EVALUATING ENVIRONMENTAL FACTORS & FIRE DISTURBANCE INFLUENCING SPECIES DIVERSITY IN A MOUNTAINOUS PROTECTED AREA

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A THESIS SUBMITTED TO THE FACULTY OF AGRICULTURE AND NATURAL SCIENCE IN FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN GEOGRAPHY, UNIVERSITY OF THE FREE STATE, PHUTHADITJHABA, SOUTH AFRICA

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Abstract

Mountain Zebra National Park (MZNP) is a unique conservation area occurring at the interface of three Biomes, i.e., Grassland, Nama karoo, and thicket. Grassland is the least protected biome in South Africa, with only approximately 2% of the biome being protected. It is estimated that 60% of the Grassland biome has been permanently transformed, while as little as 15% remains natural Grassland. Majority of the remaining natural Grassland is highly fragmented, and most is poorly managed. Grasslands and savannas are shaped by several factors, including climate change and fire. Fire plays a crucial role, particularly in influencing the structure and composition of vegetation which does have an influence on ecosystem functionality. Globally, there is a noticeable increase in the abundance of woody plants observed in Grasslands and savannas. This change in plant functional types has been ascribed to several factors, including reduced fire frequency, intense grazing pressures and elevated atmospheric CO_2. Although several ecological studies have explored different aspects of vegetation within MZNP, there still exists a considerable knowledge gap regarding the driving factors that influence this vegetation. Soil is a vital environmental factor that influences ecosystem processes and the distribution and characteristics of plant communities. The relationship between plant productivity and species richness is a fundamental focal point in community ecology, as it provides the basis for understanding plants' responses or adaptive strategies. The main objectives of this study were 1. To determine the influence of fire on woody/shrub plant species richness, diversity, and composition. 2. To determine the influence of fire on grass species richness, diversity, and composition. 3. To determine the influence of environmental factors on the species diversity and richness.4. To determine the effects of absence and presence of Fire on Woody species recruitment in a mountainous grassland. This was done using satellite imagery; the park's fire history was c between 2000 and 2020. Eighty plots (approximately 20 × 20 metres; >100 metres apart) were laid out purposively across the different fire regimes. Vegetation data was obtained using the step-point method. Biomass measurement was collected using a disc pasture meter on the transects. Environmental data except the rainfall data were extracted for each sample site using Quantum GIS 2.18.0 (Las Palmas de G.C.). All layers applied in the QGIS used the geographic coordinate system WGS84 and EPSG:4326 as spatial reference. This was done using Worldclim which

allows the extraction of raster values to points. There was no significant difference in both species' richness and diversity in burned and unburned sites ($p>0.05$) There was a significant difference in species cover for the Type B fire (2010 and 2019) compared to the Site A fire (2002 and 2010) fire. The unburned site had higher moribund material and unpalatable grasses than the burned area. The results show that the absence of fire for a prolonged period changes woody species cover in Grassland. Only one of the soil properties, soil pH, influenced plant biomass. Although soil nutrients are highly important in plant biomass production, it was found their influences on Above Ground Biomass (AGB) and plant to be insignificant. The study's main findings indicate that the chemical properties of soil (nitrogen and soil organic carbon) significantly impacted species richness and diversity and that clay and sand content (i.e., soil texture) positively affected species diversity. In contrast, the physical properties of soil (silt) did not affect plant species richness and diversity. Nitrogen showed an inversely proportional relationship with species richness. Sand content was the only physical property of soil which positively affected species diversity.

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1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other University.

3. This thesis does not contain other persons' data, pictures, graphs, or other information unless specifically acknowledged as being sourced from other persons.

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Nthabeliseni Munyai Signed: _____________________ Date: 01/12/2023

As the candidate's promoter, I certify the above statement and have approved this thesis for submission.

1. Prof. Samuel Adewale Adelabu: ____________________ Date: __________________

2. Prof. Abel Ramoelo: _________________ Date: __________________

Declaration

I, Nthabeliseni Munyai, declare that the thesis that I herewith submit for the Doctoral Degree in **Geography** at the University of the Free State, is my independent work and that I have not previously submitted it for a qualification at another institution of higher education.

Declaration 2-Publication and Manuscripts

1. **Munyai, N**., Ramoelo, A., Adelabu, S. & Bezuidenhout, H., 2023, 'The influence of fire presence and absence on grass species composition and species richness at Mountain Zebra National Park', *Koedoe* 65(1), a1738. https://**doi.org/10.4102/ koedoe. v65i1.1738.**

2. Munyai, N., Ramoelo, A., Adelabu, S., Bezuidenhout, H. & Sadiq, H., 'Influence of Environmental Factors on Species Richness and Diversity in a Semi-Arid Environment, South Africa'. *Grasses* journal 2023, *2*, x. https:// **doi.org/10.3390/grasses2040017**.

3. Munyai, N., Ramoelo, A, Adelabu, S., Bezuidenhout, H. & Sadiq, H. 'Effects of environmental factors on plant productivity in the mountain Grassland of the Mountain Zebra National Park, Eastern Cape, South Africa'. Ecologies journal 2023. **https://doi.org/10.3390/ecologies4040049**.

4. **Munyai N.;** Effects of absence and presence of Fire on Woody species recruitment in a mountainous Grassland. In preparation for Submission

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I would like to thank Dr Stefanie Freitag-Ronaldson for her support and encouragement from the start. This includes sending me to the trainings that really shaped me up and created a desire to study further the time I was with Garden route Scientific services. My move from Garden route scientific services didn't change anything as she continuously supported me throughout.

I would like to thank my mom and my husband for looking after me while pregnant with my 2nd born and looking after my 1st child who was just 7 months old when I registered for the study and with a full-time job. They carried out my responsibilities all on their shoulders just to ensure that I have enough time to study and to rest without worrying about anything else.

I would like to thank my two boys for allowing me to spend time alone studying instead of playing hide and seek and I promise that mom will now have plenty of times to play and have fun with you both. I know I haven't been fully there but you two have really walked this journey with me and I love you.

I would also like to thank everyone from family and friends who have been encouraging me and understanding when I was too busy to go out on our regular activities.

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CHAPTER 1: INTRODUCTION AND BACKGROUND TO THE STUDY

The Mountain Zebra National Park (MZNP) was proclaimed in 1937 and this was to protect and manage the last remaining Cape Mountain Zebra (*Equus zebra zebra*) population in the area. To sustain a viable population of the threatened Cape Mountain Zebra the park area has been extended in 1960. Various farms adjacent to the park were procured not only to increase the habitat for the Cape Mountain Zebra but also to introduce other wildlife species that historically occurred in the area and to maintain the natural processes and patterns of the diverse ecosystems of the park (Brown & Bezuidenhout 2018). Vegetation plays a vital role in the life of many organisms, natural preservation, and ecosystem balance (Heydari & Mahdavi, 2009). Any impact on an ecosystem, such as pollution, development, grazing, fire, and drought, is first observed through changes in vegetation. Detailed studies on species and population composition of vegetation in an area are critical for developing scientifically sound management and conservation strategies (Brown & Bezuidenhout, 2005).

Species richness and soil properties

Studies on plant species richness and diversity patterns form the foundation of ecology and conservation biology research (Noss, 1990). Local and regional plant community distribution patterns are influenced by environmental factors such as climate, topography, and soil physical and chemical properties (Wang et al., 2015). Although various ecological studies on different aspects of vegetation have been conducted within the Nama Karoo biome (Pienaar et al., 2004), much remains to be understood about the drivers that shape this vegetation. Soil is a vital environmental factor that influences ecosystem processes and the distribution and characteristics of plant communities (Pienaar et al., 2004). Soil properties affect the redistribution of rainwater, including runoff and infiltration (Le Houérou et al., 1988). Soil chemical, physical, and microbiological properties influence plant community structure, composition, distribution, and diversity (Eskelinen et al., 2009). In mountainous areas, elevation, slope, and aspect are the main topographic factors affecting plant species composition, diversity, and distribution patterns (Huang, 2002). Vegetation monitoring is essential for understanding vegetation structure and species composition over time (Bezuidenhout & Brown, 2021). However, few studies have investigated the patterns of plant biodiversity in the semi-arid Nama Karoo biome. Most historical ecological research in the region focused on livestock grazing effects on the landscape (Todd & Hoffman, 2009; Hanke et al., 2014), and several floristic studies have investigated species assemblages in some parts of the region (Brown & Bezuidenhout, 2018).

Mountain Zebra National Park (MZNP) is a unique conservation area occurring at the interface of three Biomes, i.e., Grassland, Na ma-Karoo, and thicket. Nama karoo Fire has recently become more common in the Nama karoo and other arid ecosystems, potentially threatening the persistence of native species (du Toit et al., 2015; Syphard et al., 2017). Climate change may be the reason why there is an increase in fire-conducive weather conditions (Wilson et al., 2010; Kraaij et al., 2012) and changes in the structural composition of vegetation affecting fuel attributes of ecosystems (D'Antonio & Vitousek, 1992; Syphard et al., 2017). Just like other Grassland vegetation types, MZNP Mountainous Grassland is prone to occasional lightning-caused fires (Hugo et al., 2016).

Grassland management and fire

Open grassy systems which include Grassland and savannas cover about a quarter of Earth's vegetated surfaces (Ramankurry & Foley 1999) and In South Africa 30% of the land is covered by Grassland. However, Grassland is the least protected biome in South Africa, with only 2% protected. It is estimated that 60% of the Grassland biome has been permanently transformed, while as little as 15% remains natural Grassland (Carbutt et al., 2011) and the majority of the remaining natural Grassland is highly fragmented and most is poorly managed (Mucina & Rutherford, 2006a). South African Grasslands are being increasingly degraded by several factors, such as overgrazing (Neke and Du Plessis, 2004), extensive, frequent burning (Uys et al., 2004), plantation forestry (Lipsey & Hockey, 2010), invasion by alien plant species (Le Maitre et al., 1996) and fire suppression that results in woody encroachment. Grasslands are the most primitive evolving systems of diverse plant communities (Little et al., 2015). Grasslands and Savanna are shaped by several factors that include, over the longer term, climate change (Bond & Midgley 2012; Kulmatiski & Beard 2013).

Changes in the plant functional types has been ascribed to several factors, including decreases in fire frequency (Bragg & Hulbert, 1976), intense grazing pressures (McPherson & Wright, 1990; Scholes & Archer, 1997) and elevated atmospheric CO_2 (Bond & Midgely, 2001; Polley et al., 1997). Changes in vegetation co-dominance by shrubs in Grasslands are associated with changes in plant community composition and vegetation structure (Eldridge et al., 2011), ecosystem (Barger et al., 2011), and long-term conservation of biodiversity (Gray & Bond, 2013). Some of the palatable grass species require frequent burning, for example, *Themeda triandra*, and conversely absence of fire favours species such as *Merxmuellera disticha* (Munyai et al., 2023). Fire also does have an impact on plant biomass availability which is also influenced by limited resources (Tilman et al., 2012). However, little is known regarding the interactive effects of these environmental factors influencing plant biomass (Bello et al., 2013). Environmental factors play an important role in carbon accumulation and contribute to carbon transformation (Farrior et al., 2013). Different responses of plant biomass production to environmental factors are complex and less is known about the interactive effects of potential environmental driving factors (climate, soil properties, topographic properties, etc.) on plant biomass distribution in Mountain Zebra National Park.

Vegetation biomass and species richness

Vegetation biomass distribution is a vital issue in plant life history, providing the basis for understanding the plants' response or adaptive strategies (Weiner 2004; Sims et al., 2012). Several studies have shown that plant biomass plays a vital role in shaping the community structure and ecosystem function (Anderson, 2011; McCarthy & Enquist, 2007; Van der Putten et al., 2009). This is because vegetation biomass is a key contributor to soil organic matter, which can influence greenhouse gas emissions in terrestrial ecosystems (Liu et al., 2020). Plant biomass signifies the ability of an ecosystem to acquire energy, which is one of the most fundamental quantitative characteristics for understanding community structure and function (Yu, 2011). With increased atmospheric carbon concentration over the past decades studying plant biomass is essential in understanding vegetation dynamics, terrestrial ecosystem carbon (C) stocks and their response to environmental changes (Gao et al., 2021).

1.2 Problem Statement

Open grassy systems which include Grassland and savannas cover about a quarter (¼) of Earth's vegetated surfaces (Ramankurry & Foley 1999) and In South Africa 30% of the land is covered by Grassland. However, Grassland is the least protected biome in South Africa, with only 2% protected. It is estimated that 60% of the Grassland biome has been permanently transformed, while as little as 15% remains natural Grassland (Carbutt et al., 2011) and the majority of the remaining natural Grassland is highly fragmented and most is poorly managed (Mucina & Rutherford, 2006a). South African Grasslands are being increasingly degraded by several factors, such as overgrazing (Neke and Du Plessis, 2004), extensive, frequent burning (Uys et al., 2004), plantation forestry (Lipsey & Hockey, 2010), invasion by alien plant species (Le Maitre et al.,1996) and fire suppression that results in woody encroachment. Due to fire being an important tool in Grassland management, it is important to conduct studies on Grassland fire management to enable better management of the Grassland vegetation to minimise degradation. Vegetation monitoring is essential for understanding vegetation structure and species composition over time (Bezuidenhout & Brown, 2021). However, few studies have investigated the patterns of plant biodiversity in the semi-arid Nama Karoo biome. Most historical ecological research in the region focused on livestock grazing effects on the landscape (Hanke et al., 2014; Todd & Hoffman, 2009), and several floristic studies have investigated species assemblages in some parts of the region (Brown & Bezuidenhout, 2018). Hence it is important to do a study on factors influencing plant productivity and the influence of plant biomass on plant species richness and diversity.

1.4 Objectives of the Study

The objectives of the study were:

1. To determine the effects of environmental factors on plant species richness and diversity in mountainous Grassland and how those are influenced by fire.

2. To determine the influence of environmental factors on plant productivity.

3. To determine the influence of fire has on grass species richness and diversity and grass relative abundance cover in mountainous Grassland.

4. To determine the impact of fire presence and absence on woody species composition and palatability.

1.6 Description of the Study Area

The study was conducted in MZNP (Figure 1.1) which is approximately 28 412 ha and located in the Eastern Cape Province, South Africa (32° 22′ 47′′S; 25° 47′ 88′′E) (Bezuidenhout & Brown 2008). Mountain Zebra National Park was proclaimed in 1937 protecting a remnant population of the Cape Mountain zebra (*Equus zebra zebra*) and has since played a principal role in the conservation of the biodiversity of the area (Grobler 1983). The Park is characterised by elements of three Biomes of South Africa, which are Karoo Escarpment Grassland (53%), Eastern Upper Karoo (37%), and Eastern Cape Escarpment Thicket (10%) (Gaylard et al., 2006). The Park is one of the few protected areas that protect and preserve the Grassland (Bezuidenhout & Brown, 2008). Mountain Zebra National Park is classified as Nama Karoo but falls in between arid Nama Karoo bushveld in the west and the drier Grassland in the east (Gebeyehu & Samways, 2002). The biome is characterised by grasses and dwarf shrubs (Mucina et al., 2006). The park is located on the northern slopes of the Bankberg mountain range in the Cape Midlands, Eastern Cape, which is described as having a cool and arid climate (Bezuidenhout & Brown 2008). Mountain Zebra National Park is dominated by sedimentary rock types such as sandstones, siltstones and mudstones of the Beaufort Series. Post-Karoo dolerite intrusions are prevailing in certain areas. The soil throughout the park is generally shallow with vast parts of the park rocky with very little topsoil (Brown & Bezuidenhout, 2000). The average monthly temperatures in austral summer (September to March) vary between a minimum of 6 °C and a maximum of 28 °C, whereas in winter (April to August) the temperature often drops below 0 °C and reaches a maximum of 20 °C (Novellie & Gaylard, 2013). Rain falls mostly in late summer and autumn (December to April) (Novellie & Gaylard, 2013) and the average annual rainfall is 400 mm (Pond et al., 2002).

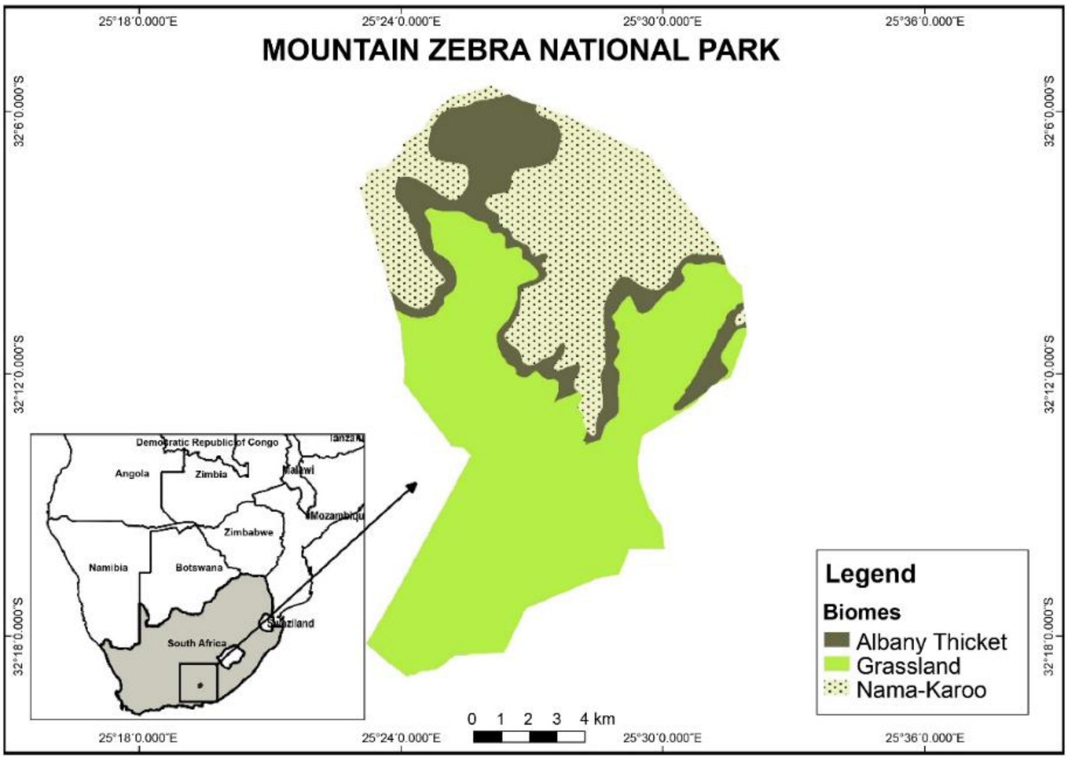

Figure 1.1 Location of the study area

1.7 Outline of the Thesis

To achieve the objectives of this study, the thesis is structured as a compilation of four research articles of which three papers have already been published and one is in preparation for submission. Each chapter was written as a stand-alone chapter and can be read independently apart from other chapters in the thesis, but the general conclusion in chapter 6 summarizes the findings of all other chapters. Thus, some repetitions crop up in the “Introduction,” “Figures,” and “Methods” sections of different chapters. The thesis consists of seven chapters.

Chapter 1 is the introductory part. It gives the background to the topic of fire disturbance and environmental factors that influence species richness and diversity and plant productivity.

Chapter 2 presents the influence of fire presence and absence on grass species composition and species richness at Mountain Zebra National Park by examining burned versus unburned areas of the park.

Chapter 3 discusses the Influence of environmental factors on the species richness and diversity in the semi-arid environment, in South Africa

Chapter 4 discusses the effects of environmental factors on plant productivity in the mountain Grassland of the Mountain Zebra National Park, Eastern Cape, South Africa

Chapter 5 Effects of absence and presence of fire on woody species recruitment in a mountainous Grassland.

Chapter 6 presents general conclusions, the contribution of the research to the body of knowledge, limitations of the study, and areas with potential for further research.

1.8 Ethical Considerations

There was no need for ethical consideration in this study.

Chapter 2: The influence of fire presence and absence on grass species composition and species richness

This chapter is based on:

Nthabe Munyai, Abel Ramoelo, Samuel Adelabu, Hugo Bezuidenhout. The influence of fire presence and absence on grass species composition and species richness. Published in Koedoe journal. **https://doi.org/10.4102/koedoe.v65i1.1738**

Abstract

It is well known that fire is a common driver in many Biomes and plays a vital role in maintaining ecosystems functioning in many southern African Biomes. The ecosystem process is an essential determinant of plant community composition and diversity and can result in structural composition and ecosystem functioning changes. The main objectives were to determine the influence of fire on grass species richness, diversity, and composition in Mountain Zebra National Park. Using satellite imagery, the park's fire history was determined between 2000 and 2020. Eighty plots (approximately 20 x 20 metres; >100 metres apart) were laid out purposively across different fire regimes. There was no significant difference in both species' richness and diversity in burned and unburned sites(P>0.05). However, there was a difference in species composition between burned and unburned sites and between different fire frequencies. The unburned site had higher moribund material and unpalatable grasses compared to burned area.

Introduction

Fire is fundamental in maintaining ecosystem functioning in many southern African vegetation types (Bond & Keeley, 2005). It is a common and regular driver of change in many ecosystems and Biomes across the Globe, from boreal forests to tropical Grasslands (Bond et al., 2005). Fire influences species composition, vegetation structure and dynamics (Bond & van Wilgen, 1996), particularly in Grassland and savanna systems. In Grassland and savanna Biomes, fire frequency, extent and intensity can significantly determine the abundance of woody and herbaceous species (Bond et al., 2005; Cavender-Bares & Reich, 2012). Fire can be used as a management tool to promote ecosystem benefits.

Grasslands are the most primitive evolving systems of diverse plant communities (Little et al., 2015). South African Grasslands are being increasingly degraded through the increasing influence of overgrazing (Neke & Du Plessis, 2004), extensive and frequent burning (Uys et al., 2004), plantation forestry (Lipsey & Hockey, 2010) and invasion by alien plant species (Le Maitre et al., 1996). It is estimated that 60% of the Grassland biome has been permanently transformed, while as little as 15% remains as natural Grassland, with only 2% formally conserved in South Africa (Macdonald, 1989; Carbutt et al., 2011). What is alarming is that the majority of the natural Grassland is vastly fragmented, and most need to be better managed (Mucina & Rutherford, 2006).

