The community ecology of herbaceous vegetation in a semi-arid sodic savanna

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Much like the community ecology I studied, this thesis would not be possible without interactions between a community of people and institutions that helped me to function during this journey.

‘Uit onsself is ons nie in staat om iets te bedink asof dit uit onsself kom nie. Ons bekwaamheid kom van God’
2 Korintiërs 3:5

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Declaration

I declare that the work presented in this PhD thesis is my own work. It is being submitted for the degree Doctor of Philosophy at the North-West University, Potchefstroom Campus. It has not been submitted for any degree or examination at any other university. All sources used or quoted have been acknowledged by complete reference.

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Abstract

Ecological conservation of savanna ecosystems is dependent upon interactive mechanisms involving bottom-up drivers such as nutrient availability, and top-down controls relating to fire, herbivory and water availability at various spatial scales. Alterations in diverse savanna herbivore communities, suppression of natural fire regimes and increased rainfall variability alter the functioning of these mechanisms. Protected areas, such as the Kruger National Park (KNP), South Africa, provide valuable natural experimental settings where vegetation structure and function are being maintained by similar drivers under which they have evolved. Since plant communities form the structural and functional basis for most terrestrial ecosystems, functional understanding of species is becoming progressively important. Despite increased awareness of understanding resilience in complex systems, there is limited information available on the underlying functions of herbaceous life forms. This is particularly true for the forb component within the herbaceous layer, which is generally overlooked in ecological studies. Research presented in this thesis primarily aimed to evaluate how the species–and functional composition of the herbaceous layer of a semi-arid sodic savanna responds to changes in herbivory, fire and rainfall. Since the observed patterns in savanna community ecology is driven by underlying effects of herbivory, fire and rainfall variability, this study furthermore aimed to evaluate how interactions within the herbaceous component relate to the drivers they are exposed to, or released from. Specific objectives were therefore to test interactive effects of long-term exposure and/or exclusion of: (1) herbivory and fire on forb and grass diversity and abundance patterns of various functional groups, and how these effects interact with rainfall variability in a nutrient-rich semi-arid savanna ecosystem without elephants, (2) elephants (partial herbivore loss) versus all large mammalian herbivores (LMH) (total herbivore loss) on forb and grass diversity patterns and differences in forb and grass abundances of various functional groups, and how these effects interact with rainfall variability in a fire-excluded nutrient-rich semi-arid savanna system, (3) herbivory and fire during an episodic drought on system function by evaluating patterns in herbaceous species composition, trait diversity and functional group assemblages in a system without elephants, and (4) herbivory during an episodic drought on system function by evaluating patterns in herbaceous species composition, trait diversity and functional group assemblages in a system without fire. Results obtained from this study suggested that semi-arid savanna herbaceous community dynamics are largely dependent on variable life-form (i.e., grass and forb) responses to common savanna drivers at both species and functional level. These findings add to current understanding of the community ecology of savanna herbaceous layers by acknowledging the important ecological role of a previously neglected herbaceous life-form, the herbaceous forb component. However, further research on forbs within sites with different soil conditions and geographical aspects is necessary to improve the understanding of savanna herbaceous communities and hence the management of herbivore forage security when considering complex environmental changes.

Key words**:** *drought, forbs, fire, grasses, herbivory, nutrient-rich, forage, browsing, grazing*

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Chapter 1

Introduction

1.1 Background and rationale

Ecological research on terrestrial ecosystems focuses mainly on the effects of environmental changes on community structure and function. Since plant communities form the structural and functional basis for most terrestrial ecosystems, an improved understanding of community ecology (i.e., species co-occurrence across temporal and spatial scales (McGill *et al*., 2006)) is necessary for the enhanced conservation of biodiversity (Pärtel *et al*., 2017).

Ecologists and managers readily recognize the importance of long-term monitoring at various spatial scales in providing valuable ecological insights (Lindenmayer & Likens, 2009). However, the interpretation of temporal and spatial patterns is often hindered by various challenges such as a lack in commitment to maintaining measurements at regular intervals over long time periods and poorly designed monitoring programs (Clarke *et al*., 2005; Lindenmayer & Likens, 2009). Exploring interactions within ecosystems which change over shorter time scales may, therefore, become a useful tool for improved understanding and management of ecological systems. Sodic patches in savannas have been shown to change over short time scales (Khomo & Rogers, 2005). These patches are sparsely vegetated and considered as potentially stressful environments for vegetation (Scogings *et al*., 2013; Siebert & Scogings, 2015). Nutrient-rich vegetation growing on sodic soil is favoured and intensely utilized by herbivores (Tarasoff *et al*., 2007; Levick & Rogers, 2008). As a result of this intense utilization, savanna sodic patches are the first to show signs of degradation (Grant & Scholes, 2006). Enhanced understanding of dynamic interactions in these environments may improve our understanding of responses of sensitive herbaceous vegetation to extreme conditions such as drought and intensive utilization by herbivores.

