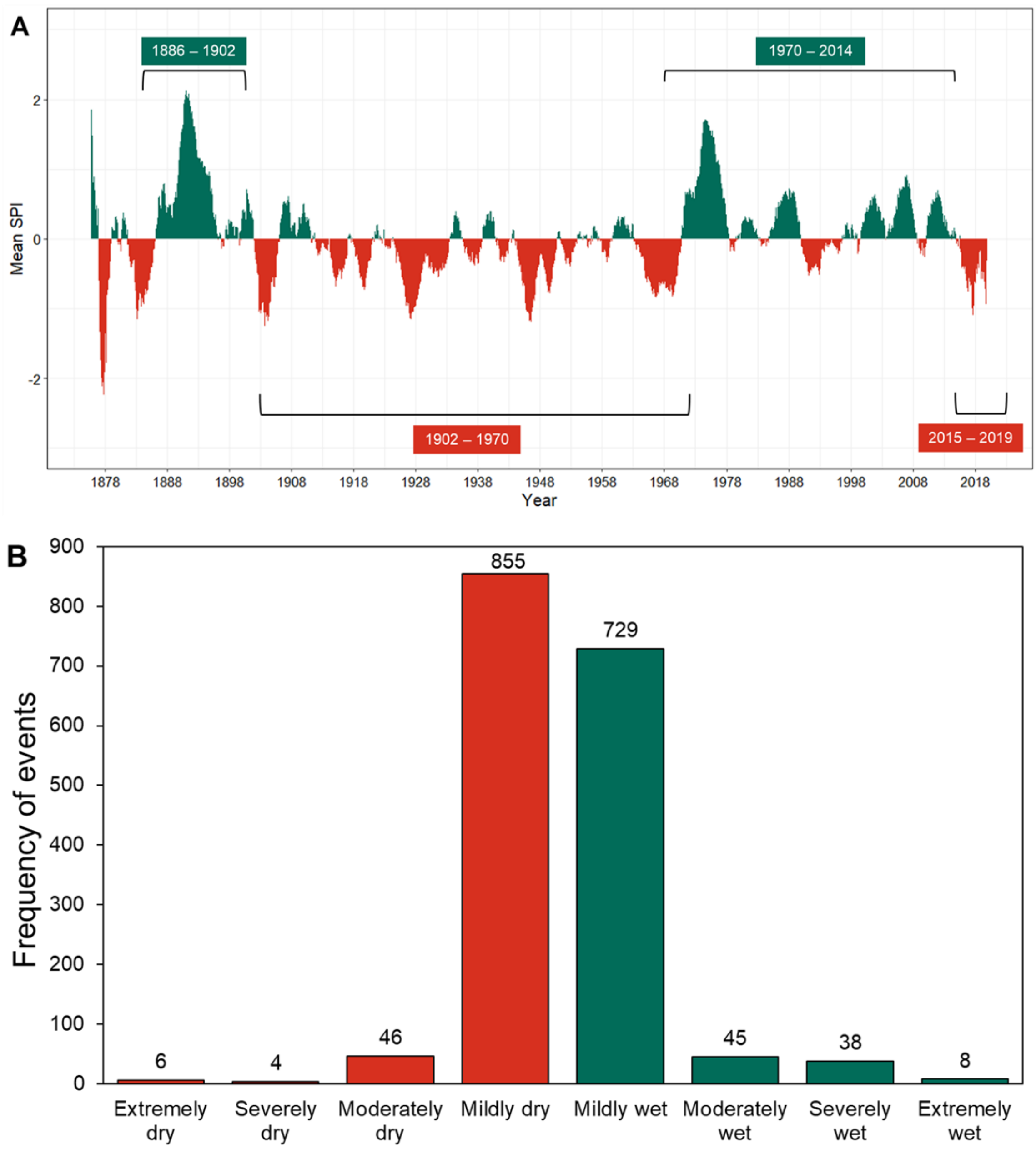

Figure 3.3 A) The long-term (141 years) 24-month Standardised Precipitation Index (SPI) averaged over all rainfall time series (n = 26) in the study area. Notably wet (above-average annual rainfall) and dry (below-average) periods are bracketed. Black dots represent the initial and repeated vegetation surveys conducted in the early 1960s, 1989-90, 2008-09 and 2017-18. B) The frequency of above and below-average annual SPI events in the time series grouped according to the drought categories defined by McKee et al. (1993). Individual SPI graphs per site are provided in Appendix B2.

3.5.2. Climate trends

Annual rainfall trends

The long-term average of annual rainfall across the rainfall gradient has increased from 376 mm/yr (from 1874 to 1969) to 414 mm/yr (from 1970 to 2019). Of the 24 annual time series, 17 (71%)

revealed positive MKVC1 values, eight (33%) of which were statistically significant (**Table 3.8**). The sites of increasing annual rainfall were largely located in the Nama-Karoo biome (below the dashed line, **Figure 3.4**). The remaining eight time series (33%) had negative MKVC1 values for annual rainfall, one of which was statistically significant. These sites occur towards the north-eastern, or Grassland biome (above the dashed line), extent of the area.

Seasonal rainfall trends

Twenty-one (88%) of all early summer (OND) time series had positive MKVC1 values, eight (33%) of which were statistically significant. In contrast, 11 (46%) of the late summer (JFM) time series had negative trends, but only three (13%) were significant. Furthermore, sites that had a negative trend in late summer rainfall, with a concomitant positive trend in early summer rainfall, were those located along the wetter extent of the rainfall gradient (north-east) where the biomes begin to merge. Based on the summer rainfall trends, two important distinctions can be made: i) several sites in the Nama-Karoo have experienced higher rainfall in the early summer months, and ii) a shift in seasonality from late to early summer rainfall along the biome boundary has occurred (**Figure 3.4**).

Fourteen (58%) of all autumn (AMJ) time series had negative MKVC1 trends, while 16 (67%) of all winter (JAS) time series were positive but non-significant. The above-average rainfall phase from 1970 to 2016 recorded in the SPI analysis (**Figure 3.3**) can be further informed by these rainfall trends. The frequency of change points detected from all the time series was highest in the 1970s (Appendix B3, B4), thus emphasising that a shift in the rainfall regime in the eastern Karoo was more likely to have occurred in this decade.

Table 3.8 Annual and seasonal rainfall trends (*Z* statistic) calculated using the variance corrected Mann-Kendall for lag-1 serial correlation test (MKVC1). Bold values indicate significant positive or negative trends at $*p < 0.05$ and $**p < 0.01$. Time periods of each dataset are in subscripts. OND = early summer; JFM = late summer; AMJ = autumn; JAS = winter

Station name	**Rainfall**				
	Annual	**OND**	**JFM**	**AMJ**	**JAS**
Blouboskuil$_{(1919-2017)}$	**4.71****	**3.20****	1.54	**2.91****	1.07
Buffelsfontein$_{(1885-2012)}$	**3.10****	**2.42***	1.14	**2.08***	0.67
Burghersdorp$_{(1887-2001)}$	**-2.30***	-0.35	**-2.34****	-1.28	-0.39
Colesberg$_{(1878-2004)}$	-0.37	1.28	-1.54	-0.26	0.75
De Aar$_{(1888-1992)}$	0.14	0.37	-1.31	0.72	1.18
Dewetsdorp$_{(1906-2013)}$	-0.60	0.40	-0.99	-0.30	-0.69
Glen Roy$_{(1923-2018)}$	1.33	1.02	**1.97***	-0.49	-1.65
Gordonville$_{(1907-2005)}$	**2.38***	**2.32***	0.87	0.61	**2.07***
Jamestown 1$_{(1879-2008)}$	-1.92	-0.30	**-2.85****	-0.55	-1.03
Kamferskraal$_{(1900-2019)}$	1.46	1.48	0.70	1.68	0.28
Kendrew Est.$_{(1890-2017)}$	0.54	1.07	1.01	-0.43	-0.39
Klipfontein$_{(1892-2018)}$	0.88	1.64	0.33	-0.29	0.43
Middelburg 1$_{(1878-2019)}$	1.68	1.81	0.87	0.47	0.39
Molteno 1$_{(1889-2001)}$	**1.96***	1.12	-0.12	**2.01***	1.40
Philipstown$_{(1878-2002)}$	-0.08	**2.13***	-1.73	-0.90	1.04
Prospect$_{(1926-2018)}$	**2.37***	1.93	1.70	1.18	0.75
Richmond$_{(1878-2013)}$	0.98	**2.43****	-0.57	-0.57	0.50
Rietvlei$_{(1914-2019)}$	**2.19***	1.13	1.73	0.52	0.64
Steynsburg$_{(1878-2002)}$	**1.99***	**2.08***	-0.23	-0.24	**3.44****
Struishoek$_{(1928-2018)}$	0.44	0.37	0.58	0.39	-0.66
Tarkastad$_{(1878-2005)}$	-1.89	0.16	**-3.03****	**-2.04***	-1.20
Trompsburg 1$_{(1913-2018)}$	-0.19	-0.38	-1.00	-0.29	-0.22
Wellwood$_{(1874-2017)}$	1.29	**4.28****	0.34	**-2.59****	0.84
Winterhoek$_{(1900-2015)}$	-0.40	-0.17	0.16	-1.42	-1.12

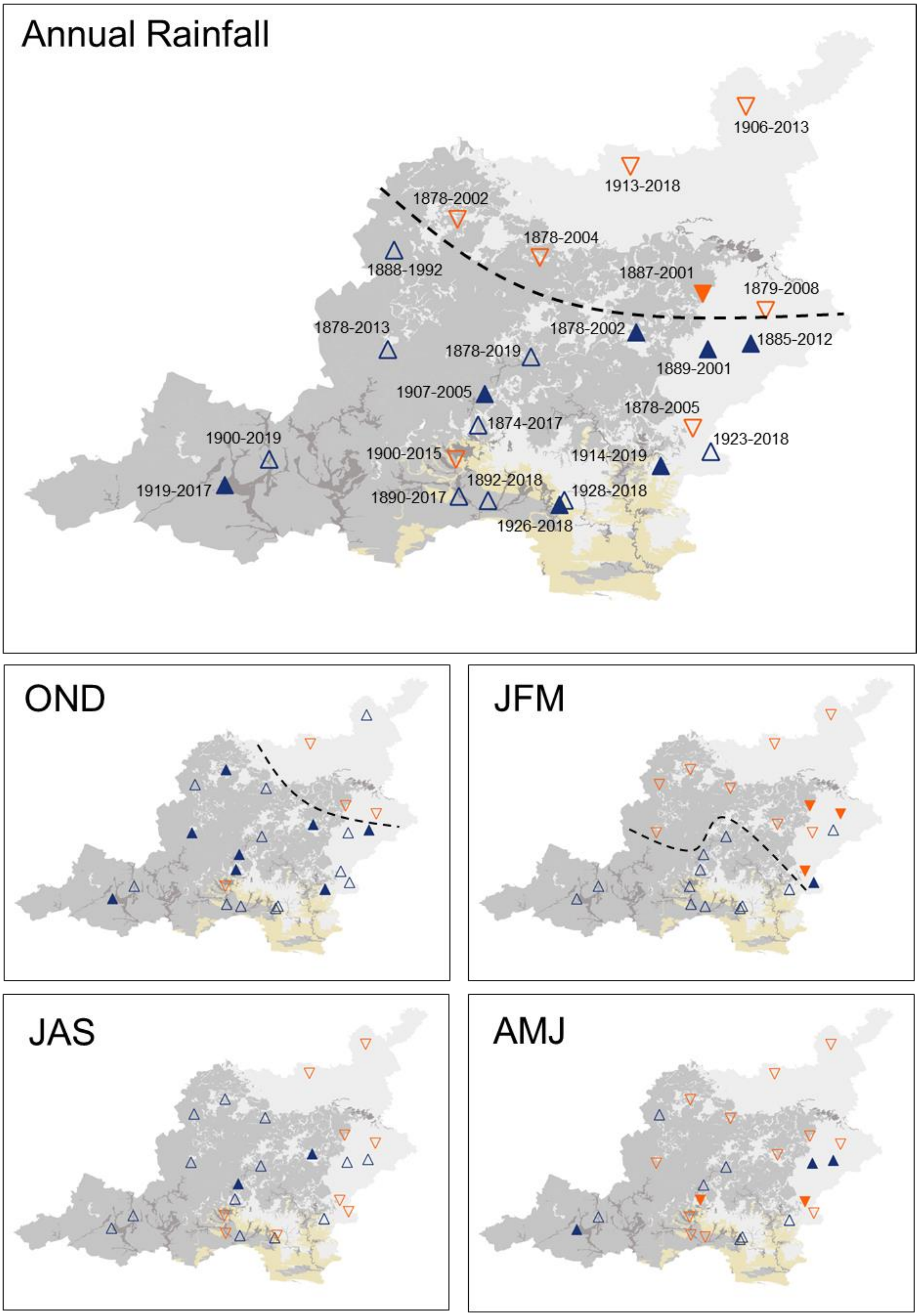

Figure 3.4 Annual and seasonal rainfall trends in the eastern Karoo, represented by the MKVC1 *Z* statistics. Maps display significant trends with blue (+) and orange-filled (-) triangles and non-significant trends are empty triangles. Dashed lines illustrating shifts are hand drawn. Time periods for each site are the same for the four maps showing seasonal trends.

Annual and seasonal temperature trends

Eleven (65%) and 12 (71%) of the temperature time series (n = 17) had positive MKVC1 values for MAT and annual TMAX, respectively. Only three (18%, MAT) and four (24%, TMAX) were statistically significant (**Table 3.9**). Nine (53%) sites had negative MKVC1 values for annual TMIN, three of which were significant (12%). On account of variable time series lengths, the time series of longest length (39 years, Buffelsfontein), indicated that TMAX increased by 1.7 °C at a rate of 0.04 $°Cy^{-1}$. TMIN decreased by 0.04 °C at a rate of -0.001 $°Cy^{-1}$. Generally, the change in TMAX across all temperature records varied between -0.8 and 5.0 °C and TMIN varied between -3.6 and 3.7 °C. These ranges indicate an overall warming has occurred. On average, seasonal trends were generally positive for TMAX and negative for TMIN (**Figure 3.5**). However, this pattern was enhanced in the months September, October, and November. March to July showed warming trends for both TMAX and TMIN. Annual and seasonal trends for TMAX and TMIN were not significantly correlated with altitude (Appendix B5).

Average seasonal trends for TMAX indicated that early summer had the largest trend in TMAX (+0.93) (**Figure 3.5**). Autumn had the largest positive trend for TMIN (+0.40), while winter had the largest negative trend for TMIN (-0.34). The summer months (January, March and December) and autumn and winter months (May, June and July) showed warming trends for both TMAX and TMIN (**Figure 3.5**). March had the largest positive trend in TMAX (+1.79), while November had the largest negative trend for TMIN (-1.16).

Table 3.9 Annual and seasonal mean maximum (TMAX), minimum (TMIN) and mean annual (MAT) temperature trends (*Z* statistic) as determined by MKVC1 tests (n = 17). Time periods of each dataset are in subscripts

Station name	MAT	TMAX (°C)					TMIN (°C)				
		Annual	OND	JFM	AMJ	JAS	Annual	OND	JFM	AMJ	JAS
Beaufort West$_{(1990-2019)}$	**5.17****	**4.46****	**3.59****	**4.85****	**2.80****	**2.00***	1.72	1.07	**2.03***	**2.25***	-0.53
Buffelsfontein$_{(1979-2017)}$	1.45	**7.23****	**2.71****	0.58	1.24	**2.32***	-0.82	0.00	1.04	-1.16	**-4.41***
Colesberg$_{(1984-2003)}$	1.59	1.01	0.42	0.16	0.49	-0.29	1.46	0.26	-0.68	0.84	-0.23
Cradock 1$_{(1986-2017)}$	0.02	**2.68****	**2.06***	**2.19***	1.35	1.28	**-2.47***	**-4.30****	**-3.47****	**-2.66****	**-2.42***
Cradock 2$_{(1972-2002)}$	**2.04***	1.29	-0.44	0.34	0.44	**4.13****	1.75	**2.19***	0.25	0.82	1.19
Gariep Dam$_{(2004-2017)}$	-0.77	0.00	-0.77	0.33	0.99	-0.18	**-1.09**	-1.20	-0.77	-0.33	-0.06
Graaff-Reinet$_{(1993-2017)}$	-0.77	-0.86	-0.26	0.82	0.07	-1.38	-0.63	-0.96	-1.38	-0.02	-0.77
Hobhouse$_{(1998-2019)}$	1.64	**2.99****	1.47	**8.84****	**1.97***	1.80	-1.80	-1.66	-1.27	0.17	-1.07
Jamestown 1$_{(1991-2017)}$	-0.75	-1.38	0.38	-0.82	-1.25	-0.92	1.86	1.30	1.42	**2.45***	0.42
Jamestown 2$_{(1985-2007)}$	**2.01***	0.74	**2.43***	0.95	0.11	-0.14	**2.38***	1.80	1.88	**2.59****	1.58
Middelburg 1$_{(1999-2019)}$	0.49	1.27	1.43	1.66	1.06	**2.37***	0.47	0.52	1.17	1.13	-0.03
Middelburg 2$_{(1980-1992)}$	0.79	0.79	-0.67	0.11	0.43	0.55	-0.06	-0.06	0.06	0.18	-0.06
Murraysburg$_{(2005-2019)}$	0.00	-0.30	-0.40	0.30	1.58	-0.88	-0.59	-0.64	-0.40	1.09	-0.33
Noupoort$_{(1994-2017)}$	-0.62	1.22	**1.99***	1.17	0.79	-0.22	-0.80	0.07	-0.22	0.12	-0.12
Smithfield 3$_{(2002-2012)}$	**-2.80****	**-2.02***	-0.62	**-12.23****	-1.80	-0.31	-1.25	-1.40	0.00	-0.86	0.26
Tarkastad$_{(1987-2019)}$	0.54	0.91	**2.35***	-0.82	0.09	0.53	0.43	0.85	0.48	0.95	0.00
Wepener$_{(2000-2017)}$	0.30	1.67	0.23	0.38	1.67	1.44	0.00	-0.76	1.14	-0.76	0.83

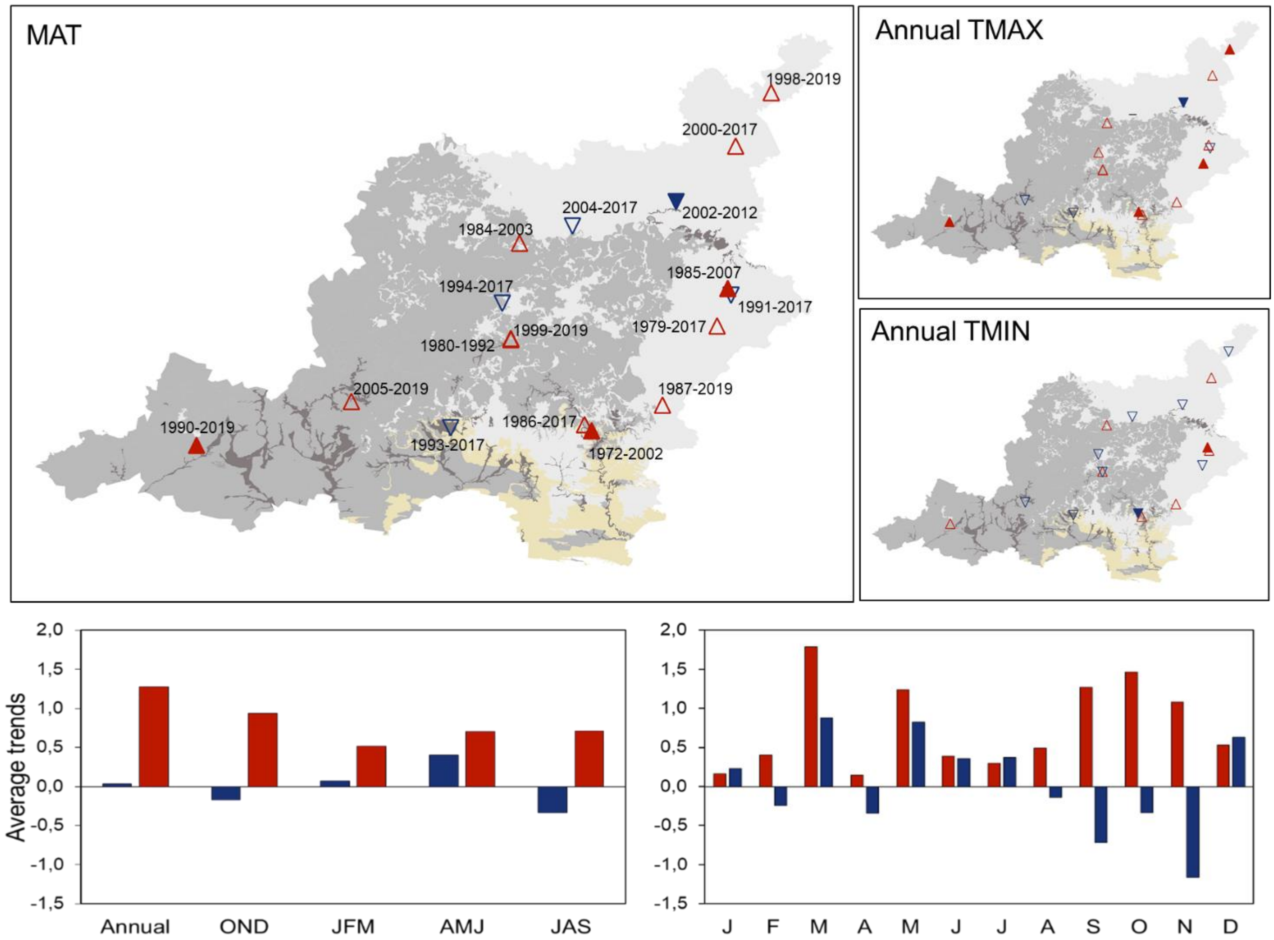

Figure 3.5 Trends in mean annual temperature (MAT), and annual maximum (TMAX) and minimum (TMIN) temperatures in the eastern Karoo represented by the MKVC1 *Z* statistic for the period 1971-2019. Maps display significant trends with red (+) and blue-filled (-) triangles. Non-significant trends are empty triangles and dashes represent no change. Time periods shown for MAT are the same for the maps showing TMAX and TMIN trends. Graphs are the averaged *Z* statistics for annual, seasonal and monthly TMAX (red) and TMIN (blue) trends in the study area.

Evaporation and Wind Run trends

The annual and seasonal trends in A-Pan evaporation were negative at all sites, but only two (29%) were statistically significant (**Table 3.10, Figure 3.6**). The magnitude of decrease in A-Pan evaporation was greatest at sites with lower mean annual rainfall (e.g., Colesberg and Cradock 2) compared to sites of higher mean annual rainfall (e.g., Jamestown and Hobhouse) (R = 0.83, P = 0.02). Evapotranspiration trends were, in contrast, all positive both annually and seasonally with one and two significant trends present during the early and late summer seasons, respectively.

Wind run, an important driver of evaporative processes, has experienced a predominantly downward trend at all sites (**Table 3.10**). Significant negative annual trends in four (44%) of the nine wind run time series were found.

Table 3.10 Annual and seasonal trends (*Z* statistic) in A-Pan evaporation (n = 7), evapotranspiration (ET; n = 5) and wind run (n = 9) as determined by MKVC1 tests. Dashes indicate where wind run data were not available and time periods for each dataset are in subscripts

Station name	**Evaporation (mm)**					**Wind Run (km/day)**				
	Annual	**OND**	**JFM**	**AMJ**	**JAS**	**Annual**	**OND**	**JFM**	**AMJ**	**JAS**
A-Pan										
Buffelsfontein$_{(1984\text{-}1997)}$	-1.86	-0.77	-1.20	-1.48	-0.55	**-2.19***	**-2.41***	-1.86	-1.75	-1.53
Colesberg$_{(1984\text{-}2003)}$	**-3.47****	**-2.69****	**-2.69****	**-2.17***	**-2.11***	0.60	0.52	-0.02	0.94	0.76
Cradock 2$_{(1972\text{-}2002)}$	**-2.51***	**-4.59****	**-3.16****	**-3.02****	**-4.28****	**-3.87****	**-3.72****	**-3.42****	**-4.89****	**-5.25****
Hobhouse 1$_{(1998\text{-}2004)}$	-0.30	-0.60	0.30	-1.50	-1.20	-	-	-	-	-
Jamestown 2$_{(1985\text{-}2007)}$	-0.60	0.45	-1.74	-0.92	-1.58	**-2.48***	-1.07	**-2.40***	-1.95	-1.64
Smithfield 2$_{(2002\text{-}2012)}$	-0.78	-1.40	-1.09	1.56	0.62	-	-	-	-	-
Tarkastad$_{(1987\text{-}2005)}$	-1.22	-0.63	-1.89	-1.61	-0.92	**-3.71****	**-2.24***	**-3.22****	**-2.10***	-1.89
ET										
Hobhouse 2$_{(2005\text{-}2019)}$	**3.24****	1.58	**1.98***	0.79	0.99	-	-	-	-	-
Middelburg 1$_{(2002\text{-}2019)}$	1.21	1.52	1.52	0.15	0.45	-1.59	**-2.14***	**-2.65****	-1.21	-1.77
Murraysburg$_{(2005\text{-}2019)}$	1.78	**2.89****	**2.62****	1.39	-0.77	-1.09	-1.13	1.29	-1.29	**-2.25***
Smithfield 1$_{(2012\text{-}2019)}$	0.87	1.36	0.12	-0.62	0.30	-0.87	0.12	1.11	-1.75	-1.50
Trompsburg 2$_{(2010\text{-}2019)}$	**3.04****	1.25	1.25	0.89	0.54	-1.79	-1.61	0.54	-1.79	-1.61

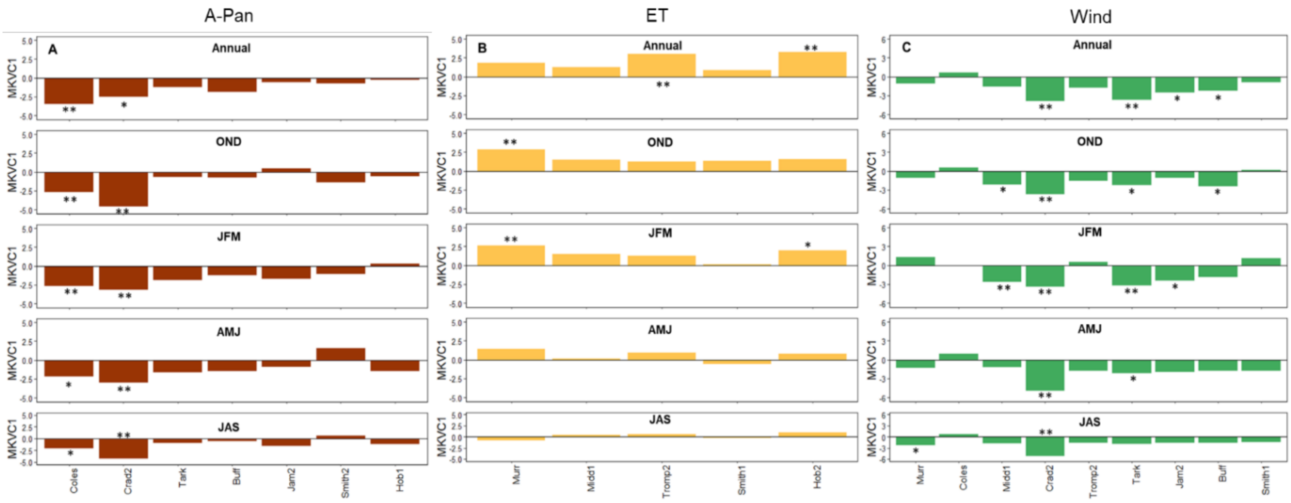

Figure 3.6 Annual and seasonal trends in the eastern Karoo represented by the MKVC1 *Z* statistics. A) A-Pan evaporation (mm) (1971-2012), B) modelled evapotranspiration (mm, ET) (2001-2019), and C) wind run (km/day) (1984-2019). Significant values are *$p < 0.05$ and **$p < 0.01$.

3.6. Discussion

3.6.1. Long-term records reveal multi-decadal wet-dry phases in the rainfall regime

Three major wet-dry phases defined the historical rainfall patterns of the eastern Karoo. A moderate-to-severely wet phase occurred in the late 1800s (1886-1902), a 7-decades long mild-to-moderately dry phase (1902-1970) followed by a 50-year recovery of a mild-to-severely wet phase (1970-2015). Vegetation surveys reported in this study initially captured the state of natural vegetation during the middle dry phase in the early 1960s (Roux, 1969). These were twice repeated in the final wet phase in 1989-1990 (Hoffman & Cowling, 1990) and 2008-2009 (Masubelele et al., 2014). The most recent survey of 2017-2018 (Chapter 4) coincided with a drought event.

Documentary-derived climate chronologies of the 19th century in South Africa provide some supporting evidence of unusually wetter years having taken place between 1885 and 1890 and in 1900 in parts of the Eastern Cape (Vogel, 1989). Tyson & Dyer (1975) also noted that the period 1890 to 1900 was one of the wettest on record.

According to the SPI analysis, the eastern Karoo experienced an unusually long dry phase from 1902 to 1970. Similar patterns for this period were found in the rainfall analysis for Grootfontein (Du Toit & O'Connor, 2014). Although this phase might reflect a period of higher interannual rainfall variability (Fauchereau et al., 2003), it was largely characterised by frequently occurring, and widespread, mild drought events. The well-known and severe, ENSO-driven droughts of the 1980s and 1990s (Archer, 2019; Botai et al., 2016; Joubert et al., 1996; Nemani et al., 2003; Richard et al., 2001; Rouault & Richard, 2003; Vogel & Drummond, 1993) were comparatively shorter and far less severe than those that took place during this long middle dry phase of the early to mid-20th century. The SPI analysis indicated that the 1980s signalled a mildly wet period in the study area (1977-1990) which was then followed by a mildly dry period (1990-1999).

The recovery wet phase in the late 20th to early 21st century was triggered by the moderately to severely wet rainfall events between 1973 and 1976 and continued into the 2010s with less intensity. Du Toit & O'Connor (2014, 2016) provide supporting evidence of prevailing wetter conditions during this period at Grootfontein. Several regional and continental studies have also emphasised the significance of this climate anomaly of the 1970s, some suggesting that this was what led to a shift in the rainfall regime over eastern and southern Africa (Harmse et al., 2020; Nicholson, 2000; Nicholson et al., 2018; Rouault & Richard, 2003). Towards the end of this wet phase, the climate entered a drought period between 2014 and 2019. This period is considered to have been one of the most severe droughts since the 1980s (Archer, 2019). However, our analysis indicated that harsher droughts than those of the 1980s and the 2010s occurred in the late 1870s and even mid-1940s. The severe droughts of the 1870s are supported by historical sources (Nash et al., 2019). Malherbe et al. (2020) have identified key drought events of comparable intensities over the past 30 years in the Lowveld region. Additionally, the drought pattern observed in our analysis is supported by those reported across South Africa at the 24- and 60-month time scales calculated from quaternary catchment data (Malherbe et al., 2016).

3.6.2. Differences in rainfall trends among sites located in the eastern Karoo

During the 20th and beginning of the 21st centuries annual rainfall trends were positive at sites in the Nama-Karoo biome and negative at sites in the Grassland biome. Significant positive annual trends (eight of 24 sites, $p < 0.05$) were represented by positive trends for early summer months (OND) at Nama-Karoo sites. In addition to a directional increase in rainfall amount, a seasonal shift in rainfall has also occurred at eight sites indicating an earlier end to the rainfall season. This is supported by the negative trends for late summer months (JFM, three of 24 sites), which were also more prevalent at Grassland sites. Positive winter rainfall trends (JAS) further suggest an earlier start to the rainfall season. Lastly, patterns in autumn rainfall were variable but non-significant at the majority of sites.

A directional increase in rainfall has been reported by several other studies for the continent and southern Africa (Du Toit & O'Connor, 2014; Harmse et al., 2020; Nicholson, 2000; Nicholson et al., 2018; Rouault & Richard, 2003). The increase in rainfall observed at Grootfontein (Du Toit & O'Connor, 2014) was also evident in our analysis, however, no significant increase in late summer rainfall was recorded. Other studies have reported increases in high intensity rainfall events in the Eastern Cape, south-central and central-interior regions of South Africa (Fauchereau et al., 2003; Kruger & Nxumalo, 2017; Mason et al., 1999; Richard et al., 2001). This has been linked to intense cut-off lows which bring heavier rainfall events most frequently in the winter and summer seasons (Molekwa et al., 2014; Tyson, 1986). Although this was not investigated from the data, the positive trend in early summer rainfall may be associated with heavier rainfall brought on by the same intense cut-off lows.

The long-term rainfall trends over Africa are shown to have strong teleconnection links that operate in an 'out-of-phase', or dipole, relationship between the Sahel-western Africa and eastern-southern African zones (Nicholson et al., 2018). Interestingly, a less than 20% positive departure from the long-term rainfall mean in eastern equatorial Africa and much of southern Africa between 1980 and 1998 in the months of October to December was found (Nicholson et al., 2018). This period was accompanied by an 'out-of-phase' pattern of extreme rainfall deficits over the Sahel-western African zone suggesting that a regime shift in climate over Africa had taken place (Nicholson et al., 2018).

3.6.3. Regional warming and greater early summer temperature extremes

Although temperature trends were less clear on account of the short length of most of the time series, patterns indicated a positive trend for maximum and a negative trend for minimum temperatures. TMAX has increased and is more pronounced in the early summer months of October to December while TMIN has decreased during the same season. Although TMIN trends were variable across seasons, positive trends were most evident in autumn. TMAX and TMIN trends have become more extreme in relation to each other between September and November, with maximum temperatures becoming hotter and minimum temperatures become colder over time. A unique study of long-term minimum temperature and frost at Grootfontein revealed that minimum temperatures were much lower from the 1930s to 1950s compared to other decades and a similar pattern was detected in later years from 2011 to 2013 (Du Toit & O'Connor, 2017). Although the time series used in the thesis did not coincide with the earlier 'cold' period highlighted by Du Toit & O'Connor (2017), the implication of increasing temperature extremes detected at some sites across the eastern Karoo between 1971 and 2019 might support their findings of an increase in cold weather spells, at least in recent decades. However, significant temperature trends that coincide with those found by Du Toit and O'Connor (2017) can only be detected from longer climate records, which at present are not currently available.

Reconstructions of the climate over southern Africa during the Last Glacial Maximum projected that mean annual temperatures were 4-6 °C cooler than present-day temperatures (Engelbrecht et al., 2019). There have been numerous studies that have reported increasing temperature and aridity over Africa and southern Africa (Davis et al., 2016; Engelbrecht et al., 2015; Hulme et al., 2001; King'uyu et al., 2000; Kruger & Nxumalo, 2017; Kruger & Sekele, 2013; Kruger & Shongwe, 2004; MacKellar et al., 2014; Nicholson, 2000; Van Wilgen et al., 2016). Evidence of rising temperatures as early as the late 19th century has been reported in Zimbabwe (Unganai, 1997). Others suggest that warming accelerated from the mid-1960s in South Africa (Kruger & Sekele, 2013). Strydom et al. (2018) illustrated an increase of as much as 4 °C since 1982 for parts of the western Karoo. Kruger & Shongwe (2004) noted that large positive trends in annual TMAX were evident in the central region of South Africa between 1960 and 2003 near Bloemfontein. Furthermore, evidence of increases in extreme warm events and decreases in extreme cold events across South Africa, as displayed by our trends between September and November, has also been found in other historical records (Kruger & Nxumalo, 2017; Van Wilgen et al., 2016). As the majority of these studies lacked data points located within the bounds of our study area, our findings fill an important gap in understanding past temperature trends in South Africa.

3.6.4. Pan evaporation and wind run trends

The pattern of evaporation (A-Pan and ET) trends from our study were consistent across sites and seasons. A-Pan trends were negative both annually and seasonally since the 1970s, while ET trends were positive, despite the low significance. Finally, trends in wind run were consistently negative across sites and seasons, with four of nine sites being statistically significant for annual wind run.

The negative trends in A-Pan evaporation reported in this study are in line with those identified in the Cape Floristic Region (Hoffman et al., 2011), in Carnavon and Grootfontein (Eamus & Palmer, 2008), in Australia (Roderick & Farquhar, 2004), China (Cong et al., 2009; Wang et al., 2015; Wang et al., 2007), the Tibetan Plateau (Liu et al., 2011) and Canada (Burn & Hesch, 2007). The most important factors for decreasing A-Pan evaporation rates have been declines in wind speed (Roderick & Farquhar, 2004), solar radiation and vapour pressure deficit (Eamus & Palmer, 2008; Nemani et al., 2003). Changes in A-Pan evaporation have an important association with changes in wind speed and declines in solar radiation, (Power & Mills, 2004). The former can be influenced by various microsite characteristics such as topography or increased tree cover surrounding the A-pans (Chapman et al., 2021; Rayner, 2007) and the latter has been detected over Grootfontein in Middelburg-EC. While Hoffman et al. (2011) suggested that rainfall had not necessarily increased in the Cape Floristic Region, broad-scale wind run declines were most likely to have contributed to the declining pan evaporation trends in the region. This, they suggested, was indicative of a large-scale change in atmospheric circulation patterns having occurred over South Africa. Notably, the trends in wind run for the study area did not show a reversal in direction at any point between 1977 and 2019, as has been found at various sites in the Northern Hemisphere (Zeng et al., 2019). Instead, Nchaba et al. (2017) have found strong correlations of declining wind speeds over southern African to both the Southern Annular Mode (SAM) and the ENSO between 1980 and 2015.

Engelbrecht et al. (2015) predict, however, that enhanced surface evaporation will continue to increase across Africa. Indeed, the positive annual and seasonal ET trends from our study align with the drying trends in South Africa (Jovanovic et al., 2015), Africa (Nicholson, 2000), and several regions around the world (Fu et al., 2009; Roderick et al., 2009; Wang et al., 2015).

However, the contradiction between A-Pan (-) and ET (+) trends reported in this study may be explained by two alternative hypotheses. First, the Penman-Monteith algorithm that calculates ET (Allen et al., 1998) utilises standard references for the aerodynamic resistance parameters, which are not calibrated to individual weather station microsite conditions. Therefore, the influence of measured wind speed used in the calculation of ET could either be over- or under-estimated based on the weighting of these standardised variables. Alternatively, these contradictory trends may simply be indicative of a complementary relationship between potential and actual evaporation, the latter being proportional to rainfall amount and surface run-off (Nash, 1989; Penman, 1948). In other words, increases in ET are expected where temperature, rainfall and cloudiness have increased, resulting in higher surface run-off and soil wetness (Brutsaert, 2006; Brutsaert & Parlange, 1998; Hobbins et al., 2004). Over time in response to a directional increase in rainfall amount, vegetation cover is expected to increase, exposed soil area to decrease and transpiration rates to increase. However, the latter hypothesis requires experimental testing because the ET trends were largely non-significant. Despite these uncertainties, the decline in wind run in this study is a strong explanation for declining A-Pan evaporation trends. Information regarding the local microsite conditions surrounding A-Pans in this study was not available, and hence, we cannot rule out the possibility that declines in wind speed and increases in surface friction as a result of woody thickening is the cause for declining A-Pan evaporation (Chapman et al., 2021).