Mountain Zebra National Park (MZNP) is a unique conservation area occurring at the interface of three Biomes, i.e., Grassland, Nama karoo, and thicket (Bezuidenhout & Brown 2008).Fire has recently become more common in the Nama karoo and other arid ecosystems, potentially threatening the persistence of native species (du Toit et al., 2015; Syphard et al., 2017). Climate change may be the reason why there is an increase in fire-conducive weather conditions (Wilson et al., 2010; Kraaij et al., 2012) and changes in the structural composition of vegetation affecting fuel attributes of ecosystems (D'Antonio & Vitousek, 1992; Syphard et al., 2017). Just like other Grassland vegetation types, MZNP Mountainous Grassland is prone to occasional lightning-caused fires (Hugo et al., 2016). Studies from the eastern Karoo suggest that fire can significantly modify vegetation structure and composition, similar to grazing and herbivory (du Toit et al., 2015). The complexity of the interaction between grazing, herbivory and climate in the region has been broadly acknowledged (Kraaij & Milton, 2006). Fire plays a huge role in shaping the structure and composition of vegetation (Veen et al., 2008). It provides a green flush of nutrient-rich grass by removing moribund grass materials (Bond & Wilgen, 1996). Although South African Grassland systems are naturally maintained by winter and spring fires (Mucina & Rutherford, 2006), there is concern over the possible detrimental effect of unnaturally frequent fires on plant diversity (Collins & Calabrese, 2012). It has been suggested that controlled burning should be based on the rate of litter accumulation and that grazing should not start until sward height reaches 250 mm (Mentis, 1981). Some of the palatable grass species require frequent burning, e.g., *Themeda triandra* and in the absence of fire, species such as *Merxmuellera disticha* and *Merxmuellera stricta* increases (Owen-Smith & Danckwerts, 1997). Although there are studies done on Grassland ecology in South Africa, limited studies exist in MZNP mountainous Grassland which to some extent, hinders the development of a suitable fire management plan for the park. Hence, this study aims to determine the influence of fire on (i) grass species richness and diversity, and (ii) grass relative abundance cover. We hypothesize that (i) burned sites will have high species richness and species diversity due to fire reducing moribund accumulation and making it easier for plants to get sunlight and other nutrients, and (ii) burned sites will have more palatable grass compared to unburned sites because fire encourages the growth of palatable grasses.

Methodology

Eighty (80) plots were laid out across the sites using purposive sampling (twenty per fire regime) with twenty plots in a site which burned in 2002 and 2010 and twenty in the unburned (control) site which is Site A. Another twenty plots were done in a site which burned in 2010 and 2019 with twenty plots on an unburned (control) site, site B (Figure 2.2). Each plot was approximately 20 metres x 20 metres (~ 0.04 ha) and spaced at least 100 metres apart. In each plot, all grasses were counted and identified to species level. The study was done during the growing season, from December to April for easy grass identification. Field identification of the grass was done during December and January. Each species was assigned a cover percentage value using the Daubenmire Cover Class Method while overall grass and shrub percentages were also estimated in each plot (Daubenmire, 1959).

Study area

The study was conducted in Mountain Zebra National Park (MZNP) (Figure 2.1), which is approximately 28 412 ha and located in the Eastern Cape Province, South Africa (32^{o} 22’ 47’’S; 25^{o} 47’ 88’’ E) (Bezuidenhout and Brown, 2008). MZNP was proclaimed in 1937, protecting a remnant population of the Cape Mountain zebra (*Equus zebra*) and has since played a principal role in the conservation of the biodiversity of the area (Grobler, 1983). Elements of three South African Biomes characterise the park: Eastern Cape Escarpment Thicket, Eastern Upper Karoo and Karoo Escarpment Grassland (53%), (Gaylard et al., 2006). The Park is one of the few protected areas that protect and preserve this vegetation (Bezuidenhout & Brown, 2008). It is classified as Nama Karoo but falls in between arid Nama Karoo bushveld in the west and the drier Grassland in the east (Gebeyehu & Samways, 2002). The biome is characterised by grasses and dwarf shrubs (Mucina et al., 2006). The park is located on the Northern slopes of the Bankberg mountain range in the Cape Midlands, Eastern Cape which is described as having a cool and arid climate (Bezuidenhout & Brown, 2008). It is dominated by sedimentary rock types such as sandstones, siltstones, and mudstones of the Beaufort Series. Post-Karoo dolerite intrusions are also prevailing in certain areas. The soil throughout the park is generally shallow with vast parts rocky with very little to no soil topsoil (Brown & Bezuidenhout, 2000). The average monthly temperatures in summer (September to March) vary between a minimum of 6 °C and a maximum of 28 °C. In contrast, in winter (April to August) the temperature often drops below 0 °C and reaches a maximum of 20 °C (Novellie & Gaylard, 2013). Rain falls mostly in late summer and autumn (December to April) (Novellie & Gaylard, 2013) and the average annual rainfall is 400 mm (Pond et al., 2002). The sites were actively grazed by the angulates in MZNP e.g. Cape Mountain Zebra, Red Hartebeest, Wildebeest etc.

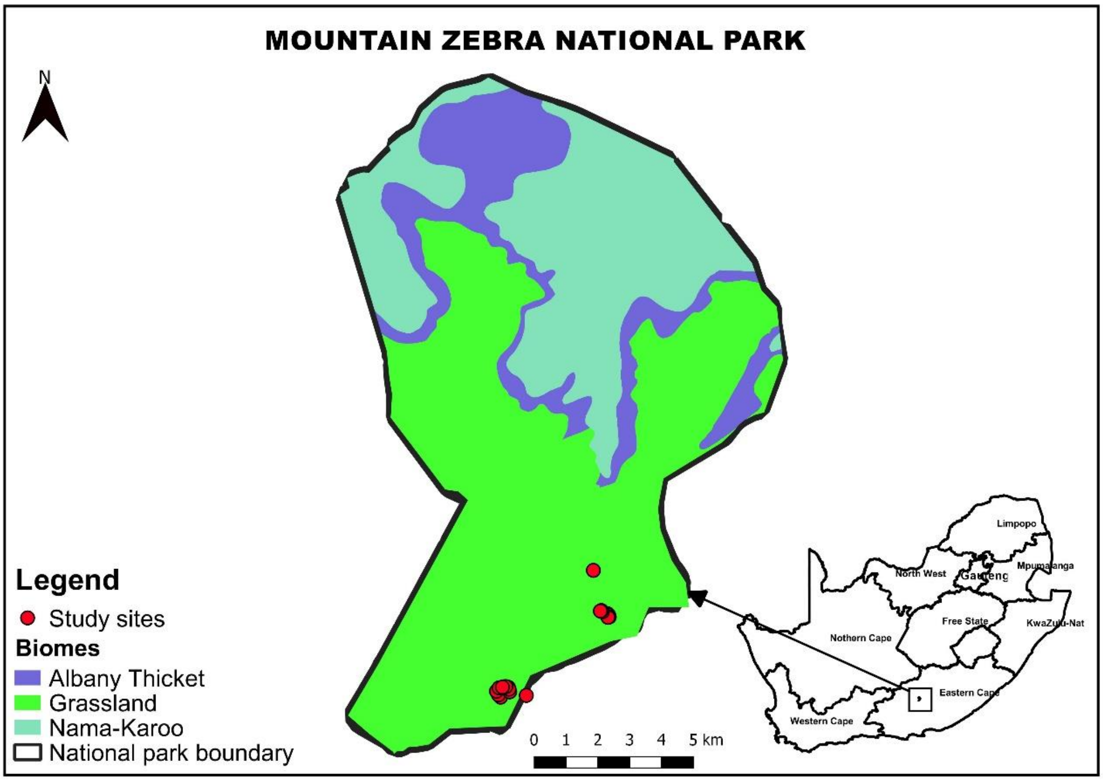

Figure 2.1: Location of the study sites within Mountain Zebra National Park

Field data collection

Fire frequency data

Historical fire data from 2000 until 2020 were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) MCD45 burned area product and Sentinel-1. The 2019 fire scar was obtained by physically mapping the fire scar on the ground. The fire data was then processed using a quantum geographic information system (QGIS) (Quantum GIS Development Team, 2016) to generate fire scar maps for the study sites. All the fires from 2000 to 2020 were in one vegetation type, i.e., mountain Grassland. Four fires have occurred in the park, i.e., in 2002, 2010, 2016 and 2019. The fire in 2016 was not used in the data because it was too small (< 10 ha). Two fire scars was used in this study, i.e., Site A (2002 and 2010) and Site B (2010 and 2019) fire scars.

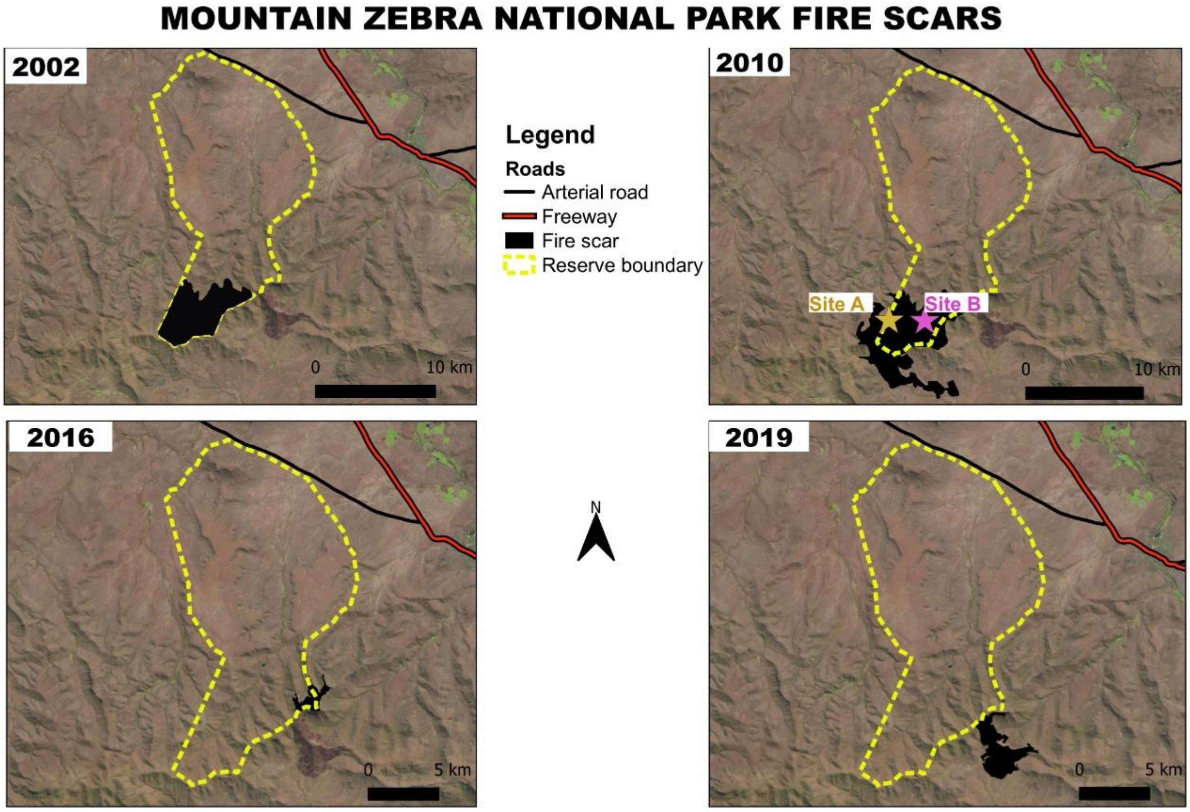

Figure 2.2: Fire scar maps showing the location of fires in MZNP between 2000 and 2020 1

Statistical Analysis

The statistical analyses were performed using R, where two response variables were investigated (R Development Core Team, 2011). These include species richness and normalised Shannon diversity index (NSDI). Species richness is calculated as absolute counts of the number of unique species at the corresponding vegetation units. On the other hand, NSDI is implemented as an extension of the original proposal by Shannon (1948). It is a fractional value that varies between zero and one. Indices closer to one imply a high degree of unevenness. The *p*-values reported in this work are adjusted for multiple testing using the Benjamini-Hochberg technique (Benjamini & Hochberg, 1995). This helps minimise the risk of incorrectly rejecting the null hypotheses verified with the statistical tests.

Results

Species Richness and Diversity

Overall, species richness was high in the burned compared to unburned areas, but not significant (*p*>0.05 Figure 2.3). There is no significant difference in grass species richness between burned and unburned sites for Site A and Site B (*p*>0.05, Figure 2.4).

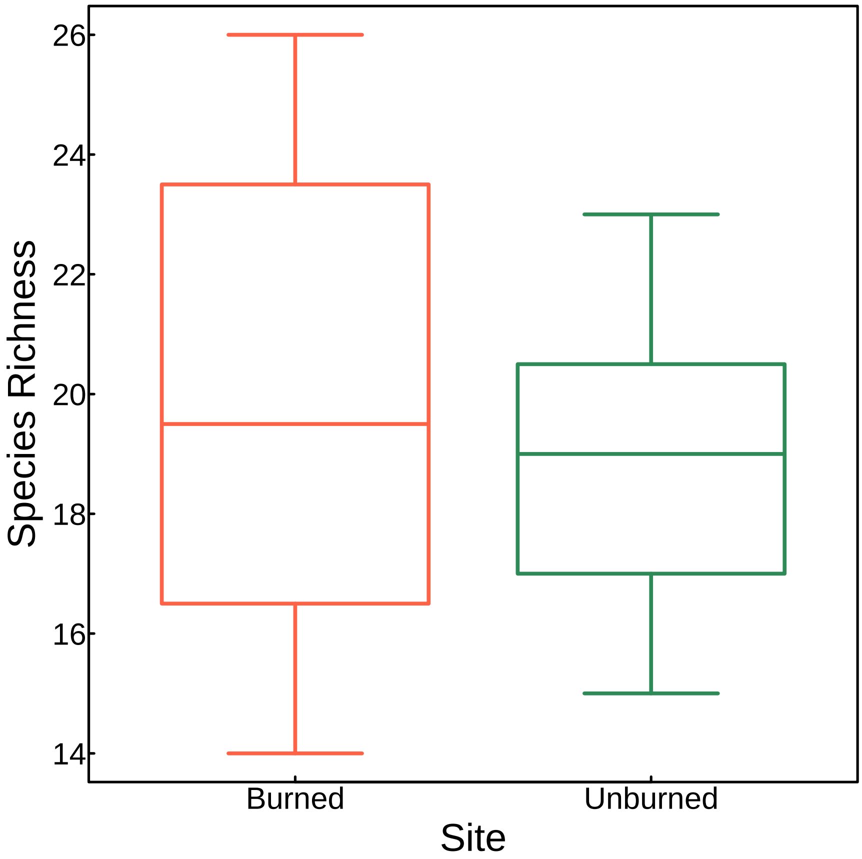

Figure 2.3: Mean difference in grass species richness between the burned and unburned sites

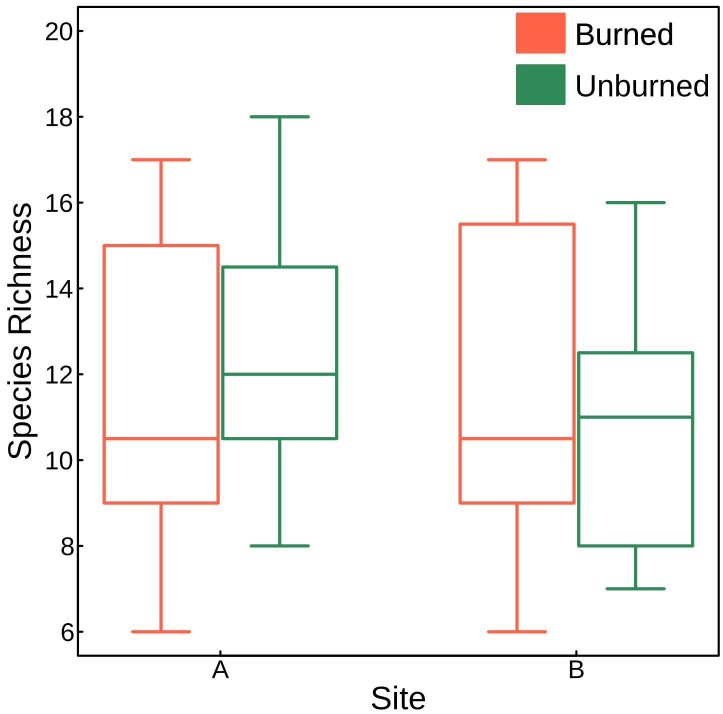

Figure 2.4: Mean differences in grass species richness between the two different fire occurrences, Site A and Site B.

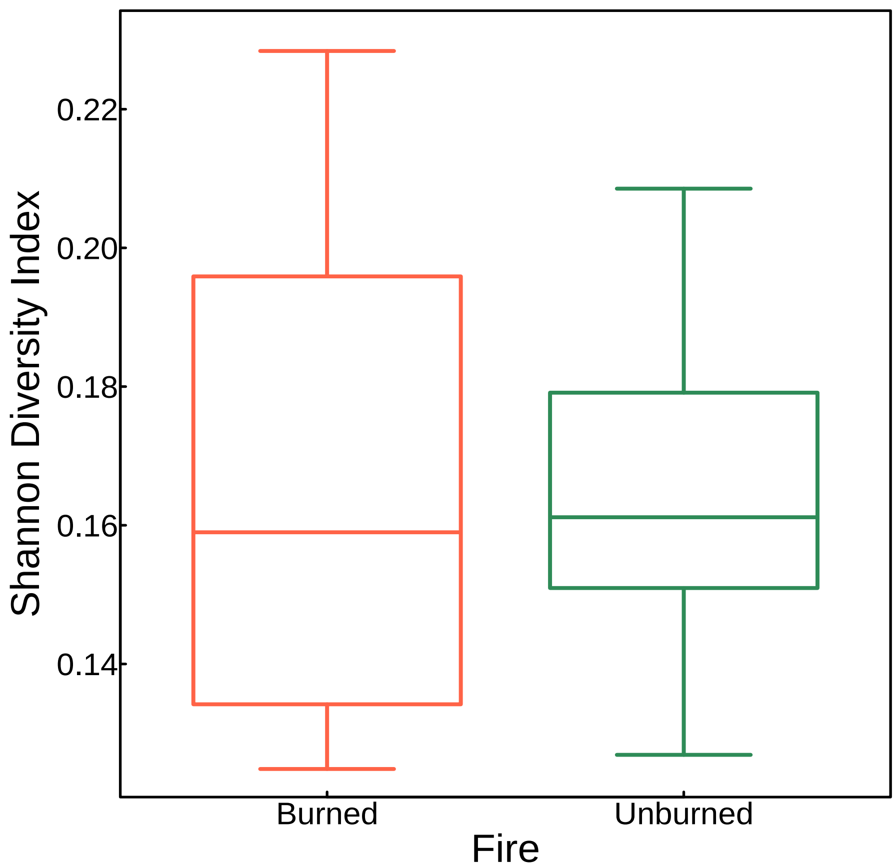

Figure 2.5: Mean difference in grass species diversity between the burned and unburned sites

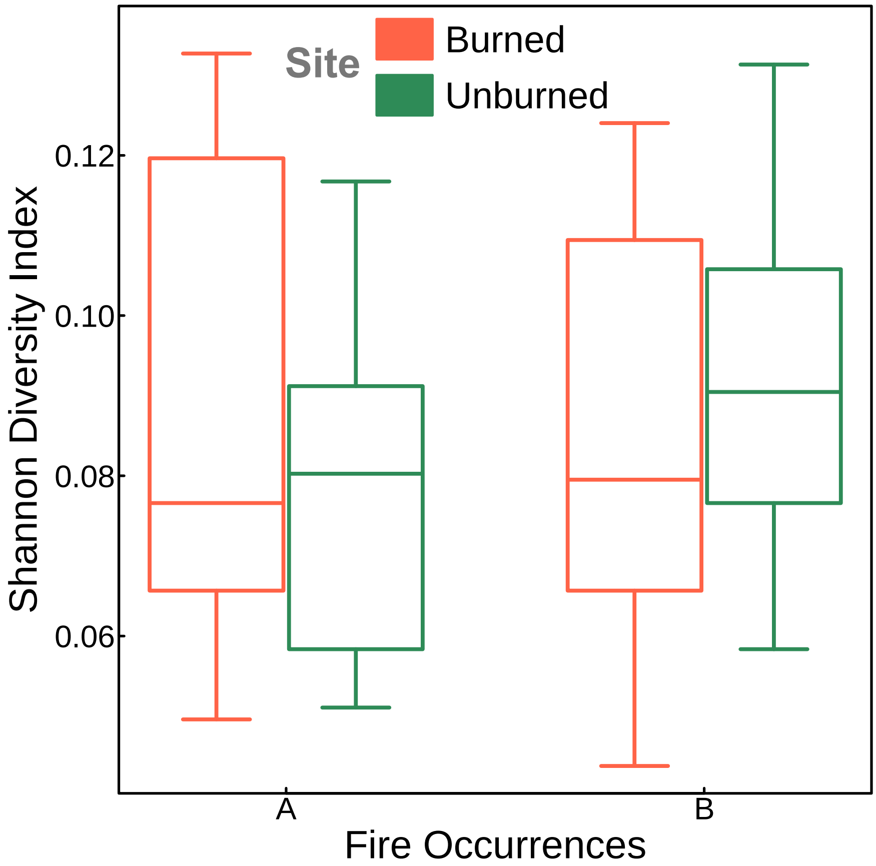

Figure 2.6: Mean difference in grass species diversity between burned and unburned areas in Site A and Site B

Percentage cover

Grass cover differed in burned and unburned sites for Site A and Site B (Figure 2.5 and Figure 2.6). While not statistically significant (p>0.05), there was greater grass percentage cover in the burned areas in Site A while in Site B, grass percentage cover was high in unburned sites versus the burned sites. However, there was no significant difference between the different fire frequencies regarding grass and shrub species composition (p>0.05). Grass percentage composition was not statistically different when comparing Site, A (2002 and 2010) and Site B (2010 and 2019) (p >0.05).