The ecological conservation of savanna ecosystems is dependent upon interactive mechanisms involving water availability, soil nutrients, fire and herbivory at different spatial scales (Skarpe, 1992; Scholes & Walker, 1993; Bergström & Skarpe, 1999; Augustine, 2003; Sankaran *et al*., 2008; Belay & Moe, 2012; Bufford & Gaoue, 2015; Yu & D'Odorico, 2015). The functioning of these mechanisms are, however, weakened by human-induced disturbances, such as the loss of heterogeneous savanna herbivore communities to single-species grazers (Daskin *et al.*, 2016), modifications to natural fire frequencies (Olff & Ritchie, 1998; Koerner *et al.*, 2014) and increased rainfall variability as a result of global climate change (Mason *et al.*, 1999). Although protected areas such as the Kruger National Park (KNP) are not secured and entirely isolated from these pressures, they provide valuable natural experimental settings where spatial heterogeneity and ecological responses still function under natural drivers (Pickett *et al.*, 2003). Savanna research usually emphasizes the negative effects of ecological drivers such as high densities of large mammalian herbivores (LMH) (Olff & Ritchie, 1998) and fire effects (Van Langevelde *et al.*, 2003). However, studies focusing on the possible implications of fire exclusion and LMH loss in ecosystems that were shaped by these drivers are limited (Koerner *et al.*, 2014).

In semi-arid savanna herbaceous communities, herbivory, fire, and rainfall variability also interact to determine plant community composition and dynamics (O'Connor, 1994; Archibald *et al.*, 2005; Masunga *et al.*, 2013; Angassa, 2014; Koerner *et al.*, 2014; Burkepile *et al.*, 2017). Herbaceous communities are characterized by forb-grass mixtures of which the grass component functions as the main source of forage, which not only supports the high diversity of African grazers, but also domestic livestock (Bell, 1971; McNaughton & Georgiadis, 1986; Murray & Illius, 1996; Smith *et al.*, 2012). Palatable perennial grasses are generally considered an important and stable source of forage to livestock in savanna systems (Uys, 2006; Trollope *et al.*, 2014, O'Connor, 2015). Consequently, assessments of range condition in savannas are largely based on dominant palatable perennial grass species (Uys, 2006; Kioko *et al.*, 2012; Treydte *et al.*, 2013; Trollope *et al.*, 2014). Increased abundances of alleged unfavourable functional groups (e.g., annual grasses and forbs) at the expense of taller, palatable perennial grass species are often used as an indication of land degradation (Scholes, 1987; Skarpe, 1991; Skarpe, 1992; Milchunas & Lauenroth, 1993; Illius & O'Connor, 1999; Fynn & O'Connor, 2000; Savadogo *et al.*, 2008; Buitenwerf *et al.*, 2011; Tessema *et al.*, 2011; Koerner & Collins, 2013). However, increases in these 'undesirable' functional groups may not necessarily be negative to the overall functioning of savanna ecosystems (Du Toit, 2003; Van Oudtshoorn, 2006; Siebert & Scogings, 2015), as there is a paucity of information on the ecological function of these plant groups. For instance, forbs (herbaceous dicotyledonous species, non-graminoid monocots and geophytes) are a particularly nutritious and high-quality food class for browsers in South African savannas (Du Toit, 2003), and may constitute an important part of ungulate diets at certain times of the year (Scholes, 1987; Van Der Merwe & Marshal, 2012). Not only are forbs functionally important, they are also significant in describing correlations of traits (e.g., vegetative traits) along disturbance gradients (McIntyre *et al*., 1999; Wesuls *et al*., 2012; Wesuls *et al*., 2013), and contribute substantially to the richness and diversity of herbaceous layers in grasslands and savannas (Uys, 2006; Buitenwerf *et al*., 2011; Trollope *et al*., 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015). Moreover, evidence of more intensely browsed herbaceous forbs on nutrient-rich patches (Siebert & Scogings, 2015) confirms their functional responses to small-scale environmental heterogeneity (Shackleton, 2000; Lettow *et al*., 2014). Forbs are overlooked or lumped into a 'non-grass,' Increaser II category in range condition assessments (Scott-Shaw & Morris, 2015). For this reason, the ecological function of forbs and the way they respond to general drivers of herbaceous vegetation dynamics (i.e., herbivory, fire, and rainfall variability) remain less explored (Lettow *et al*., 2014; Scott-Shaw & Morris, 2015, Siebert & Scogings, 2015). Although it is widely accepted that forbs and grasses co-dominate and often switch dominance in response to environmental changes (Illius & O'Connor, 1999; Koerner & Collins, 2014), the complete functional identity of herbaceous layers, and the way they respond to herbivory, fire and rainfall variability remains understudied.