3.6.5. Ecological implications of 149 years of climate change in the eastern Karoo

Important implications for vegetation dynamics and ecosystem processes in the eastern Karoo are expected to have resulted from the changes in climate reported in this study. First, even though natural vegetation was heavily impacted in the first half of the 20th century due to high livestock densities, particularly during the 1930s wool boom (Acocks, 1953), degradation would have been further exacerbated by the dry conditions that persisted between 1902 and 1970. During the last wet phase (in conjunction with declining livestock densities), vegetation is expected to have regenerated (Chapter 4, 5). Second, the directional increase in early summer rainfall since the 1970s is strong support for a vegetation response that favoured perennial grasses relative to shrubs (Milton & Hoffman, 1994). Increasing annual rainfall has already been attributed to the increase in grass relative to shrub abundance at Grootfontein (Du Toit et al., 2018). Based on our findings, the hypothesis that rainfall has increased across the rainfall gradient of the biome transition, particularly towards the western extent, and that seasonal shifts are more widespread, can be accepted. Warming trends are shown to have led to persistent increases in net primary production both globally and in south and central Africa (Nemani et al., 2003). Therefore, third, we expect that hotter early summer temperatures, coupled with higher rainfall, has stimulated vegetation (grass) growth rates. Finally, the reduction in wind run and resultant declines in A-Pan evaporation affects soil water retention, water availability and vegetation production (Scott et al., 2014). An increase in vegetation cover would, in turn, reduce soil evaporation but also result in increased rates of ET, as indicated by the positive ET trends reported in this study.

3.6.6. Conclusions

Significant climatic changes over the last century have occurred over the eastern Karoo. The climate shifts identified here are expected to have led to vegetation responses across the biome boundary indicative of an overall ‘greening’ and a shift in the dominance of major growth forms. The rainfall trends identified in Middelburg-EC (Du Toit & O’Connor, 2014, 2016) are confirmed by this study to have been spatially correlated over a larger area. However, the high spatial variation in shifting rainfall season observed in this study offers a novel contribution to the existing climate change research for the eastern Karoo and for global semiarid biome boundaries. The rainfall regime of the eastern Karoo is characterised by natural cycling between multi-decadal wet and dry phases. Up until now, the vegetation changes observed in this region (Masubelele et al., 2014) strongly reflects the effect of wet conditions in recent decades. Evidence also points towards regional warming and ‘stilling’, the latter having led to declines in evaporation. Therefore, continued observation of vegetation change in the eastern Karoo should reflect an overall positive feedback response in vegetation hypothesised to be a ‘greening’ effect and the detection of significant shifts in growth form dominance.

Chapter 4: Long-term vegetation change in the dryland rangelands of the eastern Karoo

4.1. Introduction

Biome boundary research in South Africa has received much attention in the last few years in urgent response to build our knowledge of the dynamics and drivers of vegetation boundaries in a warming climate, so much so, that an entire special journal issue was dedicated to this theme (Potts et al., 2015a). The boundary between the Nama-Karoo and Grassland biomes provides an opportunity to investigate such vegetation dynamics that are primarily driven by rainfall, but which are also influenced by an underlying environmental gradient and local land use practices. Coetzee's (1967) paleoecological analysis of vegetation shifts in the Aliwal North area in the north-east of this biome boundary 13000-9600 yr/B.P. suggests that shifts between grassland and shrubland have been driven mainly by moisture for millennia. Decadal transitions between grassland and karroid vegetation have also been studied (O'Connor & Roux, 1995), yet an extended trend of increasing grassiness across the rainfall gradient has raised questions as to whether this is a natural response to fluctuating moisture or if it is a response to global warming (Du Toit et al., 2018; Hoffman & Cowling, 1990; Masubelele et al., 2014, 2015).

Vegetation studies of global semiarid grassland-shrubland boundaries have reported trends of increasing and expanding shrublands with a relative decrease in grasses, and greater soil degradation and erosion (Bestelmeyer et al., 2018; McIntosh et al., 2019; Peters et al., 2006). Yet, the recent vegetation trends of the eastern Karoo diverge from this global narrative and therefore warrant further observation and investigation into the causes for these changes. It has been suggested that the late 20th century increase in perennial grasses was triggered by a series of high summer rainfall events, which occurred over the period 1974-75 (Roux & Vorster, 1983a). Annual rainfall in Middelburg-EC has generally been higher than the long-term average for most of the last 30 years (Du Toit & O'Connor, 2014). The findings reported in Chapter 3 have confirmed that positive rainfall trends are present along the rainfall gradient and are particularly represented by an increase in rainfall between October and December. The growth of C_4 perennial grasses are restricted to the summer months (O'Connor & Roux, 1995) and become increasingly significant in the vegetation where the Nama-Karoo and Grassland biomes merge (Werger & Ellis, 1981), while C3 grasses make up a much smaller component of the vegetation and only become more common at much higher altitudes. Annual and ephemeral grasses fluctuate in response to rainfall over shorter periods more so than perennial grasses which are shown to respond to longer-term rainfall trends (>10 years) (O'Connor & Roux, 1995). Increasing temperature during the same months, combined with annual declines in wind speed and evaporation are predicted to have had a significant impact on the vegetation of the eastern Karoo. The combined climate changes and reductions in livestock densities across the region are expected to have influenced the condition of rangelands over time in terms of condition and carrying capacity; yet this has not been determined.

Historical vegetation data sources are valuable snapshots of the past, which can be repeated and compared with present-day conditions to provide answers to key questions on the nature of decadal changes in broad vegetation patterns. A few longer-term grazing experiments at Grootfontein, for example, have recently been revived (Du Toit et al., 2018). Other useful archives, such as the vegetation surveys conducted by Dr. Piet Roux in the early 1960s, provide valuable opportunities to investigate vegetation change and shifting biomes.

4.2. Aims and objectives

The study aimed to determine the extent and nature of long-term vegetation change in the Nama-Karoo-Grassland biome boundary based on the observed trends reported in recent studies (Hoffman & Cowling, 1990; Masubelele et al., 2014). This was achieved using two approaches, i) resurveying historical vegetation plots, presented in this chapter, and 2) fixed-point repeat landscape photography (Chapter 5).

Before assessing change, it was important to first determine how the cover of grasses and shrubs was related to the underlying climatic and edaphic gradients of the biome boundary in 1962 and 2018. Vegetation change was then estimated as the percent change in the cover of growth forms between 1962 and 2018 across all sites. Changes in species composition were further examined based on the floristic clustering of species data in each year. Shifts in composition within and among plant communities were assessed through multivariate analysis and indicator species analysis. The vegetation changes, determined by the percent changes in growth forms and their relative dominance, were examined in relation to the changes in rainfall and temperature parameters. And lastly, past and present rangeland condition, based on species abundance, was assessed across sites.

4.3. Methods

4.3.1. Study area

The study area is located in the central-eastern Karoo region of South Africa and extends over an area of about 19,500 km^2 across the Western Cape, Northern Cape, Eastern Cape, and Free State provinces (**Figure 4.1**). The climate of this region is characterised as semiarid in the south-west and dry sub-humid in the north-east with an Aridity Index range of 0.1-0.5 (Hoffman & Ashwell, 2001; Trabucco & Zomer, 2018). Although historical fire has been infrequent in the region, recent studies have indicated that following the wetter conditions and subsequent increase in grass fuel loads in Middelburg-EC, fire is predicted to become a more frequent driver of these landscapes (Du Toit et al., 2015; Kraaij et al., 2017). A detailed description of the climate and vegetation of the region is provided in Chapter 2.

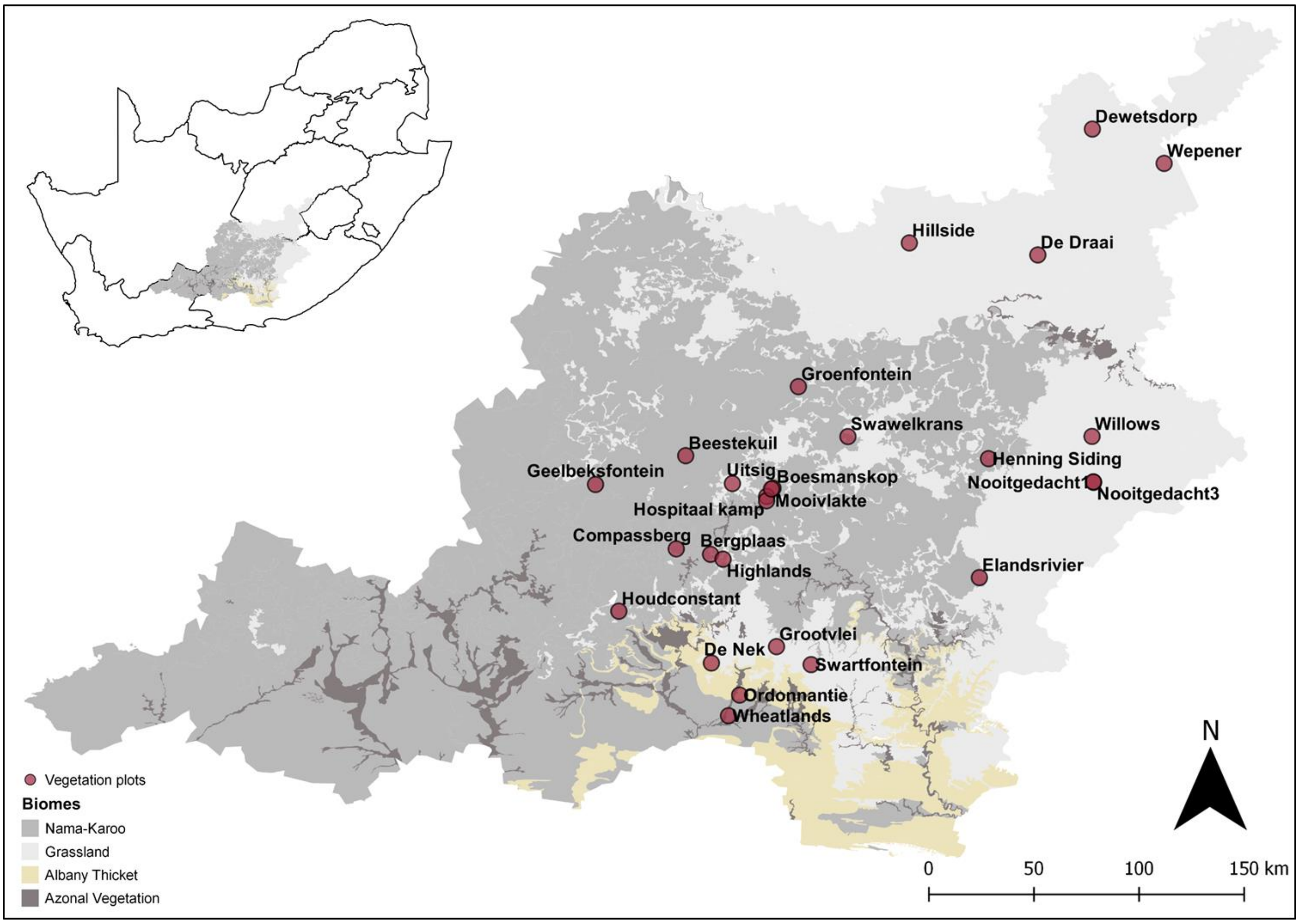

Figure 4.1 The position of 27 resurveyed historical vegetation plots situated along a south-west to north-east gradient of increasing rainfall where the Nama-Karoo biome transitions into the Grassland biome (Nama-Karoo: n = 18; Grassland: n = 9).

4.3.2. Historical vegetation surveys

Historical vegetation survey data collected by Dr. Piet Roux between 1958 and 1970 were obtained from the data archives at Grootfontein in Middelburg-EC (Roux & Blom, 1979). Although Dr. Roux carried out a total of 84 vegetation surveys spread across the broader mesic-east and arid-western Karoo, only 27 of these are positioned within the study area. He conducted these surveys as part of his work with the National Department of Agriculture, and a smaller subset was included in his doctoral thesis on the “Autecology of *Tetrachne dregei*” (Roux, 1969).

The main aims of his thesis were to study the anatomy, physiology, geography, and ecology of *T. dregei,* which is a highly palatable, C_4 perennial grass. The Stormberg Plateau escarpment is the centre of its distribution (Roux, 1969). Although the 27 sites present some bias into the present study due to their representation of the distribution of a single grass species, they still provide an acceptable representation of the two major biomes in the study area (Nama-Karoo and Grassland) (**Figure 4.1**). It is necessary at this point to mention that assessing changes in C_4 versus C_3 grass cover over time could not be adequately investigated for two reasons: first, the study was not initially designed to track the physiological responses of grasses to CO_2-enrichment or increasing temperature, and second, the sample size of sites at higher altitudes (where C_3 grasses are typically more abundant) was too low to be able to provide a statistically appropriate result. A smaller subset of these surveys (10) had previously been repeated in 1989 (Hoffman & Cowling, 1990) and again in 2009 (Masubelele et al., 2014).

4.3.3. Site selection

Although there were many more historical surveys available to be used in this study, several of these were 'non-traceable'. This was primarily due to information lacking on the specific survey locations and absence of landscape photographs to enable the accurate relocation of the original surveys. Therefore, site selection was largely dependent on the accuracy with which the transects could be relocated (Appendix C1). Only very coarse latitude and longitude readings in degrees-minutes were provided for each historical survey, therefore, additional useful metadata included, i) a farm name and magisterial district, ii) 1: 50 000 topocadastral maps, iii) the original vegetation survey number and description, iv) accompanied by a minimum of one historical landscape photograph, with a suitably descriptive caption, taken by Dr. Roux at the time of conducting each survey, and vi) contact with local farmers to source further information.

Site relocation also involved an initial desktop search using Google Earth Pro. Using the street-view and fly-over functions, landscapes that looked similar enough to each historical photograph were identified and matched to the photographs, all which were used in the field for easy relocation.

4.3.4. Vegetation survey techniques

The original vegetation surveys were conducted using two methods both of which record the number of times that a plant species is encountered along a line at regularly marked intervals. The methods are described in more detail below.

Wheel-point method

The original surveys conducted by Dr. Roux, were first carried out using a 'Tidmarsh' wheel, which was developed primarily for use in semiarid grasslands (Tidmarsh & Havenga, 1955). The wheel-point method is an adaptation of the point method first developed by Levy & Madden (1933) and provides a standard and reliable measure of basal and canopy plant cover (Tidmarsh & Havenga, 1955). With each full revolution of a spoked wheel, which has one sharpened marked spoke to indicate the point at which the observer must stop pushing the wheel, a sample point, hereafter referred to as a 'strike', is recorded. The plant species name and the part of the plant that is struck, whether at the base of the plant (basal strike) or under its canopy (canopy strike), is noted. This is repeated for a minimum of 500 points and up to as many as 2000 points per survey. Since each revolution of the wheel covers approximately 1 m, this is equivalent to a transect length of 500 m or 2000 m, respectively. From this method, basal cover is perhaps the most useful estimate because it provides a relatively accurate representation of the cover and composition of rooted plants in a marked area, despite the level of grazing of aboveground plant parts. The estimate of canopy cover can often be under- or over-estimated in grassy environments and should in all cases be used in conjunction with basal cover (Tidmarsh & Havenga, 1955). The calculation of either the percent basal or canopy cover per species is the same (**Equation 1**). For example, 10 basal or canopy strikes of a species on a 500-point transect is equivalent to 2%, or 1% on a 1000-point transect.

$$Cover\ (\%) = \frac{Sum\ of\ strikes}{Sum\ of\ points\ per\ survey} \times 100 \qquad \text{Eq. 1}$$

Descending-point method

Owing to a number of biases of the wheel-point method such as the striking of dominant species or growth forms (e.g., grasses) over less common ones (e.g., dwarf shrubs) (O'Connor & Roux, 1995; Roux, 1969), Roux (1963) developed the descending-point method in which the same principles of the wheel-point are applied. The only difference between these two methods was a small change in the design of the apparatus. In the revised method, two spokes were removed from the wheel so that a steel needle could be lowered vertically through each gap to record basal cover, canopy cover, canopy spread cover and/or plant height. These values were then used for the construction of phytographs to represent canopy layering in a plant community. Although additional cover variables were measured in his surveys, Roux (1963) indicated that not all cover variables were recorded in all his surveys when enough data could be obtained from fewer cover variables, such as basal and/or canopy cover.

Using this method of vegetation sampling, 1000 points were usually collected along 10 parallel transect lines (100 points per line) spaced 14.5 m apart. On rocky terrain, where the wheel was often too difficult to push, the chain-point method was used (Roux, 1969). This was an adaptation of the wheel-point method and followed a similar procedure. A chain was stretched in parallel lines across an area and a thin metal rod was descended vertically through marked chain links that were equidistant to each other to record basal and canopy strikes. This method was used extensively under the Stock Reduction Scheme to assess vegetation change (Roux & Vorster, 1983a).

For the present study, the point intercept method was used for the repeat surveys. This method is a modification of the wheel-point and descending-point methods as long as the spacing of plant strikes and transect lines are the same (Du Toit, 2003). A 100 m long rope, marked at 1 m intervals, is placed in the area to be surveyed and all species struck by the point of a thin rod are identified, recorded and counted. This is repeated along parallel lines spaced 15 m apart for up to 1000 strikes.

Definitions of strikes

The definition of each type of strike in the different methods used in historical surveys often varied among observers (Novellie & Strydom, 1987). Strict rules, therefore, need to be applied by the user when undertaking the survey. For the repeated surveys described in this study, the following rules were applied as close as possible to Roux's (1963) initial definition:

i) A basal strike occurred when the sharp point of a survey rod landed within the rooted perimeter of a plant;
ii) A canopy strike occurred when the sharp point of the survey rod landed anywhere within the shaded area of the canopy of a plant, or where the rod hit the canopy branches or culms of the plant.

4.3.5. Sampling error and biases

Repeating historical vegetation surveys has been used extensively in arid and semiarid research (e.g., Van der Merwe et al., 2018; Van Rooyen et al., 2018). However, there are several challenges to resampling historical surveys. In most cases, historical surveys were not permanently marked for the purposes of resurveying decades later, thus making the accurate relocation of these sites difficult (Kapfer et al., 2017).

Sampling error is usually unavoidable in repeat surveys and occurs in the form of three main sources: i) plot relocation error, ii) observer bias as a result of differences in characterisation and placement of point strikes, and iii) seasonal bias where the date of the historical survey had not been noted. These challenges can lead to some level of uncertainty in the reliability of the data. In this case, Kapfer et al. (2017) suggested that such plots should be termed 'quasi-permanent' plots. Furthermore, even though historical landscape photographs were available to aid in the relocation of historical plots, there remained a degree of uncertainty in some cases in knowing exactly where and in which direction to place the transect lines within the bounds of the photograph.

Possibly the largest bias that can occur among observers, however, is in the identification of species. To address this problem, species lists compiled from the historical surveys were always taken into the field. Before conducting each repeat survey, the abundance of dominant species was assessed visually to determine if a shift had occurred in these species since the historical survey had taken place. Long-lived species, which were recorded historically, were also used as benchmarks under the assumption that they would likely still be present in the vegetation at the time of resampling.

To increase the geographic area covered by previous repeat surveys (Hoffman & Cowling, 1990; Masubelele et al., 2014) and to test the generality of the conclusions derived from these studies, the sample size was increased from 10 to 27 sites. Sampling error was reduced by using historical photographs to help relocate the new sites. As was done historically, transect lines were also laid parallel to each other so as to ensure, as far as possible, that each survey remained within the same vegetation type and landform. Finally, every effort was made to resurvey the plots within the same month, or at least within the same season, as the original survey. Where this was unavoidable due to logistical constraints, sites were still resurveyed.

4.3.6. Environmental and land use variables

Rainfall (received as precipitation), temperature, altitude, and soil data were obtained from several different sources.

Rainfall

Monthly totals of rainfall data were provided by the historical database of Lynch et al. (2004), the South African Weather Service (SAWS), the South African Agricultural Research Council (ARC) and the Climate Systems Analysis Group (CSAG). Long-term means for i) annual rainfall (July-June of the following year, hereafter referred to as 'MAP') and ii) seasonal rainfall were calculated from a collection of weather stations that fell within a 15 km radius of each vegetation plot. Seasons were represented as summer (October-March), which was further divided into early summer (October-December) and late summer (January-March), autumn (April-June), and winter (July-September). The division of summer into two additional groups was done in order to examine the presence (or absence) of significant shifts in the concentration of rainfall over the summer months. Shifts to either earlier or later summer months will influence the timing of the growing season of perennial grasses, which will in turn influence broader community structure at greater scales along the biome boundary. The length of each time series per vegetation survey had to span at minimum the period of 1942-2018, but longer time series were also used where available. If gaps were present in a time series then neighbouring weather station data were used to patch those gaps, provided that the Pearson's correlation coefficient of the relationship of annual totals among the relevant stations was greater than 0.5. Due to several rainfall stations having been closed down several years prior to the repeated vegetation surveys in 2017-18, recent decades between 1998 and 2018 have been patched using gridded pentad data per site from the CHIRPS satellite product (Climate Hazards Group InfraRed Precipitation with Station Data version 2.0; Funk et al., 2015). Chapter 3 provides a detailed analysis of the rainfall conditions for period 1 (i.e., MAP1, Summer1, etc.) and period 2 (i.e., MAP2, Summer 2, etc.). The first period between 1942 and 1962 was largely dry (**Table 3.7**, Chapter 3) and the second period between 1998 and 2018 experienced wetter conditions, barring the last few years between 2014 and 2019 which were mildly dry.

Temperature

Time series per vegetation plot of monthly average temperature between 1958 and 2018 were obtained from the satellite product TerraClimate, a high-resolution (1/24°, ~4 km) dataset of global monthly land surface climate and water balance (Abatzoglou et al., 2018). Mean annual temperature and mean annual minimum and maximum temperatures were calculated for each site for the first (1958-1962) and second period (2014-2018), as well as for the entire length of the study period. **Table 4.1** provides a breakdown of each rainfall and temperature variable calculated for each time period used in the analyses that follow.

Table 4.1 The rainfall and temperature variables used in the multiple regression analyses for the vegetation plots surveyed in 1962 and 2018. Rainfall data (received as precipitation) were obtained from the historical database of Lynch et al. (2004), the South African Weather Service (SAWS), the South African Agricultural Research Council (ARC), the Climate Systems Analysis Group (CSAG) and the CHIRPS satellite data product. Temperature data were obtained from the TerraClimate satellite data product and differed in length on account of when the data became available

Environmental variable	**Year of vegetation survey**	**Rainfall**		**Environmental variable**	**Temperature**	
		20-yr Period	**Months**		**5-yr Period**	**Months**
MAP1	1962	1942-1962	July-Jun	MAT1	1958-1962	July-Jun
Summer1	1962	1942-1962	Oct-Mar	TMIN1	1958-1962	July-Jun
Early Summer1	1962	1942-1962	Oct-Dec	TMAX1	1958-1962	July-Jun
Late Summer1	1962	1942-1962	Jan-Mar			
Winter1	1962		Apr-Sept			
MAP2	2018	1998-2018	July-Jun	MAT2	2014-2018	July-Jun
Summer2	2018	1998-2018	Oct-Mar	TMIN2	2014-2018	July-Jun
Early Summer2	2018	1998-2018	Oct-Dec	TMAX2	2014-2018	July-Jun
Late Summer2	2018	1998-2018	Jan-Mar			
Winter2	2018	1998-2018	Apr-Sept			
MAP	-	1942-2018	July-Jun	MAT	1958-2018	July-Jun
Summer		1942-2018	Oct-Mar	TMIN	1958-2018	July-Jun
Early Summer		1942-2018	Oct-Dec	TMAX	1958-2018	July-Jun
Late Summer		1942-2018	Jan-Mar			
Winter		1942-2018	Apr-Sept			

Soil

Unfortunately, soil samples were not collected from the vegetation plots in 1962 or in 2017-18. The need to collect and track soil changes in this region is a significant one that has not been addressed in previous long-term studies. However, proxies of soil variables were obtained from the ISRIC – World Soil Information database using the SoilGrids 250 m predictive maps of soil properties and classes. These data are provided as point observations per vegetation plot taken from the topsoil layer of a recorded depth of between 0 and 30 cm. The soil fertility, chemistry and moisture variables selected for analysis were soil pH, percent silt content, percent clay content, percent sand content and soil depth (cm). These data are based on the Soil and Terrain database for Southern Africa (SOTERSAF version 1.0; Batjes, 2004), and although these maps are acknowledged to be unreliable, up-to-date and higher resolution products could not be found.

4.4. Statistical analyses

All statistical analyses were performed in R version 3.5.2. (R Core Team, 2018). Data wrangling and plotting was done using the packages tidyverse (Wickham et al., 2019), magrittr (Bache & Wickham, 2020), and ggplot2 (Wickham, 2016). Additional packages useful for statistical testing included Hmisc (Harrell Jr et al., 2019), broom (Robinson et al., 2021) and MASS (Venables & Ripley, 2002). Packages specific to each analysis are mentioned below.

Only canopy cover values per species have been used due to the inconsistency in the recording of basal cover strikes in several of the 1962 surveys. The relationship between canopy and basal cover was tested by taking a subsample of canopy and basal strike data from 1000-point surveys for each survey period (n, excludes bare ground strikes). The Pearson's correlation coefficients between canopy and basal cover percentages indicated a significant and positive correlation for both periods (1962: n = 499; $r = 0.86$; $p < 0.001$; 2018: n = 589; $r = 0.60$; $p < 0.001$). The relationship was weaker for the 2018 surveys due to the high likelihood of striking dominant growth forms (i.e., grasses have wider canopies) over less common ones (e.g., dwarf shrubs have narrower canopies), and therefore, might over-represent canopy cover. This is a shortfall of using the point intercept method in grassier environments (Roux, 1963). However, the relationship remains to be significantly positive, and hence, the use of canopy cover as an appropriate surrogate for basal cover is justified. Percent bare ground was calculated by subtracting the total number of canopy strikes per survey from 1000 points and expressing this value as a percentage.

4.4.1. Grass and shrub cover in relation to the environmental gradient

Multicollinearity

The influence of key environmental variables on vegetation composition and cover was assessed through multiple regression analysis. Prior to this, correlations among climate and soil variables were performed to inspect the degree of collinearity between altitude, soil (pH, soil depth, percent sand, clay and silt), rainfall (mean annual, summer, autumn, winter, early summer and late summer) and temperature (mean annual, mean minimum and mean maximum) variables (Appendix C2). Relationships among variables were considered highly collinear if the correlation coefficient (r) was > 0.5 and had a corresponding p-value of < 0.05. Based on their degree of collinearity and appropriateness, a set of variables was selected to represent the group of environmental variables used for further analysis.

Univariate relationships

Linear relationships among the percent cover of grasses and shrubs and selected soil, rainfall and temperature variables were investigated for 1962 and 2018. Pearson correlation values, trend line equations and p-values were obtained for univariate relationships.

Multivariate relationships

Following this, multiple regression analysis was used to examine the relative contributions and significance of climate and soil explanatory variables (continuous and independent) to explaining the percent covers of perennial grasses and perennial (palatable + unpalatable) dwarf shrubs (continuous and dependent) in 1962 and 2018. **Equations 2 to 5** below detail the full regression equations used in a forward-backward stepwise selection process to identify the best selection of explanatory variables for the final models reported in the results. The power of each final model was confirmed by the adjusted R^2 and p-values. If adding interaction effects to the model increased the adjusted R^2 value, then they were included in the final model. If multicollinearity was discovered in the models by inspecting the variance inflation factors (VIF) of each explanatory variable, then an appropriate surrogate variable was used in place of the highly correlated covariates. For example, Summer1 was an appropriate surrogate for Early1 and Late1 rainfall variables. The VIF cut-off for multicollinearity used in this study was ≤ 5 (Thompson et al., 2017). Likelihood ratio tests were used to confirm if the final model equations were significantly different from their respective null hypothesis models. The general multiple regression equations for the null and alternative hypotheses are as follows,

$$\mathrm{H}_0 : Y = \alpha + \beta_1 X + \epsilon$$
$$\mathrm{H}_A : Y = \alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \cdots$$

where the null hypothesis (H_0) assumes that β_1 is statistically no different from zero and where the alternative hypothesis (H_A) does assume statistical difference from zero for β_1. Y is the dependent variable that is being explained, a (alpha) is the constant or intercept, b_1 (beta coefficient) is the slope for X_1, X_2, X_3… the independent variables (explanatory variables) that are explaining the variance in Y. Hence, the full regression equations for each dependent variable are outlined below:

$$\%\ Perennial\ grass\ cover\ 1962 \sim pH + Soil\ depth$$ Eq. 2
$$\%\ Perennial\ grass\ cover\ 2018 \sim pH + Soil\ depth$$ Eq. 3

$$\%\ Perennial\ shrub\ cover\ 1962 \sim Early\ Summer1$$ Eq. 4
$$\%\ Perennial\ shrub\ cover\ 2018 \sim Early\ Summer2 + Late\ Summer2 + pH$$ Eq. 5

The following R packages were used for the plotting and calculation of regression statistics: corrplot (Wei & Simko, 2017), Rmisc (Hope, 2013), car (Fox & Weisberg, 2019), lmtest (Zeileis & Hothorn, 2002), mctest (Imdad et al., 2019; Imdad & Aslam, 2018), rcompanion (Mangiafico, 2020).

4.4.2. Spatiotemporal vegetation change between 1962 and 2018

Shifts in species composition

In order to identify and group the major floristic associations in the study area, the total percent cover per plant species in 1962 and 2018 were used in a Ward's hierarchical agglomerative cluster analysis performed on the Bray-Curtis dissimilarity distances. This allowed for the visualisation of the association of sites with each other, based on the similarity of species composition surveyed in each year. Species and growth form data were, thereafter, analysed and presented in accordance with these major groupings. A permutational MANOVA (Anderson, 2001) was used to determine the significance of dissimilarity among the major floristic groupings. This provides a probability associated with the null hypothesis of no differences among groups.

Additionally, indicator species analysis was used to define meaningful vegetation communities in 1962 and 2018 within these floristic groupings (Dufrêne & Legendre, 1997). In this analysis, species that were strongly associated with particular groups of sites were determined by calculating an Indicator Value index (IV). This index is calculated between each species and each group of sites and determines the group that corresponds to the highest IV for that species. The statistical significance of this relationship was then tested using a permutation test. Sample estimates, *specificity* ('A') and *fidelity* or *sensitivity* ('B'), were obtained. The specificity indicates the probability that a survey site belonged to a particular group based on the presence of a particular indicator species. The fidelity indicates the probably of finding a species in sites belonging to a particular group. The R package indicspecies (De Cáceres & Legendre, 2009) was used for this analysis.

To investigate how species composition has changed over time, non-metric multidimensional scaling (NMDS) analysis was performed using the species percent cover values at each site. Only species with ≥ 1% cover, which is equivalent to ≥ 10 strikes per species, were used in the analysis. Rare species, which are defined here as having less than 1% cover per site, were excluded from the multivariate analysis. The Bray-Curtis distances calculated for 1962 and 2018 were overlaid on the same axes to illustrate i) the temporal shifts in species composition in individual sites between years, and ii) the spatial shifts in species composition among the groupings determined from the clustering process. A secondary axis of environmental variables, namely altitude, soil pH, percent sand and MAP (1942-2018) was fitted to the ordination axes, and a goodness of fit test was used to determine the strength and significance of the environmental variables in influencing the association of sites.

Changes in growth form cover and relative dominance

Each species was then assigned to one of five plant growth forms: annual grasses, annual herbs, perennial grasses, palatable shrubs, and unpalatable shrubs. The difference in means (± standard deviation) of percent cover for each growth form between years, and within and among the floristic groups, was tested using the non-parametric Wilcoxon signed-rank and Kruskal Wallis tests by ranks.

Following the approach adopted by Gremer et al. (2018), a metric was calculated (**Equation 6**) to describe the relative dominance of perennial grasses versus dwarf shrubs (palatable + unpalatable) in 1962, 2018 and the change in dominance over time against the rainfall gradient of the study area (represented by the long-term MAP per site). The metric limits are between -1 and +1, representing the complete dominance of shrubs or grasses, respectively. This metric does not capture species-specific changes, rather it is useful in describing broad comparisons of growth form covers. The non-parametric Locally Weighted Least Squares Regression ('loess') was fitted to the relationship of relative dominance and mean annual rainfall. Relative dominance was calculated according to Gremer et al. (2018) as follows:

$$\frac{\%\ Cover_{Grass} - \%\ Cover_{Shrub}}{\%\ Cover_{Grass} + \%\ Cover_{Shrub}} \qquad \text{Eq. 6}$$

Shifts in dominant species

To identify which dominant species have been responsible for the changes in vegetation, the percent changes in the cover of dominant species (≥ 1% cover) of perennial grasses and palatable and unpalatable shrubs were calculated. The difference between percent covers per species was tested using a Wilcoxon test for paired independent samples. A basic measure of species richness (the number of species recorded in each year per site) was quantified. Multivariate analyses were conducted using the packages vegan (Oksanen et al., 2020), cluster (Maechler et al., 2019), and BiodiversityR (Kindt & Coe, 2005).

4.4.3. Environmental drivers of grass and shrub cover change

The percent changes in the cover of perennial grasses and perennial dwarf shrubs were modelled against the changes in climate variables through multiple regression analysis. The two periods preceding vegetation sampling were dry (1942-1962) and wet (1998-2018). Thus, to account for this change in rainfall conditions, the change in rainfall over the full sampling period (1942-2018) is represented by the slope of the linear trend line of each rainfall time series at each site,

$$Y = mx + c$$

where *m* is the gradient or slope and *c* is the y-intercept. The slope of the trend line (*m*) for each site was then plotted against the percent change in grasses and shrubs to determine if the relationship was significantly positive or negative. Slope values were only calculated for mean annual (ΔMAP), summer (ΔSummer) and winter (ΔWinter) rainfall. **Equations 7 and 8** below indicate the full regression equations obtained after running a forward-backward stepwise selection on all environmental variables to identify the best selection of explanatory variables for each final model. The power of each final model was confirmed by the adjusted R^2 and *p*-values.

$$\%\,Change\ perenial\ grass\ cover \sim pH + Altitude + \Delta Summer \qquad \text{Eq. 7}$$

$$\%\,Change\ perennial\ shrub\ cover \sim \Delta Late\ Summer + \%\,Sand + Soil\ depth + \Delta Summer \qquad \text{Eq. 8}$$

4.4.4. Changes in rangeland condition (1962-2018)

To determine rangeland condition in 1962 and in 2018 the Ecological Index Method based on Vorster (1982), and later revised by Du Toit (2003), was used on the species cover data collected in each year. **Equation 9** details the method to determining rangeland condition.

$$VCI\ per\ species = Sum\ of\ strikes\ per\ species\ (per\ 100\ points) \times SGIV$$

$$VCI\ per\ survey = Sum\ all\ species\ VCI\ values \qquad \text{Eq. 9}$$

$$Grazing\ capacity\ (ha/LSU) = \left(\frac{650}{VCI\ of\ survey}\right) \times 7.14\ ewes\ per\ hectare$$

A Veld Condition Index (VCI) per survey was derived by summing the VCI value for each species. This was calculated as the number of strikes for each species per 1000 points multiplied by the subjective grazing index value (SGIV). The SGIV is a score of the agronomic attributes of a species and includes its productivity, forage value and degree of perenniality (Du Toit, 1995). The VCI of the sampled veld was then used to estimate the grazing capacity of the site. This was done by relating the VCI value of the sampled veld to a benchmark site at Grootfontein in Middelburg-EC. This benchmark site has a VCI score of 650 and can support approximately 8.05 merino ewes (small stock units) per hectare for a year without deterioration of the veld (Du Toit, 2003). In order to convert the grazing capacity values obtained for each survey to hectares per Large Stock Unit (ha/LSU) the VCI value, calculated relative to the benchmark site, was multiplied by 7.14 (Du Toit, 2003). This is the LSU equivalent of a small stock unit, in this case a reproducing ewe (Meissner et al., 1983). An LSU is defined as an ox that weighs 450 kg and ingests 10 kg of dry matter per day with an average digestibility of 55-65% which grows at a rate of 500 g per day (Meissner et al., 1983). Grazing capacity was calculated for each site in 1962 and 2018. The difference between years per site were tested using a Wilcoxon test for paired independent samples.

4.5. Results

4.5.1. Grass and shrub cover in relation to the environmental gradient

Multicollinearity

Before relationships of percent grass and shrub cover to key environmental variables could be examined, multicollinearity was investigated among all soil, temperature and rainfall variables (Appendix C2). Percent sand content was negatively related to percent clay and percent silt, while soil pH was collinear with soil organic carbon, percent clay and percent silt. Thus, soil pH and percent sand were selected as appropriate soil chemistry and texture properties. Altitude was negatively related to all parameters of temperature (MAT, Tmin, Tmax = 1958-2018; MAT1, Tmin1, Tmax1 = 1958-1962; MAT2, Tmin2, Tmax2 = 2014-2018) and all temperature variables were highly collinear with one another. On this basis, altitude was chosen as an acceptable surrogate for temperature. All rainfall variables were highly collinear with each other. Therefore, summer and winter rainfall variables were used for the relevant time periods investigated below.

Univariate relationships

In general, high altitude sites received on average higher rainfall per annum than low-altitude sites (**Figure 4.2A**; $r = 0.62$, $p = 0.0006$). Altitude was negatively related to temperature ($Tmin_{1958\text{-}2018}$: $r = -0.94$, $p = 1.69e^{-13}$, $Tmax_{1958\text{-}2018}$: $r = -0.90$, $p = 1.38e^{-10}$). Grass cover in the study area increased altitudinally, and along a gradient of increasing average summer and average winter rainfall in both years. In contrast, shrub cover was unrelated to altitude, but decreased along a gradient of increasing average summer rainfall in both 1962 and 2018, and average winter rainfall in 2018 (**Figure 4.3A, B, C**). Thirteen out of 27 sites showed an increase above 50% in the cover of grasses in 2018 relative to 1962 at altitudes above 1000 m (**Figure 4.3A**). Few sites that received an average summer rainfall of ≤ 300 mm exhibited an increase above 50% in the cover of grasses. However, wetter sites (≥ 300 mm) have had an increase in both grass and shrub cover since 1962 (**Figure 4.3B**). While some interesting outlier points emerged, speculation on possible reasons for these outliers will not be offered because these points failed to mask clear relationships.