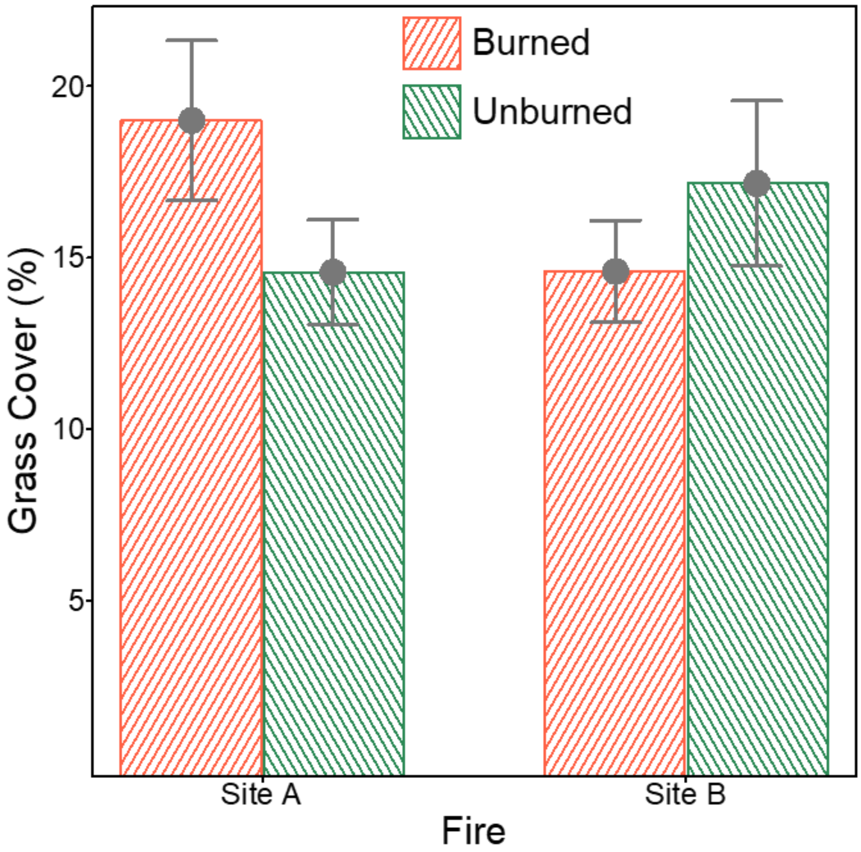

Figure 2.7: Grass percentage cover for both fire frequencies burned and unburned sites

Species composition

The species composition of the burned and unburned areas differed significantly (p<0.05). Species composition varied in both fire frequencies (Site A and Site B) burned sites compared to unburned sites, and the difference is statistically significant (p=0.00) (Figure 2.7). The results suggest that the absence of fire reduces or encourages certain species over others. For example, in Site A (2002 and 2010), there was a greater prevalence of *Themeda triandra* in the burned sites followed by *Cymbopogon pospischilli* which was similar in the burned and unburned sites and *Merxmuellera disticha* and *Merxmuellera stricta* in unburned sites (Figure 2.8). Site B also had a high percentage of *T triandra* in the burned sites compared to unburned sites followed by *Heteropogon contortus* which are both highly palatable species and *M disticha* and *M stricta* species composition higher in the unburned sites (Figure 2.9). The results from both fire frequencies show the highly palatable grass species *T triandra* to be high in burned sites compared to unburned sites. In contrast, unburned sites were dominated by *M disticha* and *M stricta* which is an unpalatable wiry grass with high moribund tendency.

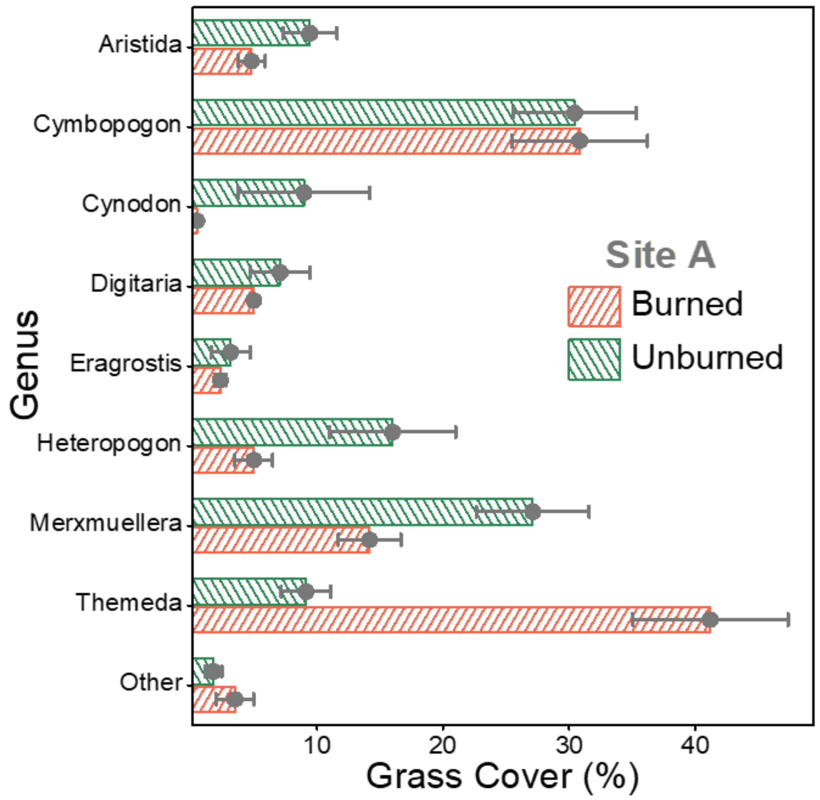

Figure 2.8: Species composition of the grass (%) in burned and unburned sites

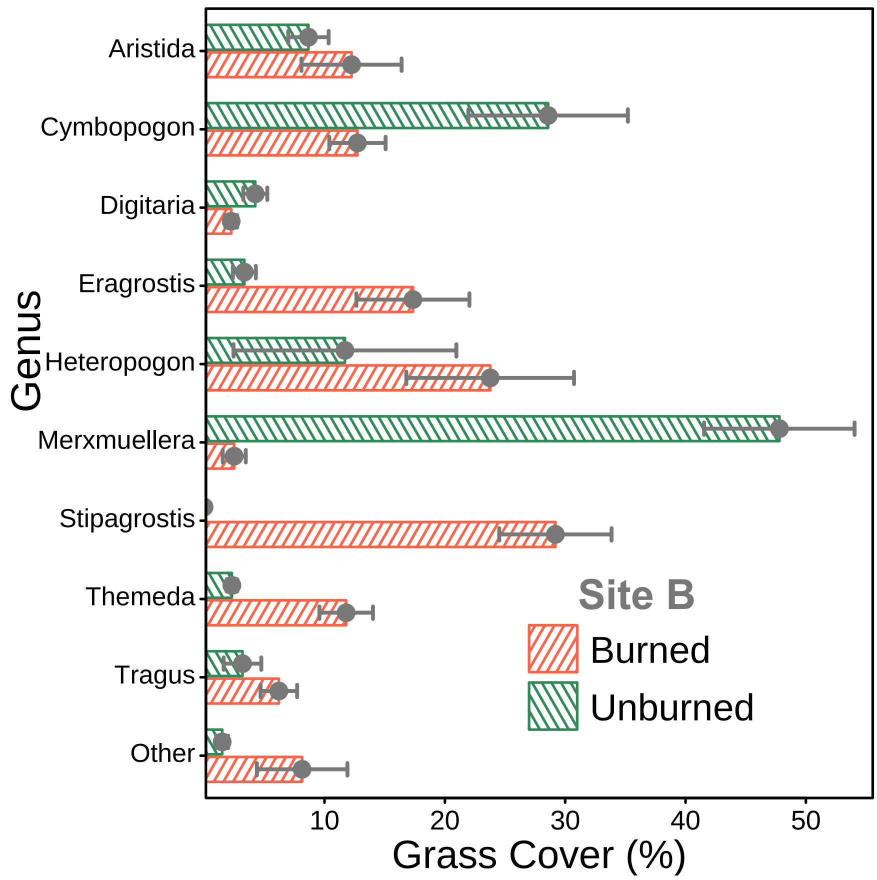

Figure 2.9: Species composition of the grass in burned and unburned sites

Discussion

Even though fire is known to cause replacement or addition in a habitat which results in species richness and diversity, there was no significant difference in terms of species richness and diversity in the burned and unburned areas (p>0.05 Figure 2.3). This is similar to a study done by Nepolo and Mapaure (2012) where there was no significant difference in burned and unburned sites' species richness in Semi-Arid Savanna woodland in Namibia. The results have shown the importance of fire in Grassland ecosystems as an ecological factor that determines the plant species composition (Bond & Wilgen, 1996). The grass with high moribund such as *Merxmuellera disticha* and *Merxmuellera stricta* were dominant in unburned (control) sites for both Site A (2002 and 2010) and Site B (2010 and 2019). The presence of *M. disticha* and *M. stricta* is a strong signal of habitat degradation or disturbance, as these two species are associated with moribund material which inhibits the growth of other species (Owen-Smith & Danckwerts, 1997). These are big tussock, wiry grasses that easily outcompete other grasses under conditions of selective grazing and the absence of fire. With fire suppression, these grasses create a huge amount of moribund, limiting sunlight and other resources for other plant species. One of the highly palatable grasses, i.e., *Themeda triandra,* was high in burned sites compared to unburned sites in both fire frequencies.

The absence of fire suppresses the palatable grass and promotes grass that does well under shady conditions. *Themeda triandra* is one of the most significant grasses in MZNP as it is the most palatable grass available for grazing animals (Zacharias, 1990). Consequently, the Grasslands dominated by *T. triandra* are of significant ecological importance at MZNP. *T. triandra* is considered a climax or sub-climax species (Smit et al., 1992) and an indicator of Grassland in good condition. It declines in abundance when overgrazed, underutilised or in the absence of fire (also commonly referred to as a 'Decreaser' species) (Van der Westhuizen et al., 2001; Wiegand et al., 2004). In South Africa, Australia and Southeast Asia, *T. triandra* dominate mainly in frequently burnt Grasslands, and their populations may decline to local extinction if fires are excluded for longer than a decade (Snyman et al., 2013). This is similar to this study, as *T. triandra* was low in composition in unburned areas. Manipulation of the fire interval is a key tool for influencing the biodiversity of vegetation stands (Bond & Keeley, 2005). Grass and shrub species composition differed significantly between burned and unburned areas.

The overall grass cover differed between burned and unburned sites however the difference was not statistically significant. Grass cover was higher in the burned area compared to an unburned area in the 2002 and 2010 fires (Site A) (Figure 2.7). Fire occurrence removes the moribund and the litter build up on the soil surface, changing the microclimate and nutrient levels in the surface soil (Lavorel et al., 1999). Therefore, removing these growth inhibitors by fire in the burned area has resulted in higher grass cover observed for this site. According to a study by Snyman (2003), fire increases plant nutrient availability in the soil, and acts as a natural selective force in the development of grass species. Fires play an important role in driving species composition in MZNP.

Although there was no significant difference in grass species richness and species diversity in burned and unburned sites, there was a significant difference in grass species composition in burned and unburned sites' species composition. Fire plays a vital role in species composition; hence there was a significant difference in Site B, where the fire burned less than three years ago, and no significant difference in Site A, where the fire burned more than ten years ago. This does show that the fire return interval should not be more than ten years as it affects grass species composition, and a site that burned more than ten years ago is almost similar to a site that has not burned in 20 years or more. One of the highly palatable grasses *T. triandra* was low in unburned sites compared to burned sites, and a decline in abundance of *T. triandra* in Grassland is usually coupled with a decrease in grazing value, species richness, and cover. Consequently, intermittent fire application for less than ten years is recommended as it could increase the abundance of palatable species. This is done to maintain a healthy, functional Grassland composition. If any natural fire occurs in a veld that has not burned in more than eight years, it must not be suppressed unless it threatens property or lives. One of the limitations of this study is the absence of prior data collected on the sites before the 2002 fire, which would bring a good comparison. In future it will be interesting to conduct a study looking at the fire frequencies influence on grass species composition.

Chapter 3: Influence of Environmental Factors on Species Richness and Diversity in a Semi-Arid Environment, South Africa.

This chapter is based on:

Munyai N.; Ramoelo, A.; Adelabu, S.; Bezuidehout, H.; Sadiq, H. Influence of Environmental Factors on Species Richness and Diversity in a Semi-Arid Environment, South Africa. *Grasses* **2023**, *2*, x. https://doi.org/10.3390/xxxxx

Abstract

The Nama Karoo biome is one of the least studied Biomes in the semi-arid region of South Africa, and essential baseline biodiversity data for this region are lacking. The present study aimed to examine the influence of environmental factors on the species diversity and richness of Mountain Zebra National Park, South Africa, which includes this vital biome. Vegetation data were obtained using the step-point method. Both species richness and diversity were unaffected by slope, aspect, coarse fragments, and soil texture. Multiple linear regression analyses indicated that a combination of four variables (nitrogen, clay, sand contents and longitude) should be included in the optimal model for species richness, and the optimal model for species diversity also revealed four influencing variables: soil organic carbon, clay content, sand contents and longitude. Overall, both species richness and diversity could be predicted by a combination of climatic, topographic, and soil properties. The findings of this study can be used as a reference for the effects of environmental factors on plant species richness and diversity in semi-arid environments.

Introduction

Vegetation plays a vital role in the lives of many organisms, as well as in natural preservation, and ecosystem balance (Hayden & Mahdavi, 2009). Any impact on an ecosystem, such as pollution, development, grazing, fire, and drought, is first observed through changes in the vegetation. Detailed studies on the species and population dynamics of vegetation in an area are critical for developing scientifically sound management and conservation strategies (Brown & Bezuidenhout, 2005). Plant species richness and diversity patterns are the foundations of ecology and conservation biology research (Noss, 1990). Local and regional plant community distribution patterns are influenced by environmental factors such as climate, topography, and soil physical and chemical properties (Wang et al., 2015). Although several ecological studies have explored different aspects of vegetation within the Nama Karoo biome (Pienaar, 2004), there still exists a considerable knowledge gap regarding the driving factors that influence this vegetation.

Soil is a vital environmental factor that influences ecosystem processes, and the distribution and characteristics of plant communities (Pienaar, 2004). Soil properties affect the redistribution of rainwater, including runoff and infiltration (Le Houérou et al., 1988). The chemical, physical and microbiological properties of soil influence the plant community structure, composition, distribution, and diversity (Eskelinen et al., 2009). In mountainous areas, elevation, slope and aspect are the main topographic factors affecting plant species composition, diversity, and distribution patterns (Huang,2002). Vegetation monitoring is essential for understanding the vegetation structure and species composition over time (Bezuidenhout & Brown, 2021). However, few studies have investigated plant biodiversity patterns in the semi-arid Nama Karoo biome. Previous ecological research in the region has primarily focused on livestock grazing effects on the landscape (Hanke et al., 2014; Todd & Hoffman 2009;), and several floristic studies have investigated species assemblages in some parts of the region (Brown & Bezuidenhout, 2018a). However, there is a need to further explore how environmental drivers affect the vegetation in the region.

Bezuidenhout and Brown (2021) divided Mountain Zebra National Park (MZNP) into 13 landscape units based on their geomorphological characteristics, land and soil types and plant species composition. These landscape units serve as management units and provide an ideal opportunity to study the species richness and diversity across various topographical areas. Mountain Zebra National Park was established to protect the threatened Cape Mountain Zebra. Since 1996, the Park has been expanded with the incorporation of various farms alongside the northern boundaries. As a result, the park more than doubled in size, from 6536 ha to approximately 21,000 ha (Bezuidenhout & Brown, 2018b).

The Nama Karoo biome, the second largest biome in South Africa, is located on the central plateau area of the country. The biome is characterized by the dominance of dwarf shrubs and grasses on the lower-lying valley bottom areas and plateaus, with medium-sized shrubs along moderate to steep mountain slopes (Dean et al., 1999; Mucina & Rutherford, 2006). The *Vachellia karroo* tree is prominent along drainage lines and streams. Although it is not as diverse as other Biomes, the fauna and flora of the region are adapted to the arid and semi-arid environments within which they occur. In the past, the biome was characterized by vast herds of springbok that used to migrate to the area in search of grazing land and water (Palmer & Hoffman, 1997). With the settlement of humans in the area, most wild animals were destroyed, while the fencing of the farms effectively cut off any animal migratory routes (Hoffman, 1988). The wild ungulates were replaced by sheep and angora goats that comprise the major agricultural activity of the area toda The stocking of the area with domestic animals leads to the heavy overgrazing of large sections of the biome (Dean et al., 1999). Alien invasive plants were also introduced into the area, which has resulted in the displacement of the natural vegetation of the biome in many areas (Lovegrove 1993; Milton et al., 1999). Moreover, mining activities in some parts have contributed to the destruction of the natural vegetation and habitat of the biome (Comley, 2016). To make scientifically justifiable decisions on the management of the remaining natural habitat, research on the vegetation of the area must be continued. This will not only provide an inventory of the biome but also of the diversity of species present (Bezuidenhout & Brown, 2018). The main objective of the present study was to determine the effects of environmental factors on plant species richness and diversity in the study area. The following hypotheses were tested: (i) species diversity and richness vary across different landscape units, and (ii) plant species richness and diversity significantly correlate with soil parameters and topographic factors.

Materials and Methods

Study Area

The study was conducted in MZNP (Figure 3.1), which covers an area of approximately 28,412 ha and is in the Eastern Cape Province, South Africa (32°22′47″ S; 25°47′8″ E). The Park comprises three Biomes of South Africa: Karoo Escarpment Grassland (53%), Eastern Upper Karoo (37%), and Eastern Cape Escarpment Thicket (10%) (Brown & Bezuidenhout, 2005). The Eastern Upper Karoo is characterized by flat and gently sloping plains, interspersed with hills and rocky areas where the dominant flora is dwarf microphyllous shrubs (*Pentzia incana* and *Eriocephalus ericoides*) (Gaylard et al.,2006). The Karoo Escarpment Grassland is characterized by low mountains and hills, with wiry tussock Grasslands and mountain wire grass (*Merxmuellera disticha*) being the dominant flora. The Eastern Cape Escarpment thicket is characterized by steeply sloping escarpment and mountain slopes with medium-high and semi-open to closed thicket, where the dominant flora are olive trees (*Olea europaea*) (Brown & Bezuidenhout, 2005). The Park is located on the northern slopes of the Bankberg mountain range (Gaylard et al.,2006). It is dominated by sedimentary rock types such as the sandstones, siltstones, and mudstones of the Beaufort Series (Novellie & Gaylard, 2013). Mountainous terrain with steep-sided drainage lines makes up the southern quarter of the park, where the highest point is found along Bankberg Mountain which is 1 957 meters above sea level, with the lowest part of the park in the northern section only reaching 1 000 meters above sea level (Pond et al., 2002; Novellie & Gaylard, 2013). The soil in the park is predominantly shallow, with large areas of the park being rocky and having minimal or no topsoil (Gaylard et al.,2006; Novellie & Gaylard, 2013). The average monthly temperature in summer (September to March) varies between a minimum of 6 °C and a maximum of 28 °C, whereas in winter (April to August), the temperature often drops below 0 °C and reaches maximums of 20 °C (Mentis, 1981). Rainfall occurs regularly from December to April (Mentis, 1981), and the average annual rainfall is 400 mm (Figure 3.2) (Bothma et al., 2004). The region experiences periodic light snow during the winter months, and frost is common between May and October (Mentis, 1981).

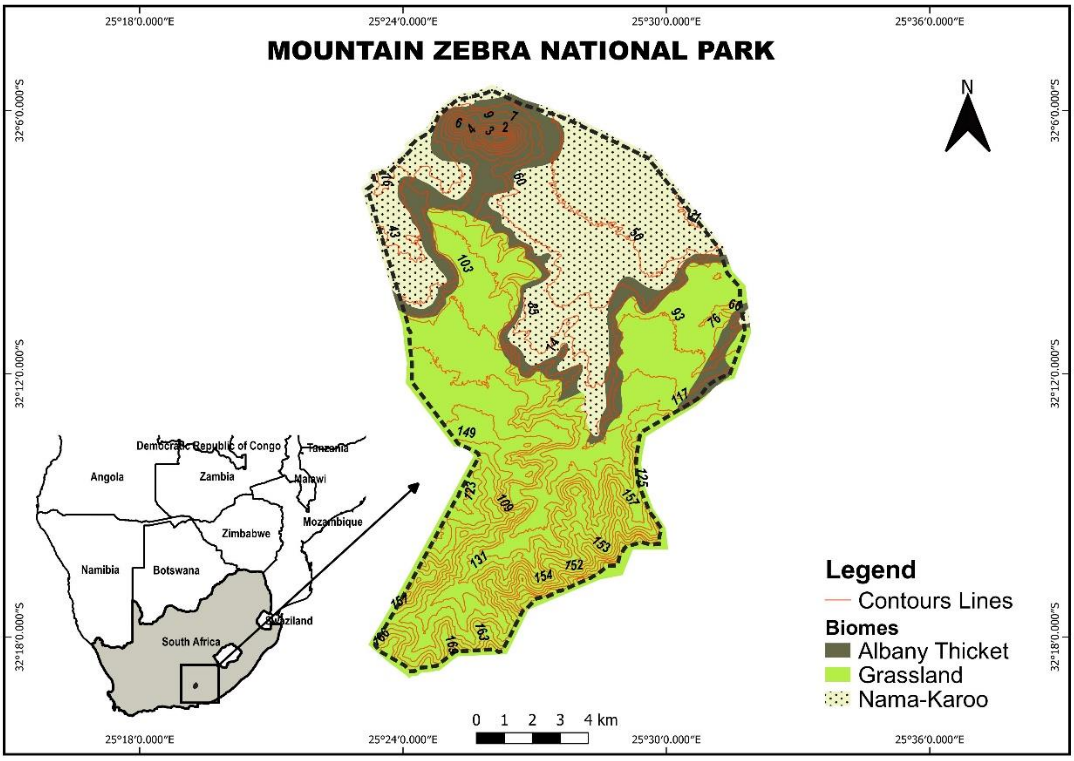

Figure 3.1: Location of Mountain Zebra National Park (MZNP) in South Africa and the three Biomes in the study area in the park (contour interval = 10 m).