1.2 Aims and objectives of the thesis

The primary aim of this study was to evaluate how the species–and functional composition of the herbaceous layer of a semi-arid sodic savanna responds to changes in herbivory, fire and rainfall.

Results chapters in this thesis were structurally designed to represent herbaceous community responses in different savanna management systems: one fire-excluded system and the other excluding elephants. Herbaceous responses within each of these systems were consistenly compared with effects of total large mammalian herbivore (LMH) loss.

Specific objectives were therefore to test the interactive effects of long-term exposure and/or exclusion of:

1. Herbivory and fire on forb and grass diversity and abundance patterns of various functional groups, and how these effects interact with rainfall variability in a nutrient-rich semi-arid savanna ecosystem without elephants;

2. Elephants (partial herbivore loss) versus all LMH (total herbivore loss) on forb and grass diversity patterns and differences in forb and grass abundances of various functional groups, and how these effects interact with rainfall variability in a fire-excluded nutrient-rich semi-arid savanna system;
3. Herbivory and fire during an episodic drought on system function by evaluating patterns in herbaceous species composition, trait diversity and functional group assemblages in a system without elephants;
4. Herbivory during an episodic drought on system function by evaluating patterns in herbaceous species composition, trait diversity and functional group assemblages in a system without fire.

1.3 Primary hypothesis

In semi-arid savanna ecosystems, fire, herbivory and rainfall variability interact to determine herbaceous community composition, structure, and function (O'Connor, 1994; Archibald *et al*., 2005; Masunga *et al*., 2013; Angassa, 2014; O'Connor, 2015; Burkepile *et al*., 2017). Savanna herbaceous layers are co-dominated by two life-forms (forbs and mainly C_4 grasses), which are floristically, morphologically and physiologically distinct (Turner & Knapp, 1996). Based on these differences, it is expected that the (i) diversity, (ii) abundance and (iii) functional attributes of forbs will differ from grasses when exposed to varying effects of fire, herbivory and rainfall variability.

1.4 Secondary hypotheses

1. Theory states that a competitive exclusion effect will become evident when productivity (biomass) is high and defoliation, disturbance and damage is low, such as when LMH are excluded from the system (Grime, 1973). This is consistent with the findings of Jacobs and Naiman (2008) and Van Coller *et al*. (2013) reporting decreased species richness as a result of increased standing biomass when herbivores are excluded. Tomlinson *et al*. (2016) furthermore reported that herbivores increase functional diversity in savanna communities. From this, it is hypothesized that if herbivores are present in a nutrient-rich semi-arid savanna system, both taxonomic and functional diversity will be higher than when herbivores are excluded, irrespective of life-form.

2. Although not mutually exclusive, it is widely accepted that community diversity of savanna ecosystems is a function of the forb component of herbaceous layers (Uys, 2006; Koerner & Collins, 2014), whilst biomass is a function of the grass component (Uys, 2006). Accordingly, it is hypothesized that forbs will contribute most to the taxonomic and functional diversity of the herbaceous layer.
3. Often considered a subdominant life form, the morphology, life history and ecophysiology of forbs may differ from that of dominant C_4 grasses (Turner & Knapp, 1996). Alternate states of life form (forbs or grasses) dominance within similar functional groups (based on palatability and life history) in response to fire and herbivore treatments are therefore expected. It is predicted that average rainfall and the presence of fire and herbivory will favour palatable perennial grasses, since indigenous African grasses are well adapted to withstand severe grazing (Scholes & Walker, 1993; Owen-Smith, 2013), depending on the type of ecosystem. It is furthermore hypothesized that unpalatable grasses and forbs will be more abundant with higher grazing pressure and drought, whilst the exclusion of herbivores and fire will favour palatable perennial grasses at the expense of other functional groups as a result of competitive exclusion effects (Van Coller & Siebert, 2015).
4. Fire and herbivory are important drivers of herbaceous vegetation composition in savanna systems (O'Connor, 1994; Archibald *et al*., 2005; Masunga *et al.*, 2013; Angassa, 2014; Burkepile *et al.*, 2017). The impacts and extent of fire is strongly affected by soil nutrients (Archibald & Hempson, 2016). For example, as suggested by Bond (2005), nutrient-poor soils would tend to reduce mammalian herbivory, in turn favouring fire. Herbivores would therefore dominate in nutrient-rich patches, and fire in nutrient-poor patches (Bond, 2005). In accordance, Van Coller *et al.* (2013) suggested that fire is considered a secondary driver of herbaceous dynamics in a nutrient-rich semi-arid sodic savanna. It is therefore hypothesized that fire weakly interacts with herbivory and rainfall variability, irrespective of life-form, in these higher-nutrient sodic patches.