Soil pH and percent sand were negatively related to altitude (**Figure 4.2B**; pH: $r = 0.52$, $p = 0.006$; percent sand: $r = 0.52$, $p = 0.006$). In both years, grass cover was higher at sites containing acidic soils, while shrub cover was higher at sites containing less acidic soils (**Figure 4.3D**). Lastly, sites containing a higher sand content had significantly lower grass cover, while shrub cover was unrelated to percent sand across the study area (**Figure 4.3E**).

The relationship between the percent cover of perennial grasses and percent cover of shrubs (with shrub cover as the dependent variable) was significantly negative in both 1962 (n = 27, $r = -0.63$, $p = 0.0005$) and 2018 (n = 27, $r = -0.83$, $p = 1.01e^{-07}$), indicating that a competitive effect between grasses and shrubs is maintained across the biome boundary.

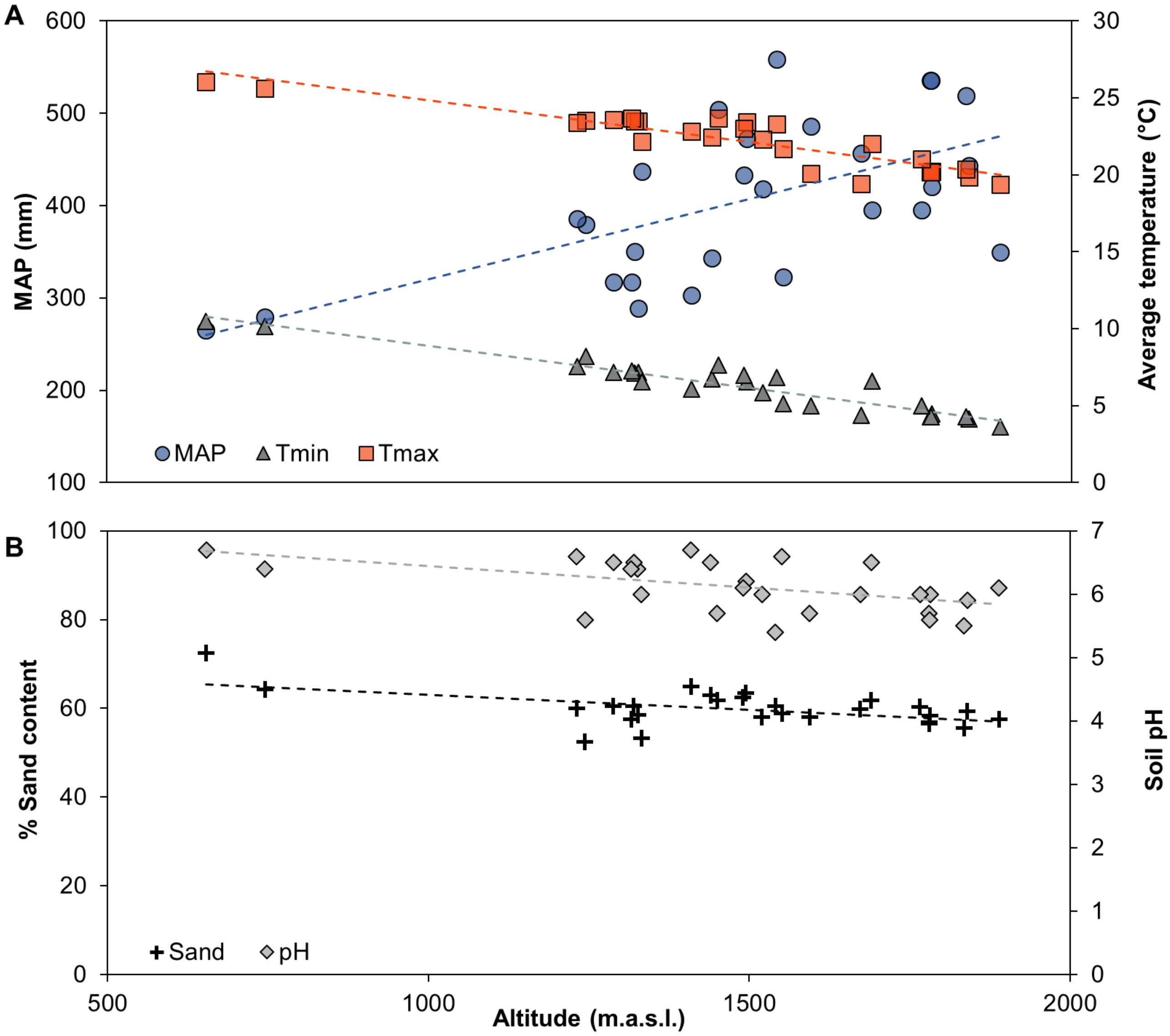

Figure 4.2 Relationships among altitude and climatic (A) and edaphic (B) variables per site (n = 27) across the biome boundary of the eastern Karoo. The time periods for which MAP and temperature spanned, were 1942-2018 and 1958–2018, respectively.

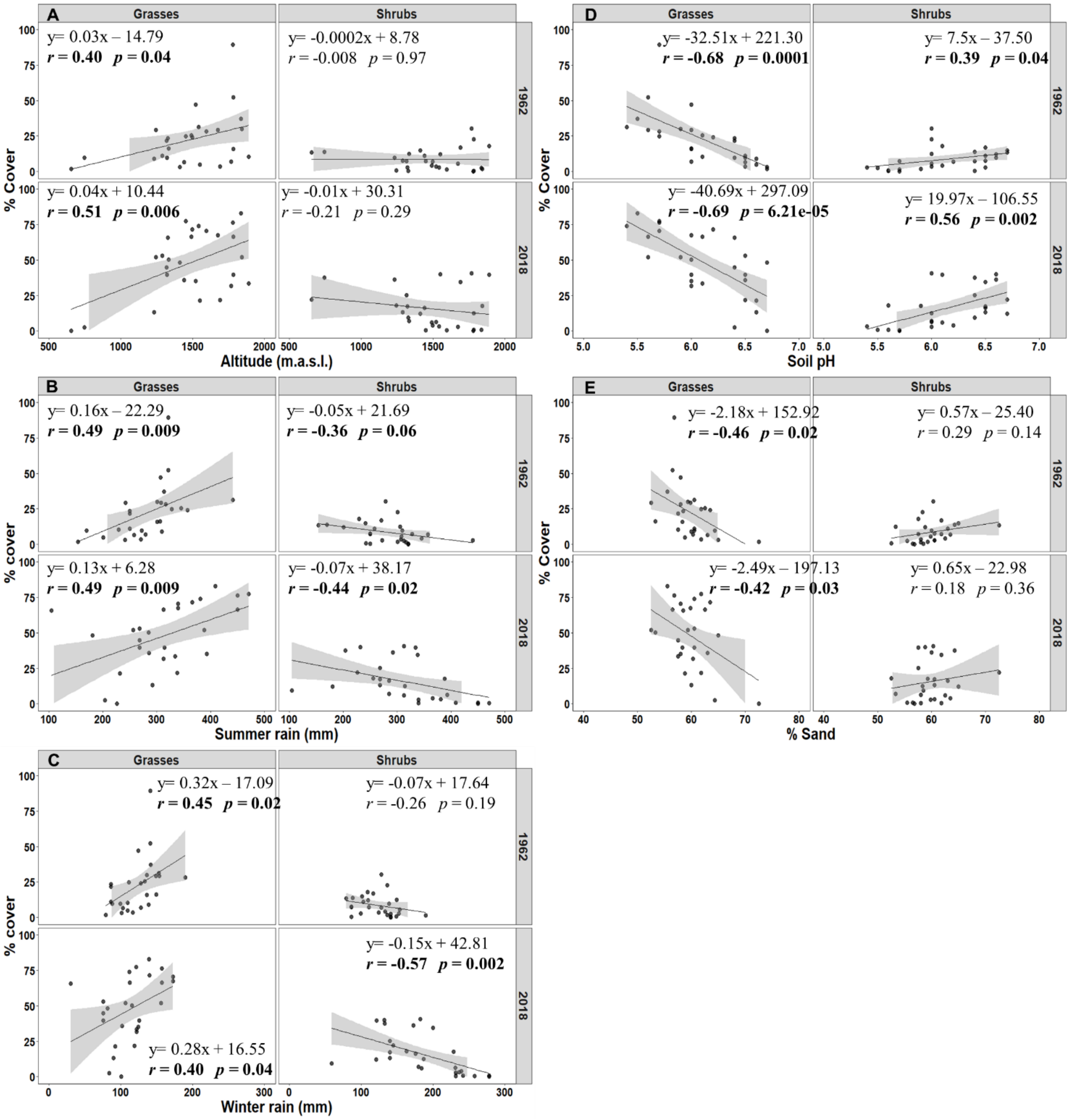

Figure 4.3 Relationships of percent cover of grasses and shrubs in 1962 and in 2018 with A) altitude, B) average summer, and C) average winter rainfall, D) soil pH and E) percent sand content. Slope equation, coefficient of correlation (*r*) and *p*-values at the 95% confidence interval (shaded bands) are indicated. Significant positive or negative relationships are in bold.

Multivariate relationships

Collectively, soil pH and soil depth explained 50% of the variation in percent grass cover in 1962 and in 2018 (**Table 4.2**). Early summer rainfall between October and December explained 14% of the variation in percent shrub cover in 1962, while a combination of summer rainfall in the early and late months (January to March) and soil pH explained 40% of the variation in percent shrub cover in 2018. This may suggest that there are unknown variables that have not been accounted for in the models to explain the response of shrubs and grasses over time.

Table 4.2 Final linear regression models of the environmental explanatory variables that best explained the variation in percent perennial grass and shrub cover in 1962 and 2018 at sites in the eastern Karoo (n = 27)

Final model	**Coefficient Estimate**	**Standard Error**	***t*-value**	***p*-value**	**Adjusted R^2**	**F-statistic**	**Model *p*-value**
% Grass cover (1962)					0.50	$14.24_{(2,24)}$	**$8.35\ e^{-05}$**
Intercept	155.83	51.31	3.04	**0.006**			
Soil pH	-28.39	6.91	-4.11	**0.0004**			
Soil depth	0.23	0.11	2.09	**0.05**			
% Grass cover (2018)					0.50	$13.91_{(2,24)}$	**$9.76\ e^{-05}$**
Intercept	230.63	63.28	3.64	**0.001**			
Soil pH	-36.51	8.52	-4.29	**0.0003**			
Soil depth	0.24	0.14	1.72	0.1			
% Shrub cover (1962)					0.14	$5.25_{(1,25)}$	**0.03**
Intercept	22.62	6.31	3.58	**0.001**			
Early summer rainfall	-0.12	0.05	-2.29	**0.03**			
% Shrub cover (2018)					0.40	$6.70_{(3,23)}$	**0.002**
Intercept	-52.55	53.86	-0.98	0.34			
Early summer rainfall	-0.26	0.10	-2.54	**0.02**			
Late summer rainfall	0.14	0.08	1.65	0.11			
Soil pH	11.85	7.55	1.57	0.13			

4.5.2. Spatiotemporal vegetation change between 1962 and 2018

Shifts in species composition

The hierarchical agglomerative cluster analysis of the covers of species (≥ 1%) of perennial grasses and shrubs (palatable and unpalatable) at each site in 1962 and 2018 produced three distinct groupings, hereafter referred to as ‘vegetation units’ (Appendix C3). These groups represent the dominant plant communities of the region and have been categorised as ‘Karoo’ (1962: n = 12; 2018: n = 10), ‘Escarpment’ (1962: n = 8; 2018: n = 9) and ‘Grassland’ (1962: n = 7; 2018: n = 8) vegetation units.

The indicator species analysis conducted on the species composition data was based on these three vegetation units. The analysis on the 1962 species data showed that *Eragrostis lehmanniana* was strongly associated with Karoo sites (B = 0.58, $p = 0.02$), while *Eriocephalus ericoides* and *Pentzia incana* were good indicators of the Karoo vegetation unit because these species occurred at sites belonging to this group only (**Table 4.3**, A = 1.00). The Escarpment vegetation unit was strongly associated with the presence of *Tenaxia disticha* (A = 1.00) but not all sites belonging to this vegetation unit included this species (B = 0.63). *Tetrachne dregei* and *Tribolium purpureum* were also both strongly associated with the Escarpment sites. *Themeda triandra* and *Digitaria* *argyrograpta* were strong indicators of the Grassland vegetation unit, with *T. triandra* occurring at all sites in this group (B =1.00).

The analysis of the 2018 species data showed subtle shifts in indicator species in all vegetation units. The Karoo vegetation unit was still strongly related to *E. lehmanniana*, but *Aristida diffusa*, and the perennial shrubs *P. incana* and *E. ericoides* were also strong indicators of sites in this group. *Eragrostis chloromelas* appeared at all sites in the Escarpment vegetation unit in 2018, while *T. disticha, T. purpurea and T. dregei* remained as good indicator species for this group. Lastly, *T. triandra* was still the strongest indicator of Grassland vegetation, while *Sporobolus fimbriatus* and *E. obtusa* became new significant indicators of this group. Plant communities that described these vegetation units in 1962 and 2018 are summarised in **Table 4.3**.

Table 4.3 Main plant communities (perennial grasses and dwarf shrubs) of the Nama-Karoo-Grassland biome boundary in 1962 and 2018 based on the indicator values (IV) and sample estimates of the specificity (A) and fidelity (B) of species identified in each vegetation unit ($p < 0.05$)

Family	Species	A	B	IV	*p*-value
1962					
Karoo: *Eragrostis lehmanniana* community					
Poaceae	*Eragrostis lehmanniana*	0.88	0.58	0.72	**0.03**
Asteraceae	*Eriocephalus ericoides*	1.00	0.25	0.50	0.10
Asteraceae	*Pentzia incana*	1.00	0.25	0.50	0.11
Escarpment: *Tenaxia disticha - Tetrachne dregei* community					
Poaceae	*Tetrachne dregei*	0.88	0.88	0.88	**0.001**
Poaceae	*Tenaxia disticha*	1.00	0.63	0.79	**0.002**
Poaceae	*Tribolium purpureum*	0.92	0.63	0.76	**0.006**
Grassland: *Themeda triandra - Digitaria argyrograpta* community					
Poaceae	*Themeda triandra*	0.98	1.00	0.99	**0.001**
Poaceae	*Digitaria argyrograpta*	0.92	0.57	0.73	**0.009**
Poaceae	*Eragrostis curvula*	0.75	0.43	0.57	0.10
Poaceae	*Aristida diffusa*	1.00	0.29	0.54	0.06
2018					
Karoo: *Eragrostis lehmanniana - Pentzia incana* community					
Poaceae	*Eragrostis lehmanniana*	0.93	0.70	0.81	**0.003**
Poaceae	*Aristida diffusa*	0.92	0.60	0.74	**0.01**
Asteraceae	*Pentzia incana*	0.97	0.50	0.70	**0.01**
Asteraceae	*Eriocephalus ericoides*	1.00	0.40	0.63	**0.03**
Escarpment: *Eragrostis chloromelas - Tenaxia disticha* community					
Poaceae	*Eragrostis chloromelas*	0.84	1.00	0.92	**0.001**
Poaceae	*Tenaxia disticha*	1.00	0.67	0.82	**0.001**
Poaceae	*Tetrachne dregei*	0.95	0.56	0.73	**0.005**
Poaceae	*Tribolium purpureum*	1.00	0.44	0.67	**0.01**
Thymelaeaceae	*Passerina montana*	1.00	0.33	0.58	**0.04**
Grassland: *Themeda triandra - Sporobolus fimbriatus* community					
Poaceae	*Themeda triandra*	1.00	0.88	0.94	**0.001**
Poaceae	*Sporobolus fimbriatus*	1.00	0.38	0.61	**0.02**
Poaceae	*Cymbopogon pospischilii*	0.97	0.38	0.60	0.06
Poaceae	*Eragrostis obtusa*	0.81	0.38	0.55	**0.05**

The permutational MANOVA test of the null hypothesis, which assumes no significant difference among vegetation units, was rejected for both the 1962 and 2018 data (Appendix C4). The NMDS of species cover per site of the first two axes indicated a distinct separation of vegetation units in both years (Appendix C5).

Non-distinct temporal changes occurred in species composition per site between years for the combined datasets (**Figure 4.4**). Changes were highly variable within sites and among vegetation units, both in terms of the direction and length of arrows. For example, Wheatlands (Wheat56 and

Wheat17) experienced a greater within-site change in species composition than did the Middelburg commonage site (Midd62 and Midd18) in the Karoo vegetation unit. Two sites (Comp61 and Uit62) experienced shifts in composition from Karoo to Escarpment over time while Swart61 shifted from the Escarpment to Grassland vegetation unit between the sampling periods (Appendix C6). Despite these shifts, the vegetation units remained significantly different from each other based on the factor centroids of each group in each year (**Table 4.4**). Bearing these shifts in mind, the number sites for each of Karoo, Escarpment and Grassland are not the same between 1962 and 2018 (see Table 4.5).

A secondary axis of the environmental variables was added to the ordination space to describe the main gradients that exist in the study area and along which the sites are aligned based on their species composition (Appendix C5). The direction of the arrows indicates positive correlation to an environmental variable, while the length of the arrow is proportional to the correlation between the ordination and environmental variable, also referred to as the strength of the gradient. Therefore, Karoo sites are best described by soil pH ($R^2 = 0.54$, $p < 0.05$) and percent sand ($R^2 = 0.33$, $p = 0.001$), while Escarpment and Grassland sites are best described by altitude ($R^2 = 0.54$, $p = 0.001$) and MAP (1942-2018; $R^2 = 0.35$, $p = 0.001$) (Appendix C5). The direction (axes) and strength (R^2 value) of each environmental variable indicated that all were sufficiently strong predictors of species composition in each year (**Table 4.4**).

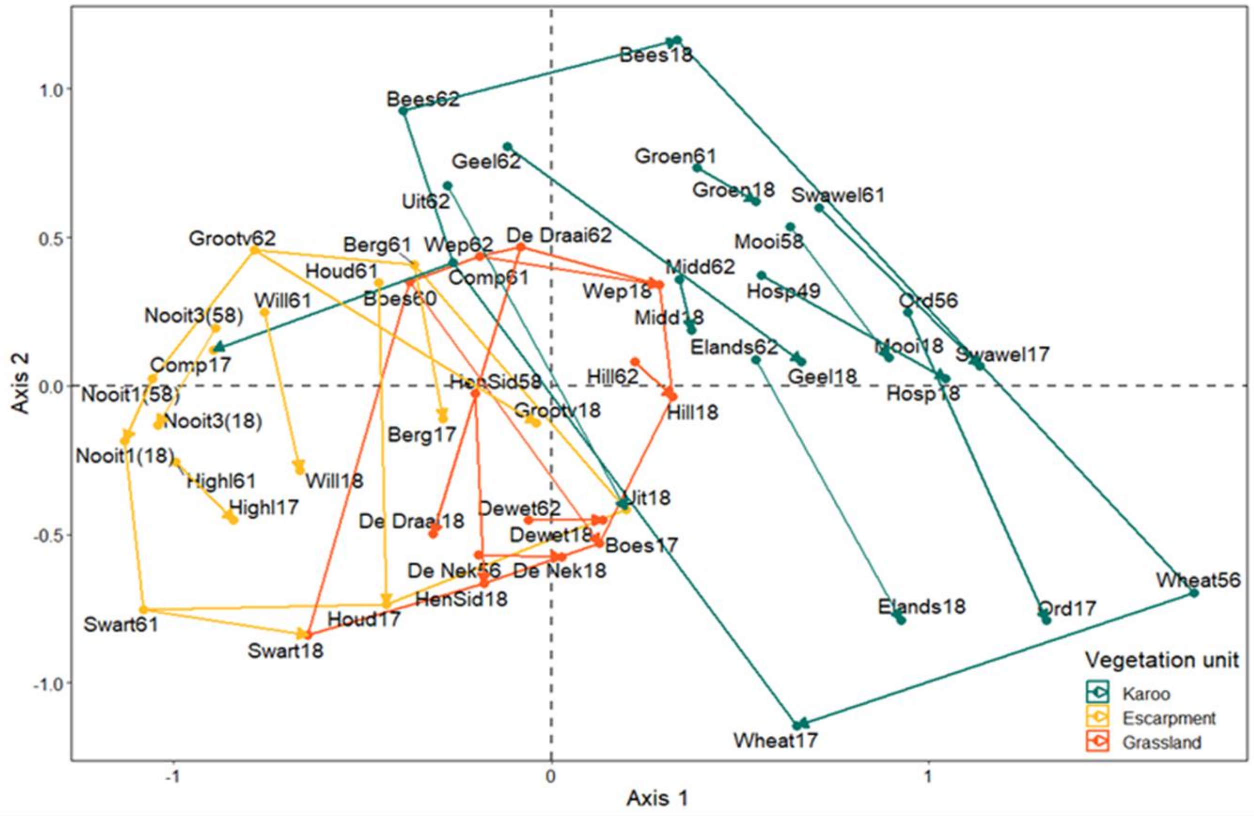

Figure 4.4 Non-metric multidimensional scaling of perennial grass and shrub species cover (≥ 1%) over a 60-year period (Bray-Curtis distance; k = 5, Stress score = 0.08, R^2 = 0.92).The lines, or arrows, show the trajectories of changes in species composition at each site, grouped according to their vegetation units determined by the cluster analysis, through time between the original (n = 27) and repeated surveys (n = 27). The direction of arrows shows the direction of changes in species composition at sites between years, some of the sites shifting from one vegetation unit into another, e.g. Swart61 (Escarpment) to Swart18 (Grassland).

Table 4.4 Goodness of fit statistics on the environmental predictors (vector centroids) of species composition of the original (1962) and repeated (2018) vegetation data and the vegetation units (factor centroids) on the first and second axes (1000 permutations)

		Axis 1	Axis 2	R^2	*p*-value
	Vector centroids				
1962					
	Altitude	0.99	0.06	0.49	**0.002**
	Soil pH	-0.93	0.37	0.65	**0.001**
	% Sand	-0.90	0.43	0.50	**0.001**
	$MAP1_{1942-1962}$	0.90	-0.44	0.47	**0.001**
2018					
	Altitude	0.66	-0.75	0.57	**0.001**
	Soil pH	-0.92	0.38	0.53	**0.001**
	% Sand	-0.95	0.31	0.28	**0.02**
	$MAP2_{1998-2018}$	0.79	-0.62	0.54	**0.001**
	Factor centroids				
1962				0.56	**0.001**
	Karoo	-0.73	0.16		
	Escarpment	0.98	0.21		
	Grassland	0.13	-0.52		
2018				0.47	**0.001**
	Karoo	-0.87	0.04		
	Escarpment	0.79	-0.17		
	Grassland	0.20	0.15		

Changes in growth form cover and relative dominance

Perennial grasses have increased uniformly across all 27 sites since 1962 (**Table 4.5, Figure 4.5**). Palatable dwarf shrubs and annual grasses have also increased significantly, but only at sites in the Karoo vegetation unit. Unpalatable dwarf shrubs and annual herbs have remained unchanged since 1962. Palatable and unpalatable shrub cover has not increased at Escarpment or Grassland sites. Percent bare ground cover has decreased significantly at all sites.

Table 4.5 Percent cover per growth form as sampled across 27 sites in two years in the Karoo (1962: n = 12; 2018: n = 10), Escarpment (1962: n = 8; 2018: n = 9) and Grassland (1962: n = 7; 2018: n = 8) vegetation units, with the calculated percent change over time. Values are means (± standard deviation). Significant changes are shown in bold at the 95% confidence level for the [1]comparison of percent cover between years (paired Wilcoxon test) and the [2]comparison of percent change among vegetation units (Kruskal-Wallis test)

Growth form	**Vegetation unit**	**% Cover 1962**	**% Cover 2018**	**% Change**	***p*-value[1]**	***p*-value[2]**
Annual herbs						0.29
	Karoo	0.8 ± 0.9	0.3 ± 0.6	-0.5 ± 0.7	0.14	
	Escarpment	1.1 ± 1.0	1.3 ± 1.4	0.2 ± 1.8	0.81	
	Grassland	0.4 ± 0.3	0.8 ± 1.0	0.4 ± 0.9	0.80	
Annual grasses						**0.03**
	Karoo	1.3 ± 1.2	7.8 ± 10.2	6.5 ± 10.7	**0.04**	
	Escarpment	0.6 ± 0.7	0.1 ± 0.2	-0.4 ± 0.8	0.18	
	Grassland	0.6 ± 1.2	1.4 ± 2.9	0.8 ± 3.2	0.68	
Perennial grasses						0.12
	Karoo	8.1 ± 5.5	28.1 ± 18.0	20.0 ± 16.7	**0.02**	
	Escarpment	31.9 ± 24.4	55.6 ± 17.6	23.7 ± 15.8	**0.01**	
	Grassland	29.1 ± 7.2	64.2 ± 13.1	35.0 ± 19.4	**0.02**	
Unpalatable						0.85
dwarf shrubs	Karoo	8.1 ± 3.8	8.1 ± 5.4	0.0 ± 4.5	1.00	
	Escarpment	9.9 ± 10.2	13.1 ± 14.8	3.2 ± 9.9	0.67	
	Grassland	2.5 ± 1.9	4.1 ± 3.4	1.6 ± 4.5	0.62	
Palatable						**0.001**
dwarf shrubs	Karoo	2.9 ± 2.7	17.4 ± 11.8	14.5 ± 10.1	**0.006**	
	Escarpment	0.5 ± 0.8	0.5 ± 0.9	0.0 ± 0.5	0.83	
	Grassland	0.8 ± 1.4	1.9 ± 2.7	1.1 ± 3.2	0.18	
Bare ground						0.07
	Karoo	78.8 ± 4.9	38.2 ± 17.3	-40.6 ± 18.2	**0.006**	
	Escarpment	56.0 ± 17.5	29.4 ± 8.4	-26.6 ± 17.4	**0.01**	
	Grassland	66.6 ± 7.3	27.7 ± 11.7	-38.9 ± 18.1	**0.02**	

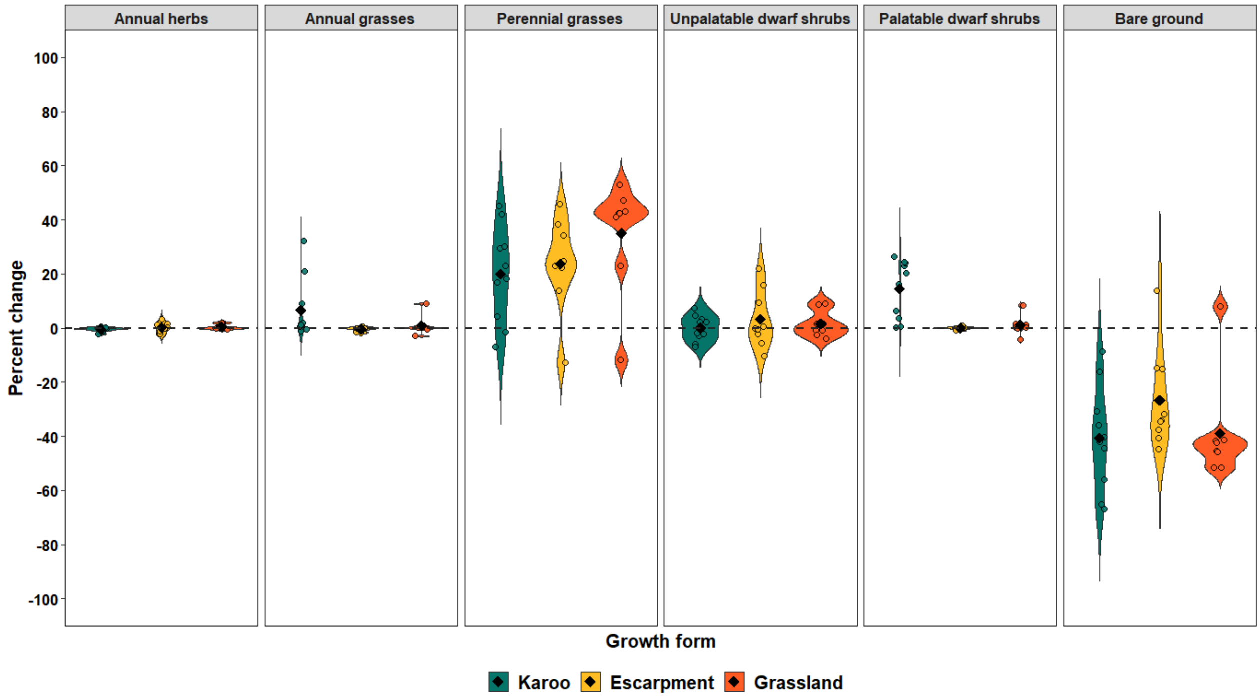

Figure 4.5 Percent change in growth form cover sampled at 27 sites in the Karoo (n = 10), Escarpment (n = 9) and Grassland (n = 8) vegetation units. Black diamonds are means and circles are the spread of data points.

The metric used to calculate the relative dominance of perennial grasses and dwarf shrubs in 1962 and 2018 indicated slightly similar patterns between years (**Figure 4.6**). Fifty-three percent of sites (nine of 17 sites) in the Nama-Karoo biome experienced a shift towards grass dominance relative to dwarf shrubs between 1962 and 2018. Ninety percent of sites (nine of 10 sites) in the Grassland biome experienced little change or only small shifts towards greater grass dominance. One Grassland site (De Nek) experienced a shift towards shrub dominance.

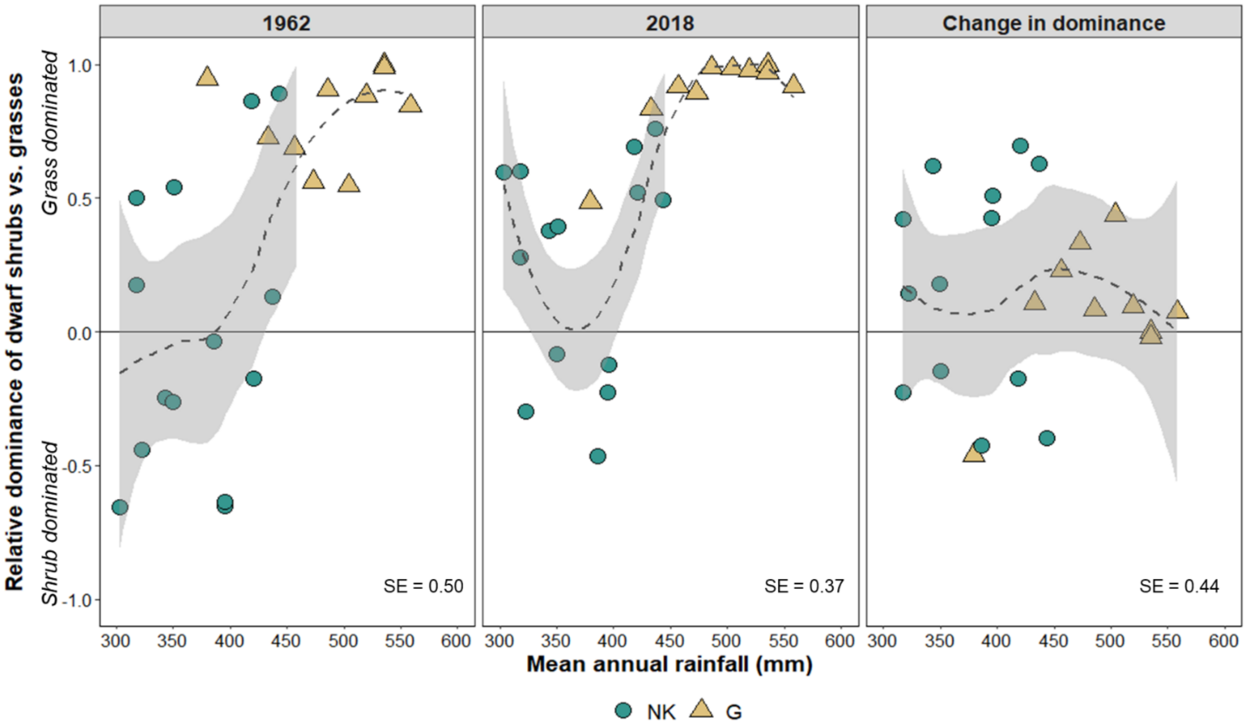

Figure 4.6 The relative dominance of perennial grasses versus dwarf shrubs in the vegetation sampled (n = 27) at sites in survey years 1962 and 2018 across the rainfall gradient of the eastern Karoo. The rainfall gradient is represented by the long-term average rainfall at each site for the period 1942-2018. The panel on the far right is the difference in the relative dominance values between start and end sampling points. The Loess regression is fitted to the data and residual standard errors (SE) reported for each.

Shifts in dominant species

A total of 46 families, 158 genera and 311 species was observed in 1962 and 2018 from the vegetation plots surveyed across the study area. The average number of species per site was similar among vegetation units (Karoo: 1962 = 26, 2018 = 22; Escarpment: 1962 = 22, 2018 = 18; Grassland: 1962 = 23, 2018 = 20). Unpalatable dwarf shrub richness decreased at Karoo sites but increased at Grassland sites and Escarpment sites (**Table 4.6**). Although perennial grasses have increased in cover since 1962, species richness of this growth form has decreased at Karoo and Escarpment sites and increased by one species at Grassland sites. Palatable dwarf shrub richness increased in 2018 at Escarpment and Grassland sites but decreased at Karoo sites. The grasses that use the C_3 photosynthetic pathway (*Bromus catharticus, Helictotrichon turgidulum, Melica decumbens, Pentaschistis airoides, Tribolium purpureum, Tenaxia disticha*) were minor components of vegetation in the surveyed plots as these did not occur as dominant in cover (Table 4.7), and therefore did not afford greater inspection.

Table 4.6 The number of species per growth form per vegetation unit across 27 sites in 1962 and 2018 as sampled along transects lines using the point intercept method. The average percent cover of each growth per vegetation unit across all sites is included in parentheses for comparison

Growth form	**Karoo (n=12)**	**Escarpment (n=8)**	**Grassland (n=7)**
1962			
Annual herbs	12 (0.8)	9 (1.1)	7 (0.4)
Annual grasses	6 (1.3)	3 (0.4)	1 (0.6)
C_4	5 (0.8)	-	1 (4.6)
C_3	1 (0.4)	3 (0.6)	-
Unpalatable dwarf shrubs	60 (8.1)	26 (9.9)	14 (2.5)
Perennial grasses	31 (8.1)	30 (31.9)	28 (29.1)
C_4	26 (2.4)	25 (5.3)	27 (3.7)
C_3	5 (0.8)	5 (10.1)	1 (0.6)
Palatable dwarf shrubs	21 (2.9)	3 (0.8)	6 (0.8)
2018	**(n=10)**	**(n=9)**	**(n=8)**
Annual herbs	5 (0.3)	8 (1.3)	5 (0.8)
Annual grasses	4 (7.8)	2 (0.1)	3 (1.4)
C_4	4 (6.6)	1 (0.8)	3 (3.2)
C_3	-	1 (0.2)	-
Unpalatable dwarf shrubs	41 (8.1)	33 (13.1)	20 (4.1)
Perennial grasses	23 (28.1)	23 (55.6)	30 (64.2)
C_4	21 (12.4)	19 (15.9)	28 (15.1)
C_3	2 (0.3)	5 (20.7)	2 (0.8)
Palatable dwarf shrubs	18 (17.4)	6 (0.6)	9 (1.9)

Sites in the Karoo vegetation unit have experienced the greatest number of dominant species changes. The perennial grass, *Enneapogon desvauxii*, has increased significantly at Karoo sites, while *Tragus koelerioides* has decreased significantly in cover at Grassland sites (**Table 4.7**). *Eragrostis chloromelas* was the only perennial grass that increased significantly in cover at Escarpment sites, while *T. triandra* increased significantly at Grassland sites. *Tetrachne dregei*, a highly palatable perennial grass, has not changed significantly within any of the vegetation units. The palatable dwarf shrubs, *P. incana* and *Pteronia tricephala,* have increased while the unpalatable dwarf shrub *Chrysocoma ciliata,* has decreased significantly at Karoo sites. *Lycium cinereum* and *Selago saxatilis* which are both relatively unpalatable shrubs have increased significantly across all vegetation units.

Table 4.7 The changes in percent covers of dominant species (≥ 1%) across sites in each vegetation unit. Subjective grazing index values (SGIV) represent palatability scores of each species according to Du Toit (2003). Bold values indicate significant differences in percent cover between 1962 and 2018 at the 95% confidence level

		Change in percent cover		
Species name	**SGIV**	**Karoo**	**Escarpment**	**Grassland**
Perennial grasses				
Aristida diffusa	5.1	5.32	-0.13	0.45
Cymbopogon pospischilii	7.6	0.35	0.20	8.92
Cynodon incompletus	4.1	-0.81	0.33	0.79
Digitaria argyrograpta	7.3	-	-1.05	-3.38
Enneapogon desvauxii	1.0	**5.68**	-	**0.60**
Eragrostis chloromelas	5.5	0.10	**14.51**	5.25
Eragrostis curvula	6.7	-0.49	-1.23	2.11
Eragrostis lehmanniana	5.4	-3.05	1.40	0.22
Tribolium purpureum	2.6	-1.20	-6.24	0.35
Sporobolus fimbriatus	9.5	0.05	-0.10	4.03
Tetrachne dregei	10.0	0.20	-7.60	-1.44
Themeda triandra	9.3	0	-0.34	**15.45**
Tragus koelerioides	2.2	**-2.33**	0.60	**-2.79**
Tragus racemosus	1.3	2.86	-	0.10
Palatable dwarf shrubs				
Eriocephalus ericoides	5.0	5.39	0.10	0.03
Nenax microphylla	7.0	-0.20	-	1.93
Pentzia globosa	4.8	0.53	-3.98	0.91
Pentzia incana	5.7	**13.02**	2.50	0
Pteronia tricephala	1.7	**2.03**	7.80	-
Oedera oppositifolia	3.0	-0.10	-7.30	-
Unpalatable dwarf shrubs				
Chrysocoma ciliata	1.5	**-0.95**	-0.86	-0.43
Delosperma sp.	5.7	3.73	-	-
Lycium cinereum	3.0	**1.33**	**1.70**	**1.18**
Mestoklema tuberosum	5.6	5.67	-	-
Passerina montana	2.0	-	7.84	-
Pentzia spinosa	4.8	3.20	-	-
Pteronia glomerata	3.9	0.40	3.70	-
Selago saxatilis	2.0	**0.36**	**1.37**	**0.88**

4.5.3. Environmental drivers of grass and shrub cover change

To determine whether the percent change in grass or shrub cover was related to a directional change in the average summer or winter rainfall, the slope of the trend lines of summer and winter rainfall (1942-2018) were obtained per site and plotted against the percent changes in perennial grasses and shrubs. Percent changes in grass cover were negatively, but not significantly, related to the average summer or winter rainfall of a site (**Figure 4.7A, B**). This was also true for its relationship to the slopes of trend lines of annual summer or winter rainfall over time, therefore indicating that changes in grass cover were unrelated to an increase in rainfall over time (**Figure 4.7C, D**). Percent changes in shrub cover were also negatively, but not significantly, related to average summer and winter rainfall, as well as to the slopes of the trend lines of annual summer and winter rainfall (**Figure 4.7C, D**). Likewise, no significant relationships were found between the percent changes in grasses or shrubs and mean annual temperature per site.