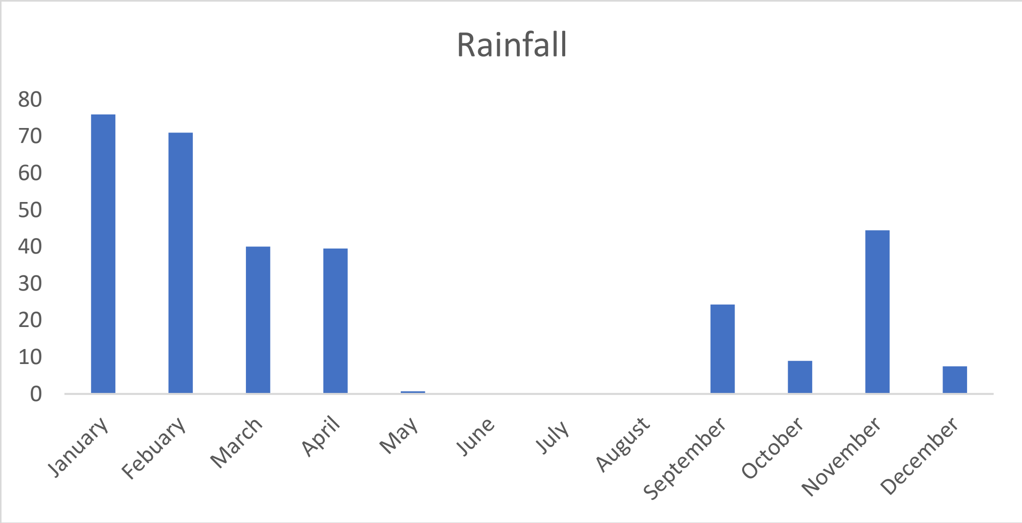

Figure 3.2: Climate and rainfall in Mountain Zebra National Park from 2019.

Field Data Collection: Plot-Based Method

Sampling was conducted using transects distributed across the different vegetation units in the park (Figure 3.3). Vegetation units are the categories of different portions in the park that are based on the dominant vegetation and the growth forms. Data were collected using the step-point method (R Core Team, 2016), using an approach based on a method reported previously (Shannon, 1948). In total, 50 transects were sampled across the eight management units. Several plots differed across the vegetation units. The transects were 50 meters long, and observations were made at 1-metre intervals, where the plant in contact with the meter stick was identified and recorded. All plants in the plots were identified to the species level. The geographical positioning system (GPS) coordinates were recorded using a Garmin GPSMAP 64s GPS device. The study was conducted during the growing season (January to February 2021) to facilitate easy plant species identification.

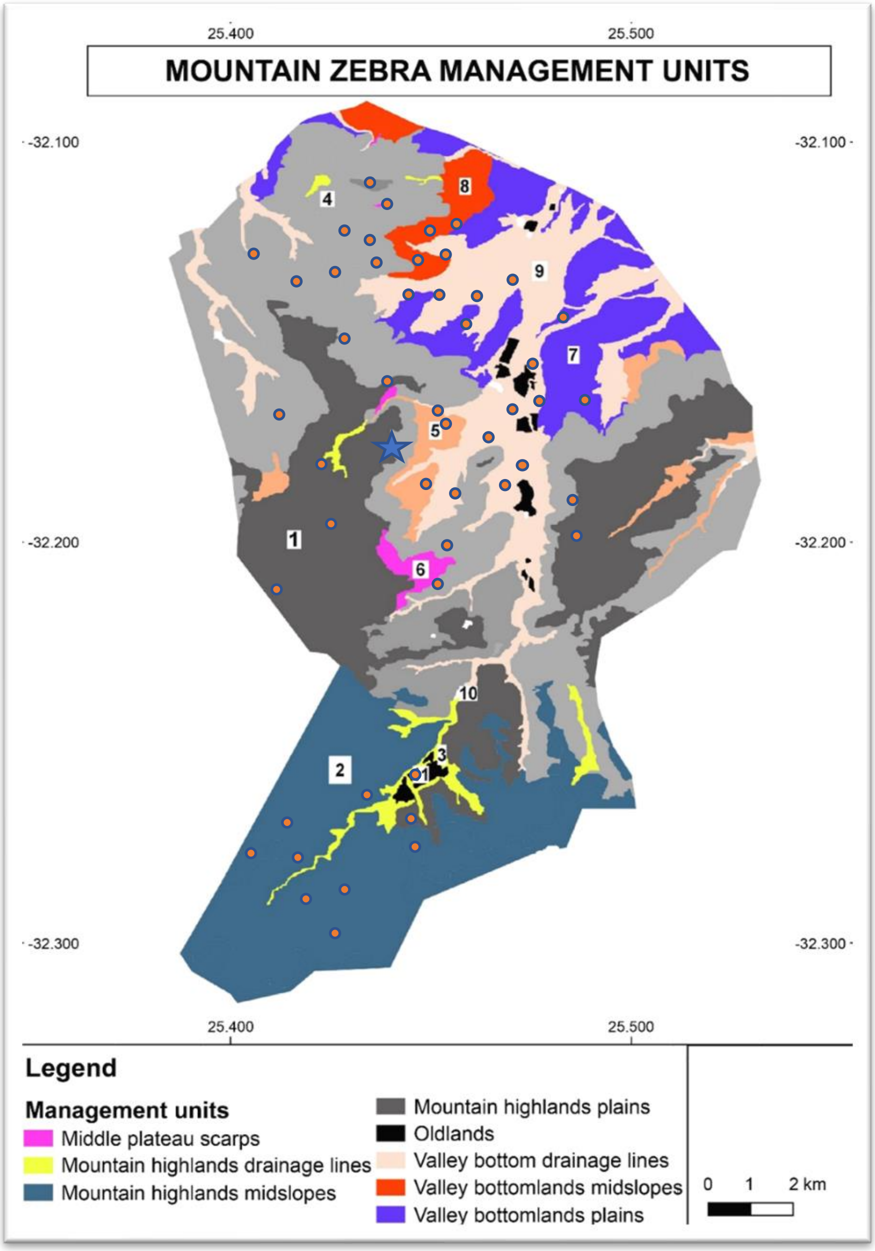

Figure 3.3: Location of the monitoring plots in the Mountain Zebra National Park management units. The star symbol on the map represents the location of the climatic weather station. Numbers 1 to 11 on the map are different vegetation units.

Climate and Soil Data

Digital elevation model (DEM) data were obtained to compute the slope and aspect data and environmental data, except the rainfall data, were extracted for each sample site using Quantum GIS (QGIS) 2.18.0 (Las Palmas de G.C.). All the layers that were applied in QGIS used the geographic coordinate systems WGS84 and EPSG:4326 as spatial references. This was completed using WorldClim, which allows for the extraction of raster values to points. The soil physical properties included organic matter content, sand, clay, coarse fragments, and silt, whereas the chemical properties included nitrogen and organic carbon (Table 3.1).

Table 3.1: Environmental variables used in the present study.

Class	Variable	Source	Scale/Resolution
Topography	Digital elevation model (DEM)	SRTM	30 m
	Slope	Derived from DEM	30 m
	Aspect	Derived from DEM	
Soil chemical properties	Nitrogen (cg/kg)	Soil grids	250 m
	pH	Soil grids	250 m
	Organic carbon (g/kg)	Soil grids	250 m
	Cation exchange capacity (mmol/kg)	Soil grids	250 m
Soil texture and physical properties	Silt	Soil grids	250 m
	Coarse fragments (cm^3 /dm^3)	Soil grids	250 m
	Bulk density (kg/cm^3)	Soil grids	250 m
	Sandy (g/kg)	Soil grids	250 m
	Clay (g/kg)	Soil grids	250 m

Statistical Analyses

Statistical analyses were performed using R (R Development Core Team, 2019). Two response variables were investigated: species richness and the normalized Shannon diversity index (NSDI). Species richness was calculated as the absolute number of unique species in the corresponding vegetation units. The NSDI (a fractional value that varies between zero and one) was implemented as an extension of the original proposal by Shannon. The association between the response variables and different environmental variables was evaluated using appropriate visual and quantitative statistical tools. Geographic coordinates were also considered as predictor variables in the models. The GPS coordinates serve as proxies for the environmental gradient, meaning that the information added to the model by the longitude and latitude variables can be considered as an indicator of the positions of the plots on the map. Because of the limited size of the dataset used for the analyses, the p-values reported in this work were adjusted for multiple testing using the Benjamini–Hochberg technique (1995), which minimizes the risk of incorrectly rejecting the null hypotheses verified with the statistical tests. Notably, all areas in each vegetation unit had similar richness and NSDI values, implying that the vegetation unit variable perfectly separated the response variables. Regression analyses were used to separate and evaluate the relationship between the overall species richness and the NSDI. These analyses required us to implicitly assume that the unobserved population data of the pairs of responses were normally distributed, depending on the predictors. Environmental variables were included as predictors in the models. The decisions regarding the parsimonious models relied on Akaike information criteria (Akaike, 1993) and an analysis of variance (ANOVA). The NSDI was estimated, such that for each vegetation unit k, $NSDI_k = -\frac{1}{\log(S)}\sum_{i=1}^{S} p_i \log(p_i)$.

The notation is $p_i = n_i/\sum n_i$, where n_i is the number of times species i was observed in vegetation unit k and $S = 54$ denotes the total number of unique species observed across all the vegetation units. Normalization permits unbiased comparisons among vegetation units.

Results

Both the species richness and the NSDI had low *p*-values (≈0.0003), indicating a statistically significant difference between richness and diversity across the vegetation units (Table 3.2). Unit 1 contained the highest number of species (Dybzinski et al., 2008), whereas Unit 11 had more than five times fewer species (6). Subsequently, the degree of pairwise relationships between the vegetation unit response and each different environmental predictor was investigated using ANOVA and linear correlations.

Table 3.2: Species richness and the normalized Shannon diversity index (NSDI), summarized concerning the vegetation units. The reported *p*-values obtained from the Chi-squared test of equal counts and proportions were adjusted for multiple testing.

	Vegetation unit									***p*-value**
	1	**2**	**3**	**4**	**5**	**7**	**8**	**9**	**11**	
Species richness	34	30	12	29	23	15	15	21	6	**0.0003**
NSDI	0.363	0.325	0.623	0.412	0.334	0.614	0.469	0.536	0.722	**0.0003**

The widths of the lines drawn in the graphical illustrations of continuous predictors were two times greater than those of the associated standard errors (Figure 3.4). The dots represent the positions of the corresponding average values. A statistically significant association was observed only between the vegetation units adopted here as a proxy for the NSDI and species richness. This inference was based on the corresponding low *p*-values ($p<0.05$). The longitude coordinate, rainfall and soil organic carbon content in Unit 2 appeared to be significantly higher than similar measurements in the other units.

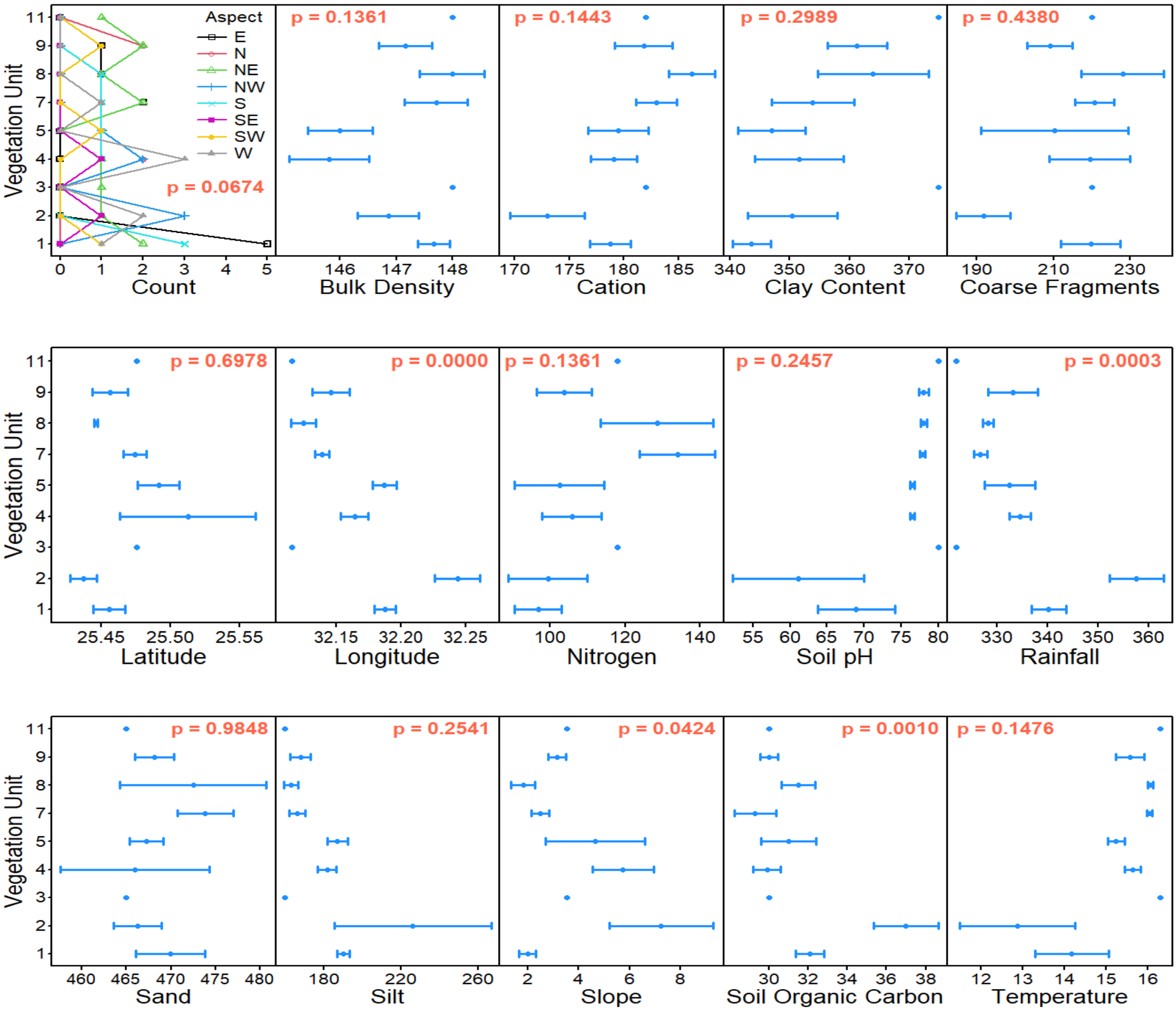

Figure 3.4: Pairwise comparison of the environmental and geographical predictor variables against the vegetation unit variable. The vegetation unit was used here as a proxy for the normalized Shannon diversity index and the species richness response variables. The reported adjusted p-values were obtained from appropriate Fisher tests of association.

Outputs from examining the magnitude and direction of the linear relationship between all pairs of continuous variables in the data are summarized in the correlation matrix (Figure 3.5). It is evident from the matrix that the coarse fragment variable had the lowest degree of linear correlation with the other continuous variables in the data. However, longitude appears to have the strongest linear relationship with the other variables. Sand exhibited the highest (approximately zero) pairwise linear correlation. These observations implied that: (1) the information provided by the longitude coordinates was similar to that provided by many of the other variables in the data, indicating that such “other” variables are likely to be redundant; (2) sand and coarse fragment variables are unlikely to be displaced from an optimal model, except if the quality of the information that they contribute is invaluable.

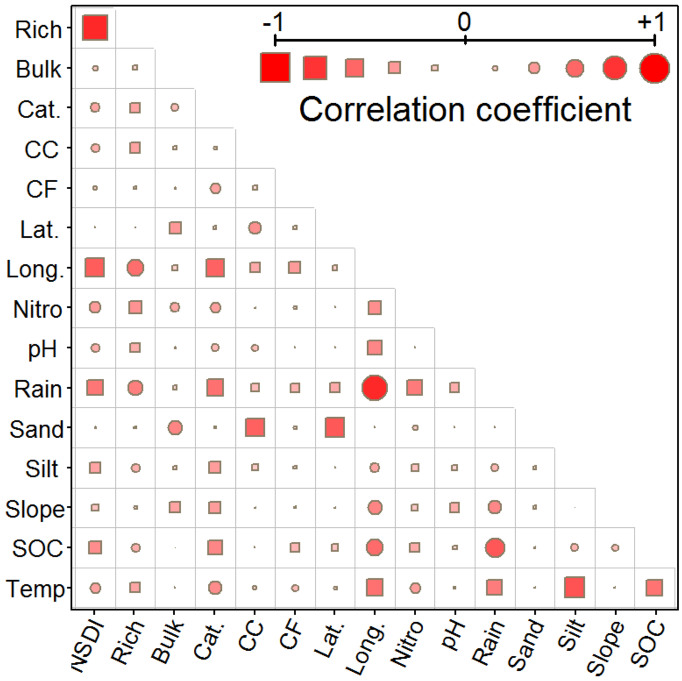

Figure 3.5: Pairwise linear correlation matrix for all the continuous variables in the analyzed data. The cells' colour, size, and shape are proportional to the corresponding coefficients. NSDI = Normalized Shannon diversity index; Rich = Species richness; Bulk = Bulk density; Cat. = Cation; CC = Clay content; CF = Coarse fragments; Lat. = Latitude; Long. = Longitude; Nitro = Nitrogen; pH = soil pH Water; Rain = Rainfall; SOC = Soil organic carbon; Temp = Temperature

The linear predictive equations for the NSDI and species richness, including all predictor variables in the dataset, are presented (Table 3.3). Note that the aspect categories were included in the model as dichotomous variables, with east being the reference category. Without a loss of generality, the East-Aspect category of vegetation units was adopted as the reference group for understanding the impact of Aspect on the response variables. The regression estimates from the regression model related to the Aspect should be interpreted relative to the East-Aspect group. In addition, owing to its perfect portioning property, the vegetation unit variable was not included as a predictor variable. The degree of the observed variation in the response variable explained by the predictive models was measured by the adjusted correlation coefficient. The estimates were 38.13% and 33.43% for the NSDI and species richness, respectively. The regression coefficient estimated that eight of the predictors in the NSDI equal zero. This implied that the predictors did not affect the NSDI values in the presented full-model expression.

Table 3.3: Parsimonious multiple linear r multiple linear regression for the species richness response as inferred through the implementation of all-subset variable selection analysis.

$\textbf{Species Richness} = \beta_0 + \beta_1 \times \text{Clay Content} + \beta_2 \times \text{Longitude} + \beta_3 \times \text{Nitrogen} + \beta_4 \times \text{Sand}$					
Coefficient	Estimate	Std. error	p-value	95% Confidence interval	
				Lower	Upper
β_0	-1528.7705	816.4972	0.0674	-3171.3511	113.8101
β_1	-0.2045	0.0778	0.0116	-0.3611	-0.0479
β_2	53.3856	25.5911	0.0424	1.9030	104.8682
β_3	-0.0715	0.0411	0.0885	-0.1541	0.0112
Adjusted correlation coefficient: 43.53%					

Consequently, it is necessary to seek less complex models, i.e., those made up of fewer influential predictors, which are almost as effective as the full models.

The clay content, longitude and sand predictor variables constituted the optimal models for both response variables (Tables 3.3 and 3.4). These three variables were also inferred to significantly influence the estimates of both the NSDI and the species richness. This claim was based on the corresponding low adjusted p-values (<0.05). The clay content and sand variables had positive impacts on the response values. In contrast, the longitude tended to be negatively associated with the NSDI, but positively associated with species richness. Two predictors, namely soil organic carbon for the NSDI, and nitrogen for species richness, were included in the final models, despite them not showing a statistically significant impact in determining the relative response value. This non-significance could result from the conservativeness related to the multiple test corrections or because these variables represent confounders. Thus, a pair of predictors could benefit from future interrogation with a larger dataset. The optimal models identified through all-subset variable selection analyses used to achieve the set objective are summarized in Tables 3.3 and 3.4 for the NSDI and species richness responses, respectively.

Table 3.4: Optimal linear regression model for the normalized Shannon diversity index (NSDI) response, as identified through the implementation of all-subset variable selection analysis.

Coefficient		**Std. Error**			
				Lower	**Upper**
β_0	26.1353	13.1958	0.0053	−0.4113	52.6819
β_1	0.0026	0.0012	0.0279	0.0003	0.0049
β_2	−0.8593	0.4119	0.0424	−1.6880	−0.0306
β_3	0.0027	0.0013	0.0416	0.0001	0.0053

Discussion

The main findings indicate that the chemical properties of soil (nitrogen and soil organic carbon) significantly impacted species richness and diversity and that the clay and sand content (i.e., soil texture) positively affected species diversity. In contrast, the physical properties of soil (silt) did not affect plant species richness and diversity. Furthermore, our results suggested that soil nitrogen content influences species richness, as the nitrogen content was inversely proportional to species richness. The negative relationship between species richness and soil nitrogen content in the present study was in accordance with the findings of Tilman (1999) as well as Harpole and Tilman (2007), but it contradicted the “fertility effect” theory of Dybzinski et al., (2008). Duprè et al., (2010) conducted a temporal analysis of species richness in Grassland and found that species richness significantly declined relative to the estimated cumulative nitrogen deposition. However, other authors have contended that species richness increases with the increase in fertility (Gentry, 1988; Stark,1970).