1.5 Structure of thesis

This thesis conforms to the guidelines stipulated for a standard research thesis at the North-West University[1]. It encompasses nine chapters, of which the scientific results and discussions are presented in four chapters (Figure 1.1). Results chapters (i.e., Chapters 5-8)

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[1] See section 6 of the manual for Post Graduate Studies (http://www.nwu.ac.za/sites/library.nwu.ac.za/files/documents/manualpostgrad-a.pdf)

were formulated to present a complete view of the research presented in that particular chapter, similarly to a format in which manuscripts are prepared for submission to scientific journals. Cited research is included as a single list of references at the end of the thesis.

Chapter 2: Literature Review

A detailed overview of literature relevant to the research title is provided in this chapter. It defines a semi-arid savanna ecosystem for this study and furthermore elaborates on savanna heterogeneity, vegetation structure, drivers and dynamics of herbaceous layers. Lastly, it provides a backdrop for linking patterns of herbaceous dynamics to ecosystem resilience.

Chapter 3: Study Area

This chapter presents a detailed account of the study area and provides more information regarding the general ecology (i.e., locality, climate, topography, geology and soil, and vegetation) of the study site.

Chapter 4: Materials and Methods

This chapter describes general methodology followed to acquire floristic and trait data, as well as statistical analyses that were applied for which results are presented in chapters 5-8. It furthermore discusses the experimental layout of the Nkuhlu exclosures, even though small variation to the design is highlighted in respective chapters.

Results and Discussion:

A layout of the results chapters summarizing research questions, data pools used and systems investigated is presented in Figure 1.1.

Chapter 5: Interactive effects of herbivory, fire and rainfall variability on herbaceous diversity and life form abundance in a system without elephants

This chapter addresses the first objective by providing visual and tabular results on how herbaceous diversity responds to LMH loss, fire treatment and rainfall variability and how the herbaceous community components interact at spatial and temporal scales.

Chapter 6: Interactive effects of herbivory and rainfall variability on herbaceous diversity and life form abundance in a system without fire

Results pertaining to the second objective are presented in this chapter. Results from statistical analyses describing forb and grass richness and diversity patterns, variation in forb and grass abundances and differences in functional group abundances in a system without fire disturbance are presented and discussed here.

Chapter 7: Drought-tolerant herbaceous community composition and function in a fire-exposed system without elephants

This chapter addresses the third objective of this study by evaluating patterns in herbaceous composition, functional diversity of the overall herbaceous layer, as well as herbaceous life forms separately and lastly, functional group assemblages across different herbivore and fire treatments during an episodic drought.

Chapter 8: Drought-tolerant herbaceous community composition and function in a system without fire

Patterns in trait assemblages and functional traits that could potentially contribute to drought resilience of a nutrient-rich semi-arid savanna herbaceous layer (i.e., objective 4) are identified, presented and discussed in this chapter.

Chapter 9: Conclusions and Synthesis

This chapter integrates the findings discussed in the respective results chapters (Chapters 5-8) to provide conclusions and a general synthesis on the relevance and implications of the presented research.