However, when explanatory variables were combined in the multiple regressions, soil pH, altitude and the change in summer rainfall (ΔSummer) significantly explained 28% of the variation in the percent change in perennial grass cover since 1962 (**Table 4.8**). The negative intercept of ΔSummer might be explained by the outlier sites, Nooitgedacht1 and Henning Siding, because upon removing these sites from the model the intercept became positive, but it did not improve the significance to the model (Appendix C7). Furthermore, while the percent change in grass cover was positively related to an increase in altitude, substituting altitude for any of the temperature variables in the equation yielded a lower adjusted R^2 value. Therefore, the temperature variables were better represented by altitude in the model. Further investigation of the relationships between percent change in grass or shrub cover and temperature, indicated that only the percent change in grasses was positively related to the change (slope) in average maximum and minimum temperatures in January (**Figure 4.7E, F**). In other words, the percent increase in the cover of perennial grasses was positively related to an increase in the average minimum temperature of January since 1958. The percent increase in the cover of shrubs was positively related to an increase in the average maximum temperature of January since 1958. The model indicated that the variables of ΔLate summer rainfall (Jan-Mar), percent sand, soil pH and ΔSummer rainfall explained 43% of the variation in the percent changes in shrub cover (**Table 4.8**). The adjusted R^2 values of both models indicated that there remains a large proportion of unexplained variation which was not accounted for in the study. Finally, the negative relationship between percent change in grass cover and percent change in shrub cover was not significant (n = 27, r = -0.11, p = 0.59).

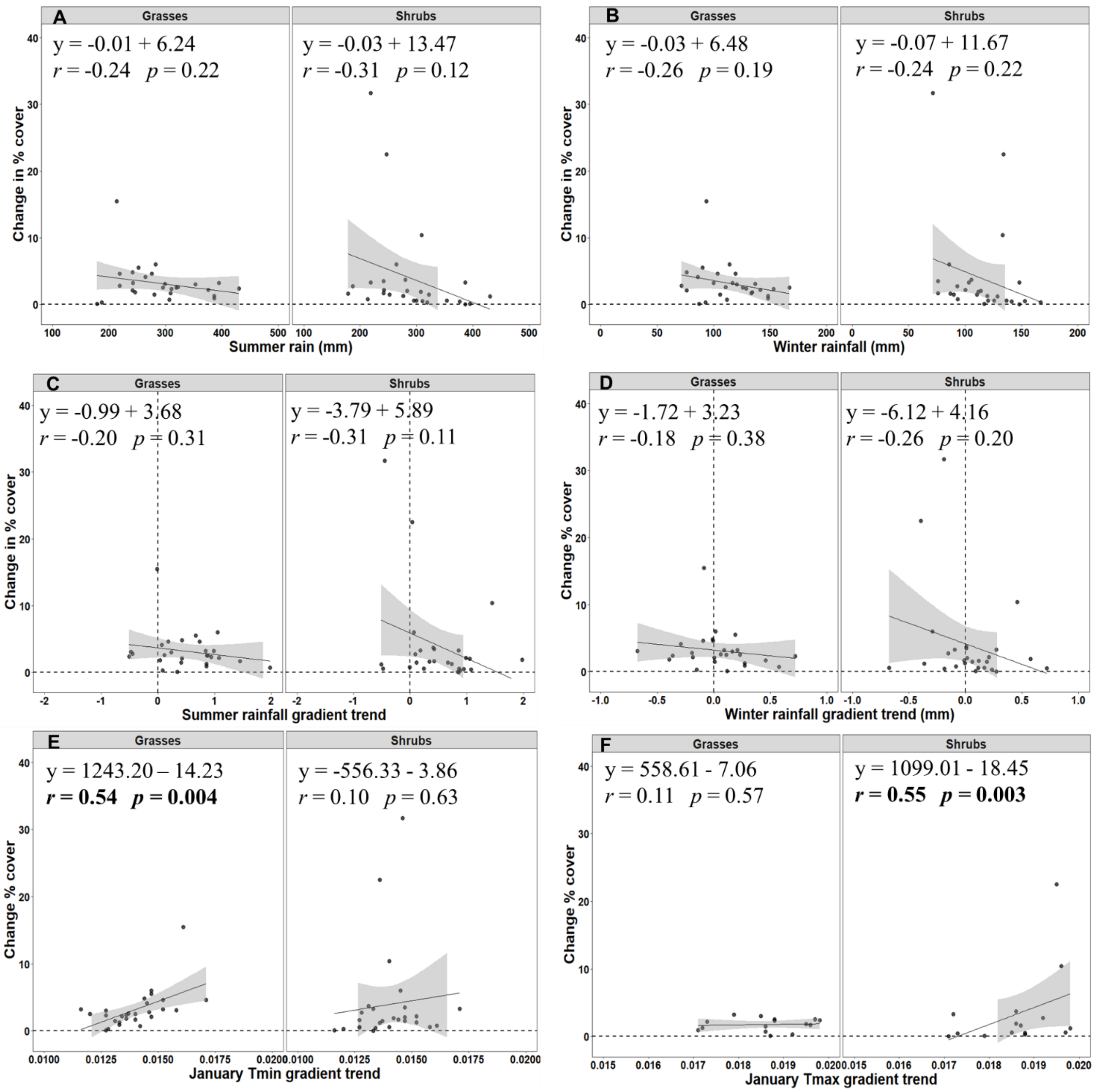

Figure 4.7 Relationships between the changes in the percent covers (between 1962 and 2018) of perennial grasses and dwarf shrubs (n = 27) and the A) average summer rainfall per site and, B) average winter rainfall per site. Changes are also plotted against the slopes of each trend line per site for the period 1942-2018 for C) annual total summer rainfall and D) annual total winter rainfall. Lastly, the relationships between the slopes of each trend line per site for the period 1958-2018 of the E) January average minimum and F) average maximum temperatures showed significant correlations to the changes in the percent covers of grasses and shrubs.

Table 4.8 Multiple linear regression models of percent change in perennial grass and shrub cover between 1962 and 2018 as explained by the relevant environmental explanatory variables

Final model	Coefficient Estimate	Standard Error	*t*-value	*p*-value	Adjusted R^2	F-statistic	Model *p*-value
% change Grass cover					0.28	$4.42_{(3,23)}$	**0.01**
Intercept	-28.59	10.52	-2.72	**0.01**			
Soil pH	4.12	1.45	2.84	**0.009**			
Altitude	0.004	0.002	2.52	**0.02**			
Δ Summer rainfall	-0.74	0.46	-1.60	0.12			
% change Shrub cover					0.43	$5.96_{(4,22)}$	**0.002**
Intercept	65.50	18.56	3.53	**0.002**			
Δ Late Summer rainfall	-20.38	8.03	-2.54	**0.02**			
% Sand	-0.70	0.28	-2.54	**0.02**			
Soil depth	-0.09	0.04	-2.02	**0.05**			
Δ Summer rainfall	8.78	4.70	1.87	0.08			

4.5.4. Changes in rangeland condition (1962-2018)

A smaller area was required to support a livestock unit in 2018 than in 1962 for all vegetation units (**Figure 4.8**). Karoo sites have experienced the greatest improvement in rangeland condition, and subsequently the number of hectares required to graze one LSU has decreased fivefold (Wilcoxon test for paired independent samples: p = 0.006; 1962 = 105 ha/LSU, 2018 = 23 ha/LSU). Sites in the Grassland and Escarpment vegetation units have also improved significantly over time. In both vegetation units there has been a twofold decrease in the number of hectares needed for one LSU (Grassland: p = 0.02; 1962 = 26 ha/LSU, 2018 = 10 ha/LSU; Escarpment: p = 0.01; 1962 = 29 ha/LSU, 2018 = 14 ha/LSU). The change in grazing capacity per site since 1962 is negatively related to the 1962 values of grazing capacity (R^2 = 0.98, p < 0.05).

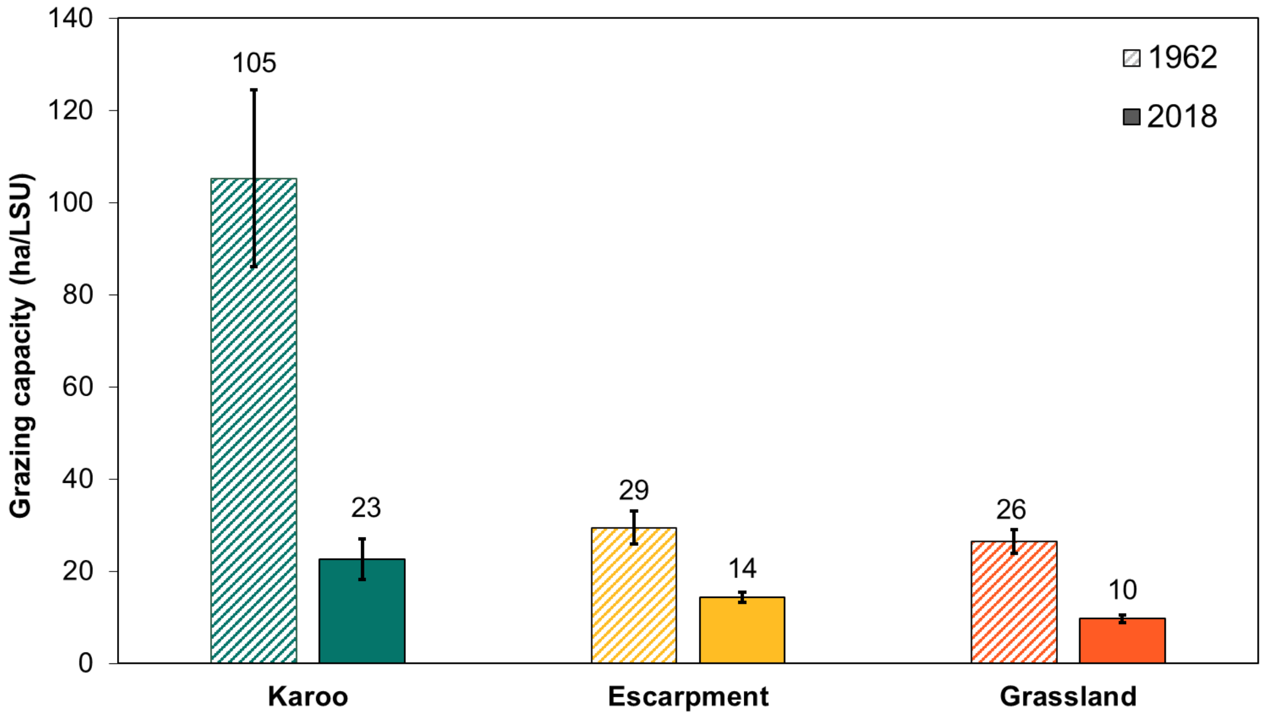

Figure 4.8 Average grazing capacity (ha/LSU) at sites in the Karoo, Escarpment and Grassland vegetation units in 1962 and 2018.

4.6. Discussion

4.6.1. Grass-shrub abundance and plant community distribution along biome and landscape transitions

Biome transition

The vegetation transitions across the eastern Karoo are best described in broad terms by its major growth forms, grasses and dwarf shrubs (Gosz & Sharpe, 1989; Peters, 2002). The distribution and abundance of grasses and dwarf shrubs is constrained along a climatic-edaphic gradient. Grass abundance increases as mean annual rainfall increases. Therefore, grasses typically become more abundant in a north-easterly direction towards the Grassland biome. Shrubs increase in abundance towards the southern and western extent of the study area as mean annual rainfall decreases towards the Nama-Karoo biome. Altitude, and subsequently temperature, also influence grass and shrub distribution and abundance. Grass cover increases with increasing altitude (and lower mean annual, minimum and maximum temperature) while shrub cover is higher on the lower-lying Karoo plains where average temperatures are generally higher. Therefore, dwarf shrubs appear to be limited at cooler sites (that also receive a higher average rainfall) where grasses are less limited by these climatic conditions. Grasses are associated with slightly more acidic soils containing a higher clay, and lower sand content, while shrubs occur in greater abundance in calcareous alkaline soils that contain a higher content of sand than clay. The flats of the Central Lower Karoo, for example, are stony and calcareous (Mucina & Rutherford, 2006), containing fewer grasses and a greater cover of dwarf shrub and succulent species. Although soil properties were not formally analysed in this study, increasing soil alkalinity and sand content towards the west might not be suitable for supporting an abundance of grass. However, this remains to be tested and future research should consider examining soil properties across the full extent of the biome transition.

Landscape transitions

These broader grass-shrub transitions can be further described at smaller hierarchies of landscape-scale mosaics, which are constrained by a climatic-edaphic-land use gradient. Three landscape hierarchies, the Karoo, Escarpment, and Grassland vegetation units, are represented by unique vegetation assemblages identified through diagnostic (or indicator) species analysis (Dufrêne & Legendre, 1997). Vegetation in the southern and western parts of the study area, in the Karoo vegetation unit, is a mixture of grasses and shrubs, characterised by an *E. lehmanniana-P. incana* community. Sites located within this plant community are dominated by the grass *A. diffusa* and the palatable dwarf shrub *E. ericoides*. Vegetation on the northern and eastern extent of the study area, occurring in the wetter and cooler Grassland vegetation unit, is largely described by a *T. triandra-S. fimbriatus* community. A suite of various climax grasses that are less specific to the Grassland biome, because they are also found in places more west of these sites but in lower abundances, are also representative of this grassveld community. Transitional vegetation of the cool mesic high-altitude sites occurring in the Escarpment vegetation unit, is identified by an *E. chloromelas-T. disticha* community, which contains C_3-grasses and Fynbos elements that are unique to these sites.

While describing the biome boundary was not within the scope of this study, and remains to be an outstanding goal of research in this region, the general description above is suitable enough for interpreting the changes in grasses and dwarf shrubs over time along a spatial continuum of climatic gradients to which more specific hypotheses could be examined. Future research that sets out to investigate how edaphic properties influence the spatial distribution of grasses and dwarf shrubs over various spatial scales along a south-west to north-east transect might alleviate the current debate around whether the transition of grasses and shrubs is a gradual intergradation or a sharp juxtaposition.

4.6.2. Vegetation changes in the eastern Karoo since 1962

Biome boundary structural shifting and compositional stability

The study set out to determine the extent and nature of long-term changes in the vegetation of the eastern Karoo since the 1960s. General vegetation cover has increased across all sites since 1962 with a remarkable decrease in bare ground cover, particularly at sites in the Karoo vegetation unit (**Figure 4.5**). Observations of increasing grass cover were recorded in 1989 (Hoffman & Cowling, 1990) and again in 2009 with a shift from dwarf shrub to perennial grass dominance (Masubelele et al., 2014). The findings from the present study show that there has been a sustained increase in perennial grasses across the biome boundary, as well as an increase in palatable dwarf shrub cover on the Nama-Karoo boundary has also occurred.

Up until now, these vegetation patterns have been highlighted as potential evidence for biome shifting, or an expansion of the grasslands (Du Toit et al., 2018), a phenomenon that starkly contrasts with that of global patterns. Indeed, dynamic vegetation models have predicted that a transition from shrubland to grassland would exhibit a slow replacement of shrubs with grasses under conditions of increased moisture availability as a consequence of competition for moisture (Moncrieff et al., 2015). This pattern has been detected in numerous local and global studies (e.g., Cable, 1969; Fitter, 1982; Masubelele et al., 2014; O'Connor & Roux, 1995; Peters, 2002). Has a slow replacement of shrubs with grasses occurred in the eastern Karoo under the conditions of increased rainfall? Based on the data, almost two-thirds (59%) of sites located in the Nama-Karoo biome underwent a shift in the relative dominance of shrubs to grasses since 1962, indicating that a significant westward expansion of grassland across a portion of the rainfall gradient has occurred.

This shift is structural in nature from the perspective of growth forms, which is not characterised by significant shifts in species composition. The structural growth form shift could be regarded as reversible if the rainfall regime enters another multi-decadal dry phase similar to that which occurred in the first 70 years of the 20th century (Chapter 3). Long dry spells, or frequent droughts, could result in the dieback of grasses and support the dominance of dwarf shrubs once again. Shrub encroachment in some parts of the eastern Karoo, which has been brought about by fire suppression (e.g., Compassberg site), could be reversed with a change in grazing management or increased fire incidence (Du Toit et al., 2015; Kraaij et al., 2017). Irreversible grassland expansion in the eastern Karoo, however, is predicted for the lower plains of the Nama-Karoo biome where fire has become increasingly more frequent. Although the effect of increasing CO_2 fertilization on grass production and the soil carbon cycle has not been investigated in the eastern Karoo, the linearly positive moisture-grass biomass relationship is supported by the data reported in this thesis. Several common dwarf shrub species display fire intolerance, or few appear to exhibit post-fire resprouting and reseeding (Du Toit et al., 2015; Kraaij et al., 2017; Rahlao et al., 2009; Van der Merwe et al., 2016), and are thus at risk of local extirpation if the positive feedback of climate and vegetation continue to promote fire in the system. Irreversible state transitions such as these can lead to functional changes in ecosystems, for example, changes in soil infiltration and nutrient cycling, and further impact ecosystem health and services.

Landscape-level shifts

At the level of landscape boundaries, there have been temporal shifts in species composition and species dominance within individual vegetation units, but again indicating structural stability in these terms. The species indicator analysis showed that present-day plant communities are remarkably similar to the original veld types that would have described these vegetation units in 1962 (Acocks, 1953). Only three sites experienced a transition to a different vegetation community. These transitions between vegetation units are unlikely to have been caused by quasi-permanent plot placement (see section 4.3.5.) because the photo descriptions detailed the position of the original surveys which were placed within the same vegetation types and topographical landforms. The shifts, however, do not represent extreme jumps from Karoo to Grassland, but instead were shifts to or away from an intermediate vegetation community, that being the Escarpment vegetation unit.

Compassberg and Uitsig, forming part of the Karoo vegetation unit in 1962, have since shifted to the Escarpment vegetation unit. These two sites are located at relatively high altitudes and contain several grass and Fynbos species unique to what was originally described as Karroid *Merxmuellera* Mountain veld (KMM; *Merxmuellera* has since been renamed to *Tenaxia*) (Acocks, 1953). Species with affinities to the Fynbos biome, and which have increased in cover since 1962, include *Passerina montana*, *Dicerothamnus rhinocerotis* and *Euryops* sp. Grasses unique to this community include *T. disticha*, *T. dregei*¸ and *E. chloromelas*.

Swartfontein, which was originally part of the Escarpment vegetation unit in 1962, now forms part of the Grassland vegetation unit in 2018. This is primarily because the dominant grass of KMM veld type, *T. disticha,* has declined significantly since being replaced by *T. triandra* and *E. chloromelas*. The Fynbos species that were present at this site have also declined in cover. Acocks (1953) suggested, when describing this veld type, that "although it [*T. disticha*] may be the natural dominant in rocky sandstone parts, it is probable that in all dolerite parts and all parts covered with soil, *Themeda* and *Tetrachne* are the natural dominants, together with such species as…*E. chloromelas*". Therefore, the main distinguishing difference between Escarpment and Grassland sites appears to be associated with a coupling of Fynbos species and a *T. disticha-T. dregei* grass complex in the Escarpment vegetation unit but the absence of this combination, or a significant reduction of Fynbos species, in the Grassland vegetation unit. It is interesting that although Fynbos species were rarely present in the 1962 surveys their re-establishment appears to be associated with higher altitudes and higher mean annual rainfall (Appendix C5). The absence or reduction of fire in these parts, discussed below, is suggested to be a key factor for the return of these Fynbos elements.

Apart from these few shifts, species composition has improved along the Karoo, Escarpment, and Grassland vegetation units. Palatable dwarf shrub species and perennial climax grasses have increased in cover, the former particularly at Karoo sites.

4.6.3. Climate and land use as drivers of change

Climate-vegetation relationships

Rainfall is the main driver of semiarid rangeland dynamics, both locally and globally. Short-term vegetation studies have illustrated the different effects of seasonal rainfall on grass and shrub growth. Grass growth, for example, is enhanced by increased summer rainfall relative to the long-term summer rainfall average, while shrub growth appears not to respond positively to trends of increasing autumn-winter rainfall (Hoffman et al., 1990; O'Connor & Roux, 1995). Grasses and shrubs also compete for moisture and space (e.g., Buffington & Herbel, 1965; O'Connor & Roux, 1995). The effects of long-term drought on reducing grass cover may permit the establishment of shrub seedlings during favourable moisture conditions. An example of this is observed in the Jornada plains where mesquite establishment during periods of extended drought affords the mesquite an opportunity to outcompete grasses for moisture in the deeper layers of the soil (Buffington & Herbel, 1965).

Warming and drying trends have been reported for the African continent (Hulme et al., 2001), the southern African subregion (Hulme, 1996) and for the central interior of South Africa (Warburton et al., 2005). Climatic conditions in the Karoo are projected to become much hotter and drier (Engelbrecht & Engelbrecht, 2016). Pollen sequence data suggests that although recent decadal climate patterns indicate trends of higher rainfall, centenary climate has overall been in a drying trend for the last 400 years within the eastern Karoo (Scott et al., 2012) . Local vegetation and palynological studies have reported cycles of significant transitions from shrub to grass-dominant systems in the eastern Karoo over a range of temporal scales. Such transitions to increased grassiness have usually been associated with wetter climatic conditions (Bousman, 2005; Coetzee, 1967; Du Toit et al., 2018; O'Connor & Roux, 1995; Scott et al., 2005). The analysis of climatic trends in the eastern Karoo (Chapter 3) confirms that directional changes in annual and seasonal rainfall, temperature, evaporation and evapotranspiration and wind speed, are likely responsible for the patterns of vegetation change observed here.

This study, therefore, predicted that positive trends in grass cover would be positively related to positive trends in summer rainfall across the study area. However, neither the increase in grass nor shrub cover was related to a trend of increasing annual or seasonal rainfall amount (**Figure 4.7C, D**). Possible reasons for this outcome might include, i) the relationships are strongly affected by outlier sites that have persisting grazing legacies that confound the effects of increasing rainfall (Du Toit et al., 2018), ii) site-level rainfall trends are not spatially correlated across the study area, iii) the impact of the drought has had variable effects among sites, thus dampening the influence of positive rainfall trends on grass abundance.

Associations between positive trends in grass cover and a warming trend in January average minimum temperatures (the hottest month), and positive trends in shrub cover and a warming trend in January average maximum temperatures, were found (**Figure 4.7E, F**). Percent change in grass cover also increased with increasing altitude (**Table 4.8**). Grass responses in terms of growth and abundance to elevated temperatures varies widely with altitude (Frei et al., 2014) but are enhanced in subtropical grasslands in South Africa (Buhrmann et al., 2016). Although the data may imply a positive feedback effect of warming on grass abundance, this requires detailed local experimental research. A complex interaction of highly variable small-scale environmental and disturbance factors operating over various time scales confound the detection of tight rainfall-vegetation linkages at broader spatial scales.

Land use-vegetation relationships

Land use practices, such as livestock or wildlife grazing, are important anthropogenic drivers of rangeland productivity, condition, biodiversity, and function (Fabricius et al., 2002; Kabir et al., 2020; Moolman & Cowling, 1994; Vanderpost et al., 2011; Weber et al., 2018). A few key factors of grazing management include herbivore density, season of grazing, length of resting from grazing, and management system (Cowling & Hilton-Taylor, 1994; Siyabulela et al., 2020; Van den Berg, 2011; Van der Merwe et al., 2018). Summer grazing, for example, is responsible for significant reductions in perennial grass cover (O’Connor & Roux, 1995). Numerous studies have tested the effects of long- and short-term grazing effects on Karoo vegetation and have reported reduced plant cover of perennial and palatable growth forms and plant diversity (e.g., McManus et al., 2018; Roux, 1967; Van der Merwe et al., 2018). One study conducted over the period 1950-1988 in the Central Lower Karoo at the farm, Ordonnantie, showed a trend of both increased grass and shrub cover after implementing a grazing practice recommended by the Department of Agriculture at the time (Palmer et al., 1990). Acocks (1953) was greatly concerned about the invasion of Karoo into numerous grass veld types as a result of livestock overgrazing. In his concept of an expanding Karoo, grasses would have been replaced by unpalatable dwarf shrub species like *C. ciliata*. Notably, this species has decreased in cover at all sites since 1962.

Historically, natural fires in the Karoo have been infrequent, or planned burning of the veld is only recorded in parts of the eastern Karoo, such as at the higher altitude Sneeuberg and Nuweberge (Kraaij et al., 2017), as a means of controlling undesirable shrub species (Roux & Vorster, 1983a). In more recent years, however, the effects of fire on shrub survival, resprouting and seedbanks have been examined (Kraaij et al., 2017; Rahlao et al., 2009), specifically on the vegetation occurring on the lower Karoo plains in Middelburg-EC (Du Toit et al., 2015). The increase in grassiness is predicted to fuel an increase in fire frequency, which could ultimately eliminate shrub seedbanks and re-enforce grass dominance (Du Toit et al., 2015; Kraaij et al., 2017). Gosz (1993) stated that "threshold dynamics are expected to occur near boundaries". An example of this is most clearly seen at the Escarpment boundary of the landscape level. The Compassberg site was regularly burned in the 1960s and 1970s to reduce shrub growth and to promote grass growth and cover when sheep were the dominant grazers on this farm (Brenda James, property owner, *pers. comm.*). Horses, which were introduced as part of an experimental breeding programme in the 1980s, increased sharply in number on the farm over the following 30 years. Following a number of key management decisions over this period, such as a change in animal type from sheep to cattle and the cessation of burning practices, an increase in Fynbos-Renosterveld vegetation replaced the grassveld community. This illustrates how specific farm-scale management decisions can lead to the triggering of critical thresholds which, when surpassed, cause a cascade response of significant changes in species composition to push an ecological site into an alternative stable state. Other high altitude Escarpment sites are similarly strongly constrained by a complex interaction of geology, fire regime, rainfall (Cowling & Potts, 2015; Kraaij et al., 2017; Roux, 1969; Roux & Vorster, 1983a; Van der Walt, 1961) and grazing management practice.

Data presented (section 2.4.2.) suggests that land use practices in the Karoo have undergone various changes since the early 1900s that may be significant enough to have had important effects on the vegetation in some locations (Hoffman et al., 2018; Walker et al., 2018). Grazing management systems, for example, have evolved in this time. While rotational grazing is the major system applied to rangelands in the eastern Karoo, management practices have been influenced in recent decades by the high-density grazing systems based on the principles of holistic management. Specifically, emphasis falls on high livestock densities, short duration grazing (1-3 days up to 2 weeks), longer resting periods and diversification of animal type to a cattle-sheep-goat combination. Magisterial district-level census data, however, still indicate a remarkable long-term decline in sheep numbers, stability in cattle and decrease in goat numbers since 1911 across the study area (section 2.4.1.). A more recent change in land use type from livestock to wildlife ranching also appears to be taking place across the broader region of the Karoo, yet little is known about the effect of this transition on the vegetation of the eastern Karoo (Clements & Cumming, 2017; Hyvärinen et al., 2019; Ramsay, 2016; Walker et al., 2018). Other key land use changes that are likely to have had important knock-on effects on vegetation change in the study area include changes in land tenure and farm size, farm abandonment after the stock reduction schemes and non-agricultural developments like solar energy, which have displaced livestock farming practices (Atkinson, 2009; Nel & Hill, 2008; Todd et al., 2016; Walker et al., 2018).

4.6.4. Implications of vegetation change for local and global drylands

Improved vegetation cover

From the view of desertification theory, drought frequency and livestock grazing are generally accepted key factors that influence shrub encroachment (Archer, 1994; Buffington & Herbel, 1965; Schlesinger et al., 1990). This process persists when water and wind erosion redistribute soil and nutrients to under shrub canopies (Allington & Valone, 2011; Reynolds et al., 2007) thereby increasing the area of bare ground. The equilibrium theory of rangeland ecology considers that vegetation-herbivore coupling is closely related and linear (Clements, 1916). Hence, on this basis, grazing exclusion (under conditions of above-average rainfall) assumes that grasses will re-establish through flowering and seeding, and a grassy layer is thereby maintained (Allington & Valone, 2011; Peters et al., 2006). Within the context of the present study, the decline in district-level sheep numbers over the last 100 years is proposed to have impacted the rate at which rangelands have been able to recover in terms of i) vegetation cover and ii) species composition. In discussions with landowners (refer to Chapter 2, section 2.4.3), their observations indicated that the reduction in livestock numbers allowed much of the vegetation to rest and recover over the years by allowing climax species to flower, set seed and re-establish in the vegetation, which thereby supports the findings of significant decreases in bare ground cover across the region. However, this vegetation-herbivore relationship is implied for the broad spatial scale and time scale that vegetation change was examined in the study. Specific experiments that test equilibrial dynamics in the eastern Karoo would need to be conducted at finer scales at the farm-level in multiple locations.

The increase in vegetation cover perhaps indicates the presence of non-equilibrial dynamics in the eastern Karoo. Event-driven increases in vegetation cover suggests that rangeland soils have greater protection from the elements thus indicating an improvement in ecohydrological and landscape functioning (García-Gómez & Maestre, 2011; Li et al., 2007). Supporting findings show a threefold increase in basal cover at a site within the study area between 1960 and 2010 (Du Toit et al., 2018). When describing False Upper Karoo in the Veld Types of South Africa, Acocks (1953) suggested that for Karoo vegetation to invade grassveld, soils would have had to erode away. Dwarf shrubs do not protect the soils from further erosion as they require harder subsoils or exposed bare rock to establish and spread (Acocks, 1953). However, on the basis of greater grass cover especially in the drier western sites, soil quality is suggested to have improved potentially by the redistribution of wind-blown sands into bare areas creating ideal sites for the establishment of grasses during favourable moisture conditions (Buffington & Herbel, 1965).

Improved rangeland condition

Under the conditions of the ‘expanding Karoo’ primarily caused by livestock overgrazing (Acocks, 1953), palatable species would have been eliminated from these environments by the year 2050, leaving rangelands dominated by undesirable and alien species. Dean & Macdonald (1994) proposed that the decreasing trends in long-term stocking rates was evidence for declining rangeland productivity on account of increases in unpalatable shrub cover. Others have shown that heavy stocking or continuous grazing in the summer months promote unpalatable and shorter-lived species (Dean et al., 1995; Van den Berg, 2011). Although our data do show that various unpalatable dwarf shrub species might have become more common at some sites (e.g., the bird-dispersed Solanaceae spiny shrub, *Lycium* spp.), this is marginal when viewed in light of the increase in dominant palatable species cover (e.g., *P. incana*, *E. ericoides* and a number of climax grasses) across the study area. Grazing capacity has improved significantly since 1960, which is representative of these significant changes in species covers over time. Similar patterns of increasing palatable cover were found in previous studies (Hoffman & Cowling, 1990; Masubelele et al., 2014).

O’Connor & Roux (1995) show that some perennial and palatable species may not necessarily be completely removed from over-utilised veld, however, the broad-scale increase in vegetation cover and palatable species cover across all sites does not provide sufficient evidence for overgrazed veld. Alternatively, improvements in livestock and land management practices alongside long-term reductions in sheep numbers across magisterial districts (Chapter 2) provide convincing support for improved grazing capacity (Hoffman et al., 1999).

Global grassland-shrubland shifts

The local evidence does, however, present contrasting patterns to the global patterns observed in grassland-shrubland ecosystems elsewhere. Buffington & Herbel (1965) indicated that shrub expansion at the expense of grasses in the Jornada plains in New Mexico had been in effect since 1858 as a consequence of livestock overgrazing in some parts, competitive advantage of shrubs over grasses during periodic droughts and rodent activity. Bestelmeyer et al. (2018) have since challenged several misconceptions around grassland-shrubland shifts including the orthodox beliefs of local livestock grazing and drought-driven shrubland encroachment. South of this area, McIntosh et al. (2019) have reported a decreasing trend in perennial grasses in the historically overgrazed Chihuahuan Desert over the period 1993-2018, despite having since applied conservative grazing intensities or destocking during drought years. This period is associated with higher temperatures, more frequent droughts and decreasing rainfall over the region (McIntosh et al., 2019). Peters et al. (2006) did, however, show that the influence of greater wind erosion (subsequent to historical overgrazing) had accelerated the conversion of grassland to shrubland. This emphasises the notion of 'grazing legacies' (Cuddington, 2011). The effects of historical overgrazing are often lagging or prolonged in nature and tends to be masked during short wetter periods where faster growing growth forms (e.g., grasses) respond quickly to the increase in moisture. In reality, grazing legacies are still present, and during unpredictable long dry periods the rate of degradation is accelerated because not enough time has lapsed for the impacts of conservative management practice to take effect, as seen in the Chihuahuan-context.

4.6.5. Conclusions

It is generally recognised that dryland ecosystems have both equilibrial and non-equilibrial dynamics operating at variable scales of time and space (Briske et al., 2020; Milton & Hoffman, 1994; Reynolds et al., 2007). Building a greater understanding of naturally-occurring transitions at the Nama-Karoo-Grassland interface should, therefore, be focused on developing an operational framework (Potts et al., 2015b) that integrates long-term cross-scale observational studies (e.g., Hoffman & Cowling, 1990; Masubelele et al., 2014) with correlative (e.g., Du Toit et al., 2015) and mechanistic modelling (e.g., Midgley & Thuiller, 2011; Peters, 2002), hypothesis-driven experimentation (e.g., Du Toit et al., 2018; Duker et al., 2015; McManus et al., 2018; Roux, 1967) and phylogenetic approaches (e.g., Scott et al., 2005). For example, experimental studies of grass-shrub competitive interactions are urgently needed particularly under multiple climate change scenarios. This is especially relevant for grassland-shrubland biome boundaries where dominant growth forms have varying response growth rates to the rapidly unpredictable and changing environmental gradients. If global warming and drying trends prove to exacerbate shrubland encroachment in other semiarid environments, then detailed fine-scale experiments to understand these disparate vegetation responses of the eastern Karoo will address a major knowledge gap in dryland rangeland ecology.

Chapter 5: Identifying vegetation shifts in the semiarid eastern Karoo using repeat photography

5.1. Introduction

Climate-induced biome shifts are being reported across global scales causing changes in ecosystem structure that affects productivity and ecosystem functioning and services (Grimm et al., 2013). Drylands are particularly susceptible to climate change as these arid and semiarid environments depend heavily on water availability for productivity (Tietjen et al., 2017). Dryland systems are facing increasing levels of land degradation as predictions indicate that droughts are to become more frequent and intense (Grimm et al., 2013; Tietjen et al., 2017). Shifts in vegetation structure and/or composition are normally detected at the boundaries between biomes where dominant growth forms can be monitored. The semiarid grassland-shrubland biome boundaries of North America, Australia, and China, are some examples of where long-term monitoring programmes have discovered persistent trends of shrubland encroachment as a consequence of historical agricultural practices, global warming, chronic drought, fire exclusion, vegetation-climate feedback loops and soil nutrient redistribution (Chen et al., 2015; Cross & Schlesinger, 1999; D'Odorico et al., 2012; Knapp et al., 2008; Nicholas et al., 2011).

Vegetation change on natural rangelands in the eastern Karoo has been documented since the mid-20th century (Hoffman & Cowling, 1990; Masubelele et al., 2014; O'Connor & Roux, 1995). A trend of increasing dominance and apparent westward shift of grasses has been reported by these studies at a limited number of sites. After increasing the number of repeated survey sites, findings indicate that these vegetation trends have persisted (Chapter 4). Based on the disparity of these vegetation trends with those global examples cited above, examination of the environmental drivers has been the focus of some important local studies (e.g., Du Toit et al., 2018; Du Toit & O'Connor, 2014). A regional trend analysis of climatic variables was performed (Chapter 3) providing credible suggestions that interactive climatic forces at play are largely responsible for the observed vegetation changes in the eastern Karoo. The combined directional increases in temperature and rainfall amount and directional decreases in wind speed and evaporation have enhanced vegetation productivity, while a seasonal shift in rainfall has favoured an increase in grass cover across the rainfall gradient. Anthropogenic factors, namely reductions in district-level livestock numbers and changes in grazing management practice over the 60-year period (section 2.4.), are suggested to have further influenced the restoration of these rangelands to improved conditions and grazing capacities as determined through vegetation sampling (section 4.5.4).

There remain some uncertainties on the extent and nature of these vegetation changes, particularly for a variety of landforms (e.g., mountain slopes or riverine areas) in the eastern Karoo. How far back in time vegetation change can be assessed is also often limited by the availability and quality of baseline data. Incorporating more than one approach to monitoring vegetation change, especially across broader spatial scales, is useful for addressing these gaps. The value of satellite-derived remote sensing approaches to analyse broad-scale change is growing as both the satellite products and methods used are continually being improved and refined (e.g., Bell et al., 2021). There is also an abundance of ground-based historical landscape photographs which, when repeated, can provide valuable insights into landscape-level change.

Fixed-point repeat photography is an effective tool used to track and assess landscape change over varying time scales (Pickard, 2002). This method has broad applications in research, environmental management, education, land degradation, ecosystem restoration, or policy, to name a few (Rohde, 1997). It has been used widely in studying the dynamics of vegetation change (Bahre, 1991; Hastings & Turner, 1966; Hendrick & Copenheaver, 2009; Herrero et al., 2017; Hoffman et al., 2019; Masubelele et al., 2015a; Michel et al., 2010; Nyssen et al., 2009; Rohde, 1997; Van der Merwe & Hoffman, 2019; Zier & Baker, 2006), for monitoring plant populations and species life histories (Jack et al., 2016; Okubamichael et al., 2016; White et al., 2016), land use change (Kull, 2005), hydrological change (Frankl et al., 2011), the effects of fire (Du Toit et al., 2015), coastal habitats (Reimers et al., 2014), and glacial retreat (Baker & Moseley, 2007; Butler & DeChano, 2001; Byers, 2007). Hence, this approach when combined with vegetation surveys, can i) provide a more nuanced interpretation of change across landforms, ii) increase the number of sites in a region and iii) lengthen the timeframe observed.

5.2. Aims and objectives

The main objective of this study was to quantify and describe landscape-scale vegetation change beyond the timeframe and area of the surveyed vegetation plots of Chapter 4 between the ~1940s and 2018 in the eastern Karoo. Based on the current vegetation and climate trends of the eastern Karoo, the aim of the study was twofold, i) to determine the growth form changes on plains and hillslopes using repeat photography, and ii) to describe the state transitions over time between grasses and dwarf shrubs across the rainfall gradient of the study area.