The results of the present study supported the hypothesis that plant species richness, diversity and soil parameters are correlated. Evaluating the factors controlling plant species richness and diversity distribution patterns is crucial to conclude the unresolved debate regarding the association between plant diversity and soil properties (Silva et al., 2013). The relationship between the soil and plant response is vital for succession and competition dynamics (Kulmatiski et al., 2008). Environmental factors such as soil properties positively and negatively influence species diversity and richness (Abbasi-Kesbi et al., 2016). In the present study, clay and sand content (i.e., soil texture) positively affected species diversity. This finding differs from the observation of Abbasi-Kesbi et al., (2016) that species diversity was negatively correlated with sand and clay content. In general, the effect of soil texture on the distribution of plant species is due to the influence of moisture on the soil. Similarly, species richness was negatively correlated with clay and nitrogen content in the present study, as previously observed by Shimono et al., (2010) who reported a negative correlation between species richness and soil clay content. This study also showed that longitude had a positive impact on species diversity and a negative effect on species richness.

Chapter 4: Effects of environmental factors on plant productivity in the mountain Grassland of the Mountain Zebra National Park, Eastern Cape, South Africa

This chapter is based on

Effects of environmental factors on plant productivity in the mountain Grassland of the Mountain Zebra National Park, Eastern Cape, South Africa

Nthabeliseni Munyai[1]* and Abel Ramoelob[2] Samuel Adelabu[3], Hugo Bezuidehout [4]and Hassan Sadiq[5]

Abstract

The relationship between plant productivity as measured by biomass and species richness is a fundamental focal point in community ecology, as it provides the basis for understanding plants' responses or adaptive strategies. Although several studies have been conducted on plant biomass and environmental factors, research on this aspect in mountainous Grassland is scarce. Therefore, in this study, I aimed to examine the influence of environmental factors on the aboveground plant biomass in the mountainous Grassland of Mountain Zebra National Park, Eastern Cape, South Africa. Biomass was not normally distributed in the park due to some species having higher biomass compared to others. These are soil chemical and physical properties which were: carbon, nitrogen, soil pH and soil texture (sand, silt and coarse fragments). A disc pasture meter was used to collect the biomass data. Multiple regression analysis revealed that most of the environmental factors did not significantly influence the plant biomass. The only environmental factor influencing plant biomass was soil pH, whereas all other factors were insignificant. The result from this study provides discernment on how environmental factors interact with plant biomass. Future study should look at how environmental factors influences plant biomass both below and above ground.

Introduction

Vegetation biomass distribution is a vital concept in plant life history, providing the basis for our understanding of plants' responses or adaptive strategies (Chen et al.,2019; Sims et al., 2012). Plant biomass determines the ability of an ecosystem to acquire energy, thus playing a vital role in shaping the community structure and the function of the ecosystem (Fei et al., 2022; Ma et al., 2021). This is because vegetation biomass is a key contributor to soil organic matter, which can influence greenhouse gas emissions in terrestrial ecosystems (Liu et al., 2020). Thus, vegetation biomass is considered to have a particular function in the global carbon (C) cycle (Wang & Lan, 2011). The general prediction is that terrestrial ecosystems globally will be affected by climate change. This is because some of the anthropogenic impacts of climate change include changes in precipitation, atmospheric C, and plant biomass production (Thakur et al., 2022; Walter 2010 and). Plant biomass contributes to food webs and overall ecosystem function (Wardle et al., 2004). With an increase in atmospheric C concentrations over the past several decades, studying plant biomass is essential for understanding vegetation dynamics, terrestrial ecosystem C stocks, and their response to environmental changes (Gao et al., 2021). Plant biomass represents the amount of total energy stored in a unit surface area during an observation period. It is influenced by the availability of limited resources such as water, carbon dioxide, and nitrogen (N) (Tilman et al., 2012) however, the interactive effects of these environmental factors on plant biomass remain unclear (de Bello et al., 2013).

Environmental factors play an important role in C accumulation and contribute to C transformation (Farrior, 2013). Environmental factors influence C absorption, thereby influencing plant growth and biomass (Lee et al., 2013). Grassland ecosystems cover approximately 40% of the Earth's land surface, and they account for 1/10 of global C storage (Hui & Jackson 2006). Consequently, it is critical to investigate plant productivity to understand vegetation dynamics, terrestrial ecosystem C stocks, and their response to environmental changes (Hui & Jackson 2006). A shift in environmental conditions would affect vegetation biomass (Maherali & DeLucia 2001). Soil nutrients influence C absorption, thereby influencing plant growth and increase in biomass (Lee et al., 2013; Reich & Hobbie 2013). Several studies have shown that plant biomass plays a vital role in shaping the community structure and ecosystem function (Anderson, 2011; McCarthy & Enquist, 2007; Van der Putten et al., 2009;). However, little is known about the interactive effects among these environmental factors on plant biomass (Bello et al.,2013 & Owens et al.,2013)

The responses of plant biomass to different environmental factors are complex, and research on the interactive effects of potential environmental driving factors (such as climate, soil properties, and topographic properties) on plant biomass distribution in Mountain Zebra National Park (MZNP) is scarce. Therefore, in the present study, plant productivity across MZNP was assessed and the influence of environmental factors on plant productivity was examined. The focus was on aboveground biomass (AGB), since it can be measured without causing any disturbance to the topsoil, compared with belowground biomass (BGB) measurements, which require the entire plant to be uprooted.The objectives of the present study were to determine whether biomass is evenly distributed across the park, whether environmental factors play a role in plant biomass production, and whether different plant genera account for different biomass values. The hypothesis was that higher N availability would enhance high plant productivity because N is one of the basic nutrients that limits plant growth and, subsequently, plant productivity (Chen et al., 2013).

Methodology

Study area

This study was conducted in MZNP (Figure 5.1). MZNP is approximately 28,412 ha in size and is located within the Eastern Cape Province of South Africa (32°22’47” S and 25°47’88” E) (Bezuidenhout & Brown 2021). The park is covered with three main Biomes: Karoo Escarpment Grassland (53%), Nama karoo (37%), and Albany Thicket (10%) (Figure 4.1) (Mucina et al., 2006). The area is characterized by a cool and arid climate, with an average annual rainfall of 400 mm (Pond et al., 2002).

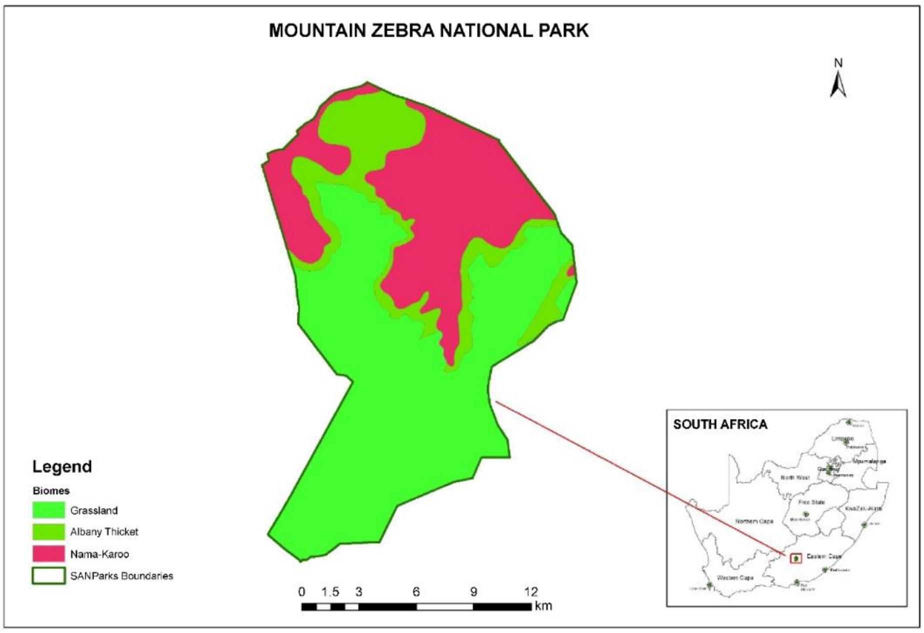

Figure 4.1: The location of the study area shows the three Biomes in the Mountain Zebra National Park and the location of the park in South Africa.

Field data collection

The data set was collected from different vegetation units across MZNP (Figure 4.2) (Bezuidenhout & Brown 2021). A total of 52 plots were sampled where biomass was collected in a transect which was 50 meters long. At each one-meter interval along the transect a disc pasture meter was used, and biomass was collected. A disc pasture meter is widely used to estimate plant productivity rapidly and non-destructively (Harmse et al., 2019) and was used to measure herbaceous biomass (De Klerk et al. 2001; Trollope & Potgieter 1986). Plant species data were collected along the same 50-metre transect using the step-point method described by Mentis (1981). The plants were identified to species level using the field identification guides and recorded. The plants were then grouped into different genus levels to determine if biomass is influenced by the plants' genera. The GPS coordinates were recorded using a GPS device (Garmin GPSMAP 64s), this was done to have the plots recorded for them to be used as baseline data in future. The following soil properties were examined: N, soil pH, clay content, silt, sand, slope, bulk density, coarse fragments, and cation exchange capacity.

Climate and Environmental Data

Digital elevation model data were obtained and used to compute the slope and aspect information using QGIS. Environmental data (Table 4.1) were extracted using QGIS 2.18.0 (Las Palmas, Spain). The geographic coordinate systems WGS84 and EPSG:4326 were used as spatial references. The environmental data included: (a) longitude (degrees), (b) latitude (degrees), (c) vegetation unit (VU; integer), (d) cation exchange capacity at pH 7 (mmol/kg), (e) N (cg/kg), (f) soil organic carbon (t/ha), (g) pH soil (pH × 10), (h) bulk density (cg/cm^3), (i) clay content (g/kg), (j) coarse fragments (cm^3/dm^3), (k) sand (g/kg), (l) silt (g/kg), (m) aspect (character), (n) slope (continuous), (o) annual mean rainfall (mm), and (p) annual mean temperature (°C).

Table 4.1: Environmental variables used in the present study

Class	Variables	Source	Scale/resolution
Topography	Digital elevation model (DEM)	SRTM	30 m
	Slope	Derived from DEM	30 m
	Aspect	Derived from DEM	
Soil chemical properties	Nitrogen (cg/kg)	Soil grids	250 m
	pH	Soil grids	250 m
	Organic carbon (g/kg)	Soil grids	250 m
	Cation exchange capacity (mmol(c)/kg)	Soil grids	250 m
Soil texture and physical properties	Silt (g/kg)	Soil grids	250 m
	Coarse fragments (cm^3/dm^3)	Soil grids	250 m
	Organic content (g/kg)	Soil grids	250 m
	Bulk density (cg/cm^3)	Soil grids	250 m
	Sandy (g/kg)	Soil grids	250 m
	Clay (g/kg)	Soil grids	250 m

Statistical analyses

Species diversity was measured using the Shannon (1948) diversity index (SDI). This choice was made without loss of generality. Species richness and Simpson's (1949) index were considered, with both generating strong correlations (87.80% and 95.20%, respectively) with the chosen SDI. The observed degree of correlation between the index pairs was expected, since all the indices are variants of the Hill (1973) index (Roswell et al., 2021). Thus, the choice of species diversity was established without bias. Given the proximity of the data points to one another, it was first checked for autocorrelation using Moran's Index (Moran, 1950) test, as implemented in the ape package (Paradis & Schliep, 2019) of the R statistical software version 4.3.0 (R Core Team, 2022). The test was conducted with biomass records. The distance between the longitude and latitude measurements was converted to weights using the population density adjustment technique (Jackson et al., 2010; Song & Kulldorff, 2005). A p-value of approximately 0.0094 was obtained. As expected, this implied that a statistically significant autocorrelation between the observations exists. As a result, all tests of association with biomass presented herewith were solved as generalized least squares regression problems (Pinheiro et al., 20021; R Core Team, 2021) with a spherical correlation structure as recommended by Beale et al., (2010). The correlation structure was formed with the latitude and longitude coordinates. Therefore, despite playing such important implicit roles, these coordinates never explicitly appeared in the outputs of any of the analyses.

The generalized least squares (GLS) were implemented in ways that optimally extracted evidence regarding biomass pattern at the MZNP. Two of the methods are noteworthy; firstly, the all-subsets variable selection technique (Heinze et al., 2018; James et al., 2021) was used to identify the "best" linear combination of the environmental variables (including SDI) that explained the observed variation in average biomass per plot. As a result, $32{,}767$ GLS subset models were fitted. Akaike Information Criterion (Akaike, 1973) was used as the selection criterion. Secondly, an approximate value was obtained for the regression correlation coefficient (R^2). This was necessary because GLS models do not return R^2 values. The reported approximation was obtained as the square of the correlation between the observed (y) and the model predicted ($\hat{y}$) biomass values.

Some adjustments were made to the data to minimize bias. Nine Vegetation unit (VUs) were observed in total. However, only one plot each was recorded for two of the units (VU3 and VU11). Thus, except for VU1, neighboring Vus were merged to ensure that each class spanned at least 5% of the plots. The resulting VU classes used in subsequent discussions were VU1, VU2-3, VU4-5, VU7-8, and VU9-11. Furthermore, thirteen plots share five latitude or longitude values. Therefore, to guarantee that the autocorrelation model was implemented successfully, duplicated values had to be eliminated. As such, random uniform (0.0001, 0.0003) values were added to the duplicated coordinates. To control the false discovery rate due to multiple tests, the Benjamini and Hochberg (1995) correction was used to adjust all subsequent p-values. Hence, all p-values reported represent the corrected estimates. Of note, in accordance with the convention, a p-value threshold of 5% was adopted in deciding the statistical significance of the evidence present in the analyzed data regarding the hypotheses considered. All the analyses were performed with R software (R Core Team, 2022).

Results

First, the biomass pattern across all 2,594 (50 × 50 + 47 × 2 plots) locations was examined. A graphical illustration is shown in 4.1, and a quantitative summary is presented in Table 4.1. The distribution was positively skewed, with only a few of the values greater than 15 g/m^2. Although the maximum biomass recorded was 36 g/m^2, 75% of the records did not exceed 10 g/m^2. Therefore, it is not surprising that the data contained significant evidence (p=0.0000) against the hypothesis that biomass was normally distributed across the MZNP. The p-values provided in red indicate the existence of statistically significant evidence against the hypothesis that the corresponding data are normally distributed.

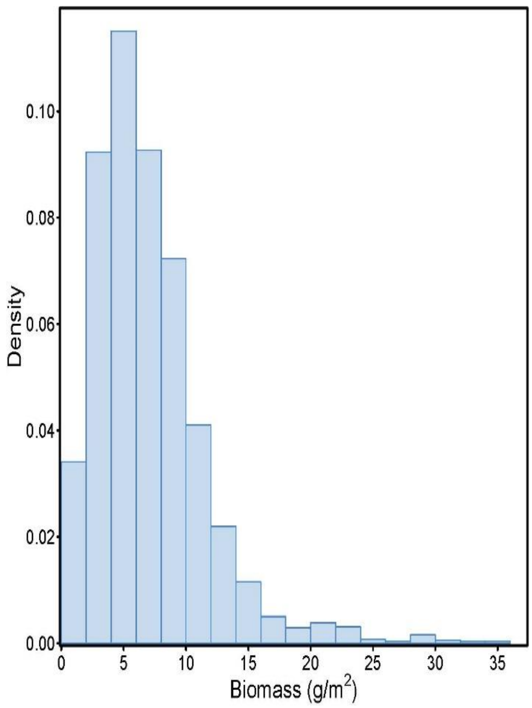

Figure *4.1*. Distribution of plant biomass across the 2594 land plots surveyed. The vertical axis shows the densities (unitless) of the observations that are within the respective intervals. In other words, the y-axis is the relative frequency that is scaled such that the area under the histogram sums to one.

Second, the distribution of average biomass as a function of the observed genus was investigated. See Figure 4.1 and Figure 4.2 for a visual illustration and a quantitative summary, respectively. The distribution was approximately normally distributed, given the concept of the central limit theorem (James *et al.,* 2021). There was insufficient evidence in the observed data (p = 0.4011) to reject the claim that mean biomass, as a function of genera, was normally distributed. It can, however, be inferred that the distribution showed a mild left tail caused by the low average biomass of the *Felicia* genus.

Table 4.2. Biomass distribution as a function of all considered locations, observed genus, species present, and plots. The p-values provided indicate the existence of statistically significant evidence against the hypothesis that the corresponding data are normally distributed.

		Total		Genera	Species	Plot
Count		2,594		43	68	52
Minimum	Biomass	0.00	Average Biomass	0.00	0.00	2.90
25% Quantile		4.00		5.87	6.08	5.85
Median		7.00		7.28	7.35	7.36
75% Quantile		10.00		8.27	8.78	8.99
Maximum		36.00		11.52	21.00	13.54
Mean		7.45		7.29	7.70	7.45
Std. Dev.		4.55		2.36	3.03	2.35
p-value		0.0000		0.40	0.50	0.96

The average biomass distribution pattern was further investigated in terms of plots and with respect to species (Figure 4.2 and Figure 4.**Error! Reference source not found.**). In both instances, the inferences were similar to those obtained with respect to genera—approximate normal distribution and high p-values that indicated insignificant evidence against the normal distribution claim. As seen for genera, the other pairs of mean biomass distributions had tails. The tail with respect to plots was mild and caused by the relatively high average biomasses of *Plot 3* and *Plot 35*. However, the tail in the case of species was heavy on both ends of the distribution. This was because of the particularly high mean biomass recorded for *Asparagus striatus* and *Diospyros austro-africana,* as well as the relatively low average biomass recorded for *Felicia filifolia*. The average biomass computed plot-wise contained the least evidence against a normal distribution hypothesis. Therefore, this justified the utilization of GLS to subsequently analyze the relationship between average biomass and different environmental factors (Table 4.1).

Vegetation Unit and soil pH ("p-value" approximately 0.0385) were the two variables that were each identified as influencing the average biomass (Table 4.1). An increase in water pH by 0.10 tended to be associated with a decrease in average plot biomass by approximately 0.069 g/m^2. Average plot biomass seemed to be similar across VUs, except for VU2-3 ("p-value" ≈ 0.0333). Compared with that at VU1, average biomass tended to be approximately 3.1 g/m^2 higher at VU2-3. The relationship between average biomass and each of the average yearly rainfall and soil organic C values merits further investigation as the significance of the associations was only eroded after the p-value adjustment. Similar post-adjustment evidence erosion was observed for VU9-11. Therefore, despite the identification of a pair of variables that were significantly associated with average biomass, more extensive study is required with data collected from more plots. To understand the optimal linear combination of the observed environmental factors, including the standard deviation index, which explained the recorded variation in average biomass (Table 4.4.4). A three-variable model that included aspect, VU, and water pH was identified as the optimal model. It was estimated that the model explained approximately 43.65% of the observed variation in average biomass. Given that VU and water pH have been previously identified to have a significant pairwise relationship with average biomass, their inclusion in the parsimonious model was not surprising. Based on a similar analogy, the presence of aspect in the model was unexpected. A possible explanation is that the aspect variable had a confounding effect. This hypothesis was investigated further.

Table 4.1. Independent generalized least square regressions fitted with average biomass per plot as the response.

Variable		n	Coeff.	p-value*	95% Conf. Int.	
					Lower	Upper
Shannon index		52	-0.3623	0.5002	-1.4339	0.7092
Aspect						
	East	9	Ref	Ref	Ref	Ref
	North	7	1.5760	0.5002	-3.0961	6.2480
	North-east	11	0.9920	0.6439	-3.3036	5.2876
	North-west	6	1.5177	0.5480	-3.5340	6.5694
	South	7	0.4668	0.9592	-17.8360	18.7697
	South-east	2	0.0631	0.9739	-3.8076	3.9338
	South-west	3	0.5944	0.9592	-22.7120	23.9009
	West	7	1.1454	0.6439	-3.8144	6.1052
Bulk density		52	0.0388	0.9622	-1.5957	1.6732
Cation exchange capacity		52	-0.0480	0.6103	-0.2361	0.1401
Clay content		52	-0.0023	0.9622	-0.0984	0.0938
Coarse fragments		52	-0.0044	0.9592	-0.1764	0.1676
Nitrogen		52	-0.0042	0.9592	-0.1682	0.1598
Annual mean rainfall		52	0.0626	<u>0.0585</u>	-0.0023	0.1275
Sand		52	0.0077	0.9592	-0.2952	0.3107
Silt		52	0.0012	0.9622	-0.0499	0.0524
Slope		52	0.1392	0.4871	-0.2601	0.5385
Soil organic carbon		52	0.1935	<u>0.1600</u>	-0.0790	0.4660
Annual mean temperature		52	-0.0275	0.9622	-1.1845	1.1296
Vegetation unit						
	1	12	Ref	Ref	Ref	Ref
	2–3	8	3.1008	0.0333	0.2564	5.9452
	4–5	14	-0.0715	0.9622	-3.0879	2.9449
	7–8	11	0.9058	0.6103	-2.6463	4.4580

9–11	7	2.3487	0.0993	-0.4610	5.1584
pH Water	52	-0.0690	0.0385	-0.1341	-0.0038

Table 4.4. Analysis of variance for the "best" subset generalized least squares (GLS) model.

Variable	**DF**	**F-value**	**p-value***	**Approx. R^2**
Aspect	7	0.5672	0.9622	0.4365
Vegetation unit	4	4.5107	**0.0385**	
pH water	1	8.2016	**0.0416**	

* Bold p-values correspond to variables detected to be significantly associated with plot-wise mean biomass.

Figures 4.3 and Figure 4.4 were used to investigate whether the importance of the aspect in the optimal biomass model was because of its potential role as a confounder. For the purpose of representation, the aspect variable used to generate the graphs in the figures was adjusted. North-east and north-west were re-classified as north. Similarly, south-east and south-west were re-classified as south.