The community ecology of herbaceous vegetation in a semi-arid sodic savanna

RESEARCH QUESTIONS

DATA POOL

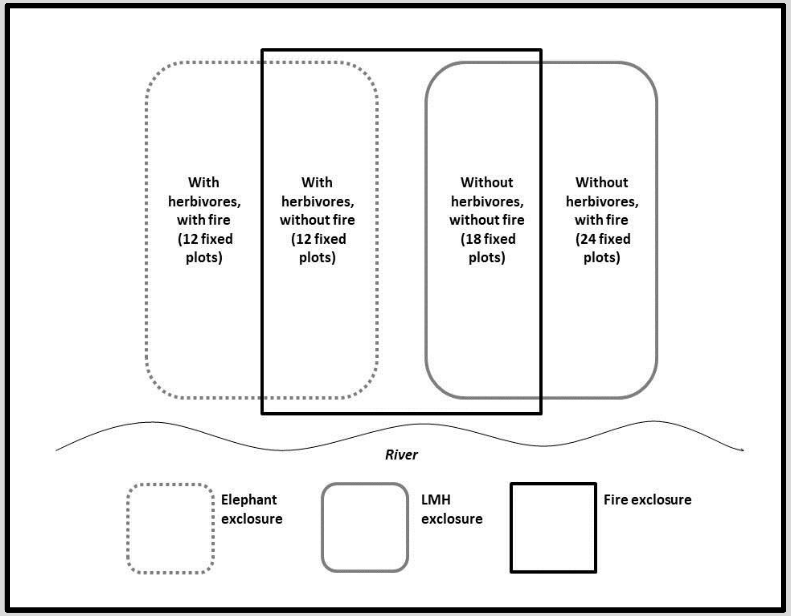
SYSTEMS INVESTIGATED

1: What are the long-term responses of herbaceous vegetation to rainfall variability and various treatments of herbivory and fire at:

- ❖ Species level (diversity data)
- ❖ Life form level (abundance data)
- ❖ Pre-identified functional group level (abundance data)?

RAINFALL:

- ❖ **2001: 659 mm**
- ❖ **2010: 567.1 mm**
- ❖ **2015: 350.4 mm**

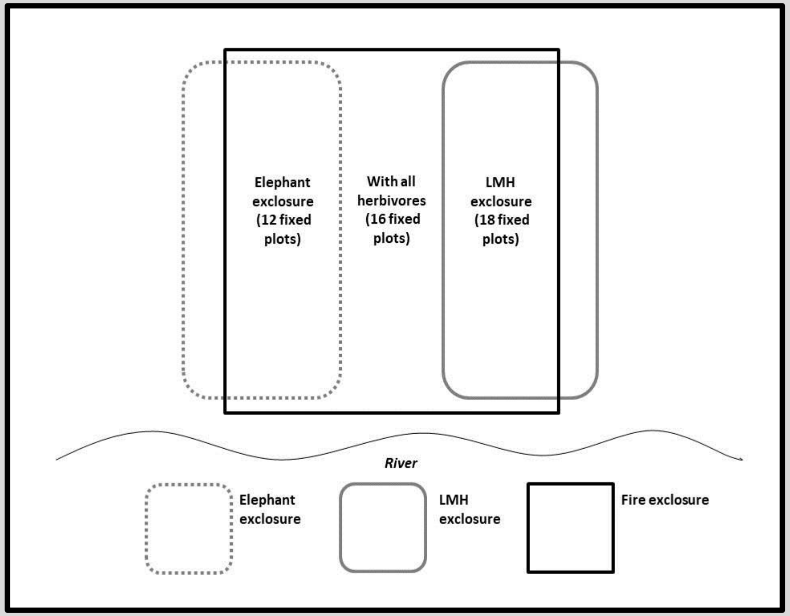


Without elephants
Chapters 5 & 7

2. What are the effects of various treatments of fire and herbivory on the functional diversity and–group assemblages of the herbaceous layer during an episodic drought?

RAINFALL:

- ❖ **2015: 350.4 mm**



Without fire
Chapters 6 & 8

Figure 1.1. Layout of results chapters summarizing research questions, data pool used and systems investigated.

Chapter 2

Literature Review

2.1 Defining semi-arid savanna ecosystems

Savannas cover 20 % of the global land surface (Baudena & Rietkerk, 2013) and 40 % of the land surface of the African continent (Scholes & Walker, 1993). In South Africa, savannas occupy approximately 33 % of land area (Higgins *et al*., 1999; Van Wilgen *et al*., 2000; Mucina & Rutherford, 2006). Savannas are generally described as having ecosystem types with strong seasonal plant communities which, in their natural state, have a relative continuous herbaceous layer and a discontinuous woody component (Walker *et al*., 1981; Knoop & Walker, 1985; Scholes, 1987; Belsky *et al*., 1989; Skarpe, 1991; Couteron & Kokou, 1997; Scholes & Archer, 1997; Mucina & Rutherford, 2006; Sankaran *et al*., 2008; Baudena & Rietkerk, 2013). Semi-arid savannas are characterized by an annual rainfall of below 650 mm and are considered water-limited systems of which annual primary production interacts strongly with rainfall (Scholes, 1987; Sankaran *et al*., 2004). The definition of a semi-arid savanna proposed for the purpose of this study is '*a strongly seasonal and water-limited plant community with a relatively continuous herbaceous layer, consisting of forbs and grasses, and a discontinuous woody component.*'