5.3. Methods

5.3.1. Historical photograph collections

Photograph collections taken by three photographers were used in this study (**Table 5.1**). The original photographs are archived in the Plant Conservation Unit (PCU) at the University of Cape Town. Original photograph slides and accompanying metadata were digitally scanned by research assistants at the PCU. The majority of photographs (64%) used in this study came from the collection donated by Dr. Piet Roux which he built up over his time working at Grootfontein in Middelburg-EC. Dr. Roux took the majority of these photographs from the late 1950s to the late 1960s during his doctoral studies on the autecology of *Tetrachne dregei*, a highly palatable C_3 grass species occurring in the region (Roux, 1969). This collection is unique in that the photographs are of natural rangelands in the eastern Karoo showing mostly plains and hillslope landforms where clumps of *T. dregei* had established or were likely to establish under improved conditions. Four additional collections were included to increase the number of photo sites (n = 85), to diversify the vegetation types assessed, and to extend the timeframe analysed. The earliest photograph was taken in 1925 by I.B. Pole Evans which documented severely degraded veld. The most recent photographs used in this analysis were taken in 2002 by R.M. Cowling which documented several vegetation types of the Lower Karoo. The location and description of each site is summarised in Appendix D1.

Table 5.1 Historical photograph collections used for the comparison of vegetation cover between original and repeated photographs

Year	Photographer	No. of photos
1925	I.B. Pole Evans	3
1945	J.P. Acocks	1
1946	J.P. Acocks	7
1953	J.P. Acocks	6
1960	P.W. Roux	13
1960-61	P.W. Roux	14
1962	P.W. Roux	1
late 1950s to late 1960s	P.W. Roux	40
	Total	**85**

A subset of photographs from the Roux collection showed the position of the vegetation plots, which he surveyed for his PhD thesis, and which were subsequently resurveyed (Chapter 4). These photographs either showed a metre pole in the foreground of the image and/or included notes describing the number assigned to that survey and the location of the site or farm name. Therefore, these sites formed the core subset of sites for this thesis and were prioritised for the repeat photography study. However, the addition of other photograph sites from his and other collections further aided in increasing the sample size.

5.3.2. Study area

The photographs were all taken in the eastern Karoo where the Nama-Karoo and Grassland biomes merge and the vegetation becomes a mix of Karoo dwarf shrubs and grasses (Mucina & Rutherford, 2006). Albany Thicket and Azonal vegetation make up a smaller area of the study area (**Figure 5.1**). According to Mucina and Rutherford (2006), the study area comprises six bioregions, which are made up of 12 vegetation types (**Table 5.2**). The average annual rainfall ranges from 200 mm in the south-west to 590 mm in the northeast and occurs predominantly in the summer months between October and March. Altogether, the photograph sites span a 500 km transect between Beaufort West in the Western Cape and Dewetsdorp in the Free State. The grassland-shrubland composition of this region is primarily limited by a moisture gradient that increases north-eastwards and influences the overlying soils of the dominant Karoo Supergroup substrates to be uniquely more clay-rich than the soils of the western Nama-Karoo (Mucina & Rutherford, 2006). Chapter 2 provides a detailed description of the vegetation, soils, climate, and land uses that make up this region.

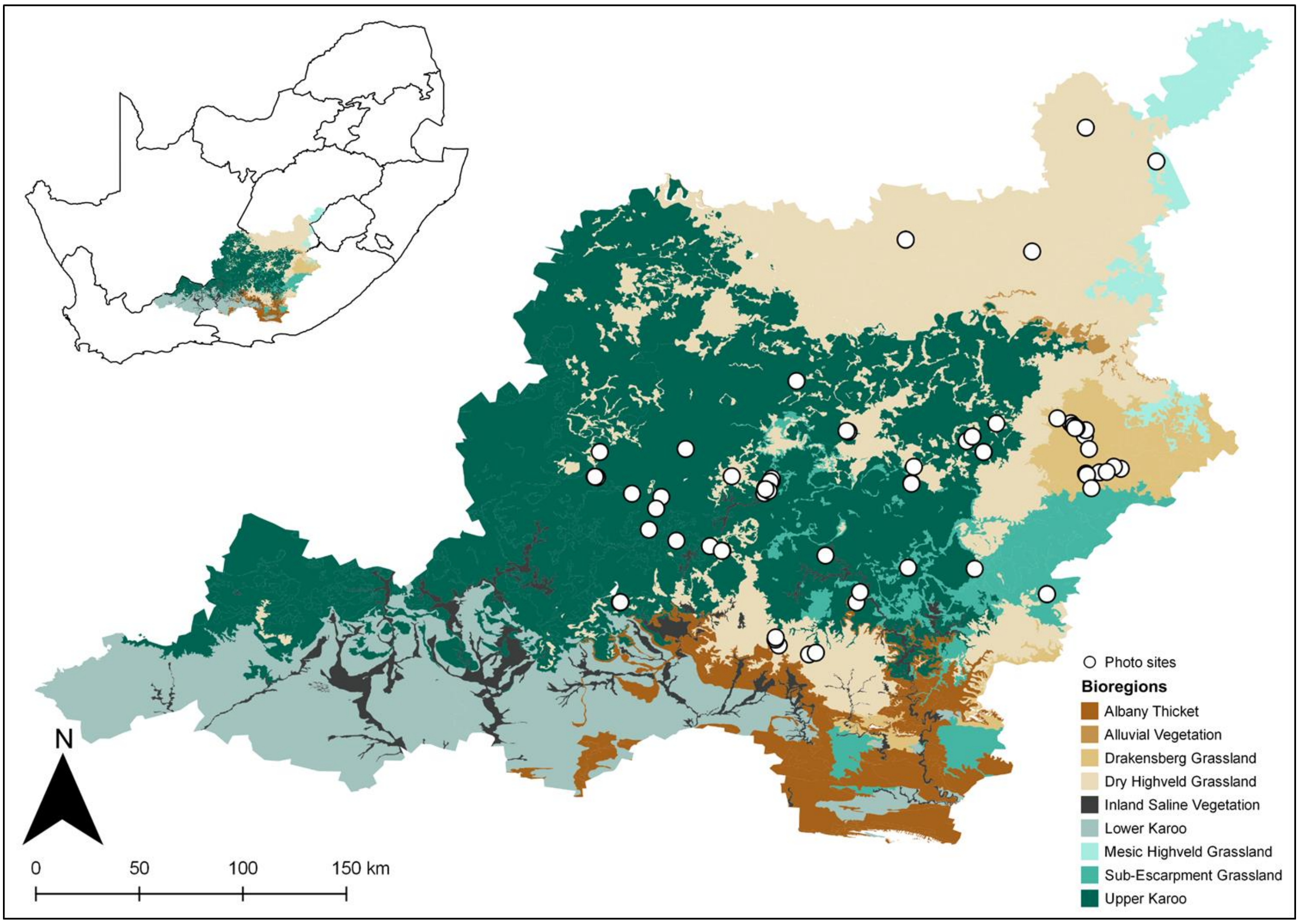

Figure 5.1 The position of photo stations (n = 85) used in this study across the Nama-Karoo and Grassland biomes in South Africa.

Table 5.2 The number of photograph sites grouped by bioregion in the Nama-Karoo, Grassland and Albany Thicket biomes in the study area

Biome	Bioregion	No. Photos
Nama-Karoo		
	Lower Karoo	16
	Upper Karoo	42
Grassland		
	Drakensberg Grassland	21
	Dry Highveld Grassland	23
	Sub-Escarpment Grassland	3
Albany Thicket		1

5.3.3. Repeat photography and the estimation of growth form cover

The majority of photograph sites were initially relocated in Google Earth Pro using the original images prior to relocation in the field. The ‘fly-over’ and ‘street view’ functions were used to search for general landscape features, such as mountain ranges or koppies (mesas and buttes), that matched features in the photographs. Google Earth sites were roughly matched to the original photographs and latitude-longitude coordinates were obtained from Google Earth to guide relocation of the sites in the field. This desktop method was only used for photographs that were repeated for the first time. A smaller subset of photo sites, which had been repeated previously (Hoffman & Cowling, 1990; Masubelele et al., 2014), provided latitude and longitude coordinates that were used to easily relocate those sites.

Once in the field, the method of repeating photographs followed the approach outlined by Rohde (1997). The exact photo site and camera position was relocated by identifying and lining up unique landscape features such as mountain peaks, large boulders, or rocks in the foreground. The photo site was marked with a cairn built from stones and the GPS coordinates and altitude were recorded. Other important site details were recorded including date, time, grid reference, original photo source and date, vegetation type and geological features. The field of view at each photo site was divided into distinct regions or landform units, such as plains and hillslopes. After retaking the photographs, each landform unit was surveyed by walking into the field of the image to record dominant species and their estimated percent covers. Percent covers of dominant grass, dwarf shrub, tall shrub species and bare ground were estimated for each landform. Lastly, a description of the landscape and the major changes were recorded.

The repeated images were matched with their respective original images in Photoshop CS5. The two images were superimposed, rescaled, rotated and cropped to create a perfect matched pair of original and repeat photographs. Each site was divided into the relevant landform units, namely, plains and hillslopes. Calibration sheets of actual growth form cover calculated from the repeated vegetation surveys analysed in Chapter 4 were used to guide the estimations of cover from the photograph pairs. The vegetation surveys were originally carried out by Dr. Roux in the 1960s. The biases around relocation and resampling of these surveys in 2017-18 has been discussed previously in the thesis (section 4.3.5.), however, the same person conducted the repeated surveys at every site thereby ensuring any inherent sampling biases were consistent.

Three observers visually estimated the percent covers of the major growth forms in each landform unit from the original and repeat photograph pairs. In some cases, if both landform units were present in a photograph and both were clear enough to be estimated for percent covers, then both landform units were scored. However, in many instances, hillslopes were either not present in all photographs, or if present were not clear enough to have estimated percent covers and thus were not always included in the total number of comparisons. Hence, the total sample size per landform unit was $n = 85$ for plains and $n = 29$ for hillslopes. The measured growth forms were grasses, dwarf shrubs (< 1 m in height), tall shrubs (≥ 1 m) and bare ground (including rock and plant litter).

Once the cover estimates had been determined by consensus among the three observers, an average value for the percent cover of each growth form in each landform unit was obtained for the original and repeat image. The difference in covers between the original and repeat images was then calculated and these percent changes were correlated against mean annual rainfall to determine the direction and significance of vegetation trends across the rainfall gradient.

5.4. Statistical analyses

The Standardised Precipitation Index (SPI; McKee et al., 1993) was used to investigate the long-term rainfall and drought patterns from 1940 to 2018 at two locations representing the Nama-Karoo and Grassland biomes in the study area. Rainfall data for these sites was obtained from the South African Weather Service. Monthly rainfall totals were applied to a 24-month time scale to calculate the SPI events, defined as the number of standard deviations from the long-term mean at which a negative or positive event occurred. Each SPI value provides a comparison of the accumulated rainfall in a period of 24-months to the long-term mean (Guenang & Kamga, 2014). Section 3.4.1. provides a detailed description of this method.

In order to determine a level of confidence in the cover estimates measured from the photograph pairs through the consensus exercise, the linear regression relationship of cover estimates between field methods (vegetation survey versus repeat photograph) was initially examined. Then the trends of percent changes in the covers per growth form (continuous variable) from the photograph comparisons were analysed against the rainfall gradient. Least squares linear regressions were used to investigate the slope and direction of relationships.

Lastly, to describe the relative dominance of grasses versus dwarf shrubs in 1960, 2018, and the change in dominance over time against the rainfall gradient of the study area, the same approach outlined in section 4.4.2 was used. The metric limits are between -1 (representing complete dominance of shrubs) and +1 (representing complete dominance of grasses) (**Equation 1**). Because this metric does not capture species-specific changes, its utility in describing broad comparisons of growth form covers is fitting for the method of repeat photography. The non-parametric Locally Weighted Least Squares Regression ('loess') was fitted to the relationship of relative dominance and mean annual rainfall. Relative dominance was calculated according to Gremer et al. (2018) as follows:

$$\frac{\%\ Cover_{Grass} - \%\ Cover_{Shrub}}{\%\ Cover_{Grass} + \%\ Cover_{Shrub}} \qquad \text{Eq. 1}$$

All graphing and statistical analyses were conducted in R version 3.5.2. (R Core Team, 2018) using the packages tidyverse (Wickham et al., 2019) and ggpubr (Kassambara, 2020).

5.5. Results

5.5.1. Rainfall patterns in the eastern Karoo

The SPI analysis of rainfall time series from the Nama-Karoo and Grassland biomes (**Figure 5.2**) reflect the long-term rainfall patterns of the eastern Karoo illustrated in Chapter 3. In the Nama-Karoo, SPI events were mostly negative in the 1960s (64% of events between 1963 and 1970) and positive from the 1970s to 1980s (84% of events between 1984 and 1990). In the Grassland biome, SPI events in the 1960s were only positive from 1960 to 1963 and 1968 to 1969, with a dry period in between. SPI events were also positive from the mid-1980s (71% of events between 1986 and 1990). The 2010s in the Nama-Karoo were almost equally wet and dry, but the years 2017-2018, when the repeat photographs were taken were particularly dry owing to the drought conditions at this time. Ninety-two percent of SPI events in the Grassland, however, were negative during the 2010s. Forty-two percent of these negative SPI values are categorised as 'extremely dry'.

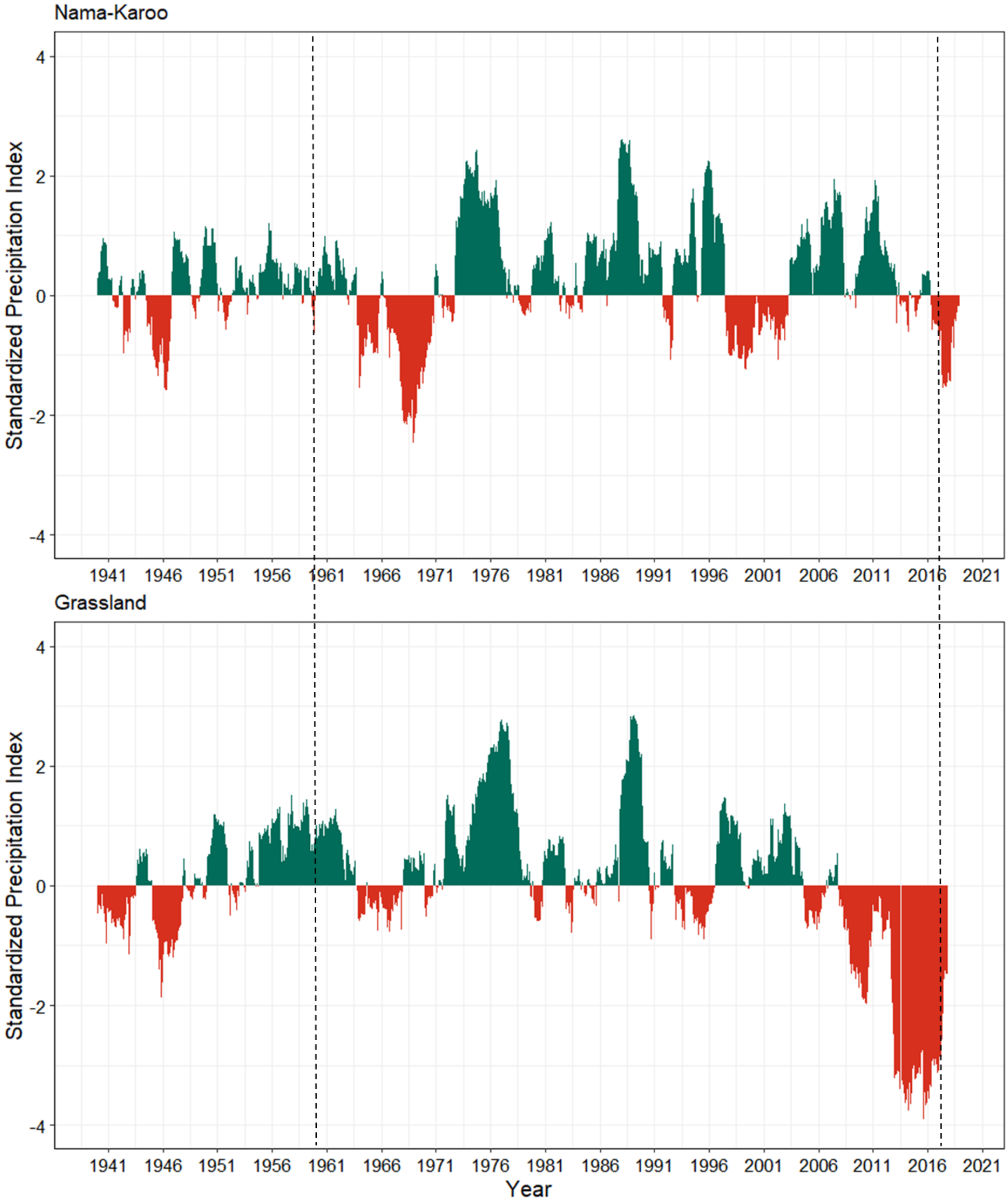

Figure 5.2 A 24-month Standardised Precipitation Index (SPI) representative of the Nama-Karoo (Middelburg-EC) and the Grassland (Trompsburg) biomes from 1940 to 2018. Dashed lines indicate periods when photographs were taken.

5.5.2. Growth form cover changes distributed across the rainfall gradient

Estimates of percent cover from both field methods in 2017-18 (fixed-point repeat photographs and vegetation point intercept surveys) were significantly and positively correlated over time for 19 out of the 27 surveyed plots (Appendix D2; R = 0.92, $p < 0.05$). The eight remaining sites did not have accompanying landscape photographs and were therefore excluded from this correlative exercise. The comparison between field methods confirms that the estimation of cover from both was consistent and that both methods are reliable tools for estimating vegetation change.

The trends in percent changes per growth form cover as calculated from the cover estimates in the original and repeat photograph pairs were similar between plains (**Figure 5.3**) and hillslopes (**Figure 5.4**) across the rainfall gradient. Percent changes in total vegetation cover was negatively related to mean annual rainfall on the plains (R = -0.26, $p = 0.02$) but showed no significant relationship on the hillslopes (R = 0.13, $p = 0.51$). The percent changes in grass cover were significantly negatively related to mean annual rainfall for both plains (R = -0.39, $p = 0.0004$) and hillslopes (R = -0.50, $p = 0.006$). By contrast, the percent changes in dwarf shrub cover increased significantly with mean annual rainfall for both landforms (Plains: R = 0.34, $p = 0.002$; Hillslopes: R = 0.48, $p = 0.008$). The percent changes in tall shrub cover, however, were unrelated to mean annual rainfall (Plains: R = 0.07, $p = 0.77$; Hillslopes: R = 0.02, $p = 0.90$). Generally, grass cover has increased on plains and hillslopes in the Nama-Karoo biome and shrub cover has increased on plains and hillslopes in the Grassland biome.

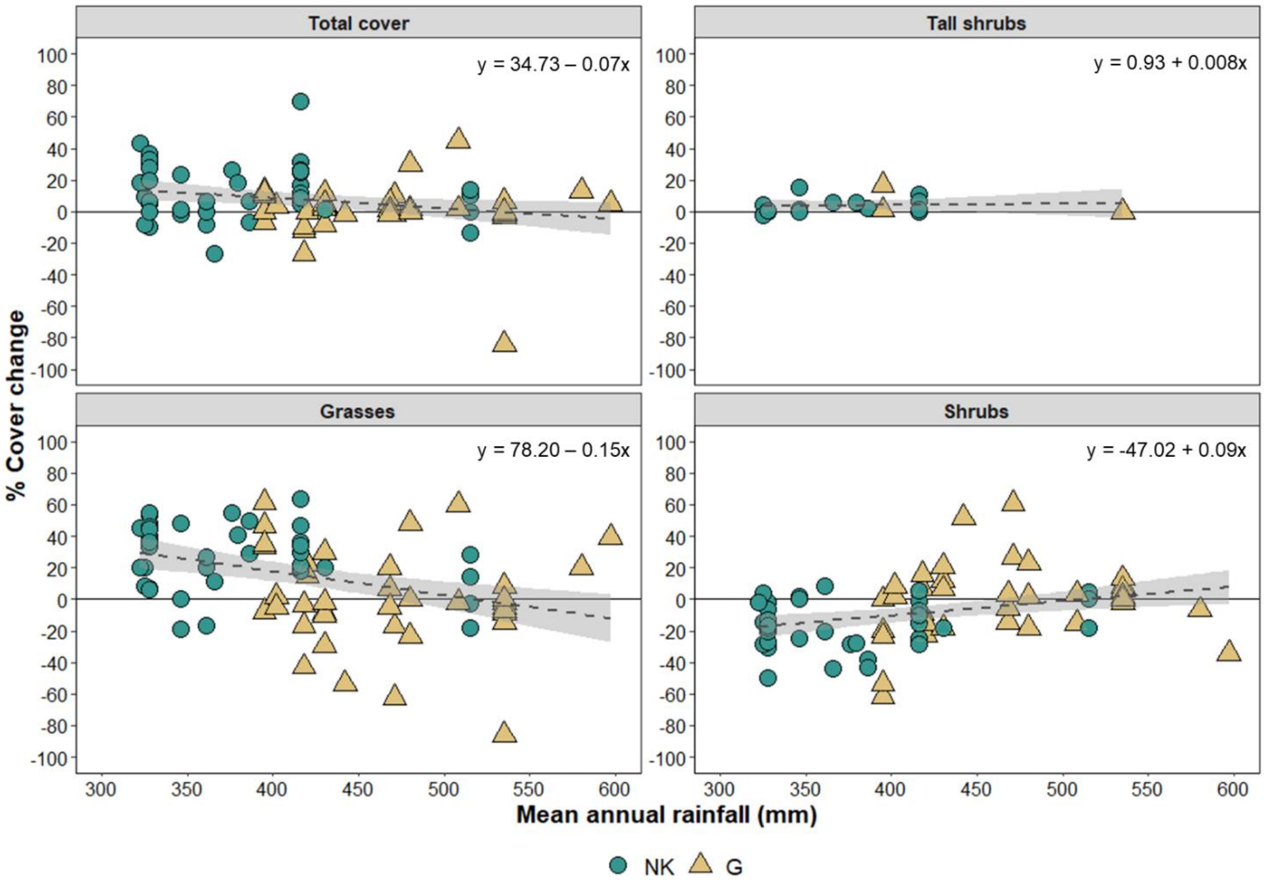

Figure 5.3 Percent changes in total vegetation, grass, dwarf shrub and tall shrub covers on the plains (n = 85) as calculated from photograph comparisons between original and repeated images taken along the rainfall gradient of the eastern Karoo. Dashed trend lines include the upper and lower bounds of the 95% confidence interval with associated linear regression equations.

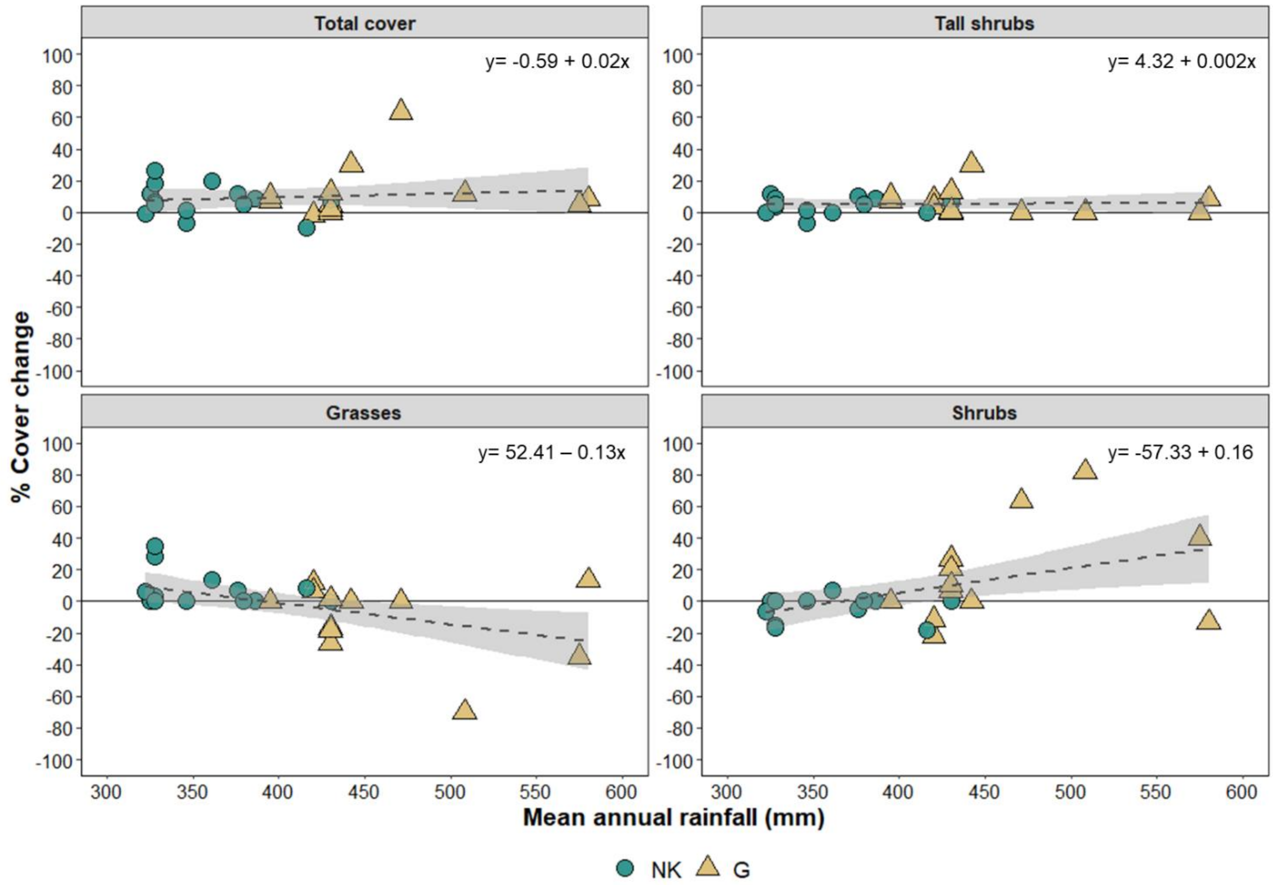

Figure 5.4 Percent changes in total vegetation, grass, dwarf shrub and tall shrub covers on the hillslopes (n = 29) as calculated from photograph comparisons between original and repeated images taken along the rainfall gradient of the eastern Karoo. Dashed trend lines include the upper and lower bounds of the 95% confidence interval with associated linear regression equations.

The metric used to calculate the relative dominance of grasses and dwarf shrubs in the 1960s and 2018 indicated similar patterns between plains and hillslopes (**Figure 5.5**). Ninety percent of plains sites in the Nama-Karoo experienced a shift towards grass dominance relative to shrubs over time. A change to grass dominance on the hillslopes of the Nama-Karoo occurred at 100% of sites. No prominent trends in either grass or shrub dominance were identified for either plains or hillslopes of the Grassland biome: 53% of plains sites experienced a shift towards shrub dominance but 47% of other plains sites had a shift towards grass dominance. No notable trends were identified for the hillslope sites in the Grassland biome either because 50% of sites had either a shift towards grass or towards shrub dominance. Therefore, no significant shifts between vegetation states were evident at Grassland sites despite there being variable changes in the percent covers of grasses and dwarf shrubs among Grassland sites (**Figure 5.4**).

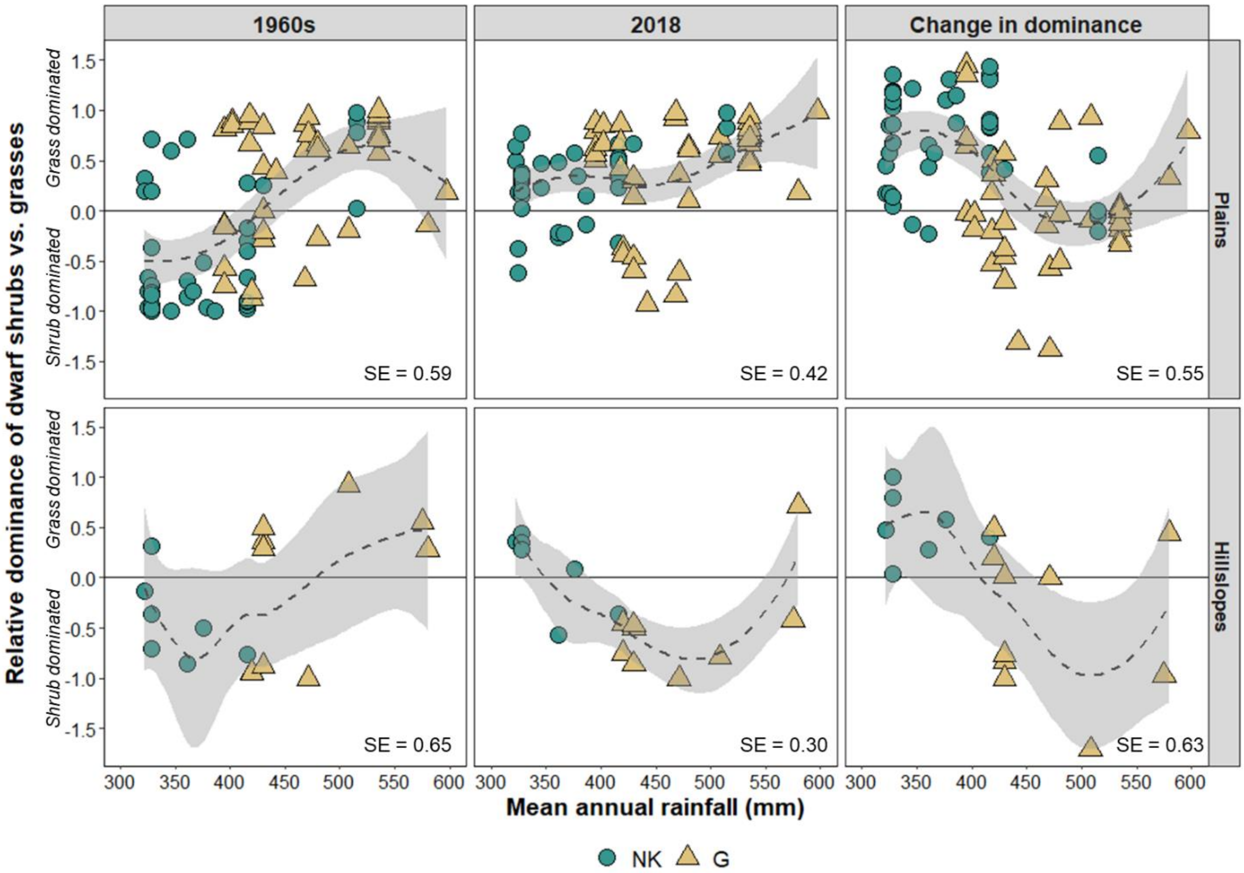

Figure 5.5 The relative dominance of grasses versus dwarf shrubs in the vegetation of the plains (top panel, n = 80) and hillslopes (bottom panel, n = 17) at photo sites in the 1960s and 2018 across the rainfall gradient of the eastern Karoo. The panel on the right is the difference in the relative dominance values between start and end sampling points. The Loess regression is fitted to the data and residual standard errors reported for each.

In summary, the vegetation of the plains and hillslopes of the Nama-Karoo biome boundary is shown to have had an increase in grass cover and associated decrease in dwarf shrub cover (**Figure 5.6**). On the Grassland biome boundary, however, little indication of a decrease in grass cover and an increase in dwarf shrub cover was detected for either the plains or hillslopes, despite there being site-level differences in land management that would have led to either grass or shrub dominance (**Figure 5.7**). An example of such changes had occurred at Compassberg and Highlands where regular burning was historically implemented to control the cover of unpalatable dwarf shrub species and sour grasses such as *Dicerothamnus rhinocerotis* and *Tenaxia disticha*, respectively. However, in speaking to the current landowners, veld burning has since been intentionally excluded from their management practices for at least the last 30 years (apart from the natural fires that are ignited by lightning strikes).

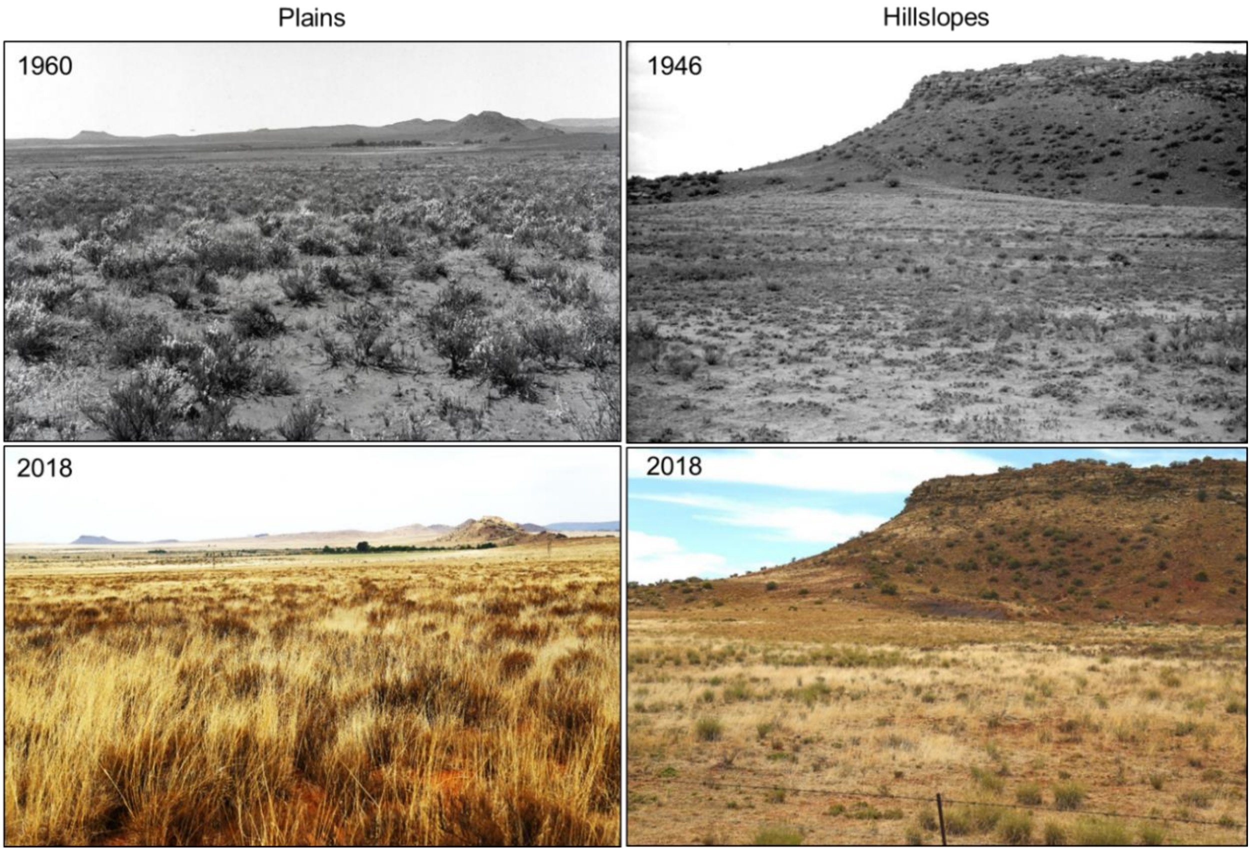

Figure 5.6 Nama-Karoo biome. **Left:** Perdekamp on Grootfontein Agricultural Development Institute, Middelburg-EC (No. 1854). Old grazing trials where *Eriocephalus ericoides* (Kapokbos) was the dominant plant cover and very little, if any, grass cover was present (**Top left:** Roux, 1 October 1960). The grazing trials were discontinued after the 1960s and the camp is currently lightly grazed by sheep. Vegetation currently comprises equally of grasses (*Aristida congesta* subsp. *barbicollis*) and dwarf shrubs (*E. ericoides*) (**Bottom left:** Arena and Hoffman, 13 November 2018). **Right:** Goodhope, Steynsburg (No. 1842). 19.8 miles ENE of Steynsburg. *Tenaxia disticha* persisting on hillside (**Top right:** Acocks, 25 July 1946). A fire burned through the site in 2014. Tall shrubs, mostly *Searsia erosa*, on the hillslope have grown in size but cover has remained stable. A borrow pit was dug at the base of the slope in the centre of image and an old fenceline runs to the left of the pit where a line of *S. erosa* shrubs have grown. On the right side of the pit on the hillslope *T. disticha* is the dominant grass, while left of the old fenceline, *A. congesta* subsp. *barbicollis* dominates (**Bottom right:** Arena and Hoffman, November 2018).

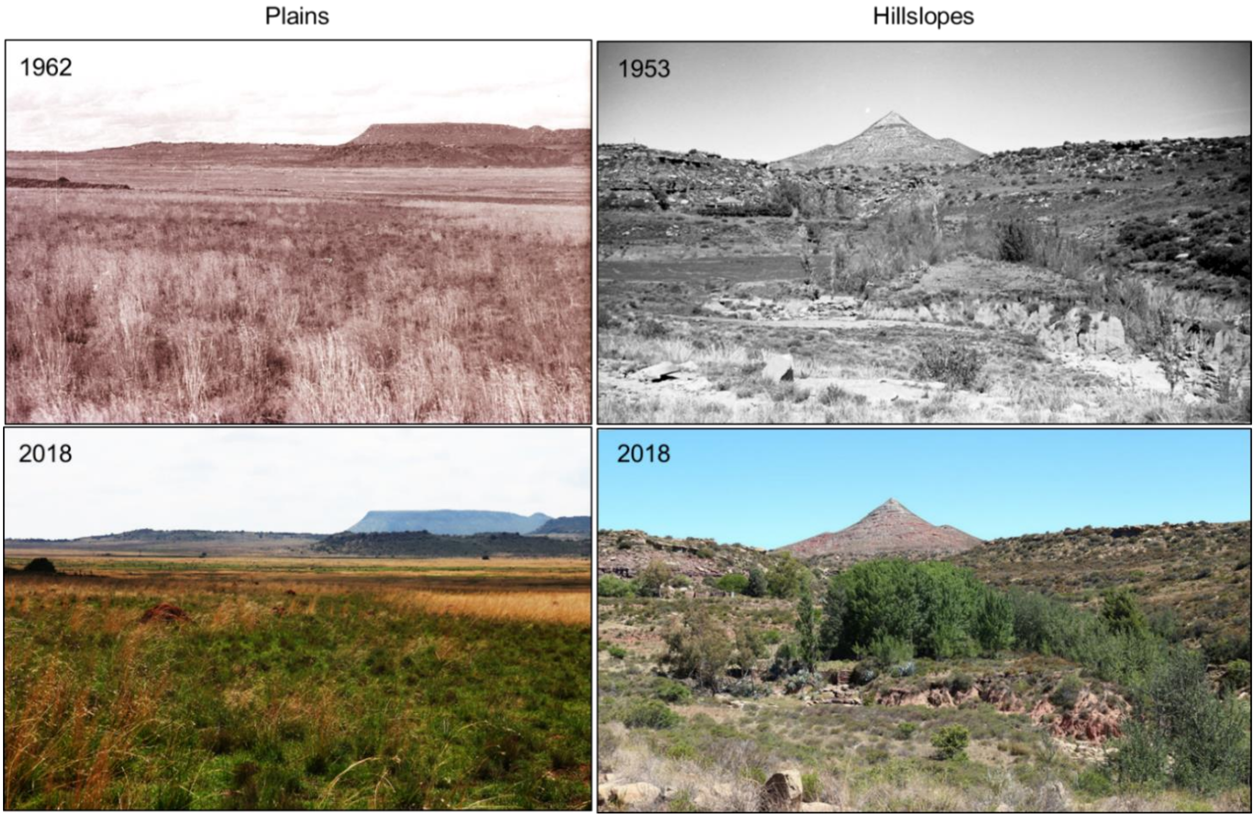

Figure 5.7 Grassland biome. **Left:** Hillside farm, Springfontein (No. 014b). Portion of survey 34, showing a small depression, forms a transitional area between a sandy hill and the area on which *Themeda triandra* is dominant, a portion of which is seen in the centre, right of the photo. (**Top left:** Roux, February 1962). Xhariep Karroid Grassland, little change has occurred in total cover and the proportion of grasses and dwarf shrubs have remained much the same. Dominant grass cover is *T. triandra* (**Bottom left:** Arena and Hölscher, 14 February 2018). **Right:** Near Witkop (No. 1834). Deep dongas in escarpment below peak. (**Top right:** Acocks, 22 April 1953). The immediate foreground has a higher grass cover in 2018 than in 1953, but grass cover on the hillslope right of the erosion gully has decreased and dwarf shrubs have increased in cover. Alien vegetation, mainly poplar trees, has increased in cover in the gully (**Bottom right:** Arena and Hoffman, 9 November 2018).