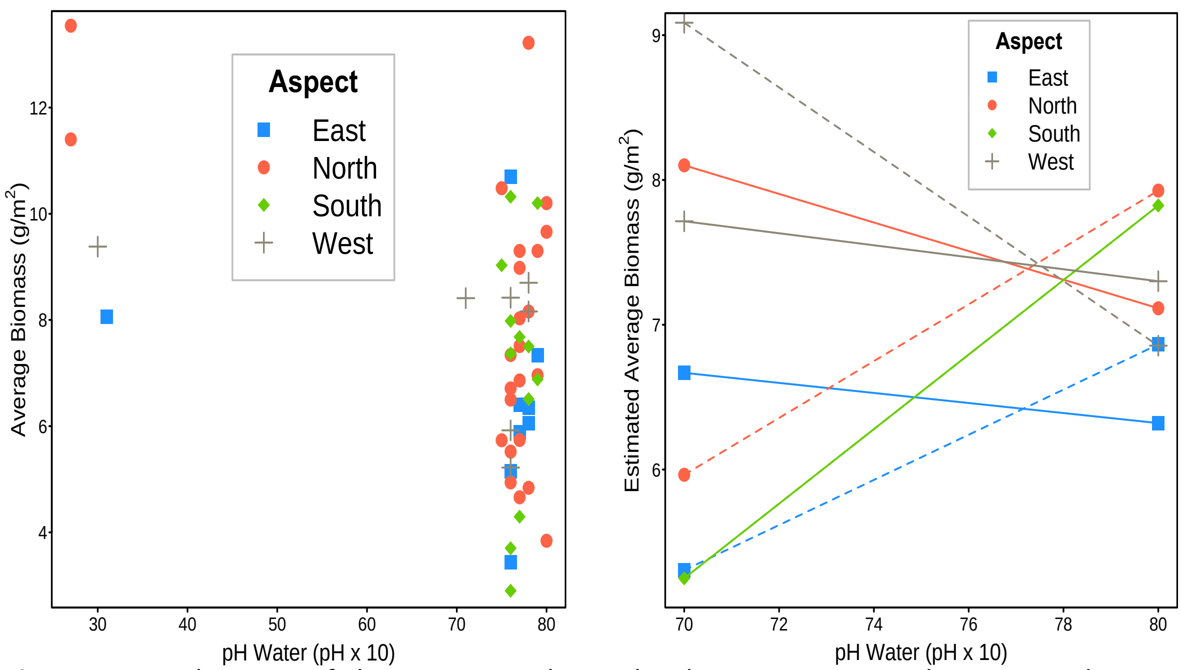

Figure 4.4 Exploration of the pairwise relationship between average biomass and pH water, conditional on aspect. The plot on the right exhibits the generalized least squares (GLS) regression lines restricted to values of pH water between pH 7 and 8 to avoid extrapolation. The dashed lines denote cases where extreme pH water values (<pH 4) were excluded. The unbroken lines were generated from the complete data.

Figure 4.3 shows that VU9-11 had the highest average at the eastern and southern aspects, whereas it did not appear in the west. Moreover, VU2-3 was among those with the highest mean at all aspects, except at the east where it did not appear. Therefore, the aspect played a confounding role in the association between mean biomass and VU. More stimulating features were evident in Figure 4.4, where the confounding effect of the aspect on the association between pH water and biomass was explored. Except for the south, all the aspect categories had extreme water pH values that skewed the distributions leftward. Notably, the extreme values were influential. The directions of the slopes of the regression lines changed from negative to positive for the eastern and northern aspects. For the western aspect, exclusion of the extreme values only caused the regression slope to increase. Therefore, it is plausible to claim that there was a negative association between water pH and average biomass at the western aspect. Conversely, at the southern aspect, the association between water pH and average biomass appeared to be strictly positive. This contrast validates the suspected confounding attribute of the aspect variable on the pairwise relationship between water pH and average biomass.

Discussion

Mountain Zebra National Park is the interface between three Biomes, namely, Grassland, Nama Karoo, and Albany thicket. The biomass across the park was not normally distributed, owing to the high biomass of the genera *Asparagus* and *Diospyros* as well as the relatively low average biomass recorded for *F. filifolia*. *D. austro-africana* and *Asparagus* are dominant within the Nama Karoo biome, while *F. filifolia* dominates the Grassland biome within the park. The high biomass species were visibly dominant in the study area while *F. filifolia* was not dominant, which may explain their higher biomass contribution. Soil pH was the sole factor investigated in this study that affected plant biomass production markedly. Other soil factors that were examined did not demonstrate significant effects on plant biomass production. This is inconsistent with the findings of studies by Baraloto et al., (2011), Sun et al., (2013) and Yang et al., (2009), which report significant relationships between biomass and soil properties in Grasslands. Furthermore, Sun et al., (2012) reported a positive relationship between soil C density and AGB. Soil N content did not influence plant biomass production in the present study. This is in line with the findings of several studies that soil N content has little to no influence on plant biomass production in most terrestrial ecosystems

(Heggenstaller et al., 2009; Wu et al., 2013). Bhandari and in Zhang (2019) and Liu et al., (2014) observed a negative relationship between soil N content and plant biomass production, in which relatively high N content resulted in relatively low biomass production, while relatively low N content translated to relatively high biomass production. A study conducted in an alpine meadow also revealed that N content is a major factor affecting AGB, influencing the richness (Brown & Bezuidenhout, 2019).

Vegetation biomass is an important factor as biomass is a major contributor to soil organic matter, which can influence greenhouse gas emissions in the terrestrial ecosystem (Little, et al., 2015). Biomass also plays a major role in energy production, which is one of the greatest essential quantitative characteristics for understanding community structure and ecosystem function. The positive association observed between plant biomass and soil pH in the present study is consistent with the findings of a study conducted by Bhandari & Zhang (2019) that soil pH and plant biomass production have a positive relationship at the southern aspect (Li et al., 2012) Although most of the environmental factors did not influence biomass distribution in the present study, studies that examine environmental factors and plant biomass remain invaluable for an overall understanding of plant biomass distribution in an area. Regionally, AGB is primarily determined by altitude, climate, and soil fertility (Fornara & Tilman 2009; Ma et al., 2010). However, in the present study there was no significant relationship between AGB and mean annual precipitation.

Above Ground Biomass and the environmental factors across 52 sites were analyzed. Based on the results, only one of the soil properties, soil pH, influenced plants biomass. Although soil nutrients are highly important in plant biomass production, their influences on AGB is insignificant. The results of the present study show that the spatial distribution of plant biomass abundance is explained by various factors that may also be influenced by various vegetation types, geology, and rainfall of an area. Furthermore, spatial distribution may be affected differently by environmental factors. The main limitation of our study was that only AGB was considered, rather than the whole plant biomass, which includes both above and belowground biomass. Future studies should focus on the whole plant as this may provide a better understanding of how soil properties influence plant biomass production and allocation.

Chapter 5: Effects of absence and presence of Fire on palatable woody species recruitment in a mountainous Grassland.

This Chapter is based on. Effects of absence and presence of Fire on Woody species recruitment in a mountainous Grassland. The paper is being prepared for publication.

Abstract

Fires play a crucial role in maintaining the structure and function of many ecosystems. In the absence of fires, the structure of open ecosystems undergoes changes that subsequently alter their functioning. In this study, we aimed to determine the influence of fire on woody/shrub plant species richness, diversity, composition, and palatability in Mountain Zebra National Park, South Africa. The park's fire history were collected for the period 2000 and 2020 using satellite imagery and we established that there were two combinations of fires; one area had fires in 2002 and 2010 and another in 2010 and 2019. We used these two fire combinations as two fire treatments paired with control areas that did not experience fire. A total of 80 plots (approximately 20 m × 20 m in size and spaced more than 100 m apart) were established. Shrub cover was not related to fire treatment, however, species richness and species diversity each had statistically significant associations with the fire cycle. Furthermore, shrub palatability was discovered to be strongly associated with the fire state of the site i.e., (whether a site was burned or not burned). In summary, our results demonstrate that the absence of fire over a prolonged period tends to impact the characteristics of woody species in grassland ecosystems.

Introduction

Open grassy systems, which include grasslands and savannas, cover approximately one-quarter of the vegetated surfaces on Earth (Ramankutty & Foley, 1999). Grasslands have undergone significant degradation and transformation, which has resulted in significant alterations in community composition and habitat loss (Stevens, 2018). The distribution of open systems are governed by climate (rainfall and rainfall seasonality) and soils (Lehmann et al., 2011). Open systems are however disturbance driven, and their physiognomies are shaped by herbivory (Bond 2008) and fire (Archibald & Hempson 2016). Beyond structure, fire also influences the composition of vegetation and the abundance of woody and herbaceous species (Cavender-Bares & Reich, 2012), thereby impacting ecosystem functionality (Higgins et al. 2012).

Globally, there is a noticeable increase in the abundance of woody plants observed in grasslands and savannas (Cavender-Bares & Reich, 2012). This change in plant functional types has been ascribed to several factors, including reduced fire frequency (Luvuno et al., 2018; Ling et al., 2023), intense grazing pressures (Scholes & Archer, 1997; McPherson & Wright 1990), and elevated atmospheric CO_2 (Bond & Midgely, 2001). The shifts in plant community composition and alterations in vegetation structure (Eldridge et al. 2011) that accompany woody encroachment is linked to shifts in ecosystem functioning (Barger et al. 2011) and long-term conservation of biodiversity (Gray & Bond, 2013).

The grassland biome has the lowest level of protection in South Africa, with a mere 2.8 % of its area being formally protected (O'connor & Kuyler 2009). It is estimated that 60% of the grassland biome in South Africa has undergone permanent transformation, leaving as little as 15% in its natural state (Carbutt et al., 2011). Moreover, the majority of the remaining natural grassland is highly fragmented and poorly managed (Mucina & Rutherford, 2006a). Several factors, such as overgrazing (Neke and Du Plessis, 2004), extensive and frequent burning (Uys et al., 2004), plantation forestry (Lipsey & Hockey, 2010), invasion by alien plant species (Le Maitre et al., 1996) and fire suppression resulting in woody encroachment (Mucina & Rutherford, 2006a), are major contributors to grassland degradation. Mountain Zebra National Park (MZNP) encompasses three distinct biomes: grassland, Nama-karoo, and thicket (Fig. 1). Of these, the grassland biome is the largest and serves as a crucial habitat for numerous grazing animals in the park.

A lack of disturbance (e.g., fire and grazing) has been found to result in decreased grass species richness (and evenness and diversity) in other grasslands (Fynn et al., 2004; Smith et al., 2013. However, few studies have considered the effects of fire on shrub cover, composition, and palatability. In Mountain Zebra National Park there are some concerns that fire had been removed from the system. The fire scars that were used in this study are the results of an escaped natural fire or unnatural fire that escaped from the surrounding farms. The absence of fire in grassland can lead to woody encroachment (Mucina & Rutherford, 2006a), and changes in grassland ecosystem function. As a large proportion of the park is covered by grassland it is important that fire management is incorporated in the management of the park following Consequently, the objectives of this study were as follows: (i) to assess the effect of the absence or presence of fire on woody (trees and shrubs) species composition, (ii) to determine the effect of fire absence or presence on the percentage cover of shrubs, and (iii) to evaluate the impact of fire absence or presence on shrub species richness and diversity. We hypothesized the following: (i) burned sites would exhibit high shrub species richness and species diversity, (ii) burned sites would have fewer grass species compared with unburned sites, and (iii) burned sites would harbor more palatable shrub species.

Materials and Methods

Study area.

The study was conducted in Mountain Zebra National Park (Fig. 5.1), an expanse covering approximately 28,412 ha situated in the Eastern Cape Province, South Africa (32°22’47” S; 25°47’’8 E). The average monthly temperature in summer (September to March) varies between 6°C and 28°C, whereas in winter (April to August), the temperature often drops below 0°C and reaches a maximum of 20°C (Novellie & Gaylard 2013). Rainfall occurs regularly from December to April, with an average annual rainfall of 400 mm. The region experiences periodic light snow during the winter months, while frost is common between May and October. The park is located on the northern slope of the Bankberg Mountain Range (Gaylard, 2013).

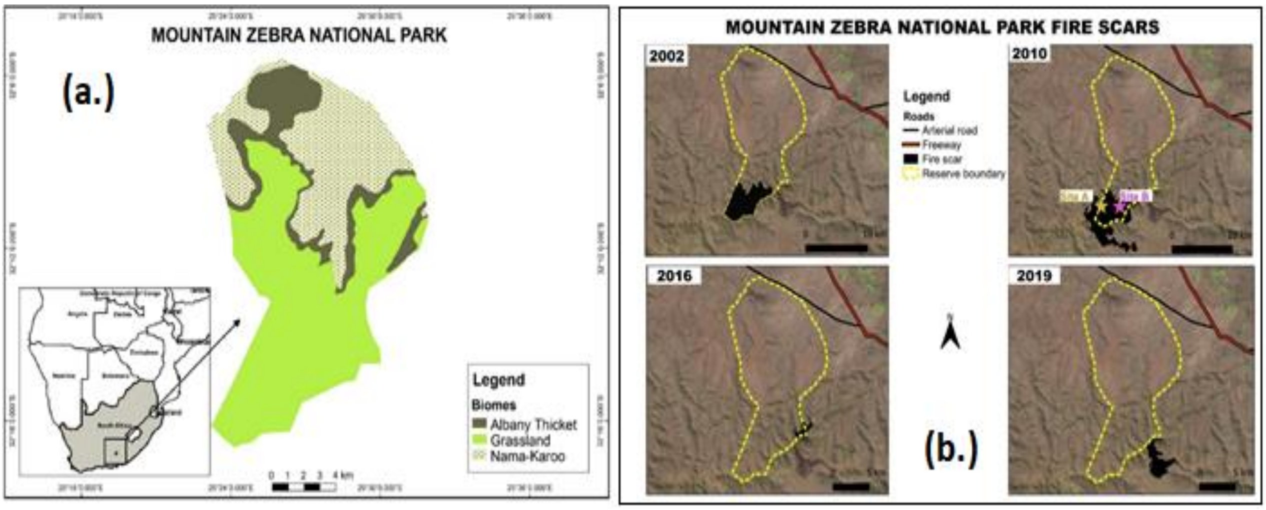

Figure 5.1: (a.) Location of the Mountain Zebra National Park (MZNP) in South Africa and (b.) the three Biomes in the study area in the park.

Field data collection

Eighty plots were laid out across the sites using purposive sampling, with 20 plots in each fire regime. These plots were categorized into site type A, which encompassed 20 plots in an area burned in 2002 and 2010, and an additional 20 plots in an unburned (control) site. Site Type B consisted of 20 plots in an area burned in 2010 and 2019, along with 20 control plots. Each plot measured approximately 20m × 20m (approximately 0.04 ha) and was spaced at least 100 m apart. The field work was conducted during the growing season, specifically between December and April, to facilitate plant identification. Within each plot, all shrub and woody plants were counted and identified at the species level. A shrub, in this context, refers to a small to medium-sized perennial woody plant with persistent woody stems above ground. The cover percentage for each species was determined using the Daubenmire Cover Class Method. Overall shrub percentages were estimated for each plot (Daubenmire, 1959).

Fire frequency data.

Historical fire data from the years 2000 to 2020 were obtained from various sources, including the Moderate Resolution Imaging Spectroradiometer (MODIS), MCD45 burned area product, and Sentinel-1. The fire scar for 2019 was physically mapped on the ground. These fire data were then processed using a quantum geographic information system (Quantum GIS Development Team, 2016) to generate fire scar maps for the study sites. All fires that occurred from 2000 to 2020 occurred in one vegetation type, namely, karroid Grassland. Four fires were recorded in the park in the years 2002, 2010, 2016, and 2019. The 2016 fire, being too small (less than 10 ha), was excluded from the dataset. The two fire scars used in this study were labelled as Site A (2002 and 2010) and Site B (2010 and 2019).

Statistical Analyses

The outputs presented in this section were obtained from the total 459 shrubs that were observed in all the 80 plots. The analyses were presented in six subsections. First, it was discussion about some exploratory outputs where was interrogated species abundance – counts of how many times each species was encountered. In the second subsection, I investigated species richness – number of different shrub species observed to each plot. Thirdly, I assessed species diversity – an index that measures relative species prevalence. Percentage cover was then explored in the fourth subsection. I considered how shrub palatability responded to fire in the penultimate subsection. In the concluding subsection, I analysed a combination of the four primary variables which is species richness, species diversity, percentage cover and palatability of shrubs. Species diversity was investigated using Rényi's (1961) index with different tuning parameter (α) values. An advantage of Rényi's index is that some popular diversity indices, such as Hill (1973) entropy, are special cases (Tothmérész, 1995). For example, Shannon (1948) index is obtained when $\alpha = 1$ and when $\alpha = 2$ it corresponds to the Simpson (1949) index. For our purpose, the wealth of Rényi entropy was exploited using diversity profiles (**Error! Reference source not found.**). A diversity profile is a plot of Rényi diversity indices for different tuning parameter values. To ensure that evidence of discrepancies was pronounced, the diversity indices were estimated for each plot in terms of the species recorded at that specific 20m $\times$ 20m area.

Some exploratory and comparative statistical tools, such as analysis of variance (ANOVA), correlation matrix, diversity and abundance profiles and principal components were used to support our exposition of biodiversity at the MZNP. Our focus remained firmly on shrubs. All computational and graphical analyses were performed using R statistical software (R Core Team, 2022). In all, the methodology adopted in this study was inspired by the compilation by Kindt and Coe (2005). The traditional 0.05 threshold was used in the decisions about statistical significance and, except if stated otherwise, the reported p-values were adjusted for multiple tests bias using the Benjamini & Hochberg (1995) technique.

Results

Species Abundance

The number of times each of the observed shrub species were encountered throughout the study (that is, species abundance) was summarised in **Error! Reference source not found.**. With respect to fire cycle (that is, A *vs.* B): *Dicerothamnus rhinocerotis* appears to be the most abundant shrub species ($n = 24$ times) on sites affected by the 2002 & 2010 fire, while *Melolobium candicans* was observed most frequently on sites affected by the 2010 & 2019 fire ($n = 15$ times). Regardless of the fire state (burned *vs.* unburned), *Melolobium candicans* was most abundant. A more interesting deduction from **Error! Reference source not found.** was the possible consequence of the interaction between fire state and fire cycle on species abundance. There was no clear pattern of the distribution of species abundance in any of the images in the figure. For example, with respect to fire cycle (**Error! Reference source not found.**: bottom row) *Aptosium spinecens* was not recorded on burned cycle A sites whereas it was more frequent on burned cycle B sites. The discussion of species abundance presented above allowed for the prevalence of each species to be properly appreciated in a way that is not always possible with respect to species richness. I however acknowledge that species richness avails an opportunity for more powerful quantitative analyses.

Species Richness

Species richness was calculated as the number of unique shrub species recorded. The values obtained across all the 80 plots were between 1.0 and 11.0. The average species richness was 5.32 and the standard deviation was 2.73 (see **Error! Reference source not found.**). The greater shrubs species richness at cycle A (mean ≈ 6.68 and s.d. ≈ 2.59) compared to cycle B sites (mean ≈ 3.98 and s.d. ≈ 2.15) despite the similar variability, was another highlight of **Error! Reference source not found.**. **Error! Reference source not found.** contains a summary of the analysis of variance (ANOVA) conducted with respect to the plot-wise richness estimates. I confirmed the validity of our implementation of ANOVA for species richness by conducting a Shapiro-Wilk (1965) normality test with the model residuals. I obtained an unadjusted p-value ≈ 0.1125. Hence, the outputs in **Error! Reference source not found.** may be considered valid and it may be observed therein that fire cycle was significantly associated with species richness (p-value ≈ 0.0000).

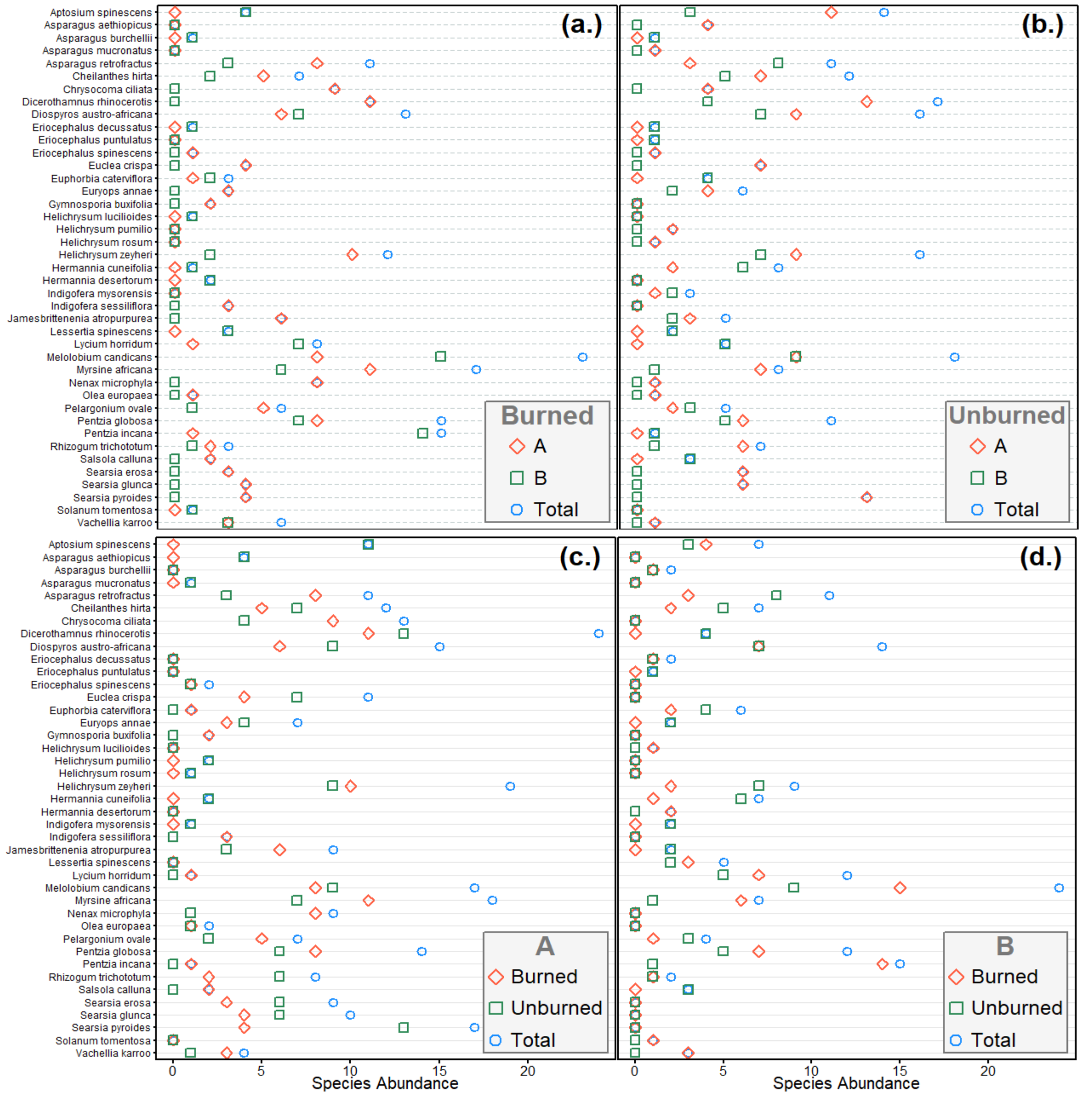

Figure 5.4: Frequency of occurrence of shrub species across the sampled landscape at Mount Zebra National Park. The vertical axes are labelled with all 41 shrub species recorded during the field study. (a.) Burned sites (b.) Unburned sites (c.) Cycle A sites, experienced fires in 2002 and 2010 (d.) Cycle B sites, experienced fires in 2010 and 2019.