2.2 Semi-arid savanna heterogeneity

Savanna heterogeneity can be expressed as the variety of plant communities and habitat assemblages in space and time as determined by variations in environmental factors such as topography, soil conditions, fire regimes, competition, rainfall variability, and distribution of soil moisture and herbivores (Baker, 1992; Bergström & Skarpe, 1999; Van Wilgen *et al*., 2003; Scogings *et al*., 2012). Although savannas are generally not considered as extremely diverse ecosystems, species richness of all biotic types is mostly above the global average (Scholes & Walker, 1993). Heterogeneity is considered the source of biodiversity (Pickett *et al*., 2003). Spatially heterogeneous environments can accommodate a greater variety of species by providing various microhabitats and microclimates (Begon *et al*., 2006). In other words, increased heterogeneity generally leads to increased species richness and diversity as a result of niche differentiation, allowing more species to inhabit the same space (Mouquet *et al*., 2002). According to the intermediate disturbance hypothesis (IDH), this increase in variety is however limited at high levels of stress or disturbance at one extreme and low levels of disturbance at the other. Species richness and diversity is therefore generally the highest at intermediate levels of biomass corresponding to moderate levels of disturbance or competition, limiting diversity at high levels of disturbance through low productivity at the one end, and by competitive exclusion at the other (Figure 2.1) (Grime, 1973; Pollock *et al*., 1998; DeForest *et al*., 2001; Bhattarai *et al*., 2004; Michalet *et al*., 2006).

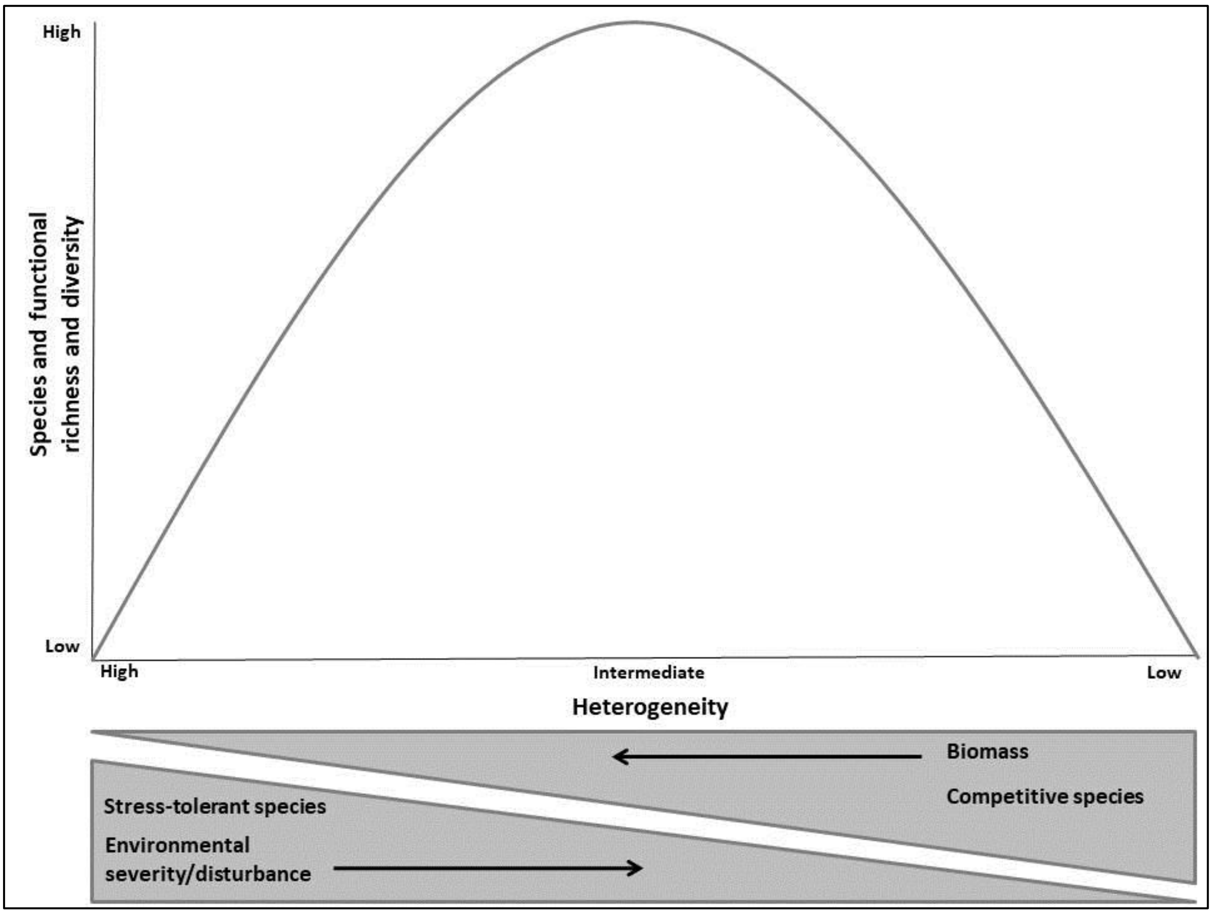


Figure 2.1. Illustration of the proposed response of species and functional diversity to various levels of biomass and environmental heterogeneity or disturbance (Adapted from Michalet *et al*., 2006).