5.6. Discussion

5.6.1. Spatiotemporal patterns of vegetation change

The aim of the study was to describe the landscape-scale vegetation changes in the study area between 1940 and 2018. The photographs document stability in terms of total vegetation cover for both plains and hillslopes, yet important shifts in growth form dominance were identified. The cover of grasses has increased and dwarf shrubs have decreased on plains and hillslopes in the Nama-Karoo biome the seasonal rainfall trends were detected (Chapter 3). While vegetation cover has remained stable, a shift in the dominance of dwarf shrubs to grasses has occurred. Although decreasing dwarf shrub cover since the 1960s was initially not significant in 2010 (Masubelele et al., 2014), by extending the observed timeframe to 2018, a significant negative trend is now identified. The general findings from this study are consistent with those reported by others for the biome boundary (Masubelele et al., 2013, 2014).

The cover of tall shrubs has, however, remained unchanged on the plains and hillslopes of both biomes. These findings are somewhat consistent with those found in the Camdeboo National Park near Graaff-Reinet where the cover of tall shrubs on plains and riverine areas was relatively unchanged between 1988 and 2010 (Masubelele et al., 2013). However, others have previously reported increases in tall shrubs on hillslopes in the Grassland biome (Masubelele et al., 2015a), and more recently, on some hillslopes where Azonal and Karoo Escarpment Vegetation occur (Du Toit et al., 2020). Woody plant encroachment is a phenomenon that has been documented across Africa (Venter et al., 2018) and has been taking place for decades in southern Africa (O'Connor, 1995; O'Connor et al., 2014). While this study provided important insights into grass-shrub transitions on plains and hillslopes, it lacked data for other landform types, particularly the riverine areas where trends in bush encroachment are variable and unclear in the region (Du Toit et al., 2020; Hyvärinen et al., 2019; Masubelele et al., 2013). Therefore, the extent of bush encroachment in the eastern Karoo deserves greater inspection.

5.6.2. Vegetation change driven by shifts in the rainfall regime

While the 1960s experienced below-average annual rainfall, significantly high rainfall events occurred in the mid-1970s over the summer rainfall region in southern Africa, which appeared to cause an important climatic shift in the rainfall regime (Nicholson et al., 2018). The directional change in the rainfall trend for the eastern Karoo commenced after these high rainfall events. According to the rainfall trends, two important changes must be recognised. First, mean annual rainfall has increased significantly at several locations in the eastern Karoo. Second, a significant shift in rainfall season from the late summer months (Jan-Mar) to the early summer months (Oct-Dec) has occurred in this area (Chapter 3). These trends coincide with a shift from dwarf shrub to grass dominance from 1960 to 2018 as determined by the photographic comparisons in this study (**Figure 5.5**) and by the vegetation survey comparisons in Chapter 4 (**Figure 4.6**). Although largely variable, the photographic comparisons for sites in the Grassland biome indicate that grasses have potentially decreased and dwarf shrubs have increased for both landforms (**Figures 5.3 and 5.4**). These changes are suggested to reflect the impact of recent droughts. However, grazing and fire management impacts cannot be ruled out because grasslands are strongly mediated by rainfall, fire and grazing pressure (Bond et al., 2003). While bush encroachment is a prevailing issue for grasslands and savannas in South Africa (O'Connor, 1995; O'Connor et al., 2014; Venter et al., 2018; Wigley et al., 2009), the data did not support patterns of woody thickening in the Grassland biome boundary.

5.6.3. Conclusions

It is evident that the interactions between climate and vegetation responses in this region are both spatially and temporally highly dynamic. The repeated monitoring of a smaller subset of these sites (Hoffman & Cowling, 1990; Masubelele et al., 2015a) confirms that the transition to grass-dominance has been ongoing for the last 30-40 years. The findings reported in previous chapters confirms that increasing grassiness has coincided with wetter rainfall conditions. The present study using repeat photography augments this understanding of the trajectories of vegetation change in the eastern Karoo. This has important implications for the agricultural and conservation management practices in these environments as they adapt to the effects of global warming. Incorporating a plot-level analysis of vegetation change (Chapter 4) enriches the interpretations gained from a landscape-level analysis that uses repeat photography.

Chapter 6: General discussion and synthesis

6.1. Problem statement

Persistent and increasing dryland degradation due to climate and anthropogenic change threatens ecosystem health, biodiversity, and human livelihoods (Burrell et al., 2020). Monitoring and assessing these impacts develops our understanding of how dryland systems respond to drivers, and therefore informs management and conservation efforts. Biome boundaries, which are often characterised by highly dynamic and interacting environmental gradients, are ideal systems to monitor and assess biome shifts, particularly in dryland ecosystems that are predicted to expand across boundaries under global warming and anthropogenic change. Identifying important ecosystem thresholds that maintain stable vegetation states at various scales, for example, can greatly improve our understanding of the nature of biome shifts.

Much like around the world, signs of rangeland degradation in the arid and semiarid parts of South Africa were detected early in the 20th century. The encroachment and replacement of perennial grasses with Karoo shrubland and decreasing vegetation cover due to livestock overgrazing was reported by John Acocks (Acocks, 1953), as well as by earlier government reports (e.g., the Drought Investigation Commission of 1923 and the Desert Encroachment Committee of 1948). A number of interventions were implemented to delay, or reverse, this onset of degradation, such as the stock reduction schemes, veld reclamation trials and the development of the group-camp system of grazing (Roux & Vorster, 1983a). Acocks (1953) further speculated that if livestock overgrazing and various ecosystem processes continued at the same rate, these vegetation trends would persist into the 2050s and would be specifically observed as an eastward encroachment of Karoo into the grasslands. Much knowledge had been produced from small-scale, short-term studies regarding the various roles of rainfall and grazing impacts on Karoo vegetation (Roux & Vorster, 1983b, 1983a). After several decades, long-term studies on vegetation changes in the eastern Karoo reported increasing grass cover across the biome boundary (Hoffman & Cowling, 1990; Masubelele et al., 2014, 2015a, 2015b).

These findings clearly contradicted the 'expanding Karoo' hypothesis but were also in contradiction to the global trends of vegetation change for semiarid grassland-shrubland biome boundaries (e.g., Bestelmeyer et al., 2018; Peters, 2002). While evidence pointed towards biome stability (Masubelele et al., 2015b), there remained gaps in understanding the specific mechanisms that drove this increase in grasses and the relative response of woody shrubs. Furthermore, little was yet known about what these changes meant for the overall condition of rangelands in the region and how these changes may have impacted local land management. Various local studies on the long-term rainfall trends in the eastern Karoo have determined that rainfall amount has increased and seasonal shifts have occurred, particularly during the last 30 years (Du Toit & O'Connor, 2014; Harmse et al., 2020). Speculations were made that these rainfall trends were spatially extensive across the biome boundary and thus responsible for driving the increase in grass cover. Yet this hypothesis had not been formally investigated until now. Furthermore, other climate variables that are also important drivers of vegetation dynamics (e.g., temperature, evaporation, and wind) have been excluded from studies of long-term vegetation change in the eastern Karoo. Previous studies have also only alluded to the role of grazing as an important driver of these extensive changes, but few have provided data for this.

The aim of this thesis, therefore, was to assess the nature and extent of long-term vegetation changes in the eastern Karoo within the context of long-term climate trends and changes in land use. A key objective of the thesis was to determine the direction of vegetation, climate, and land use changes across the Nama-Karoo-Grassland biome boundary and the potential implications of these changes for ecosystem processes and services. Identifying the spatial extent of these changes required an appropriate number and spread of sites across the rainfall gradient that also captured change in each of the major topographical landforms and vegetation units of the region. Therefore, the spatiotemporal extent of change examined in this thesis is more comprehensive than has previously been assessed. The findings have provided novel insights into long-term change in this region of the Karoo making a significant contribution to the existing knowledge on dryland degradation and vegetation shifts in South Africa.

6.2. Analytical approaches to address the problem

An integrated theoretical framework acknowledges that the heterogeneous nature of vegetation dynamics in response to abiotic and biotic drivers varies considerably over multiple scales of space and time (Briske et al., 2020). Therefore, this requires an operational framework focused on integrating long-term, cross-scale observational studies using a variety of methodological and statistical approaches (Potts et al., 2015b). Studies of long-term vegetation change that represent multiple spatial and temporal scales, and which integrates a variety of historical records and methodological approaches, can aid in providing suitably comprehensive broad-scale interpretations of change. The thesis was, thus, framed within this theoretical-operational framework.

To address the aim of the thesis the following broad approaches were undertaken:

i) an analysis of long-term climate trends (Chapter 3),
ii) the estimation of vegetation change using vegetation survey data (Chapter 4) and repeated landscape photographs (Chapter 5), and
iii) an analysis of supporting information on land uses, livestock trends and local perceptions (Chapter 2).

An analysis of climate trends in the eastern Karoo was undertaken to describe the long-term trends in rainfall, temperature, wind speed, A-Pan evaporation, and evapotranspiration (ET). The climate time series were subjected to trend analyses and the resultant trends (negative and positive) were mapped across the study area to determine their spatial distributions. This chapter also included an analysis of long-term drought frequency, intensity and duration using the Standardised Precipitation Index to describe the major wet and dry phases of the climate record.

Estimating vegetation change focused primarily on examining the changes in growth forms, species composition, the relative dominance of grasses and dwarf shrubs, as well as the changes in rangeland condition and grazing capacity, within the context of the climate and land use trends. Studies that assess long-term vegetation change often rely on the availability of repeatable historical data sources. A number of historical vegetation surveys with accompanying landscape photographs collected by Dr. Piet Roux in the eastern Karoo during the 1960s provided an ideal opportunity for repetition and comparison. Vegetation change was examined at the spatial scales of vegetation units, landforms and biomes represented across the rainfall gradient of the study area.

Lastly, due to the general poor quality and/or lack of up-to-date data on livestock stocking rates in the Karoo, the long-term trends of land use changes have only been alluded to in previous studies of this nature. In order to alleviate some of the speculations of the role of grazing in driving these broad-scale vegetation changes, semi-structured interviews with landowners and managers were conducted to obtain local perceptions of the historical and present land use, vegetation, and climatic changes for the eastern Karoo. Local perceptions of the various social challenges that farmers presently face further enriched the interpretations of vegetation change by shedding light on the current social-ecological system of the eastern Karoo. These local-level qualitative data were paired with magisterial district-level livestock census data to provide some idea of the general trends in livestock numbers for the region.

The objective of this chapter is to synthesise the findings from each of the data chapters in relation to each other and the broader context of change in the eastern Karoo. This synthesis includes a set of conceptual models adapted to best illustrate the long-term ecological transitions and thresholds of vegetation dynamics specific to this semiarid biome boundary in South Africa. Lastly, the implications of these findings for semiarid rangeland research, management and conservation are discussed, concluding with the study limitations and future research directions of the field.

6.3. Climatic drivers of change

Rainfall in the eastern Karoo is characterised by fluctuations between wet (above-average rainfall) and dry (below-average) phases which appear to span over 50-70 years each. These wet-dry phases contextualise the rainfall conditions of the eastern Karoo from a multi-decadal scale offering a new perspective that has led to greater understanding of the role of long-term rainfall patterns in influencing vegetation change. Although the rainfall records collectively only date back to the late 1800s, enough data were available to construct the past rainfall conditions. The late 1800s and the most recent half century (1970-2015) were characterised by wet conditions, with the middle period (1902-1970) defined by dry conditions. This middle dry phase completes an important piece of the historical picture of climate-driven land degradation, at least in part for the eastern Karoo, because the narrative of 20th century land degradation in South Africa (Acocks, 1953) has largely emphasised the influence of livestock overgrazing with limited understanding of the underlying role of long-term rainfall patterns.

Trends of increasing annual rainfall over Africa and southern Africa have been observed in recent decades (Nicholson et al., 2018). This, as well as a seasonal shift to earlier season rains, has also been identified locally (Du Toit & O'Connor, 2014, 2016), while trends of increased annual rainfall have been identified for the Upper Karoo bioregion northwest of the eastern Karoo (Harmse et al., 2020). The rainfall trends, however, had yet to be determined across the rainfall gradient of the biome boundary to test the assumptions of a rainfall-driven grassland expansion. Novel findings obtained from this thesis suggest that a directional increase in annual rainfall is evident along the Nama-Karoo extent of the gradient which can be described by a significant seasonal shift towards earlier summer rains between October and December. However, a directional decrease in annual rainfall is evident along the Grassland extent of the gradient and is described by a directional decrease in later summer rains between January and March. Spatially variable positive trends in winter rainfall across the gradient suggest that some parts of the study area have experienced an earlier start to the rainfall season, and may also account for the observed local increases in shrub cover in those areas.

Regional warming since the 1970s was also evident from the temperature record of the eastern Karoo, with particular emphasis falling on greater extremes in average minimum and maximum temperatures. Warming is more pronounced in the early summer months in conjunction with the increase in early season rainfall. Due to the general scarcity of long-term temperature records in South Africa, these findings have begun to fill a crucial gap in our understanding of regional microclimate trends for the eastern Karoo. Patterns of global terrestrial stilling, or declining wind speeds, have been reported since the 1980s (McVicar et al., 2012). This phenomenon has not received much attention in ecological studies in South Africa, barring those by Eamus & Palmer (2008) and Hoffman et al. (2011). In spite of this, the directional decreases in wind speed determined over the eastern Karoo supports earlier suggestions that consistent large-scale changes in atmospheric circulation patterns over South Africa have led to regional terrestrial stilling in parts of the country (Hoffman et al., 2011; Nchaba et al., 2017). These negative trends are suggested to have driven the concomitant negative trends in A-Pan evaporation identified because wind is an important driver of surface evaporation (McVicar et al., 2012). Indistinct potential ET trends over the study area, however, produces uncertainty regarding the quality and reliability of ET data recorded by weather stations, as well as the mechanisms operating within the complementary relationship between potential and actual evaporation. Emphasis here should be placed on improving and maintaining infrastructure and continuing long-term climate observations.

The climate analysis conducted for the thesis is the first to have identified the long-term trends of several climate variables that each influence the change in vegetation along the environmental gradient. The findings, thus, make significant contributions towards understanding and appreciating the role of long-term climate observation in the eastern Karoo. The analytical approach also dispels the various speculations and local perceptions of climatic changes, particularly by highlighting the highly variable and complex rainfall patterns found across multiple temporal and spatial scales. The findings also help to differentiate between climate change and natural climatic variation by shedding light on the multi-decadal natural variation of rainfall conditions of the region (Du Toit & O'Connor, 2014, 2016). Local perceptions of climate change are often limited by the timeframe of one's memory or ability to analyse a rainfall record. Therefore, the perceptions by farmers generally reflected climatic changes of the most recent 5-10 years due to the immediate impacts of rainfall on available forage for livestock. For example, farmers tended to over-emphasise the recent drought that started around 2015, but few were able to identify the longer-term trend of increased annual rainfall unless record-keeping had been personally maintained and studied. Although landowners did display some understanding that a seasonal shift in rainfall had occurred, their responses differed substantially with respect to the exact timing of rainfall and the start of this trend. The formal analysis of seasonal trends in this study alleviated these incongruences and provided necessary insight into understanding the relative shift between growth forms across the region.

6.4. Biome and landscape vegetation change in the eastern Karoo since the 1960s

Growth forms and species composition

The dominant growth forms (grasses and dwarf shrubs) of the biome boundary are best understood and described along an environmental gradient that extends in a south-west to a north-easterly direction. The south-western end is dominated by dwarf woody and spiny shrubs that are gradually replaced by grasses towards the north-eastern end of the gradient. The relative proportions, or dominance, of grasses and dwarf shrubs also fluctuate over time and these vary in space in response to local climate and land use patterns described above.

Since the 1960s, estimates of total vegetation cover obtained from point intercept vegetation surveys and repeat photographs indicated significant increases. Increasing perennial grass cover, in particular, has been maintained since it was first observed in 1990 (Hoffman & Cowling, 1990) and again in 2009 (Masubelele et al., 2013, 2015a). Dwarf shrub cover has also increased across the biome transition since the 1960s as determined by the vegetation surveys, but this increase is predominantly evident more so at Karoo sites than at the mesic and high altitude Escarpment and Grassland sites. The photographic comparisons, by contrast, indicated a decrease in dwarf shrub cover at plains sites in the Nama-Karoo biome and increases at plains and hillslopes sites in the Grassland biome. The differences in dwarf shrub cover trends between vegetation survey and photograph comparisons are likely to have occurred because the tall canopies of perennial grasses on the Nama-Karoo plains obscured the visibility of general shrub cover in the photographs, thus leading to an under-estimation of shrub cover. Vegetation sampling, in this case, provided a more accurate representation of growth form cover as estimated in the field. The relative dominance of grasses versus dwarf shrubs calculated from both methods, however, provided evidence of shifts from shrub-dominant to more grass-dominant vegetation states as organised along the rainfall gradient of the biome boundary over time. It should be emphasised that shifts between states in this region are more likely to be occurring along a continuum of varying levels of shrubbiness or grassiness in response grazing and/or rainfall over many decades. However, the nature of intergradation of grasses and shrubs between these biomes (i.e., sharp and abrupt, or gradual) remains to be a gap in this research. According to these observed changes, and as depicted by Milton & Hoffman's (1994) state-and-transition model, rangelands in the study area have transitioned from degraded to less degraded states. The general state of current vegetation comprises of "perennial grasses in a matrix of dwarf shrubs" (Milton & Hoffman, 1994). The unexpected increase in palatable dwarf shrub cover determined from the vegetation surveys, emphasises, however, how little we understand about grass-shrub competitive interactions at increasing spatial scales from the levels of plant to communities to landscapes across the rainfall gradient (Hoffman et al., 1990; Pierce et al., 2019; Smith, 2001; Smith et al., 2005).

In terms of species composition, vegetation has remained relatively stable over time within the three main vegetation units of Karoo, Escarpment and Grassland. Local climate-fire-grazing interactions drives the structure of these plant communities. Where sites underwent shifts towards shrub-dominant states and thus 'shifted' across ecotonal boundaries, shorter-term local land use change, for example fire suppression, was responsible for promoting shrubland dominance. Recently surveyed plant communities within the Karoo, Escarpment and Grassland vegetation units, however, resembled species compositions similar to those of the 1960s indicating that compositional stability and integrity has still been maintained (Masubelele et al., 2015b) despite the shift in growth forms. These findings provide evidence of a biome-level growth form shift, while landscape-level integrity and stability of species composition within plant has been maintained. This structural shift between growth forms is spatially aligned with the distribution of positive trends in annual rainfall, early season rainfall and temperature.

Although this structural shift is defined by growth form shifts and not by species shifts, it is predicted that persisting grass-dominance could promote increased fire frequency resulting in irreversible structural and compositional shifts at both the landscape and biome scales (D'Antonio & Vitousek, 1992; Rahlao et al., 2009; Van der Merwe et al., 2016). Fire is shown to negatively impact dwarf shrub communities and re-enforce grass dominance (Du Toit et al., 2015; Kraaij et al., 2017; Rahlao et al., 2009), which is evident in the middle zone of the rainfall gradient where rangelands receive between 250 and 420 mm of rainfall per year. There remain gaps, however, in our understanding of the flammability of growth forms and/or species, and of the interactions between and impacts of fire and drought on dwarf shrub species composition and structure within the context of the current vegetation and rainfall trends. Increasing fire and drought frequency could have important ramifications for the condition of these rangelands, such as accelerating rangeland degradation towards grassland-dominant patches that have significantly reduced shrubland diversity and cover (Bestelmeyer et al., 2015). Degraded rangelands in these parts would alter the provision of major ecosystem services, such as the provision of forage for livestock production, and in turn lead to alterations in land uses and changes in livestock animals (Bestelmeyer et al., 2006). Therefore, while the shift to grass dominance in the eastern Karoo is evidently climate-driven, and refutes Acocks' 'expanding Karoo' hypothesis (Acocks, 1953), concerns of increasing drought and fire frequency puts these environments at greater risk of becoming irreversibly degraded over time.

Rangeland condition

South-western US rangelands have experienced invading non-native grass species associated with altered fire regimes (D'Antonio & Vitousek, 1992; Fusco et al., 2019), as well as ongoing shrubland encroachment owing to a multitude of historical and present livestock overgrazing, drought, soil erosion and nutrient redistribution (e.g., Bestelmeyer et al., 2018; Buffington & Herbel, 1965; Hastings & Turner, 1966). In contrast, the persistent grass dominance in the eastern Karoo is comprised of native perennial and annual species and an increase in palatable dwarf shrub species. These trends, coupled with increasing vegetation cover, have ultimately led to an improvement in grazing capacities as calculated from vegetation surveys across the rainfall gradient. This, in turn, represents a greater foraging value of the veld for grazing livestock. Local perceptions shared by farmers in the study area reflected an awareness that climax grasses had increased in cover in the region and that general veld condition has improved. Interestingly though, they attributed these changes in the vegetation less to rainfall trends and more to significantly reduced livestock numbers compared to the past, as well as to improved grazing systems (i.e., rotational grazing) and significantly longer periods of rest from grazing. Several also noted that although grazing densities may differ among systems, the length of stay inside paddocks has generally become shorter and total livestock numbers are still comparatively much lower than historically, particularly during drier years. Although not measured for the thesis, the general increase in vegetation cover is also expected to have positively influenced ecosystem processes (e.g., soil water retention and reduced erosion), which aids in the restoration of ecosystem services (Scott et al., 2014).

6.5. Land use trends and drivers of change

Sheep agriculture has been the dominant land use in the eastern Karoo since European settlement in the late 18th century. Agricultural census data indicated that the number of sheep across the magisterial districts in the eastern Karoo have steadily declined since 1911. A recent study of land use and land cover change throughout the Nama-Karoo biome also indicated a significant reduction in livestock numbers, particularly of sheep, goats, and equines (Hoffman et al., 2018). The local perceptions that emerged in the thesis also supported this trend of declining livestock densities as all farmers agreed that they carried far fewer livestock than did previous generations. Widely held perceptions supported previous suggestions by Nel & Hill (2008), Atkinson (2009) and Hoffman et al. (1999, 2018) that a number of important socioeconomic and agricultural factors are responsible for the reduced sheep numbers and not necessarily declining rangeland productivity (Dean & Macdonald, 1994). Their perceptions encapsulated positive factors, specifically the adoption of more ‘veld-friendly’ grazing management practices (i.e., rotational grazing and holistic resource management), significantly longer periods of rest (6-18 months) from grazing to allow vegetation to recover and to set seed and the diversification of land use types and animals as additional income sources. However, several negative factors were also highlighted as being responsible for the overall decline in sheep numbers, such as frequently long and intense droughts, increasing natural fires, livestock losses to theft and vermin, farm abandonment and a general lack of government support over the last three decades.

A relatively recent trend of the integration of ‘lifestyle’ game ranching into livestock farming has become a more common practice in the Karoo (Walker et al., 2018) and local perceptions gathered from farmers have also alluded to this trend in the eastern Karoo. Although current formal and informal protected areas in the eastern Karoo would be able to provide data on the trend in game numbers over time within those areas, the relative trend in game ranching on commercial livestock farms has not been reported for the region. Thus, the extent to which wildlife numbers have increased in the region remains unknown and could add significantly to the official stocking rate data.

6.6. Contribution to the conceptual framework of dryland rangeland research

A combination of the equilibrium, non-equilibrium and resilience theories of rangeland science provide a framework to understand semiarid vegetation dynamics in the eastern Karoo. The findings of this thesis can contribute to this theoretical framework by modifying and improving the existing conceptual ecological models of the eastern Karoo.

The results emphasise the importance of the rainfall-grazing threshold, within which fire will potentially become an important driver of vegetation on account of the rainfall-driven increase in grass fuel loads, which operates to moderate shifts between alternative vegetation states at the levels of the ecological site, landscape, and biome boundary. The state-and-transition model for the eastern Karoo (Milton & Hoffman, 1994) and by Stringham et al. (2001) have provided a basic foundation from which to build upon using the findings obtained from this thesis (**Figures 6.1**). We already know from previous studies, that an altered grazing regime consisting of high livestock densities and heavy and/or continuous grazing can induce a shift from a grassland to shrubland state (1) dominated by unpalatable species and, when exacerbated by drought, can lead to significantly reduced cover and eroded soils (4) (**Figure 6.2**; Acocks, 1953; Milton & Hoffman, 1994). The long-term rainfall trends determined in Chapter 3 confirms the role of increased annual rainfall, and specifically increased early summer rainfall, on causing a vegetation shift from a shrubbier to grassier state (2) that is dominated by perennial grasses in a matrix of shrubs. This shift is evident at multiple spatial scales of individual sites, vegetation units, landforms and across the rainfall gradient of the biome boundary (**Figure 6.2 and 6.3**). Increased vegetation cover is expected to influence ecosystem processes through soil stabilization, soil infiltration, and water retention (Belnap, 1995; Eldridge et al., 2002), water use efficiency, carbon storage, and nitrogen deposition (February et al., 2011, 2020; Zhang et al., 2020).

Stemming from an altered rainfall regime, is the prediction that the fire regime will be altered due to the accumulation of grass fuel loads, leading to increased fire frequency. This alteration of the fire regime may lead to two different outcomes. First, under persistent conditions of above-average rainfall, fire could induce a positive feedback of grass regrowth and re-enforce grass dominance.

Second, following a post-fire grass-dominant state and a subsequent shift from a high rainfall to a low rainfall regime (i.e., prolonged drought) the dieback of grasses may occur and fire will cease, and drought will become the dominant driver of an irreversible shift from a high cover, grassland state to an eroded state of greatly reduced vegetation cover and altered species composition (3). The predictions of increasing drought and fire frequency places these environments at greater risk of becoming structurally and compositionally degraded over time. Fire, drought and grazing thresholds that accelerate degradation are irreversible and such environments require active rehabilitation and restoration measures (5) to return ecosystem processes, productivity, services, and species composition to a pre-disturbance state (Milton & Dean, 2015). However, the opportunity to investigate the true impacts of drought in a post-fire vegetation state in the eastern Karoo is yet to present itself, placing greater value and emphasis on experimentally designing and testing vegetation responses to these drivers.

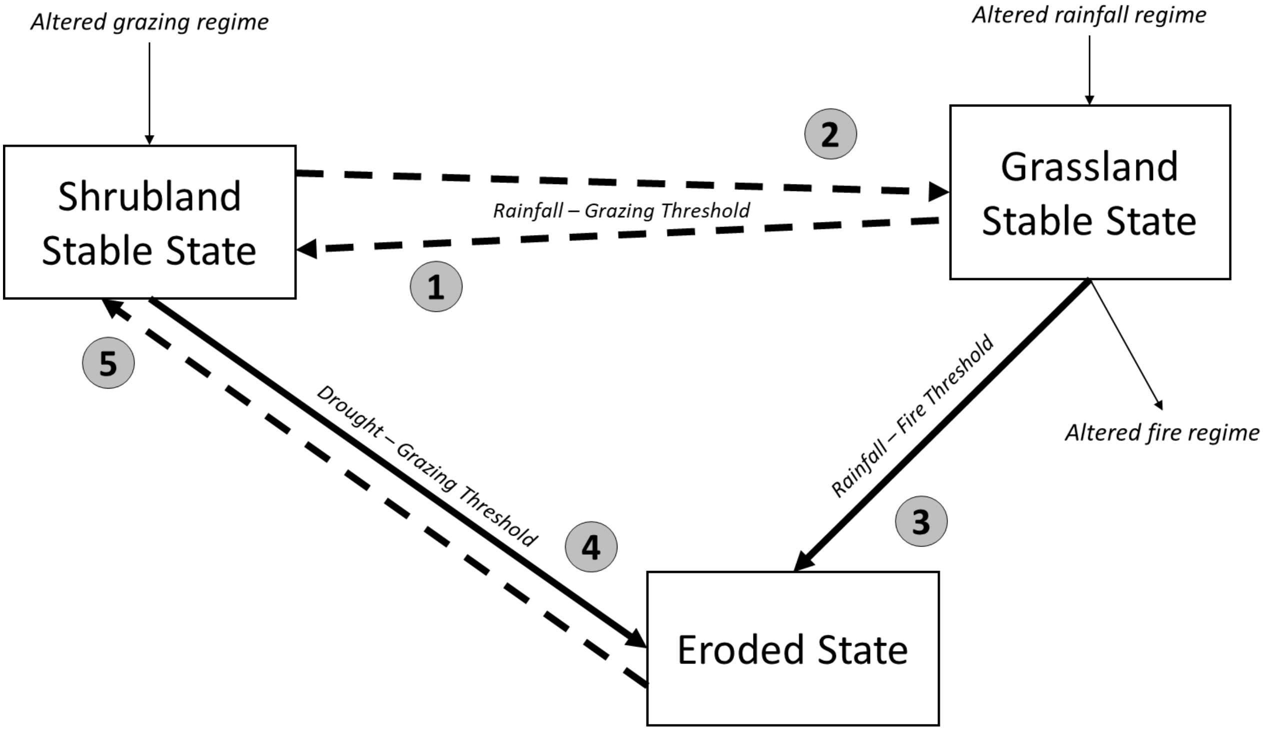

Figure 6.1 A conceptual model that incorporates aspects of the 'state-and-transition' management model for the eastern Karoo. Arrows indicate the directions of transitions, which are triggered by significant changes in the rainfall, grazing or fire regimes. Thresholds maintain transitions between states depending on the extent and duration of the altered regime. Reversible transitions (dashed lines) are caused by a change in the dominant regime, for example decreasing annual rainfall. Irreversible transitions (solid line) require active intervention to rehabilitate a degrading site. The numbers refer to the 1) historical and 2) present trends of vegetation change in the eastern Karoo, 3) a future scenario of rangeland degradation that has not previously been considered but which is expected to occur under persisting wet conditions, followed by increased fire frequency (co-occurring drought will only exacerbate degradation), 4) prolonged drought and continued grazing will lead to irreversible erosion and loss of ecosystem function, a condition that has persisted on rangelands in the arid western Karoo, but 5) ecological restoration might alleviate severe degradation. Modified from Stringham et al. (2001) and based upon Milton & Hoffman's (1994) model for the eastern Karoo.

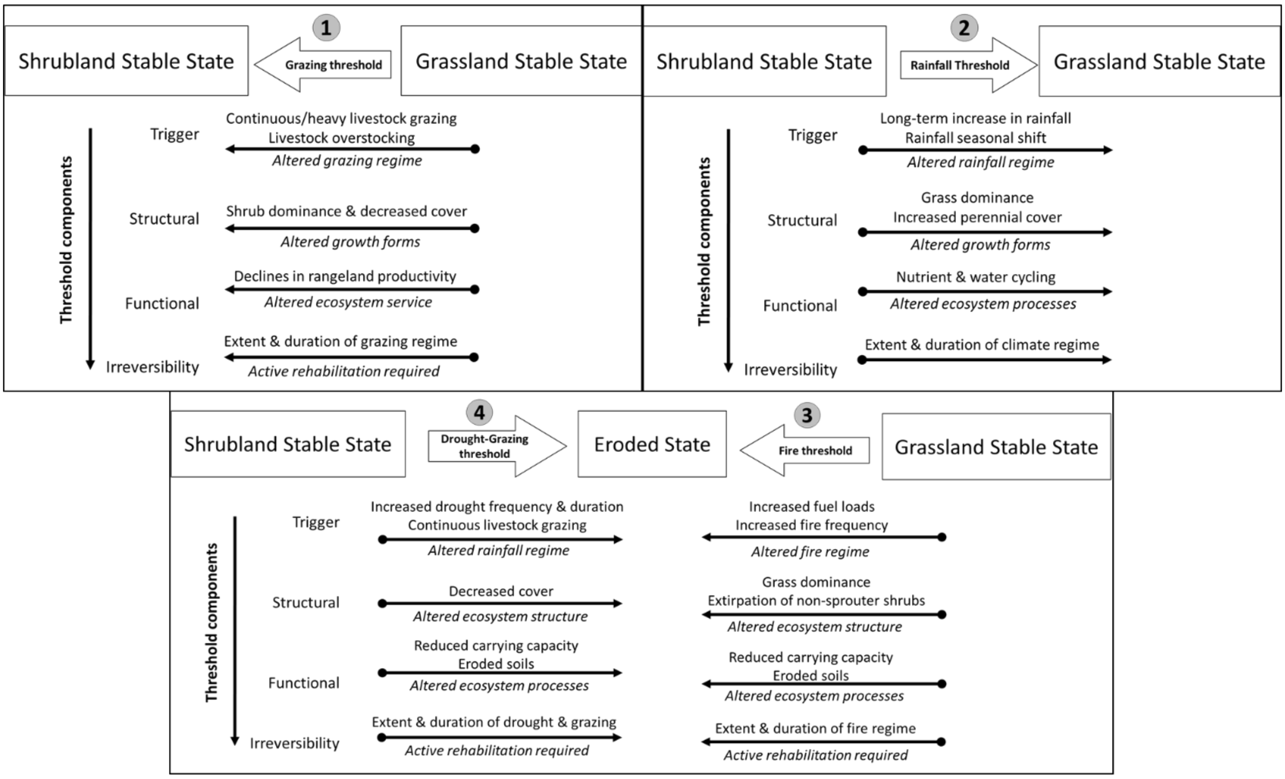

Figure 6.2 An extension of the state-and-transition model detailing the specific characteristics of the threshold components observed at the scales of the ecological site and/or landforms under different scenarios of altered climate, grazing and fire regimes. The numbers correspond to those described in Figure 6.1. and the figure follows the logic of ecological thresholds illustrated by Briske et al. (2005b). These ideas are formulated with structural changes between growth forms (grasses and shrubs) in mind and is not indicative of compositional changes, observed under different scenarios. These scenarios are simplistic and unidirectional and so do not take into account the sequence or timing of various interacting thresholds and the combination of outcomes that each might lead to.

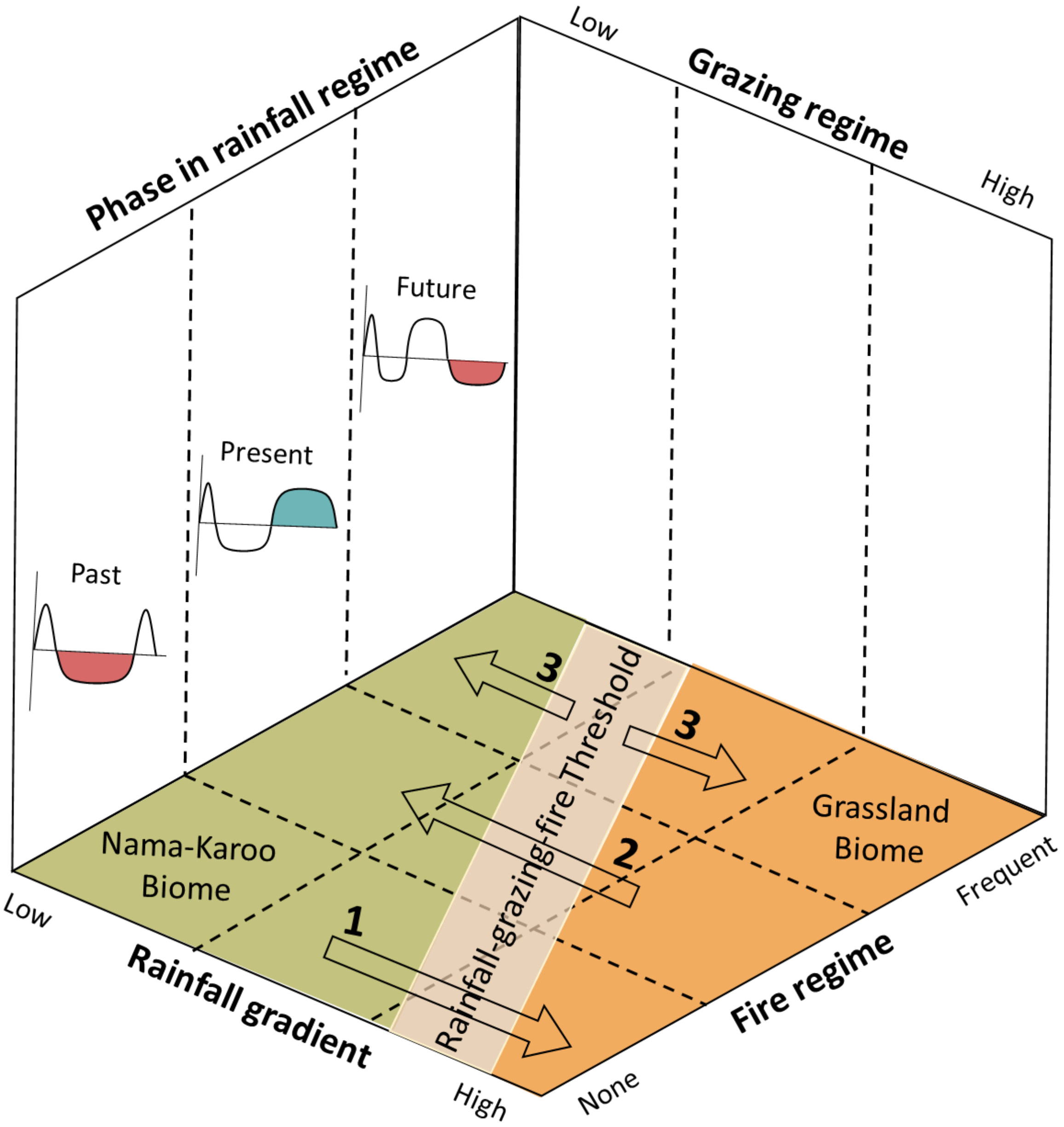

Figure 6.3 The conceptual model developed for the Nama-Karoo-Grassland biome transition illustrating the ecological thresholds of the state transitions of Figures 6.1. and 6.2. These dynamic state transitions, occurring at varying spatial scales, trigger a number of structural and functional changes in the ecosystem which leads to either the encroachment of shrublands or grasslands depending on the dominant altered regime that is driving the change. Arrows indicate the direction of the compounded state transitions (measured by the relative dominance of grasses and shrubs) organised along the rainfall gradient of the eastern Karoo. The numbers refer to the 1) historical and 2) present trends of vegetation change in the eastern Karoo, as well as 3) the future scenario of rangeland degradation. The conceptual framework is based on the findings from this thesis and informed by previous studies (Hoffman & Cowling, 1990; Masubelele et al., 2014; O'Connor & Roux, 1995) and is a modification of models presented by Milton & Hoffman (1994) and Briske et al. (2005).