Table 5.1: Quantitative summary of species richness of shrubs estimated across randomly sampled 20m × 20m plots at the MZNP.

Fire	n	Min.	Quantile 25%	Quantile 50%	Quantile 75%	Max.	Mean	Std. dev.
Total	80	1.00	3.00	5.00	7.25	11.00	5.32	2.73
A	40	2.00	5.00	6.50	8.00	11.00	6.68	2.59
B	40	1.00	2.00	4.00	5.00	9.00	3.98	2.15
Burned	40	2.00	3.00	5.00	7.25	10.00	5.18	2.60
Unburned	40	1.00	3.00	5.00	7.25	11.00	5.47	2.87
A & Burned	20	2.00	5.00	7.00	8.00	10.00	6.45	2.50
A & Unburned	20	2.00	5.00	6.00	10.00	11.00	6.90	2.71
B & Burned	20	2.00	2.00	3.50	5.00	9.00	3.90	2.05
B & Unburned	20	1.00	2.00	4.00	5.25	9.00	4.05	2.31

The species accumulation curves in **Error! Reference source not found.** were intended to enable a better understanding of the inferred association between species richness and fire cycle. The species accumulation curves show the richness pattern as the number of plots increased (Kindt & Coe, 2005). Following from the outputs in **Error! Reference source not found.**, there was insufficient evidence in the observed data to infer that interaction between fire state and fire cycle was significantly associated with shrub richness. Thus, implementing pairwise tests of association was not necessary and can only result in loss of power. I made up for this limitation with the accumulation curves in **Error! Reference source not found.**(b.).

Table 5.2: Analysis of variance output with respect to species richness (response variable). The p-values were adjusted for multiple tests bias.

Variable	Deg. of Freedom	Sum of Square	F-value	p-value
Fire State	1	1.80	0.3113	0.7810
Fire Cycle	1	145.80	25.2123	0.0000
Fire State × Fire Cycle	1	0.45	0.0778	0.7810
Residuals	76	439.50		

Inference of significant difference from accumulation curves requires that the compared curves do not intersect. For example, see fire cycle A vs. fire cycle B in **Error! Reference source not found.**(a.). When accumulation curves intersect, then it is said that the evidence available in the observed data is too weak to discern if the compared groups truly differ. Example of this may be observed in **Error! Reference source not found.**(b.) with respect to burned vs. unburned cycle B sites. For similar groups, accumulation curves tend to fully overlap. See burned vs. unburned sites in **Error! Reference source not found.**(a.) and burned vs. unburned cycle A sites in **Error! Reference source not found.**(b.) for example of this scenario. Therefore, it may be deduced from **Error! Reference source not found.** that species richness was greater for fire cycle A, similar between fire states and the impact of the interaction between fire cycle and state was inconclusive. These deductions were consistent with the contents of **Error! Reference source not found.**.

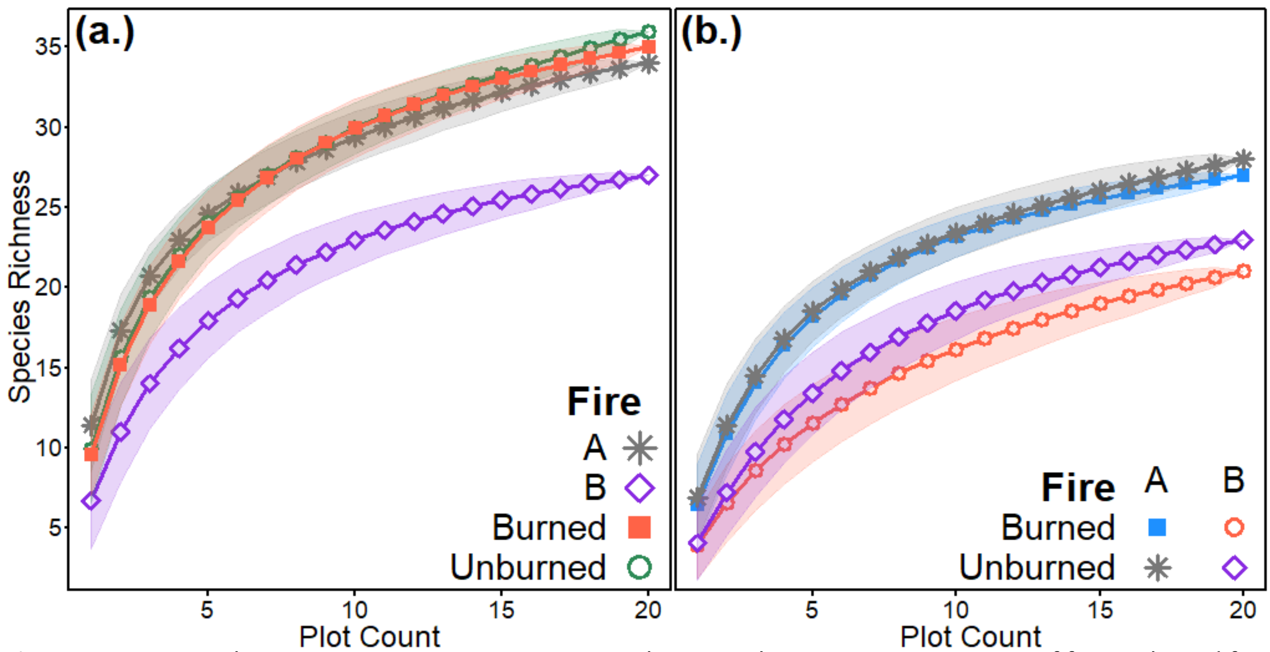

Figure 5.5: Accumulation curves comparing species richness with respect to categories of fire cycle and fire state. The lines and points trace the average values for all the possible subsets of the observed MZNP plots with respect to the associated count. The shaded regions show the corresponding standard deviations. (a.) Independent effect of fire state and fire cycle. (b.) Effect of interaction between fire state and fire cycle.

Species Diversity

It is evident from **Error! Reference source not found.** that sites that were exposed to the 2002 and 2010 fire (that is, cycle A sites) had higher species diversity and differences in diversity between burned and unburned sites were only marginal. It may also be seen in **Error! Reference source not found.**(b.) that the difference in diversities between fire states was slightly more pronounced within cycle A sites. In sum, it may be deduced from **Error! Reference source not found.** that (1.) fire cycle was likely to be significantly associated with shrub species diversity and (2.) Interaction between fire state and fire type may slightly influence shrub species diversity. Observe that the diversity profiles were monotonous. Hence, no clear discriminant feature could be used to select a preferred index. Thus, without loss of generality, a transformed Simpson diversity index (1949) was adopted as the measure of species diversity for the remainder of this study. In **Error! Reference source not found.**, our choice corresponds to the Rényi diversity index with a parameter value of $\alpha = 2$ (Kindt & Coe, 2005).

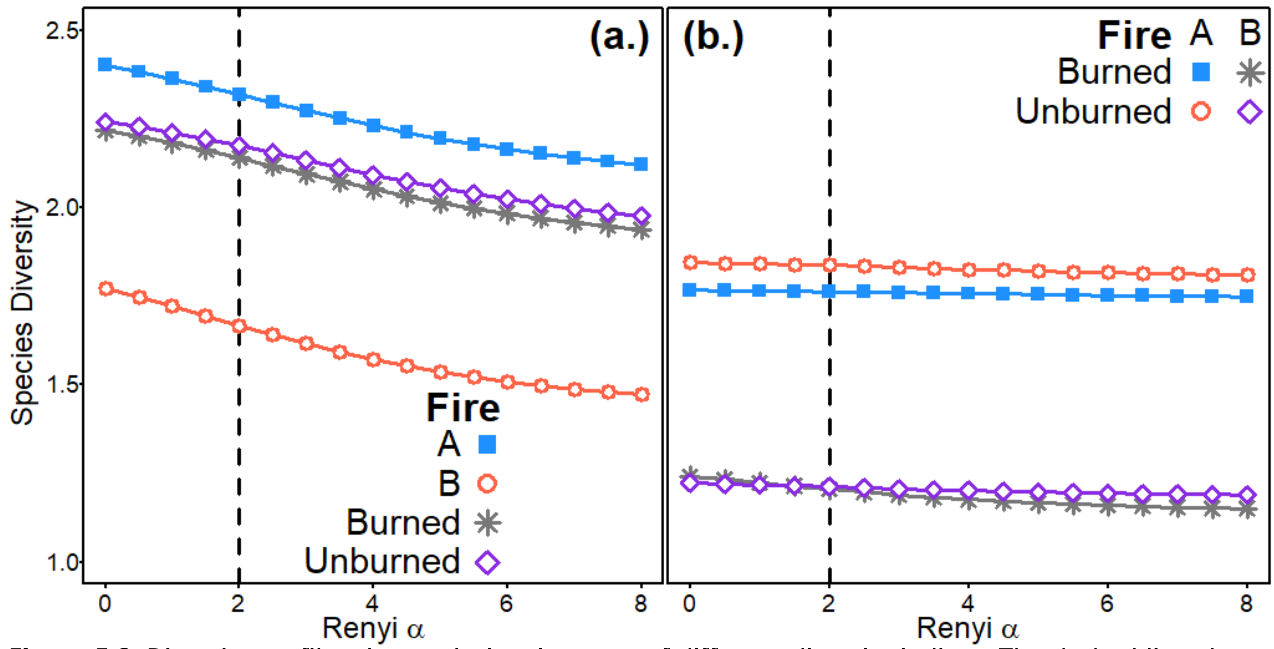

Figure 5.6: Diversity profiles that rank sites in terms of different diversity indices. The dashed line shows points that correspond to the Simpson (1949) indices. (a.) Independent analysis. (b.) Interaction

Error! Reference source not found. and **Error! Reference source not found.** contain quantitative summaries of the chosen diversity measure. The contents of the tables support the claim from **Error! Reference source not found.** about the influence of fire cycle on species diversity in at least two ways. First, the low ANOVA p-value (≈ 0.0000) associated with fire cycle. Second, the relatively large average diversity at cycle A (1.81 vs. 1.21) coupled with the comparatively higher standard deviation at cycle B sites (0.56 vs. 0.47). The marginal improvement in diversity for unburned over burned areas at cycle A sites observed in 5.4(b.) was not sufficient (p-value ≈ 0.7810) to be able to assume that the impact of the interaction term was statistically significant. A Kolmogorov-Smirnov (Feller, 1948) normality test was implemented (unadjusted p-value ≈ 0.1232) to verify validity of the ANOVA inferences.

Table 5.3: Descriptive statistics obtained for the diversity of shrub species that were observed across some 20m × 20m plots at the MZNP.

Fire	n	Min.	Quantile 25%	Quantile 50%	Quantile 75%	Max.	Mean	Std. dev.
Total	80	0.00	1.10	1.61	1.98	2.40	1.50	0.59
A	40	0.69	1.61	1.87	2.08	2.40	1.80	0.47
B	40	0.00	0.69	1.30	1.61	2.20	1.21	0.56
Burned	40	0.59	1.10	1.61	1.98	2.30	1.48	0.56
Unburned	40	0.00	1.10	1.61	1.98	2.40	1.52	0.63
A & Burned	20	0.69	1.61	1.95	2.08	2.30	1.76	0.49
A & Unburned	20	0.69	1.61	1.79	2.25	2.40	1.84	0.45
B & Burned	20	0.59	0.69	1.19	1.61	2.20	1.21	0.50
B & Unburned	20	0.00	0.69	1.39	1.63	2.20	1.21	0.64

Table 5.4: ANOVA outputs obtained with respect to shrub species diversity at the MZNP.

Variable	Deg. of Freedom	Sum of Square	F-value	p-value
Fire State	1	0.03	0.1176	0.7810
Fire Cycle	1	6.98	25.3721	0.0000
Fire State × Fire Cycle	1	0.02	0.0821	0.7810
Residuals	76	20.89		

Percentage Cover

Records of percentage cover were obtained for each of the shrub species observed at every plot. So, the analyses discussed herein were executed with estimates of percentage cover that were obtained for each plot, as the average of the values recorded at that specific plot. The resulting plot-wise cover values ranged between 0.10 and 10.00 (Table 5.5). The values failed the normality tests, except after they were log-transformed. The transformed variable yielded an unadjusted Shapiro-Wilk (1965) normality test p-value of approximately 0.1229. Consequently, the ANOVA outputs in Table 5.6 were generated with log of the plot-wise percentage cover estimates. The large p-values in the table imply that the evidence from the data set was insufficient to be able to infer that there existed statistically significant relationship between percentage cover and any of the fire features. It is noteworthy that the p-value associated with fire state was less than the 5% threshold prior to adjustment for multiple test bias. It may therefore be worthwhile to investigate that association further in subsequent studies. The deductions from Table 5.5 and Table 5.6 were supported by the illustrations in **Error! Reference source not found.**. The inter-state bars in **Error! Reference source not found.**(a.) appeared similar especially since the standard error arrows overlapped. That supported the large p-value associated with fire cycle from the ANOVA outputs in Table 6. Visually, the difference in percentage cover between the burned and unburned sites seemed evident. As stated in the previous paragraph, the evidence could however not survive multiple test adjustment, probably because of the larger variability associated with the burned sites. It is therefore necessary for the relationship between percentage cover and fire cycle to be considered in subsequent studies. The lines in **Error! Reference source not found.**(b.) hardly intersected. Thus, the inference about the insignificant interaction effect of fire features on percentage cover remained consistent.

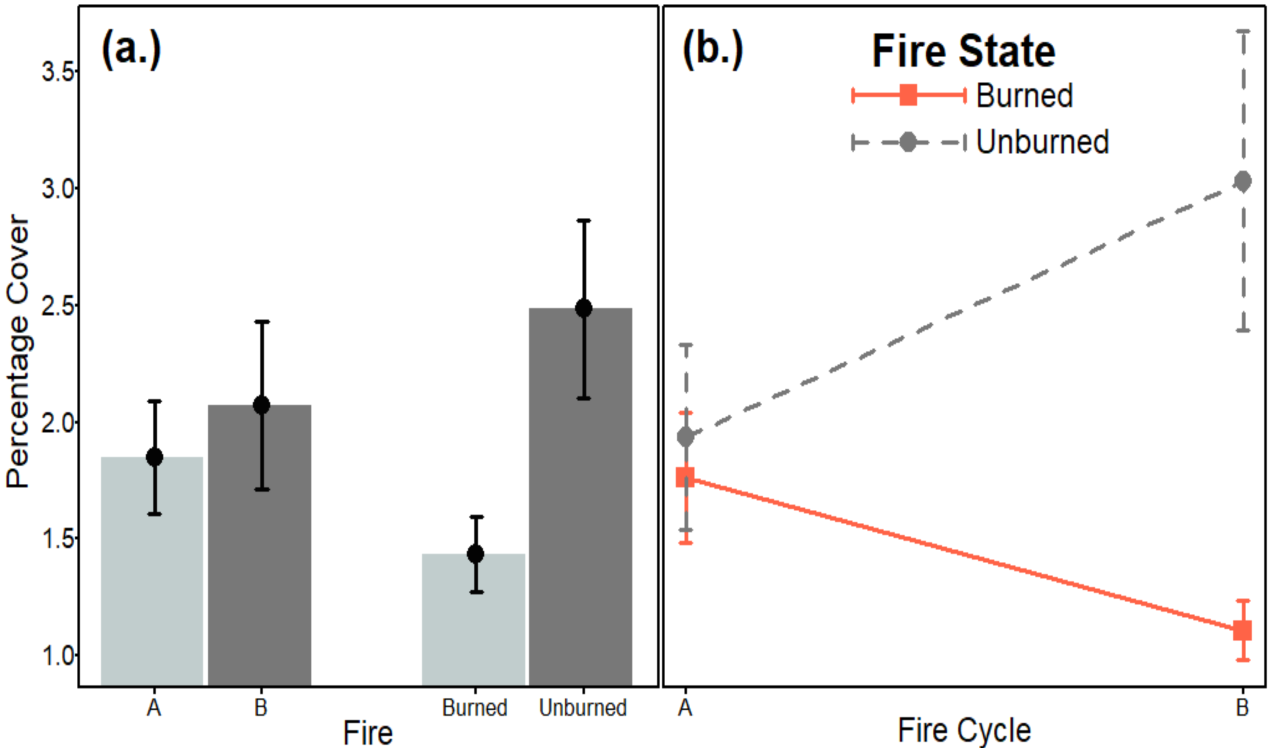

Figure 5.7: Summaries of the percentage cover estimated for all the 20m × 20m study areas from the MZNP in terms of (a.) separate fire features and (b.) interaction between fire characteristics. The bar heights and points indicate the corresponding overall averages whereas the arrows span twice the magnitude of the standard errors.

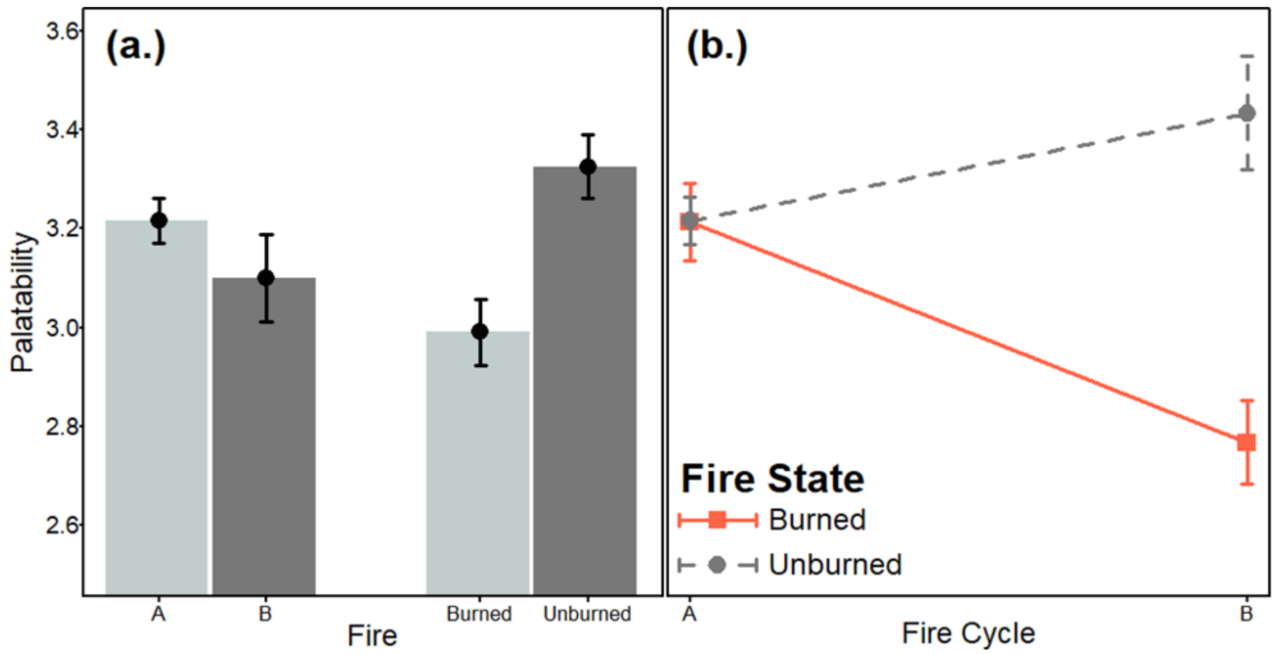

Figure 5.8: Graphical analyses of the relationship between shrub palatability and (a.) separate fire properties (b.) interaction between fire features at the MZNP. The width of the arrows equal to two times the corresponding standard error. The points and the bar heights indicate the respective sample means.

Table 5.5: Summaries of plot-wise percentage cover as a function of fire state and fire cycle.

Fire	n	Min.	Quantile 25%	Quantile 50%	Quantile 75%	Max.	Mean	Std. dev.
Total	80	0.10	0.81	1.43	2.34	10.00	1.96	1.91
A	40	0.20	0.89	1.46	2.23	7.75	1.85	1.52
B	40	0.10	0.79	1.38	2.34	10.00	2.07	2.26
Burned	40	0.14	0.68	1.25	1.67	5.00	1.43	1.01
Unburned	40	0.10	0.99	1.50	2.62	10.00	2.48	2.42
A & Burned	20	0.20	0.85	1.46	2.76	5.00	1.76	1.24
A & Unburned	20	0.50	1.07	1.45	1.91	7.75	1.93	1.78
B & Burned	20	0.14	0.67	1.15	1.50	2.50	1.11	0.57
B & Unburned	20	0.10	0.99	2.04	4.10	10.00	3.03	2.86

Table 5.6: Analysis of variance with respect to the log of percentage cover estimated from each of the MZNP study area.