Related to species richness and diversity, functional diversity and richness have been found to follow similar response patterns, with higher functional richness and diversity found at intermediate disturbance intensities, compared to high and low disturbance intensities (Figure 2.1) (Biswas & Mallik, 2010; Cadotte *et al*., 2011). Heterogeneity is produced by different processes such as fragmentation and disturbance at different scales (Farina, 2007). Scale is a central concept in landscape ecology (Wiens, 1989; Wu & Li, 2006; Farina, 2007; Wu, 2007), and refers to the spatial or temporal dimensions at which a pattern or process is recognizable (Farina, 2007). Observable ecological patterns may be affected by the scale at which these patterns are being studied (Wiens, 1989). Biodiversity is a scale-dependent property (McCann, 2000), and changes in diversity patterns occurring at large scales, may have their origins at smaller scales (Farina, 2007). An example of such a source of heterogeneity is the characteristic catenary sequence which develops on granite-derived soil (Scholes, 1987). Catenas are defined as predictable soil profile sequences and plant-soil associations along a slope (Alard, 2010). Crests and midslopes are characterized by coarse, shallow, sandy soil, which are relatively low in nutrients, overlying weathered rock, whilst foot slopes below the seep-line are characterized by deep, duplex nutrient-rich, clay-rich soil (Khomo & Rogers, 2005; Siebert & Eckhardt, 2008; Scogings *et al.*, 2012). Semi-arid savannas may include both dystrophic ('moist') and eutrophic ('arid') parts over short distances, which reveal variations in responses to ecological drivers (Scholes, 1987; Mucina & Rutherford, 2006). The type, as well as the biotic and abiotic diversity of savanna systems at any given time, is largely determined and controlled by soil conditions (Venter, 1986; Scholes & Walker, 1993; Venter *et al.*, 2003).

Soil fertility, as a bottom-up driver, influences not only the relation between annual rainfall and annual aboveground herbaceous production of savannas, but also strongly affects and shape other components of their structure and function, such as species composition, cover, morphology, forage chemistry and-quality and herbivore community structures (Scholes, 1990; Verweij *et al.*, 2006). However, differences between eutrophic and dystrophic systems are not only attributed to the amount of nutrients present, but also to the rate at which these nutrients are turned over (Scholes & Walker, 1993). Semi-arid African savannas or fine-leafed savannas are generally categorized as being nutrient-rich or eutrophic and are associated with fertile soil, as opposed to the moist nutrient-poor soil associated with dystrophic, broad-leafed savannas (Scholes, 1990; Du Toit & Cumming, 1999; Verweij *et al.*, 2006). Usually situated in the nutrient-rich bottomlands, close to the drainage line (Bailey & Scholes, 1997; Khomo & Rogers, 2005), sodic patches can be classified as eutrophic savanna systems. The extent (the spatial span of a study, i.e., the study area (Wu, 2007)) of sodic patches may be relatively small, but like termite mounds, their effects may disappear or be averaged out at coarser scales (Pickett *et al.*, 2003). Although not prominent at coarser scales of observation, sodic patches still play an important functional role in the broader landscape as nutrient hotspots and are therefore functionally linked with the larger spatial context (Pickett *et al*., 2003). Sodic patches have a global distribution and occur mainly in arid and semi-arid regions of North America, Australia and Africa (Khomo & Rogers, 2005). They are dynamic and change over a relatively short time scale (Khomo & Rogers, 2005). In southern Africa, sodic patches are generally open areas associated with foot slopes of undulating granitic landscapes (Venter, 1990; Alard, 2010). Sodic plant communities host distinct vegetation and herbivore activities that differ from those found on upland soil (Du Toit *et al*., 2003). Given the unique character of these communities they are viewed as key resources requiring rigorous examination, although many questions surrounding their ecology remain unanswered (Pickett *et al*., 2003). Sodic patches produce palatable, high-quality forage for large herbivores, particularly grazers and mixed feeders (Grant & Scholes, 2006; Scogings, 2011). Despite having a lower standing herbaceous biomass, grasses growing on sodic soil are considered productive (Grant & Scholes, 2006). Herbivores tend to congreagate on sodic soil, where they are provided with nutrient-rich forage that sustains high quality body condition for improved dry season survival and reproduction, while providing open spaces for enhanced predator vigilance (Venter, 1990; Bailey & Scholes, 1997; Khomo & Rogers, 2005; Grant & Scholes, 2006). Consequently, sodic patches are often associated with overgrazed and trampled vegetation (Van Coller *et al*., 2013). Sodic patches form an important part of the heterogeneous landscapes of savanna ecosystems (Khomo & Rogers, 2005; Grant & Scholes, 2006; Levick & Rogers, 2008). Studying herbaceous vegetation interactions with herbivory and fire, which are considered important drivers of herbaceous vegetation dynamics in such systems (Van Coller *et al.*, 2013) may enhance the management, conservation, and sustainability of these unique and ecologically important plant communities. Furthermore, nutrient-rich sodic patches within the Kruger National Park (KNP) are examples of natural systems where spatial heterogeneity and ecological responses still function unhindered over time and space (Foxcroft & Richardson, 2003; Pickett *et al*., 2003). Since being favoured and intensely utilized by herbivores, sodic areas will primarily show signs of degradation (Grant & Scholes, 2006), making them ideal to study effects of important savanna drivers (i.e., herbivores and fire) on savanna herbaceous vegetation.