6.7. Implications, limitations, and knowledge gaps

Implications

This study has enabled an understanding of how grasses and dwarf shrubs, the two dominant growth forms of vegetation structure in the eastern Karoo, have responded to the changes in climate drivers over the last 70 years. It has shown that shifts in biomes that have occurred is defined by a structural shift in growth form abundance and not by a change in species composition. While species composition has remained relatively stable between the biomes, the structural shift is defined by an overall improvement in species composition and cover. This is reflected by an increase in grazing capacity, which implies that there has been a significant recovery of rangelands from 20th century drought and livestock overgrazing. While these changes are positive, the shift from a shrub to grass-dominated system prompts significant concern about the future risks of increased fire frequency, particularly for the lower-lying plains where fire disturbance is not common.

Complex interacting environmental and disturbance factors operate at multiple spatial and temporal scales to influence vegetation dynamics and control biome distributions (Gosz, 1993; Gosz & Sharpe, 1989; Moncrieff et al., 2015; Potts et al., 2015a). Spatially non-uniform vegetation shifts are also expected across multiple scales across the eastern Karoo. For example, Du Toit et al. (2018) reported that dwarf shrub cover determined by vegetation sampling has decreased at one site, but this pattern contradicts those found in this thesis of increasing dwarf shrub cover at multiple sites across the rainfall gradient. Spatially non-uniform grassland-shrubland shifts have also been documented on the rangelands of south-eastern Arizona (Allington & Valone, 2011; Bestelmeyer et al., 2018; McIntosh et al., 2019). Therefore, grazing management systems that are uniquely adapted to local climate (annual and seasonal rainfall), edaphic and vegetation conditions for relevant landforms will help farmers to conserve and maintain species composition and veld condition at various levels. In scenarios where unpalatable shrublands are increasing, appropriate mechanical removal and/or planned burns might be necessary to maintain rangeland productivity for cattle and sheep, such as where Fynbos and Renosterveld species are unique to the vegetation distributed at the higher altitudes of the Escarpment. The trend of increasing grass cover, particularly for the region where rainfall seasonality has undergone shifts, has negative implications for the stability and integrity of species composition due to the risk of increasing fire frequency (Du Toit et al., 2015).

Limitations

Just as the newer techniques of satellite remote sensing are limited by the accuracy of validation points and ground-truth observations, studies like this thesis have their own biases and shortcomings. Studies of this nature, that is, those which rely upon historical data sources, often have only two time-steps of observations from which to interpret long-term change (Stuble et al., 2021). Repeating historical landscape photographs or vegetation surveys provide valuable opportunities to compare between time-steps but should be done cautiously and with as much supporting climate and land use data as possible. Although it has been argued in the literature, for example, that repeat photography, if not used systematically, can introduce biases into the interpretations around vegetation change (Knight & Fitchett, 2020; Pickard, 2002), historical landscape photographs still provide an invaluable baseline (sometime the only baseline) of past environmental conditions with which to compare over time (Hoffman et al., 2020). Photographs naturally only capture the changes in a small area and, hence, caution should be used when extrapolating to greater spatial scales (Pickard, 2002) particularly where there is an insufficient number of data points and repetitions over time (Hoffman et al., 2019). However, the value in using two sampling techniques, i.e., vegetation surveys and repeat photos, is that each captures a unique set of information that can be used together to formulate an interpretation of species-level and growth form changes for one or more landform units. Landowner involvement and knowledge can provide further understanding of site-specific changes in land use and climate. Hoffman et al. (2020) point out that historical photographs are rarely repeated, as was the case for the majority of the photos repeated for this thesis, and therefore provide only two samples in time from which to compare. Snapshot resampling is a common feature of long-term observational studies (Stuble et al., 2021), however with enough time and regular repetitions, these studies have the potential to provide a useful interpretation of global change impacts.

The logistical challenges of relocating historical vegetation plots and photographs are not trivial. Finding the exact location of previous sites is time-consuming and often limited by a lack of site-level metadata, such as accurate GPS locations and detailed information about the plot placement. Old roads may no longer be accessible or in good condition, access to remote sites is difficult to reach by foot and on-site permission may not always be granted by landowners. These factors can all influence the final sample size of sites that is used in a study of this spatial breadth, and therefore, can result in a limited interpretation of vegetation change for larger regions. However, in spite of these challenges the combined number of repeated photos and vegetation surveys used in the thesis is the most obtained for the eastern Karoo, and therefore improves our current understanding of broader scale changes.

Future directions

An unresolved item of research for the eastern Karoo is the study of vegetation responses in relation to edaphic properties across the region. Specifically, the thesis has highlighted the gaps in understanding how perennial grasses and dwarf shrubs facilitate and/or compete for resources and space within different contexts of soil, climate, fire, and grazing across the length of the biome transition (Pierce et al., 2019). The nature of the intergradation of grasses and shrubs at varying spatial scales across the eastern Karoo remains largely unresolved as to whether or not the changes described in this thesis are a normal response, and whether climate change is having an unprecedented impact on structural biome shifting in the region. For example, we do not know the relative carbon sequestration value and water use efficiencies of various grasses and dwarf shrubs, how life history traits differentiate niche separation and, therefore, how growth forms impact ecosystem processes, functions, and services at broader scales across the rainfall gradient. The combined effect of rising CO_2 and warming has been found to enhance productivity and soil water content in semiarid grasslands in America (Morgan et al., 2011). While these relationships have not been experimentally determined in the eastern Karoo, the findings from this thesis of increasing grass and dwarf shrub cover seem to suggest that the vegetation response to increasing temperature and CO_2 might be similar. However, basic applied research that investigates the effect of different species of shrubs on grasses would be an initial step towards enhancing the current state-and-transition model for the eastern Karoo, as well as to stimulate further research into understanding the relationships between ecosystem structure (grassland vs. shrubland-dominant) and function (e.g., ecohydrology) and how these respond under different climate change scenarios (Scott et al., 2014).

Another avenue of research that would be a worthwhile undertaking is the design and implementation of a long-term in-situ rainfall-fire-grazing experiment situated in the eastern Karoo, e.g. at Grootfontein in Middelburg-EC. A randomized block design containing treatments of combinations of rainfall (rain-out shelters), fire (controlled burns) and grazing (clipping experiments) applied in high and low concentrations, after which vegetation responses are systematically measured, may uncover valuable insights into the differences between structural and functional biome responses. Such an experiment could be expanded to multiple sites along a transect that spans the rainfall gradient in order to capture the varying responses of species and growth forms along the rainfall-edaphic gradient of the eastern Karoo.

The climate analysis contributed new insights into the long-term trends of different climate variables but has raised various questions around the interactions of seasonal temperature and rainfall, specifically regarding how increased rainfall and temperature at certain times of the year affects differences in growth form abundance. While similar trends of increasing annual rainfall have been reported further west of the eastern Karoo (Harmse et al., 2020), there is uncertainty about how far west increasing grass abundance extends and whether other environmental drivers (e.g. underlying geology and soil) are stronger limiting factors of grass abundance. There is also considerable ambiguity around the trends in actual evaporation determined from an A-Pan, and potential evapotranspiration derived from an algorithm in the region, especially in terms of how these are related and how wind speed, temperature and rainfall influence these patterns. The continued monitoring of climate, as well as increasing the number of climate stations in the Karoo, is of utmost importance for long-term environmental studies.

There remain several gaps in understanding the combined impacts of fire, drought, and rainfall on Karoo dwarf shrublands barring the more recent studies that have emerged in areas adjacent to the eastern Karoo (Du Toit et al., 2015; Kraaij et al., 2017; Rahlao et al., 2009; Van der Merwe et al., 2016; Van der Merwe & Van Rooyen, 2011). Previous studies have tried to model the relative impacts of fire and climate on biome distributions in South Africa (Bond et al., 2003; Moncrieff et al., 2015) but the effectiveness of these models has largely been limited to tree-dominant biomes. As a result, they have under-estimated the impacts of increased rainfall and positive feedbacks of fire on eastern Karoo grasslands. This thesis, therefore, contributes new and important knowledge about the growth form responses to climate, which can inform future studies that model biome distributions and rangeland degradation in South Africa. However, biome-level models will also benefit from specific studies that identify trait-based responses to fire (i.e., flammability) within a suite of grass and dwarf shrub species in the eastern Karoo (e.g., Calitz et al., 2015). Such studies may provide greater understanding of the factors that influence flammability in species and how these might change under conditions of extended drought and high temperature. Experimental studies that examine the relative influences of multiple drivers of growth form characteristics may also be useful in separating annual and seasonal differences between drivers. A study by Knapp et al. (2020), for example, has recently disentangled the important seasonal rainfall-temperature relationships that drive C_3-C_4 grass abundance in the Great Plains of America through a series of experiments. Another study by Gherardi & Sala (2015), who identified important differences between grass and shrub productivity in response to experimental increases in interannual variability of rainfall in the south-western US, gives important clues to the types of vegetation dynamics that can be tested in future experiments in the eastern Karoo.

While it is challenging to separate the effects of climate from land use on rangeland vegetation, small-scale grazing experiments have provided important insights on the influence of grazing treatments on vegetation dynamics (Du Toit et al., 2018; O'Connor & Roux, 1995; Roux & Vorster, 1983a). Various landscape-regional analyses using remotely sensed satellite data have also found ways around this challenge of providing estimates of land use-driven cover change (Bastin et al., 2012; Wessels et al., 2007; Xie et al., 2019). Although Hoffman et al. (2018) produced a useful assessment of land cover change for the Nama-Karoo and Succulent Karoo biomes, a similar assessment has not been attempted for the eastern Karoo and would provide new insights into land use-driven land cover changes for the region. In addition to assessing land use/land cover change in the Karoo, the value of this thesis in determining the trend of improved rangeland condition across the rainfall gradient has highlighted the need to extend long-term monitoring along broader environmental gradients in the arid and semiarid Karoo to determine the spatial extent of specific vegetation changes. An integrated approach that includes cross-scale experimental and long-term observations at multiple spatiotemporal scales across the rainfall gradient may be useful in helping to disentangle some of the questions relating to vegetation responses induced by global warming, increasing atmospheric CO_2, land use change and fire.

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Appendix A: Semi-structured interview template

Semi-structured interview questions

1. How big is the farm (in hectares)?
2. How long has the farm been owned by your family?
3. What type of grazing system is practiced on the farm? Why have you chosen these grazing strategies? Please describe the system/s used.
4. How many camps is the farm currently divided into?
5. Does each camp have its own watering point, or are points shared among camps?
6. How long have you farmed these livestock/animals? Do you plan to change breeds/races, or have you ever changed/included new breeds etc.?
7. Do you provide fodder/supplements to your animals? If yes, why, when or how often, and which types of feed are used?
8. Do you move the animals between farms? If so, what is the approximate distance between the two farms?
9. Which types of water sources are available (e.g., fountains, streams, rivers) and which types of boreholes are used (e.g., electric, windmill, solar)?
10. Do you have any knowledge of the farming management practices used on this farm in the past (i.e., as way back as the early 1900s to present?)?
11. Please describe the vegetation changes that you have witnessed taking place in the veld since you/ancestors/previous owners have farmed the land.
12. How are you able to determine if the veld is ‘healthy’ and good enough for grazing, i.e. what indicators of veld condition do you look for?
13. How has the drought impacted your ability to farm?
14. Do you keep climate records, or is there a weather station nearby?
15. Are there any other environmental factors that affect your ability to manage your livestock and the veld (e.g., fire, locusts, hail, frost)?
16. What are the most significant challenges you face as a farmer?

Appendix B: Equations and additional data for the climate analysis

Variance corrected Mann-Kendall for lag-1 serial correlation (MKVC1)

The MKVC1 test uses the following steps:

$$S = \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} sign(y_i - y_j), \qquad \text{Eq. 1}$$

where

$$sign(y_i - y_j) = \begin{cases} +1, & if \ y_i - y_j > 0 \\ 0, & if \ y_i - y_j = 0 \\ -1, & if \ y_i - y_j < 0. \end{cases} \qquad \text{Eq. 2}$$

n is the number of data points in the time series $y_1, y_2, \ldots, y_n$ and $i = 1, 2, \ldots, n-1$, and $j = 2, 3, \ldots, n$, for $j > i$. To calculate the variance of S in the case of autocorrelated data:

$$V^*(S) = var(S). \frac{n}{n_S^*} = \frac{n(n-1)(2n+5)}{18} . \frac{n}{n_S^*}, \qquad \text{Eq. 3}$$

where n / n_S^* represents a correction due to the autocorrelation in the data:

$$\frac{n}{n_S^*} = 1 + \frac{2}{n(n-1)(n-2)} \times \sum_{i=1}^{n-1} (n-i)(n-i-1)(n-i-2)\rho_S(i) \qquad \text{Eq. 4}$$

where n is the actual number of observations and $\rho_S(i)$ is the autocorrelation function of the ranks of the observations (Hamed & Rao, 1998). In so doing, the variance of S can be evaluated without requiring normalised data.

Sen's slope estimator

Sen's slope estimator was then used to compute the magnitude of the trend, that is, the slope and the intercept (Sen, 1968). A set of linear slopes is calculated as follows:

$$d(t) = Q(t) + b, \qquad \text{Eq. 5}$$

where Q is the slope. If the trend is linear, the magnitude is estimated using Sen's slope, where y_i and y_j are data points at times i and j and $j > i$ as,

$$Q_k = \frac{(y_j - y_i)}{j - i}, \qquad \text{for } k = 1, 2, \ldots, N. \qquad \text{Eq. 6}$$

The variance of Sen's slope is given by Equation 3 above. Qs, which is the median of the Q_k values, is obtained as follows:

$$Q_s = \begin{cases} Q_{\frac{N+1}{2}}, & \text{if } N \text{ is odd} \\ \dfrac{\left(Q_{\frac{N}{2}} + Q_{\frac{N+2}{2}}\right)}{2}, & \text{if } N \text{ is even} \end{cases} \qquad \text{Eq. 7}$$

The *z* test statistic indicates positive and negative values of Z for increasing and decreasing trends, respectively. If $|Z| > Z_{1-\frac{\alpha}{2}}$, the null hypothesis of no trend is rejected indicating that there is a trend present in the time series. The *z* test statistic is calculated as follows:

$$Z = \begin{cases} \dfrac{S-1}{\sqrt{V^*(S)}}, & if\ S > 0 \\ 0, & if\ S = 0 \\ \dfrac{(S+1)}{\sqrt{V^*(S)}}, & if\ S < 0 \end{cases} \qquad \text{Eq. 8}$$

Pettitt's Test for change-point detection

This approach is used to detect a single change-point in a climate series of continuous data, such as a rainfall record (Pettitt, 1979). The null hypothesis of this test predicts that *T* observations are independent and identically distributed. The alternative hypothesis suggests that a change point does exist somewhere in the series. The statistic for a two-sided test (i.e., the direction of change is not specified) is calculated as:

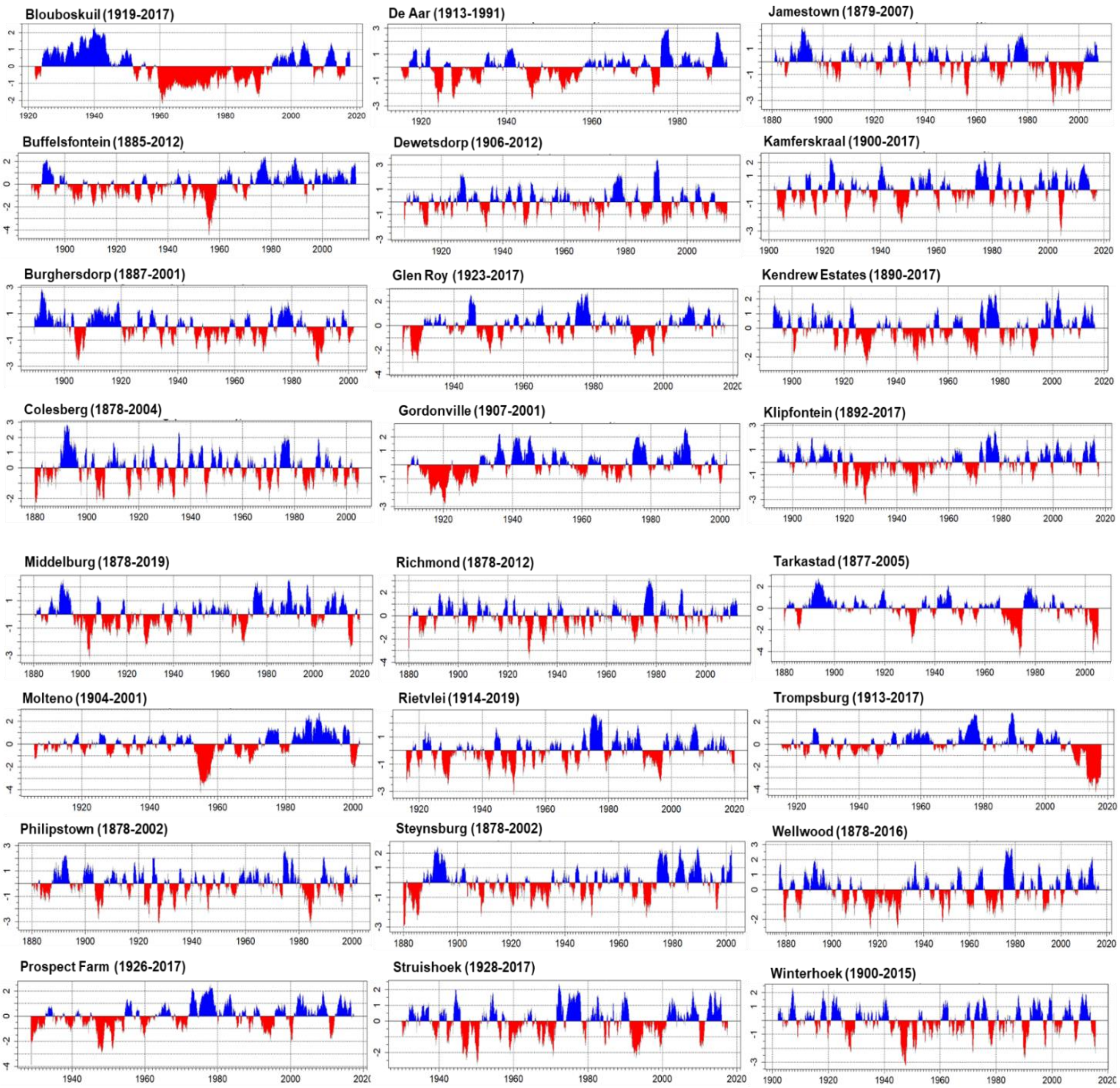
$$K_T = \max |\ U_{t,T}\ |, \qquad \text{Eq. 9}$$

where

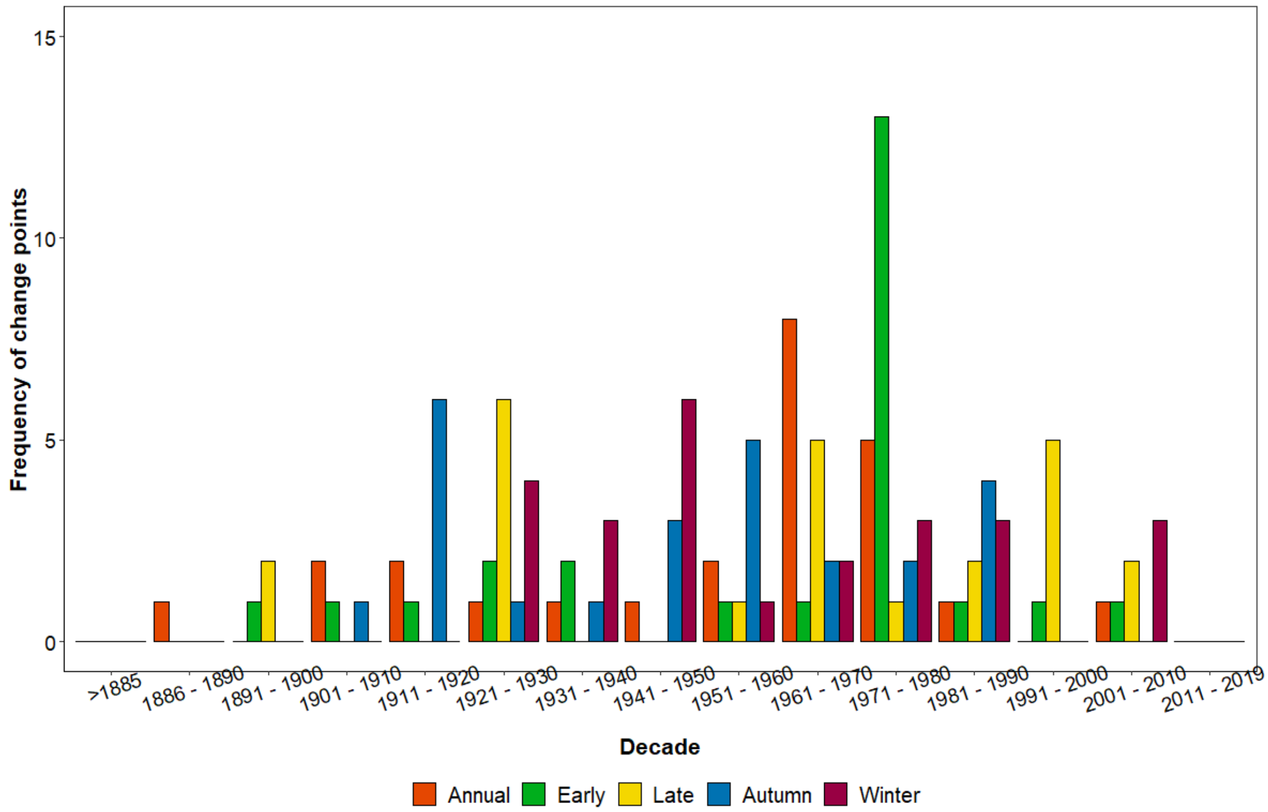
$$U_{t,T} = \sum_{i=1}^{t} \sum_{j=t+1}^{T} sgn\left(X_i - X_j\right) \qquad \text{Eq. 10}$$

K_T is where the change-point of the series is located, and this is only important where the statistic is significant for $p \leq 0.05$ as

$$p \simeq 2\ exp\left(\frac{-6K_T^2}{T^3 + T^2}\right) \qquad \text{Eq. 11}$$



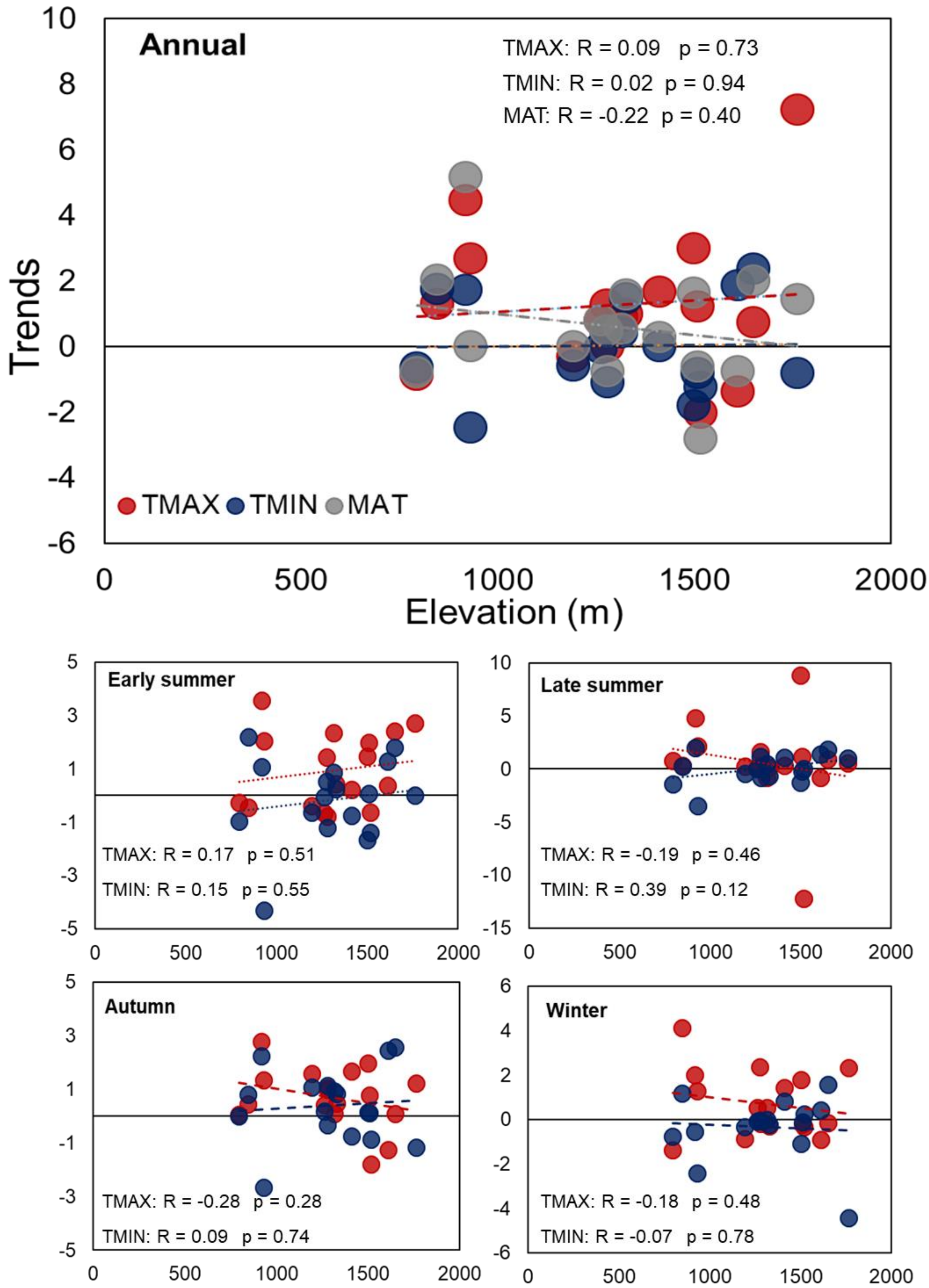
Appendix B2. The 24-month Standardised Precipitation Index (SPI) of individual rainfall time series in the study area. Gaps in time series have been removed prior to the SPI analysis, therefore time frames may not reflect the full length of the records as indicated in Table 3.2.



Appendix B3. Frequency of change points detected in 25 rainfall time series each determined by the Pettitt Test.

Appendix B4. Frequencies of change points detected in the rainfall time series of 25 locations scattered across the eastern Karoo as estimated by the Pettitt Test

Decade	Month												Total
	J	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	
≥ 1885	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1886-1890	0	0	0	0	0	0	0	1	0	0	0	0	**1**
1891-1900	2	0	2	0	1	0	0	1	1	0	1	1	**9**
1901-1910	0	0	0	0	1	1	3	2	0	0	0	4	**11**
1911-1920	3	1	0	2	0	2	1	0	3	2	5	0	**19**
1921-1930	2	5	4	3	1	3	8	1	2	1	0	1	**31**
1931-1940	1	1	7	5	2	0	0	1	1	6	3	2	**29**
1941-1950	0	2	0	3	1	2	3	7	1	2	3	2	**26**
1951-1960	1	2	1	2	1	11	4	5	6	2	1	2	**38**
1961-1970	1	5	0	3	4	3	2	2	1	2	0	5	**28**
1971-1980	1	5	7	6	2	2	0	1	5	7	9	3	**48**
1981-1990	7	2	3	1	11	0	2	1	0	0	1	2	**30**
1991-2000	6	0	1	0	0	1	0	2	0	2	1	2	**15**
2001-2010	1	2	0	0	0	0	2	1	5	0	1	1	**13**
2011-2019	0	0	0	0	0	0	0	0	0	0	0	0	**0**



Appendix B5. Relationship between temperature trends (*Z* statistic) and altitude (m) from annual and seasonal time series in the eastern Karoo for the period 1971-2019.

Appendix C: Site information and supporting multivariate analyses for the vegetation analysis

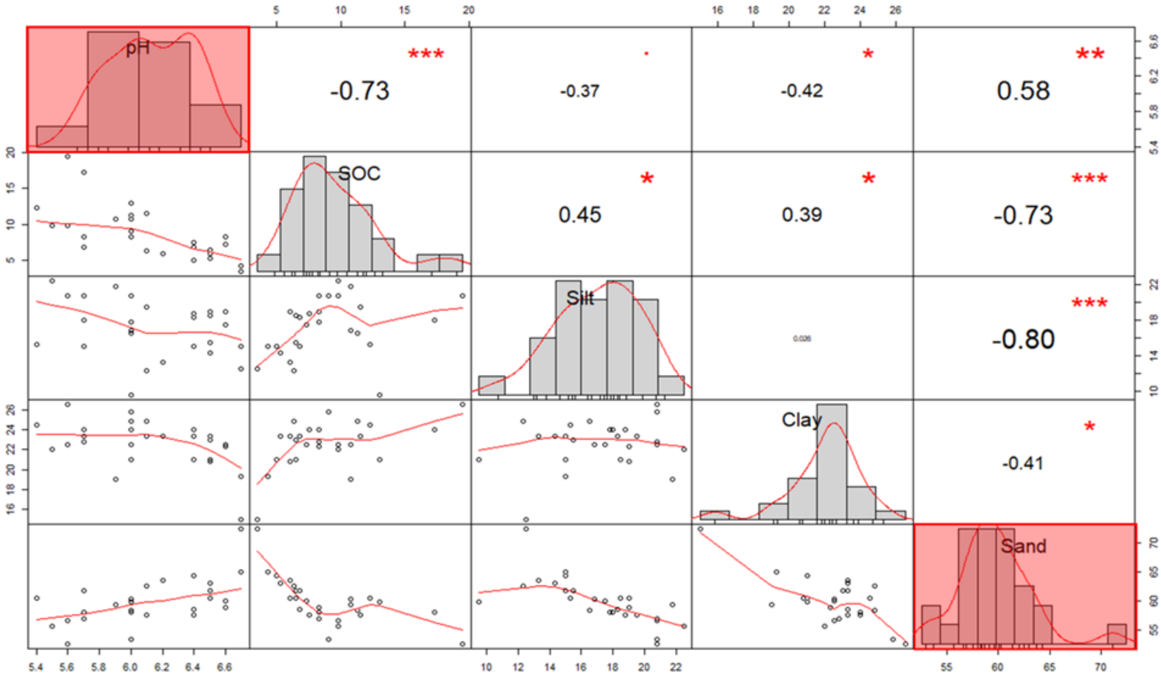
Appendix C1. Site information of sites originally surveyed by P.W. Roux and repeated by the G. Arena across the Nama-Karoo-Grassland biome boundary. Asterisk indicates sites that were resurveyed in 1989 (Hoffman & Cowling, 1990) and in 2009 (Masubelele et al., 2014)

Farm name	District Municipality	Latitude	Longitude	Altitude (m)	Biome	Vegetation type	Survey no.	Survey date (points per survey)		Repeat Photo ID.	Rainfall (mm/yr)
								Roux	Arena		
Beestekuil *	Pixley Ka Seme	31.24888	24.57958	1409	NK	Eastern Upper Karoo	18	Dec 1962 (1000)	Feb 2018 (1000)	008 Beestekuil 1 009 Beestekuil 2	322
Bergplaas	Chris Hani	31.75556	24.70586	1782	NK	Eastern Upper Karoo	23	Dec 1961 (1000)	Oct 2017 (1000)	1788 Bergplaas	436
Boesmanskop	Chris Hani	31.41588	25.02706	1326	NK	Eastern Upper Karoo	20h	No date (1000)	June 2017 (1000)	1769 Boesmanskop 1	360
Compassberg	Chris Hani	31.72711	24.53083	1889	NK	Upper Karoo Hardeveld	22	Nov 1964 (1000)	Feb 2017 (1000)	1791 Compassberg	434
De Draai *	Xhariep	30.21953	26.38974	1495	G	Aliwal North Dry Grassland	35	Feb 1962 (500)	Feb 2018 (1000)	011 De Draai	516
De Nek	Sarah Baartman	32.35065	24.71515	1356	G	Karoo Escarpment Grassland	26	Aug 1956 (2000)	Jan 2018 (1000)	none	360
Dewetsdorp commonage *	Manguang	29.57575	26.66358	1541	G	Central Free State Grassland	37	Feb 1962 (500)	Feb 2018 (1000)	013 Dewetsdorp	535

Farm name	District Municipality	Latitude	Longitude	Altitude (m)	Biome	Vegetation type	Survey no.	Survey date (points per survey)		Repeat Photo ID.	Rainfall (mm/yr)
								Roux	Arena		
Elandsrivier	Chris Hani	31.87458	26.08523	1231	NK	Eastern Upper Karoo	29	Jan 1962 (1000)	Jan 2018 (1000)	1799 Bonhills	309
Geelbeksfontein *	Pixley Ka Seme	31.39686	24.11677	1551	NK	Upper Karoo Hardeveld	21	Jan 1962 (1000)	Jan 2018 (1000)	1808 Geelbeksfontein 1	324
Groenfontein *	Pixley Ka Seme	30.89594	25.15758	1440	NK	Eastern Upper Karoo	32	Dec 1961 (1000)	Feb 2018 (1000)	010 Groenfontein	385
Grootvlei	Chris Hani	32.22868	25.04497	1673	G	Karoo Escarpment Grassland	26	Feb 1962 (1000)	Jan 2018 (1000)	1796 Grootvlei 3	495
Henning Siding	Chris Hani	31.26455	26.13201	1520	NK	Eastern Upper Karoo	12	Apr 1958 (1000)	Jan 2018 (1000)	1803 Henning Siding 1	496
Highlands	Chris Hani	31.77911	24.77056	1840	NK	Eastern Upper Karoo	24	Nov 1961 (1000)	Nov 2017 (1000)	1789 Valdrif 1 1790 Valdrif 2	533
Hillside *	Xhariep	30.15700	25.72783	1490	G	Xhariep Karroid Grassland	34	Feb 1962 (1000)	Feb 2018 (1000)	014a Hillside 014b Hillside	423
Hospitaal kamp	Chris Hani	31.45819	24.99457	1320	NK	Eastern Upper Karoo	54	- 1949 (2000)	Nov 2018 (1000)	1853 Perdekamp 1	360
Houdconstant *	Cacadu	32.75006	27.03267	1332	NK	Upper Karoo Hardeveld	25	Dec 1961 (1000)	Nov 2017 (1000)	1792 Houdconstant 1	354
Middelburg commonage *	Chris Hani	31.47972	24.99168	1289	NK	Besemkare e Koppies Shrubland	20a	Jan 1926 (1000)	Feb 2018 (1000)	004 Middelburg	361

Farm name	District Municipality	Latitude	Longitude	Altitude (m)	Biome	Vegetation type	Survey no.	Survey date (points per survey)		Repeat Photo ID.	Rainfall (mm/yr)
								Roux	Arena		
Mooivlakte	Chris Hani	31.41964	25.01917	1316	NK	Eastern Upper Karoo	20c	Dec 1958 (1000)	Feb 2018 (1000)	1783 Mooivlakte	360
Nooitgedacht	Chris Hani/ Joe Gqabi	31.38663 31.38278	26.67159 26.66974	1780 1781	G	Stormberg Plateau Grassland	1 3	Mar 1958 (500,1000)	Nov 2019 (1000)	1821 Nooitgedacht 1 1823 Nooitgedacht 5	598
Ordonnantie	Sarah Baartman	32.47713	24.85574	745	NK	Eastern Lower Karoo	31	Aug 1956 (2000)	Aug 2017 (1000)	None	278
Swartfontein	Chris Hani	32.32091	25.22241	1594	G	Karoo Escarpment Grassland	27	Dec 1961 (1000)	Jan 2018 (1000)	1797 Swartfontein 1	495
Swawelkrans	Joe Gqabi	31.15887	25.41114	1490	NK	Eastern Upper Karoo	15	Nov 1961 (1000)	Oct 2017 (1000)	1785 Swawelkrans 1	451
Uitsig	Chris Hani	31.39198	24.81881	1766	NK	Besemkaree Koppies Shrubland	19	Feb 1962 (500)	Jan 2018 (1000)	1806 Uitsig 1 1807 Uitsig 2	431
Wepener commonage *	Mangaung	29.75006	27.032667	1450	G	Aliwal North Dry Grassland	36	Feb 1962 (500)	Feb 2018 (1000)	012 Wepener	587
Wheatlands	Sarah Baartman	32.58318	24.79878	654	NK	Eastern Lower Karoo	29	Aug 1956 (2000)	Aug 2017 (1000)	none	314
Willows	Joe Gqabi	31.15117	26.66381	1835	G	Stormberg Plateau Grassland	6	Nov 1961 (1000)	Oct 2017 (1000)	1787 Willows	522

Soil texture and chemistry

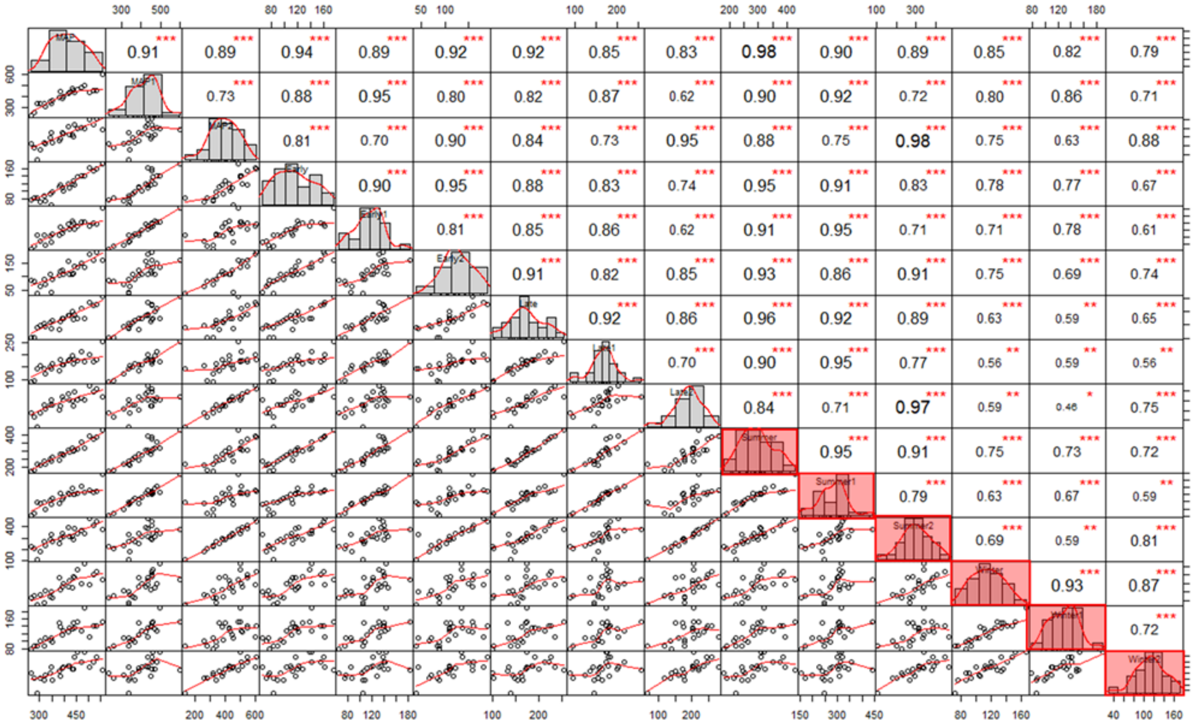


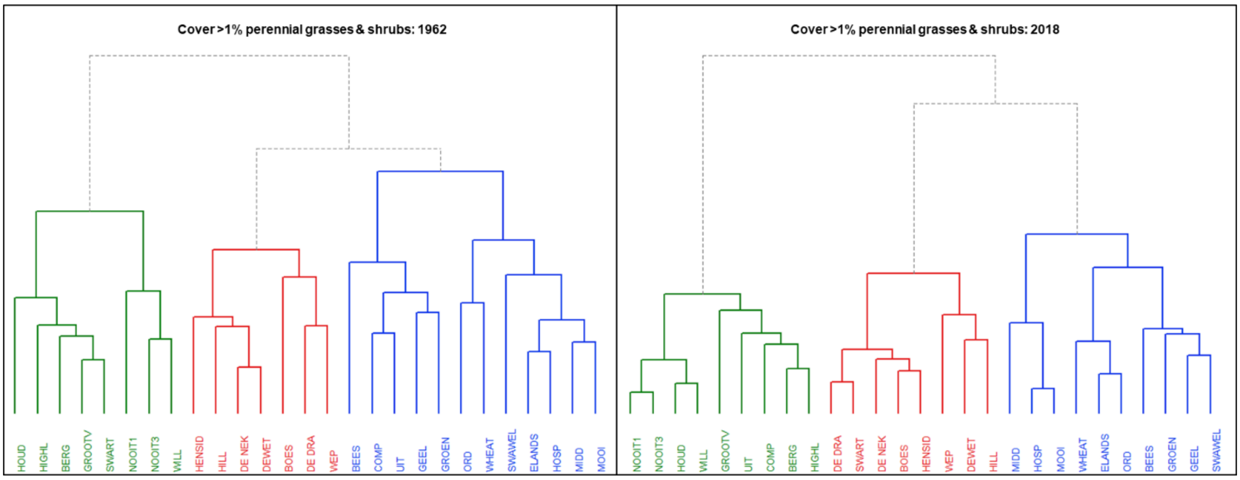
Temperature

Appendix C2. Correlation matrices of soil (acquired from SoilsGrid) and temperature variables (obtained from TerraClimate for the period 1958-2018). Spearman's correlation matrix of rainfall variables (obtained from a number of varying sources). MAP = Mean annual precipitation (1958-2018); Summ = summer rainfall mean (Oct-Mar); Wint = winter rainfall mean (Apr-Sept). 1 = 20-year mean (1942-1962); 2 = 20-year mean (1998-2018); 3 = change in mean between 1 and 2.