Variable	Deg. of Freedom	Sum of Square	F-value	p-value
Fire State	1	3.11	4.2570	0.1020
Fire Cycle	1	0.15	0.2085	0.7810
Fire State × Fire Cycle	1	1.67	2.2889	0.2689
Residuals	76	55.43		

Palatability

During the data collection phase palatability was recorded as an integer between 1 and 5 for each observation at every plot. All the analyses discussed in the preceding subsections were implemented with data that comprised a single estimate per plot. Thus, to ensure consistency, palatability was approximated as a continuous random variable such that the value for each plot was obtained as the average value. Summary outputs of the distribution of the plot-wise palatability variable and the corresponding analysis of variance were presented quantitatively in Table 5.7 and Table 5.8 as well as graphically in Figure 5.6.

Table 5.7: Descriptive summaries with respect to the palatability of the shrub species observed at specific areas at the MZNP.

Fire	n	Min.	Quantile			Max.	Mean	Std. dev.
			25%	50%	75%			
Total	80	2.33	2.79	3.20	3.47	4.25	3.16	0.45
A	40	2.50	3.16	3.25	3.34	3.75	3.22	0.29
B	40	2.33	2.50	3.00	3.52	4.25	3.10	0.56
Burned	40	2.33	2.55	3.00	3.34	3.75	2.99	0.42
Unburned	40	2.50	3.18	3.29	3.52	4.25	3.33	0.40
A & Burned	20	2.50	3.00	3.27	3.39	3.75	3.21	0.35
A & Unburned	20	2.71	3.18	3.22	3.33	3.60	3.22	0.21
B & Burned	20	2.33	2.50	2.67	3.00	3.60	2.77	0.38
B & Unburned	20	2.50	3.17	3.50	3.81	4.25	3.43	0.52

The validity of the ANOVA model summarised in Table 5.8 was verified by confirming that the model residuals were approximately normally distributed using the Shapiro-Wilk (1965). The test returned an unadjusted p-value of approximately 0.1687. Interestingly, based on the low p-values (≈ 0.0006) from the ANOVA output, evidence from the data supported claims that (a.) fire cycle and (b.) the interaction between fire state and fire cycle were significantly associated with shrub palatability. Observe from the outputs in Table 5.7 and Figure 5.6 that the variability was higher at the burned sites (0.42 vs. 0.40) while the mean was larger at the unburned sites. Also, while not more than half of the estimated plot-wise palatability at the burned sites were greater than 3.00, at least 75% of the estimates at the unburned sites were not less than 3.18. In terms of the interaction effect, average palatability was indifferent between burned and unburned sites that were exposed to the 2002 and 2010 fire, whereas sites exposed to the 2010 and 2019 fire showed significantly improved palatability at the unburned areas.

Table 5.8: Linear regression model of shrub palatability against fire features at the MZNP summarised as an ANOVA output.

Variable	Deg. of Freedom	Sum of Square	F-value	p-value
Fire State	1	2.34	15.5098	0.0006
Fire Cycle	1	0.26	1.8256	0.3097
Fire State × Fire Cycle	1	2.21	15.3131	0.0006
Residuals	76	10.95		

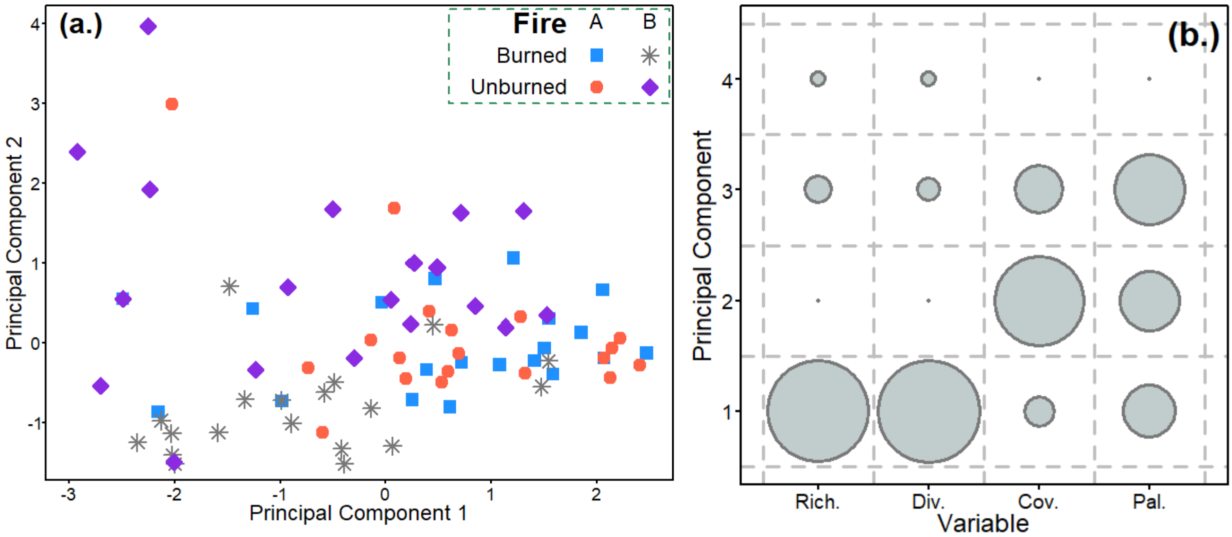

Figure 5.9: Classification of the studied MZNP region in terms of site exposure to fire as well as shrub species measurements including, **`Rich.:`** Richness, **`Div.:`** Diversity, **`Cov.:`** Percentage Cover and **`Pal.:`** Palatability. (a.) Discriminant analysis of the sensitivity of shrub species to fire at the MZNP. (b.) Correlation matrix where the sizes of the circles are proportional to corresponding coefficients and the area of each of the dashed squares equals one.

Shrubs Response to Fire

Principal component analysis was used to investigate whether the recorded shrub measurements (that is, richness, diversity, percentage cover and palatability) may be used to partition the studied area in terms of the fire exposure. The outcome is presented in Figure 5.7.

The two principal components used in the axes of Figure 5.7(a.) accounted for approximately 80.03% of the observed variability in the four shrub species measurements discussed in this work. That is, species richness, species diversity, percentage cover and palatability. The correlation between the measurements and all the principal components was illustrated in Figure 5.7(b.) Observe from Figure 5.7(b.) that the first component mostly captured the information from species richness and species diversity while the second component mostly contained information about percentage cover. The observed variability in palatability was captured approximately equally by the first three components. Therefore, it was less straightforward to discuss about palatability from the 2-dimensional summary in Figure 5.7(a.). Regardless, Figure 5.7 represents a comprehensive summary of the inferences from this section. Based on the clustering of the points in Figure 5.7(a.), it may be deduced that (i.) at the MZNP sites exposed to the 2002 and 2010 fire, species richness and species diversity were relatively high with no significant difference between the burned and unburned areas, (ii.) burned areas within sites exposed to the 2010 and 2019 fire tend to be associated with relatively low species richness and species diversity and (iii.) percentage cover contained weak evidence useful to partition the studied area.

Discussion

Fire frequency and intensity are two important drivers of vegetation structure and diversity in Grassland ecosystems (Bond et al., 2005; Cavender-Bares & Reich, 2012). In this study, I explored the effects of the absence and presence of fires on shrub species richness and diversity in Grasslands. the results showed that there was statistically significant difference in shrub species richness between burned and unburned areas, even with different fire cycles (P=0.00) (2002 and 2010 fires and 2010 and 2019 fires). There was no difference in species diversity between the burned and unburned areas in this study. This aligns with the findings of Öster et al. (2008), where the use of plant species diversity was shown to be an ineffective indicator of disturbance. It has been suggested that fire fosters the establishment and growth of grasses in burned areas, effectively reducing competition with woody species (Booysen & Taintmentison, 2012).

The percentage cover of shrub species in both burned and unburned sites during the Type A fire, encompassing the years 2002 and 2010, yielded statistically insignificant results (p=0.00). Notably, it was the shrub species composition during the Type B fire, involving the years 2010 and 2019, that exhibited statistical significance. The lack of statistical significance in shrub species composition during the Type A fire could potentially be attributed to the substantial gap between the last fire event and the data collection, spanning approximately 11 years. This duration surpasses the recommended timeframe for the Grassland burning regime, which typically operates on a four-to-six-year cycle. The outcomes of our study underscore the critical role of the burning regime in preserving Grassland species cover. The absence of fire for over 11 years resulted in cover levels akin to those of sites that had remained unburned for 20 years.

According to Akeredolu & Isichel, (1990) fire is known to suppress the growth of some plants and stimulate the growth of others, which results in the replacement of the former species in burned areas by opportunistic ones, resulting in changes in plant species composition. This is similar to mesic Grasslands, including the North American tallgrass Prairie, where changes in the timing, intensity, and frequency of fires have been associated as significant drivers of shifts from Grasslands to shrublands and woodlands (Bond 2008; Fuhlendorf et al., 2008; Gibson 2009; Twidwell et al., 2013a). Fire occurrence removes the moribund and litter build up on the soil surface, which changes the microclimate and nutrient levels of the soil surface (Lavorel et al., 1999). There was a statistically significant difference between the burned and unburned sites for type B fires, which were the 2010 and 2019 fires, respectively. This may be because when the sampling was conducted, it was only three years after the previous fire, which is still below the burning regime in Grassland vegetation. It was expected that there would be differences in shrub species cover between burned and unburned area. The implication of this study is to ensure that areas of the park with low herbivores accessibility needs to be burned at least every 6 to 8 years to maintain Grassland vegetation structure and functioning. The study limitation is there was no enough fire that occurred in the park for us to test fire frequency and it would have been good if fire frequency impacts on vegetation was tested to ensure that we know the exact frequency required in years for better management of this Grassland.

Chapter 6 synthesis and conclusion

Synthesis and summary of findings

Grasslands and savannas are shaped by several factors which includes fire (Bond 2012, Fuhlendorf 2008). Fire plays a crucial role, particularly in influencing the structure and composition of vegetation and the abundance of both woody and herbaceous species (Bond & Keeley, 2005;Cavender-Bares & Reich, 2012), thereby impacting ecosystem function. There is a noticeable increase in the abundance of woody plants observed in Grasslands and savannas globally (Briggs et al., 2002; Roques et al. 2001; Van Auken 2000). Chapter 2 examined the influence of fire presence and absence on grass species composition and species richness. Chapter 2 findings showed that the absence and presence of fire does have an impact on grass species composition. It was clear from the results that burned site was dominated by grass palatable species. Fire presence and absence did have impact species composition and dominant species. There was a significant difference in species composition in burned and unburned area of site B, where the fire burned less than three years ago. There was no significant difference in species composition in burned and unburned area of site A (an area that has not burned in more than ten years). This shows that fire return interval should not be more than ten years as it affects grass species composition. Conclusion can be made that if a site has not burned for more than 10 years species composition is similar to the site that have not burned in 20 years or more. The highly palatable species *Themeda triandra* was high on burned sites while *M disticha* and *M stricta* were higher in unburned sites. This study offered an understanding of the importance of fire in the management of the Karroid escarpment Grassland.

Chapter 3 examined the influence of environmental factors on plant biomass production, plant species diversity and plant species richness. Plant species richness and diversity patterns are the foundations of ecology and conservation biology research (Noss, 1990). Local and regional plant community distribution patterns are influenced by environmental factors such as climate, topography, and soil physical and chemical properties (Wang et al., 2015). It is important to note that vegetation monitoring is important for understanding the vegetation structure and species composition over time (Bezuidenhout & Brown, 2021). However, few studies have investigated plant biodiversity patterns in the mountainous Grassland in Mountain Zebra National Park. Previous ecological research in the region was primarily focused on livestock grazing effects on the landscape (Hanke et al., 2014; Todd & Hoffman 2009), and several floristic studies have investigated species assemblages in some parts of the region (Brown & Bezuidenhout, 2018). Hence, there is a need to further explore how environmental factors affect the vegetation distribution and structure in the region. The results of the present study supported the hypothesis that plant species richness, diversity, and soil parameters are correlated. It was evident from the results that soil properties can positively and negatively influence species diversity and richness. In this study, clay, and sand content (i.e., soil texture) positively affected species diversity. This may be because of the impact that the soil texture has on the moisture availability of the soil. Soil nitrogen content influences species richness with nitrogen being inversely proportional to species richness.

Vegetation biomass distribution is a vital concept in plant life history, providing the basis for our understanding of plants' responses or adaptive strategies (Chen et al.,2019; Sims et al., 2012). Plant biomass contributes to food webs and overall ecosystem function (Wardle et al., 2004). Although it is well known that vegetation biomass is controlled by the availability of limited resources (Tilman et al., 2012), the interactive effects of these environmental factors on plant biomass remain unclear (de Bello et al., 2013). In Chapter 4 the effects of environmental factors on plant productivity were investigated. Although soil nutrients are highly important in plant biomass production, it was found that their influences on AGB and plant to be insignificant. Soil pH was the sole factor investigated in this study that markedly affected plant biomass production. Other soil factors that were examined did not demonstrate significant effects on plant biomass production.

The absence of fire in Grassland systems enhances woody encroachment, which threatens many grassy ecosystems worldwide. Chapter 5 examined the presence and absence of fire on shrubs species composition and palatability in mountainous Grassland. There was a difference in palatable species richness and diversity between the different fire cycles. There was higher shrubs species richness at cycle A (2002 and 2010) with no difference in burned and unburned area compared to cycle B (2010 and 2019).

Conclusions

The main conclusions are based on the following findings from the different objectives addressed in this study:

1. Fire does have an influence on grass species composition and reducing the unpalatable grass species. This is done to maintain healthy functional Grassland with high palatable grass and shrubs. Based on the results of this research, it is recommended that intermittent fire application should be done every 7 years as it could increase the abundance of palatable species.

2. Chemical properties of soil (nitrogen and soil organic carbon) significantly impacted species richness and diversity and that clay and sand contents positively affected species diversity.

3. Only the soil pH had an influence on plant biomass. Although soil nutrients are highly important in plant biomass production, I found their influences on above ground biomass to be insignificant in this study.

4.Fire does have an influence on palatable shrubs species composition on the karroid escarpment Grassland.

Future research

It would be interesting if future studies focus on the whole plant when examining the influence of environmental factors on plant biomass. This may provide a better insight on how environmental factors such as soil influence plant biomass production and allocation between above ground biomass and below ground biomass. The study did look at the influence of environmental factors on species diversity and species richness, I however recommend that future study be conducted on the influence of environmental factors on different growth forms or different plants functional traits distribution throughout the park. As fires will be recorded in the park and control burn will be implemented, it is recommended that the impacts of different fire frequency on grass and shrubs palatable species be studied at karroid escarpment Grassland. Impacts of fire frequency on dominance and palatable species distribution can be a valuable study to work on. The post fire recruitment is also something that can be of interest to study if there is fire in the park. Incorporating herbivores distribution in the park in relation to different fire occurrences e.g., burned area that burned in the last eight years, twenty years and more than twenty years without fire would also be something to look at.

Study Limitation

One of the limitations of this study was the absence of prior fire occurrence data collected on the sites before the year 2002 fire, this limited the study as there was no data to serve as reference data for comparison. This would have allowed for functional traits study comparisons in the areas with different fire frequency. Recruitment after the fire data would have been great to have but unfortunately this project was registered a year after fire which was too late for post fire recruitment studies.

Recommendations for further studies

Mountain Zebra National Park is the interface of three Biomes: Grassland, Nama Karoo, and Thicket, so it would be interesting to look at species richness, diversity, and species composition comparisons across the three Biomes in the park. As this study obtained the environmental factors data from GIS, it would be good to the actual field data collection. Still, instead of using GIS to obtain soil properties, physical soil sampling, testing for those environmental properties, and comparing the results with the remote sensing results to check the reliability of remote sensing in obtaining soil properties. The study looked at grass species composition, but it would be interesting to do a study looking at grass functional traits on burned versus unburned sites. There are plans to control burn in the park, and it would be an excellent opportunity to do a study that looks at how long it takes for species composition to change after fire. This will enhance our understanding of the structure of plant communities and the relationships between environmental factors and plant species in semi-arid vegetation types. In addition, using remote sensing to map species composition and richness is recommended for future studies.

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Appendix A

Table A: Management Units at Mountain Zebra National Park and their description

Table A 1: Management units at Mountain Zebra National Park and their description

Unit numbers	**Vegetation units**	**Plant communities**	**Description**
1	Mountain highland plains	*Eragrostis lehmanniana-Eragrostis curvula* Grassland	This Grassland is found on the western and eastern sections of the rugged mountain highland plains. The dominant growth form of this Grassland is the herbaceous stratus (canopy cover varies from 50% to 70%).
3	Mountain highland drainage lines	*Searcia lucida-Diospyros lycioides* woodland	This Grassland is associated with the altitudinal range, and climatic gradient together with a more intricate pattern of differing soil conditions, gives rise to a complicated vegetation pattern. This resulted in a dense *Merxmuellera disticha*-dominated tussock Grassland (0.3 m height) and shrub representatives (0.3 m–1.3 m tall).
4	Middle plateau midslope	*Carissa macrocarpa-Rhigozum obovatum* shrubland and *Pentzia globosa-Searsia longispina* shrubland	These shrublands are located on the footslopes, midslopes, and steep northern and north-western midslopes of the rolling middle plateau. The woody layer is not very prominent with only a few trees (<4 m tall) covering an estimated 2% of the area, while the shrubs (1.5 m–2.5 m tall) cover between 15% and 30% of the area. The herbaceous layer (0.5 m–0.7 m tall) is the most prominent layer, covering between 50% and 60% of the area.
5	Middle plateau plains	*Enneapogon scoparius-Acacia karroo* woodland	This woodland is characteristic for plateau midslopes of the rolling middle plateau. Average tree canopy cover is between 1% and 50%, with a height of more than 3 m. The shrub layer covers between 5% and 25% of the area and is approximately 1–3 m in height. The average canopy cover of the herbaceous layer is estimated to be between 15% and 50% of the area, with an average height of 0.35 m.

6	Middle plateau scarps	*Searsia lucida-Buddleja glomerata* shrubland	This shrubland is found on the very steep higher midslopes and middle plateau scarps. Tree and shrub canopy cover are estimated to be between 15% and 40% with an average height of 1.8–2.2 m, while the canopy cover of the herbaceous layer is estimated to be between 30% and 50% of the area, with an average height of 0.3–0.6 m.
7	Valley bottomland plains	*Pentzia incana-Eragrostis lehmanniana* Forbland and *Pentzia globosa-Eragrostis obtusa* forbland	These forblands are found on the lower footslopes and midslopes of the undulating valley bottomland plains. The vegetation consists mainly of grasses and dwarf shrubs with no tree layer present. The shrub layer has an average height of 0.3 m and canopy covers between 25% and 30% of the area, while the herbaceous layer height is between 0.1 m and 0.3 m, with a 25%–60% coverage.
8	Valley bottomland midslopes	*Sporobolus africanus-Enneapogon scoparius* Grassland	This Grassland is found on the lower footslopes and midslopes of the valley bottomland plains. The vegetation consists mainly of grasses and dwarf shrubs with no tree layer present. The shrub layer has an average height of 0.3 m and covers between 25% and 30% of the area, while the herbaceous layer height is between 0.1 m and 0.3 m, with a 25%–60% canopy coverage.
9	Valley bottomland drainage lines	*Aristida adscensionis-Chloris virgata* Grassland	This Grassland is situated on the floodplains/old cultivated fields in the valley bottomland plains. The tree layer, which is taller than 3 m, has a canopy cover between 1% and 50%, the shrub layer (1 m to 3 m tall) between 5% and 25%, and the herbaceous layer (0.2 m to 0.5 m tall) between 15% and 50%.
11	Oldlands	Transformed	Annual and pioneer plant species.

Figure 2. Location of the study area showing biomass distribution across the vegetation units in the Mountain Zebra National Park, South Africa.

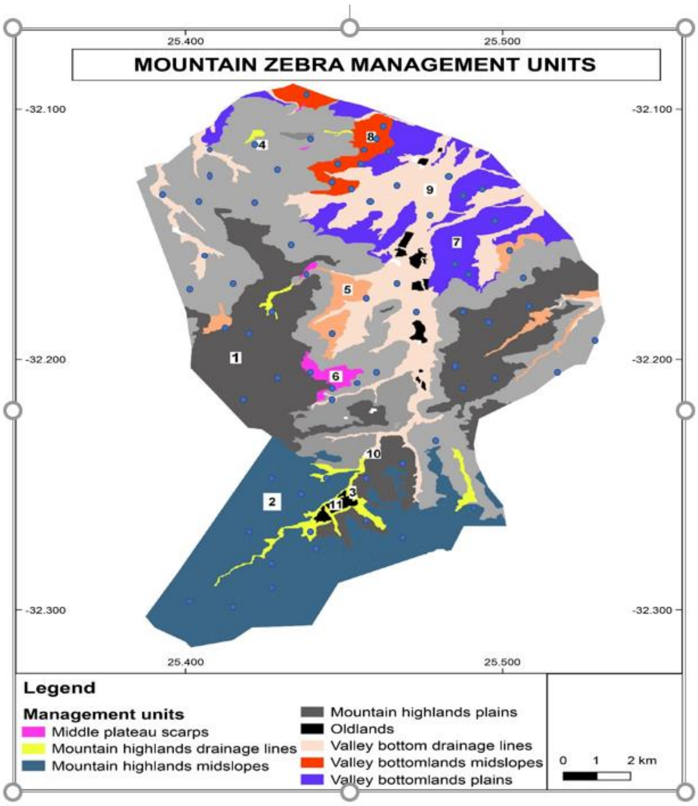

Figure 1 Location of the study area showing biomass distribution across the vegetation units in the Mountain Zebra National Park, South Africa.