Appendix C2. continued

Rainfall

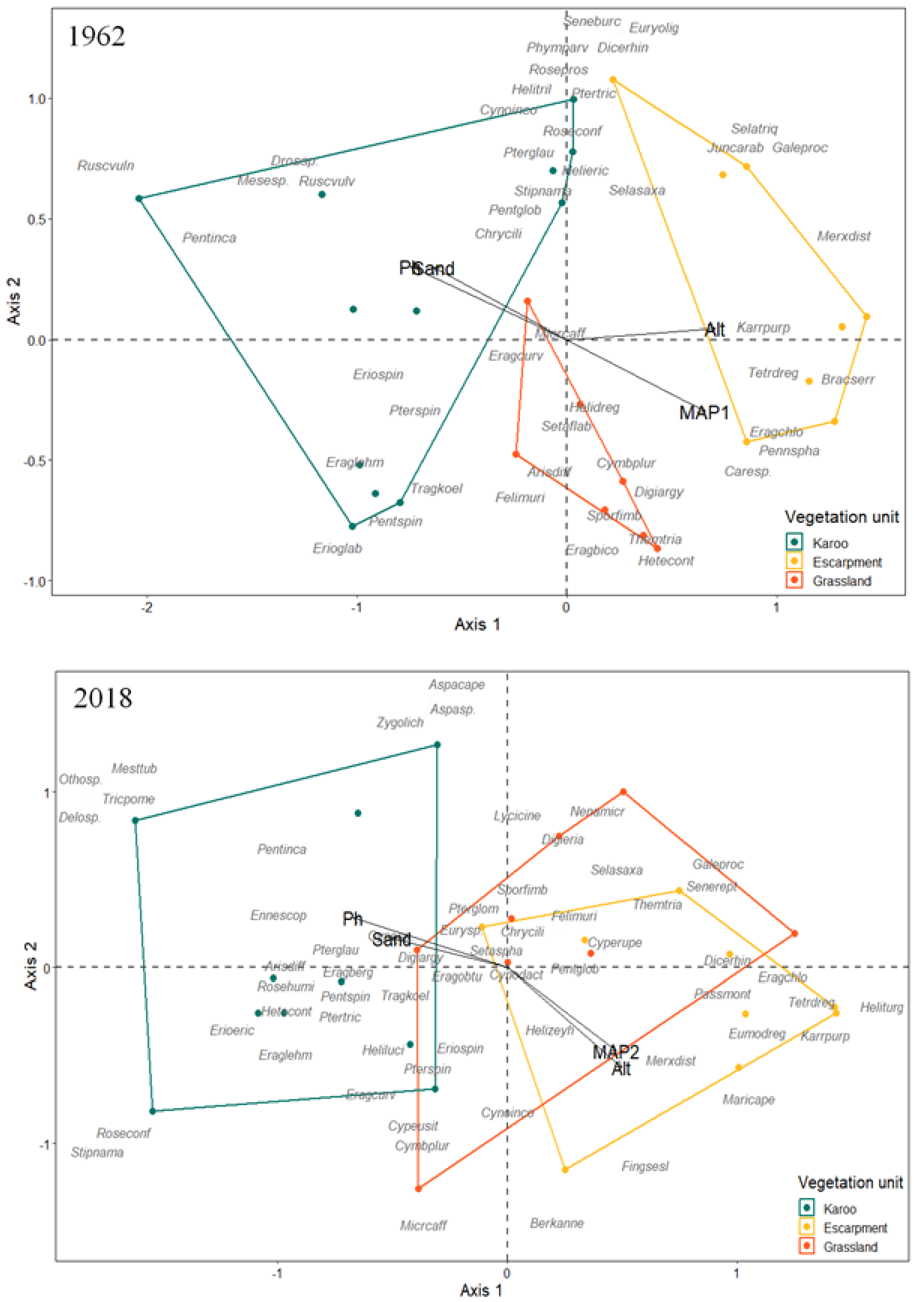




Appendix C3. Ward's hierarchical agglomerative cluster analysis of perennial grass and shrub (palatable + unpalatable) species cover of ≥ 1% sampled at 27 sites across the biome boundary using the Bray-Curtis distance measure. Groups represent 'Escarpment' (green), 'Grassland' (red) and 'Karoo' (blue) sites.

Appendix C4. Permutational MANOVA of Bray-Curtis dissimilarity distances of the original (1962) and repeated (2018) data on species composition at 27 sites in relation to vegetation unit. *P*-values are based on 1000 permutations at the 95% confidence limits

	Degrees of freedom	**Sum of Squares**	**Mean Squares**	**F-model**	**R^2**	**P**
1962						
Vegetation unit	2	2.5	1.3	3.8	0.2	**0.001**
Residuals	24	8.1	0.3		0.8	
2018						
Vegetation unit	2	3.4	1.7	6.0	0.3	**0.001**
Residuals	24	6.9	0.3		0.7	



Appendix C5. Non-metric multidimensional scaling of perennial grass and shrub species abundance ≥ 1% cover from historical and repeated vegetation plots in the eastern Karoo in relation to the environmental predictors of altitude (Alt), soil pH, percent sand, and mean annual precipitation (MAP = 1942-2018) (Bray-Curtis distance; k=4 dimensions; Stress scores: 1962 = 0.06. 2018 = 0.07; Linear fit R^2: 1962 = 0.97, 2018 = 0.94). MAP1 = 20-year mean annual precipitation for 1942-1962; MAP2 = 1998-2018. Species names in alphabetical order are as follows: Arisdiff = *Aristida diffusa*; Aspacape = *Asparagus capensis*; Aspasp. = *Asparagus sp.*; Berkanne = *Berkheya annectens*; Bracserr = *Brachiaria serrata*; Caresp. = *Carex sp.*; Chrycil = *Chrysocoma ciliata*; Cymbplur = *Cymbopogon plurinodis*; Cynodact = *Cynodon dactylon*; Cynoinco = *Cynodon incompletus*; Cyperupe = *Cyperus rupestris*; Cypeusit = *Cyperus usitatus*; Delosp. = *Delosperma sp.*; Dicerhin = *Dicerothamnus rhinocerotis*; Digiargy = *Digitaria argyrograpta*; Digieria = *Digitaria eriantha*; Drossp. = *Drosanthemum* sp.; Ennescop = *Enneapogon scoparius*; Eragberg = *Eragrostis bergiana*; Eragbico =

Appendix C5. cont.

Eragrostis bicolor; Eragchlo = *Eragrostis chloromelas*; Eragcurv = *Eragrostis curvula;* Eraglehm = *Eragrostis lehmanniana*; Eragobtu = *Eragrostis obtusa;* Erioeric = *Eriocephalus ericoides*; Erioglab = *Eriocephalus glaber* (Eriospin = *Eriocephalus spinescens*); Eumodreg = *Eumorphia dregeana*; Euryolig = *Euryops oligoglossus*; Eurysp. = *Euryops sp.*; Felimuri = *Felicia muricata*; Fingsesl = *Fingerhuthia sesleriaeformis*; Galeproc = *Galenia procumbens*; Helieric = *Helichrysum ericaefolium*; Helidreg = *Helichrysum dregeanum*; Helitril = *Helichrysum trilineatum*; Heliturg = *Helictotrichon turgidulum*; Helizeyh = *Helichrysum zeyheri*; Hetecont = *Heteropogon contortus*; Juncarab = *Juncus arabica*; Karrpurp = *Karroochloa purpurea*; Lycicine = *Lycium cinereum*; Maricape = *Mariscus capensis*; Merxdist = *Merxmuellera disticha*; Mesesp. = *Mesembryanthemum* sp.; Mesttub = *Mestoklema tuberosum*; Micrcaff = *Microchloa caffra*; Nenamicr = *Nenax microphylla*; Othosp. = *Othonna sp.*; Passmont = *Passerina montana*; Pennspha = *Pennisetum sphacelatum*; Pentglob = *Pentzia globosa*; Pentinca = *Pentzia incana*; Pentspin = *Pentzia spinescens*; Phymparv = *Phymaspermum parviflorum*; Pterglau = *Pteronia glauca*; Pterglom = *Pteronia glomerata*; Ptertric = *Pteronia tricephala*; Pterspin = *Pterothrix spinescens*; Roseconf = *Rosenia conferta*; Rosehumi = *Rosenia humilis*; Rosepros = *Rosenia prostrata*; Ruscvuln = *Ruschia vulnerans*; Ruscvulv = *Ruschia vulvaria;* Selasaxa = *Selago saxatilis;* Selatriq = *Selago triquetra;* Seneburc = *Senecio burchellii;* Senerept = *Senecio reptans;* Setflab = *Setaria flabellata;* Setaspha = *Setaria sphacelata;* Sporfimb = *Sporobolus fimbriatus*; Stipnama = *Stipagrostis namaquensis;* Tetrdreg = *Tetrachne dregei;* Themtria = *Themeda triandra;* Tragkoel = *Tragus koelerioides;* Tricpome = *Trichodiadema pomeridianum;* Zygolich = *Zygophyllum lichtensteinianum.*

Appendix C6. Bray-Cutis dissimilarity distances of the first and second axes for each site in 1962 and 2018 (n = 27) with their relevant group membership (vegetation unit) according to the hierarchical agglomerative cluster analysis

	1962		**2018**		**Vegetation unit**	
	Axis 1	**Axis 2**	**Axis 1**	**Axis 2**	**1962**	**2018**
Beestekuil	-0.04	-0.56	-1.54	-0.82	Karoo	Karoo
Bergplaas	0.21	-1.08	0.34	0.15	Escarpment	Escarpment
Boesmanskop	0.19	0.70	0.23	0.74	Grassland	Grassland
Compassberg	0.02	-0.79	0.97	0.08	**Karoo**	**Escarpment**
De Draai	-0.19	-0.16	0.37	0.08	Grassland	Grassland
De Nek	0.42	0.78	0.02	0.28	Grassland	Grassland
Dewetsdorp	0.37	0.88	0.00	0.03	Grassland	Grassland
Elandsrivier	-1.02	-0.12	-0.65	0.88	Karoo	Karoo
Geelbeksfontein	-0.07	-0.67	-0.72	-0.08	Karoo	Karoo
Groenfontein	-0.73	-0.11	-0.31	-0.69	Karoo	Karoo
Grootvlei	0.72	-0.69	0.25	-1.15	Escarpment	Escarpment
Henning Siding	0.27	0.59	0.51	1.00	Grassland	Grassland
Highlands	1.31	-0.06	1.04	-0.26	Escarpment	Escarpment
Hillside	-0.24	0.47	-0.40	0.10	Grassland	Grassland
Hospitaal kamp	-1.02	0.78	-1.09	-0.25	Karoo	Karoo
Houdconstant	0.85	-0.72	0.75	0.44	Escarpment	Escarpment
Middelburg	-1.00	0.53	-0.42	-0.43	Karoo	Karoo
Mooivlakte	-0.91	0.65	-0.98	-0.25	Karoo	Karoo
Nooitgedacht1	1.29	0.31	1.42	-0.22	Escarpment	Escarpment
Nooitgedacht3	1.17	0.16	1.43	-0.26	Escarpment	Escarpment
Ordonnantie	-1.17	-0.59	-1.62	0.84	Karoo	Karoo
Swartfontein	1.41	-0.11	1.25	0.19	**Escarpment**	**Grassland**
Swawelkrans	-0.78	0.68	-1.02	-0.06	Karoo	Karoo
Uitsig	0.03	-0.98	-0.11	0.23	**Karoo**	**Escarpment**
Wepener	0.07	0.27	-0.39	-1.26	Grassland	Grassland
Wheatlands	-2.02	-0.62	-0.31	1.27	Karoo	Karoo
Willows	0.87	0.43	1.00	-0.57	Escarpment	Escarpment

Appendix C7. Models after removing two outlier sites, Nooitgedacht1 and Henning Siding. GC = grass cover; SC = shrub cover

Final model	Coefficient Estimate	Standard Error	*t*-value	*p*-value	Adjusted R^2	F-statistic	Model *p*-value
% GC (1962)					0.64	43.21 $_{(1.23)}$	**1.04 e-06**
Intercept	175.64	23.94	7.34	**1.83e-07**			
Soil pH	-25.56	3.89	-6.57	**1.1e-06**			
% GC (2018)					0.45	20.78 $_{(1.23)}$	**0.0001**
Intercept	293.29	54.06	5.43	**1.64 e-05**			
Soil pH	-40.03	8.78	-4.56	**0.0001**			
% SC (1962)					0.08	3.29 $_{(1.23)}$	0.08
Intercept	-32.38	22.89	-1.41	0.17			
Soil pH	6.74	3.72	1.81	0.08			
% SC (2018)					0.26	9.28 $_{(1.23)}$	**0.006**
Intercept	-99.21	38.14	-2.60	**0.02**			
Soil pH	19.87	6.19	3.05	**0.006**			
% change GC					0.32	4.77 $_{(3.21)}$	**0.01**
Intercept	-44.08	21.75	-2.75	**0.06**			
Altitude	0.06	0.02	3.47	**0.002**			
Δ Summer	63.97	45.52	-1.41	0.17			
Altitude * ΔSummer	-0.05	0.03	-1.73	0.09			
% change SC					0.21	4.16 $_{(2.22)}$	**0.03**
Intercept	-42.18	34.70	-1.22	0.24			
Soil pH	17.49	6.06	2.89	**0.009**			
% Sand	-0.96	0.60	-1.60	0.12			

Appendix C8. Ratios of percent covers of grasses (annual and perennial) and shrubs (palatable and unpalatable) taken from Table 4 of Chapter 4.

Vegetation unit	**1962**		**2018**	
	Grasses (%)	**Shrubs (%)**	**Grasses (%)**	**Shrubs (%)**
Karoo	9	11	36	26
	1	**1.2**	**1**	**0.7**
Escarpment	33	10	56	14
	1	**0.3**	**1**	**0.2**
Grassland	30	3	66	6
	1	**0.1**	**1**	**0.1**

Appendix D: Metadata on the historical photographs used in the repeat photography study

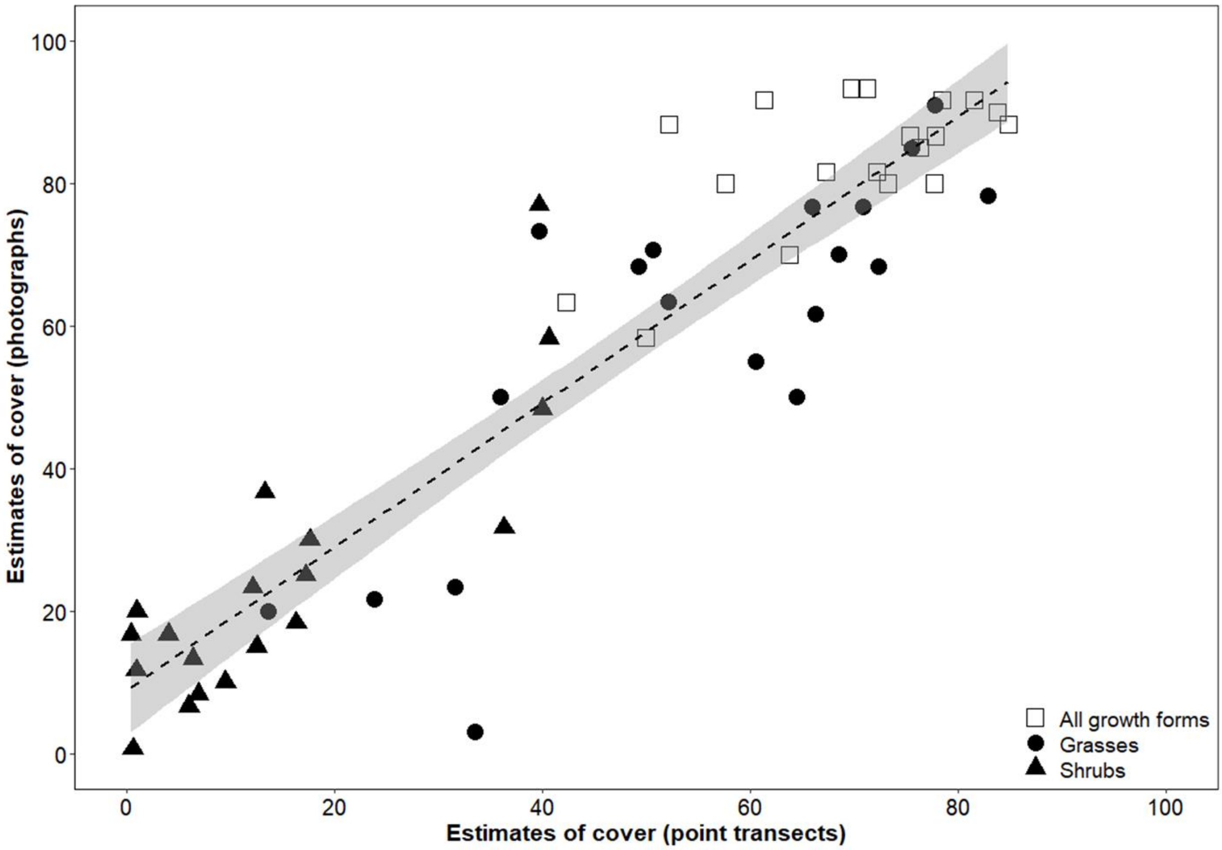
Appendix D1. Metadata on the historical photographs used for analysis in Chapter 5. Latitude and longitude are reported in decimal degrees (dd). DIN = Digital image number; QDS = Quarter Degree Square; AT = Albany Thicket; NK = Nama-Karoo; G = Grassland

Record ID	DIN	Photographer	Historical date	Repeat date	Latitude (dd)	Longitude (dd)	Altitude (m)	QDS	Site Name	Biome
1769	RouxPW05_061	PW Roux	1960-09-01	2017-06-21	31.41683	25.02728	1326	3125AC	Boesmanskop 1	NK
1770	Timm_1550	MT Hoffman	1989-03-01	2017-08-12	32.48053	24.82361	729	3224BD	Ordonnantie 1	NK
1771	Timm_1562	MT Hoffman	1989-03-01	2017-08-12	32.47058	24.82112	739	3224BD	Ordonnantie 2	NK
1772	Timm_1524	MT Hoffman	1989-03-01	2017-08-12	32.43232	24.83760	776	3224BD	Ordonnantie 3	NK
1773	Cowling_006_0100	R Cowling	2002-05-01	2017-08-14	32.36428	24.89019	927	3224BD	Wolwekloof	AT
1774	Cowling_003_006	R Cowling	2002-05-01	2017-08-14	32.38938	24.93670	1362	3224BD	Kondoa 1	G
1775	Cowling_003_007	R Cowling	2002-05-01	2017-08-14	32.39054	24.91012	1345	3224BD	Kondoa 2	G
1776	Cowling_003_009	R Cowling	2002-05-01	2017-08-14	32.38939	24.91202	1354	3224BD	Kondoa 3	G
1777	Timm_593	MT Hoffman	1986-03-21	2017-08-15	32.49236	24.83163	724	3224BD	Ganna kamp 1	NK
1778	Timm_1535	MT Hoffman	1986-03-21	2017-08-15	32.49295	24.83086	725	3224BD	Ganna kamp 2	NK
1779	Timm_1542	MT Hoffman	1986-03-21	2017-08-15	32.49728	24.84766	720	3224BD	Blakeridge 1	NK
1780	Timm_592	MT Hoffman	1986-03-21	2017-08-15	32.52149	24.85159	705	3224BD	Blakeridge 2	NK
1781	Timm_1554	MT Hoffman	1986-03-21	2017-08-15	32.52300	24.87535	708	3224BD	Blakeridge 3	NK
1783	RouxPW01_098	PW Roux	~1960s	2017-10-24	31.41933	25.02002	1325	3125AC	Mooivlakte 1	NK
1784	Roux 139	PW Roux	~1960s	2017-10-26	31.40391	25.02797	1369	3125AC	Grootfontein 1	NK
1785	RouxPW02_034	PW Roux	~1960s	2017-10-26	31.15886	25.41113	1490	3125AB	Swawelkrans 1	NK
1786	RouxPW02_035 / Roux 149	PW Roux	~1960s	2017-10-26	31.15516	25.41786	1477	3125AB	Swawelkrans 2	NK
1787	RouxPW02_005 / Roux 104	PW Roux	~1960s	2017-10-27	31.15116	26.66383	1831	3126BA	Willows 1	G
1788	Roux 129	PW Roux	~1960s	2017-10-31	31.75555	24.70586	1782	3124DB	Bergplaas 1	NK
1789	RouxPW02_021 / Roux 111	PW Roux	~1960s	2017-11-01	31.77911	24.77055	1840	3124DD	Valdrif 1	G
1790	RouxPW02_024	PW Roux	~1960s	2017-11-01	31.78052	24.76794	1859	3124DD	Valdrif 2	G
1791	RouxPW04_067 / Roux 137	PW Roux	1961/1963	2017-11-02	31.72730	24.53094	1886	3124DA	Compassberg 1	G
1792	RouxPW03_040 / Roux 118	PW Roux	1960/1961	2017-11-03	32.09777	24.23877	1336	3224AA	Houdconstant 1	G
1793	RouxPW03_049	PW Roux	1960/1961	2017-11-03	32.04905	24.23613	1334	3224AA	Houdconstant 2	G
1794	RouxPW05_048	PW Roux	1960-09-19	2018-01-09	32.27333	25.06431	1844	3225AA	Grootvlei1	G
1795	RouxPW05_049	PW Roux	1960-09-19	2018-01-09	32.24272	25.04747	1696	3225AA	Grootvlei2	G
1796	Roux 112	PW Roux	~1960s	2018-01-10	32.23155	25.04855	1673	3225AA	Grootvlei3	G

Record ID	DIN	Photographer	Historical date	Repeat date	Latitude (dd)	Longitude (dd)	Altitude (m)	QDS	Site Name	Biome
1797	RouxPW03_017	PW Roux	1960/1961	2018-01-09	32.32010	25.22212	1585	3225AC	Swartfontein 1	G
1798	RouxPW03_020	PW Roux	1960/1961	2018-01-09	32.31125	25.25793	1476	3225AC	Swartfontein 2	G
1799	Roux146	PW Roux	~1960s	2018-01-11	31.87366	26.08541	1232	3126CC	Bonhills	NK
1800	Roux 156	PW Roux	1960/1961	2018-01-12	32.00526	26.46217	1208	3226AB	Lilyvale 1	NK
1801	RouxPW03_015	PW Roux	1960/1961	2018-01-12	32.00658	26.46254	1211	3226AB	Lilyvale 2	NK
1802	RouxPW03_060	PW Roux	1960/1961	2018-01-12	32.00585	26.46228	1211	3226AB	Lilyvale 3	NK
1803	RouxPW05_042	PW Roux	1960-04-01	2018-01-13	31.26450	24.13200	1514	3126AC	Henning Siding 1	NK
1804a	RouxPW03_021	PW Roux	1960/1961	2018-01-13	31.26540	26.13277	1516	3126AC	Henning Siding 2	NK
1804b	RouxPW03_022	PW Roux	1960/1961	2018-01-13	31.26540	26.13277	1516	3126AC	Henning Siding 2	NK
1805	RouxPW05_043	PW Roux	1960-04-07	2018-01-13	31.26445	26.13199	1508	3126AC	Henning Siding 3	NK
1806	Roux 116	PW Roux	~1960s	2018-01-15	31.39157	24.81890	1763	3124BD	Uitsig 1	NK
1807	RouxPW04_032	PW Roux	~1960s	2018-01-15	31.39132	24.81956	1785	3124BD	Uitsig 2	NK
1808	RouxPW04_049	PW Roux	~1960s	2018-01-16	31.39697	24.11702	1554	3124AC	Geelbeksfontein 1	NK
1809	Roux 69	PW Roux	1960-05-09	2018-01-16	31.39356	24.10497	1573	3124AC	Geelbeksfontein 2	NK
1810	RouxPW05_056	PW Roux	1960-05-09	2018-01-16	31.39402	24.10716	1575	3124AC	Geelbeksfontein 3	NK
1811	RouxPW05_054	PW Roux	~1960s	2018-01-16	31.49901	24.45201	1496	3124CB/ 3124AD	Leeufontein 1	NK
1812	RouxPW04_056	PW Roux	~1960s	2018-01-16	31.56001	24.42515	1562	3124CB	Stone fence	NK
1813	RouxPW04_054	PW Roux	~1960s	2018-01-17	31.66947	24.38756	1671	3124CB	Vergelegen	NK
1814	RouxPW_05_016	PW Roux	1960-09-03	2018-02-06	31.47912	24.99265	1291	3124BD	Middelburg 2	NK
1815	RouxPW_05_059	PW Roux	1960-08-27	2018-02-06	31.47941	24.98937	1298	3124BD	Middelburg 3	NK
004	Roux140	PW Roux	~1960s	2018-02-06	31.48222	24.299415	1287	3124BD	Middelburg 1	NK
005	Roux 145	PW Roux	1962-03-01	2018-02-07	31.80447	25.30809	1045	3125CD	Cypress Grove	NK
008	Roux 150 / RouxPW01_004	PW Roux	1962	2018-02-09	31.24911	24.57938	1403	3124BA	Beestekuil 1	NK
009	Roux 55	PW Roux	1962	2018-02-09	31.24894	24.57948	1411	3124BA	Beestekuil 2	NK
010	Roux 151	PW Roux	1962	2018-02-07	30.89493	25.15706	1436	3025CC	Groenfontein	NK
011	Roux 160	PW Roux	1962	2018-02-11	30.21945	26.38484	1503	3026AB	De Draai	NK

Record ID	DIN	Photographer	Historical date	Repeat date	Latitude (dd)	Longitude (dd)	Altitude (m)	QDS	Site Name	Biome
012	Roux 161	PW Roux	1962	2018-02-12	29.74994	27.03253	1452	2927CA&CB	Wepener commonage	G
013	Roux 162	PW Roux	1962	2018-02-13	29.57383	26.66462	1543	2926DA	Dewetsdorp commonage	G
014a	Roux 153 / RouxPW04_026	PW Roux	1962	2018-02-14	30.15789	25.72606	1490	3025BA	Hillside 1	G
014b	Roux 154 / RouxPW04_027	PW Roux	1962	2018-02-14	30.15789	25.72606	1490	3025BA	Hillside 2	G
1816	RouxPW03_037	PW Roux	1960/1961	2018-05-30	32.04781	24.23884	1336	3224AA	Houdconstant 3	G
1817	RouxPW03_038	PW Roux	1960/1961	2018-05-30	32.04781	24.23884	1336	3224AA	Houdconstant 4	G
1818	RouxPW03_039	PW Roux	1960/1961	2018-05-30	32.04781	24.23884	1336	3224AA	Houdconstant 5	G
1819	Roux 86	PW Roux	Unknown	2018-11-06	31.37762	26.66624	1852	3126BC	Nooitgedacht 1	G
1820	Roux 87	PW Roux	Unknown	2018-11-06	31.37754	26.66628	1855	3126BC	Nooitgedacht 2	G
1821	Roux 85	PW Roux	Unknown	2018-11-07	31.38585	26.67115	1787	3126BC	Nooitgedacht 3	G
1822	Roux 95	PW Roux	Unknown	2018-11-07	31.38312	26.66962	1779	3126BC	Nooitgedacht 4	G
1823	Roux 88	PW Roux	Unknown	2018-11-07	31.38312	26.66962	1779	3126BC	Nooitgedacht 5	G
1824	Roux 97	PW Roux	Unknown	2018-11-07	31.38413	26.67077	1781	3126BC	Nooitgedacht 6	G
1825	Roux 92 / RouxPW03_033	PW Roux	1960/1961	2018-11-08	31.35218	26.84661	1767	3126BD	Rooiberg	G
1826	Roux 102 / RouxPW04_010	PW Roux	Unknown	2018-11-08	31.34169	26.81063	1757	3126BD	Snymanskraal 1	G
1827	Roux 94 / RouxPW04_004	PW Roux	Unknown	2018-11-08	31.36828	26.77368	1830	3126BC/BD	Snymanskraal 2	G
1828	Roux 108 / RouxPW04_006	PW Roux	Unknown	2018-11-08	31.37110	26.73685	1825	3126BC	Buffelsfontein	G
1829	Acocks_4307	JP Acocks	1945-01-27	2018-11-08	31.45359	26.69385	1776	3126BC	Penhoek Pass	G
1830	Acocks_bw_4957	JP Acocks	1946-07-25	2018-11-09	31.13989	26.61590	1807	3126BA	Witkop 1	G
1831	Acocks_bw_5806	JP Acocks	1953-04-22	2018-11-09	31.08933	26.51657	1629	3126BA	Kapokfontein	G
1832	Acocks_bw_5807	JP Acocks	1953-04-22	2018-11-09	31.11511	26.58699	1678	3126BA	Kalkfontein 1	G
1833	Acocks_bw_5808	JP Acocks	1953-04-22	2018-11-09	31.12910	26.60052	1748	3126BA	Kalkfontein 2	G
1834	Acocks_bw_5809	JP Acocks	1953-04-22	2018-11-09	31.12959	26.60066	1749	3126BA	Kalkfontein 3	G
1835	Acocks_bw_4956	JP Acocks	1946-07-25	2018-11-09	31.13652	26.61072	1797	3126BA	Witkop 2	G
1836	Acocks_bw_5814	JP Acocks	1953-04-22	2018-11-09	31.14010	26.60880	1814	3126BA	Witkop 3	G
1837	Acocks_bw_5815	JP Acocks	1953-04-22	2018-11-09	31.18064	26.65968	1844	3126BA	Streepfontein	G
1838	Roux 93 / RouxPW06_003	PW Roux	~1970s	2018-11-09	31.24924	26.68130	1852	3126BA	Van Aardt Siding	G
1839	Acocks_bw_4955	JP Acocks	~1960s	2018-11-10	31.11631	26.19885	1536	3126BC	Leeuwfontein	NK
1840	Acocks_bw_4953	JP Acocks	1946-07-25	2018-11-10	31.18429	26.07360	1585	3126AA	Goodhope 1	NK
1841	Acocks_bw_4952	JP Acocks	1946-07-25	2018-11-10	31.18429	26.07360	1585	3126AA	Goodhope 2	NK
1842	Acocks_bw_4954	JP Acocks	1946-07-25	2018-11-10	31.18432	26.07375	1586	3126AA	Goodhope 3	NK
1843	Acocks_bw_4951	JP Acocks	1946-07-25	2018-11-10	31.20844	26.04424	1586	3126AA	Blesbokvlakte 1	NK
1844	Acocks_bw_4950	JP Acocks	1946-07-25	2018-11-10	31.20844	26.04424	1586	3126AA	Blesbokvlakte 2	NK

Record ID	DIN	Photographer	Historical date	Repeat date	Latitude (dd)	Longitude (dd)	Altitude (m)	QDS	Site Name	Biome
1845	PE_CF10_035	P Evans	1925	2018-11-11	31.34184	25.76877	1351	3125BC/BD	Ouplaas	NK
1846	PE_CF10_033	P Evans	1925	2018-11-11	31.42565	25.75549	1244	3125BC/BD	Middelplaats	NK
1847	PE_CF10_034	P Evans	1925	2018-11-11	31.43009	25.75583	1245	3125BC/BD	Weltevreden	NK
1848a	Roux 138 / RouxPW05_036	PW Roux	~1960s	2018-11-12	31.86813	25.73867	1381	3125DC	Elandsberg 1	NK
1848b	Roux 138 / RouxPW05_036	PW Roux	~1960s	2018-11-12	31.86823	25.73870	1384	3125DC	Elandsberg 1	NK
1849	RouxPW07_013	PW Roux	~1960s	2018-11-12	32.04876	25.46933	964	3225AB	Spekboomberg 1	NK
1850	RouxPW07_012	PW Roux	~1960s	2018-11-12	31.99494	25.48820	963	3125CD/ 3225AB	Spekboomberg 2	NK
1851	RouxPW07_031	PW Roux	1960-10-01	2018-11-13	31.45829	24.99488	1319	3126AA	Hospitaal kamp 1	NK
1852	RouxPW05_018	PW Roux	1960-10-04	2018-11-13	31.46698	25.01199	1319	3125AC/ 3124BD	Perdekamp 1	NK
1853	RouxPW06_030	PW Roux	~1960s	2018-11-13	31.45251	24.99395	1316	3125AC/ 3124BD	Hospitaal kamp 2	NK
1854	RouxPW07_030	PW Roux	1960-10-01	2018-11-13	31.45856	24.99547	1299	3124BD	Perdekamp 2	NK
1855	Cowling_007_0036	R Cowling	1994/1995	2018-11-14	32.30677	22.89812	1089	3222BD	Elandsfontein 1	NK
1856	Cowling_007_0037	R Cowling	1994/1995	2018-11-14	32.29537	22.99982	970	3222BD	Elandsfontein 2	NK
1857	Cowling_007_0038	R Cowling	1994/1995	2018-11-14	32.29482	22.98397	981	3222BD	Elandsfontein 3	NK
1858	Cowling_007_0034	R Cowling	1994/1995	2018-11-14	32.29715	22.97780	987	3222BD	Elandsfontein 4	NK
1859	Cowling_007_0035	R Cowling	1994/1995	2018-11-14	32.29676	22.97766	985	3222BD	Elandsfontein 5	NK
1860	Timm_608	MT Hoffman	1986-03-20	2018-11-15	32.32668	22.83996	946	3222BD	Sunnyside 1	NK
1861	Timm_1560	MT Hoffman	1986-03-20	2018-11-15	32.36123	22.86061	906	3222BD	Sunnyside 2	NK
1862	Timm_609	MT Hoffman	1986-03-20	2018-11-15	32.35925	22.89015	907	3222BD	Sunnyside 3	NK
1863	Timm_610	MT Hoffman	1986-03-20	2018-11-15	32.35620	22.88762	911	3222BD	Sunnyside 4	NK



Appendix D2. Relationship of percent vegetation cover over time estimated using two methods, repeat photography and vegetation point-intercept surveys at the same sites (n = 19). Shaded trend line indicates the upper and lower bounds of the 95% confidence interval.

Appendix E: R Markdown scripts used for the analysis of data

Code

R scripts used for the analysis of data in each chapter can be accessed via these private links on Figshare:

- Chapter 2 - https://figshare.com/s/3286e1368e21099dce74
- Chapter 3 - https://figshare.com/s/ea7bc388747279eb159a
- Chapter 4 and Chapter 5 - https://figshare.com/s/38d88f1a024763d92f74

The R code is the product of work completed solely by the student, unless otherwise referenced in the thesis. In an effort to share open access data that is reproducible for research and/or teaching purposes, refer to the citations provided below. The DOI's, which are currently inactive, will be activated upon acceptance and publication of this thesis by the University of Cape Town.

Citations

Arena, G. (2021): R code: Descriptive climate, land use and text mining analyses. University of Cape Town. Dataset. https://doi.org/10.25375/uct.14179757

Arena, G. (2021): R code: Climate trends analysis. University of Cape Town. Dataset. https://doi.org/10.25375/uct.14179853

Arena, G. (2021): R code: Vegetation change analysis. University of Cape Town. Dataset. https://doi.org/10.25375/uct.14179898