2.3 Vegetation structure

Savanna distribution, structure and function is primarily determined by water and nutrient availability, fire and herbivory (Scholes & Walker, 1993; Bergström & Skarpe, 1999;

Augustine, 2003; Sankaran *et al*., 2008; Belay & Moe, 2012; Bufford & Gaoue, 2015; Yu & D'Odorico, 2015). Savannas are unique among terrestrial biomes in having no one single dominant plant growth form, but rather a co-dominance between trees and the herbaceous layer (Scholes, 1987; Sankaran & Anderson, 2009; Smith *et al*., 2012; Barbosa *et al*., 2014).

Tree-grass coexistence

The identification of mechanisms allowing trees and grasses to coexist in savanna systems, without one life form out-competing the other, remains a widely discussed topic in savanna ecology (Ward *et al*., 2013; Bufford & Gaoue., 2015). The coexistence and complex interactions between the herbaceous layer and the woody component makes the ecology of savannas unique (Scholes & Walker, 1993). One of the most common and debated concepts in attempting to explain the tree-grass balance is spatial resource partitioning or the 'spatial-niche-separation' hypothesis (Scholes & Archer, 1997; Jeltsch *et al*., 2000; Ward *et al*., 2013). According to Walter (1971), who postulated that water is the limiting factor in semi-arid savannas, trees and grasses have different access to this limiting factor because of their different rooting profiles. Grasses, having shallower rooting systems than trees, can, therefore, access water from subsurface layers, whilst trees use little of the water in the subsurface layers since they have exclusive access to the subsoil water below grass roots, allowing for these life forms to coexist (Walter, 1971; Mordelet *et al*., 1997; Ward *et al*., 2013). Although there is some support for this hypothesis (Knoop & Walker, 1985; Scholes & Archer, 1997; Ludwig *et al*., 2004a), there are also arguments against it (Scholes & Archer, 1997; Ludwig *et al*., 2004b), suggesting that the two-layer hypothesis cannot account for the large variation in the tree-grass ratio within a single climate-soil combination, and that many trees in savannas are quite shallow-rooted. Furthermore, some studies have indicated that the manifestation of the spatial-niche-separation hypothesis is dependent on climate, suggesting that niche separation occurs in drier areas, but not when soil moisture levels are high (Ward *et al*., 2013). The principal role of niche separation has not yet been demonstrated in savannas (Priyadarshini, 2016). Other hypotheses attempting to explain tree-grass interactions include the 'pulse reserve hypotheses' which proposes that different functional types (grasses and trees) respond differently to rainfall events, for example, fast growth in grasses and slow growth in trees (Reynolds *et al*., 2004), and the 'demographic bottleneck' hypothesis which states that a tree faces adverse conditions at different stages of its life history which limits its growth and survival (Sankaran *et al*., 2004). Sankaran *et al*. (2004) furthermore suggested an integration of the ‘demographic bottleneck’ hypothesis and ‘pulse reserve’ hypothesis to explain tree-grass coexistence in savannas.

African savannas, in particular owe their existence to interactions between fire and large herbivores, and are therefore sensitive to changes in climate (primarily rainfall), soil nutrient content, fire regime and herbivory (Skarpe, 1991; Skarpe 1992). Anthropogenic effects such as land transformation (e.g., mining, agriculture and human settlements (Mucina & Rutherford, 2006)) and increased greenhouse gas accumulations have altered the global environment and global biogeochemical cycles (Chapin III *et al*., 2000). The African continent will not escape these human-induced changes (Hulme *et al*., 2001). Atmospheric carbon dioxide (CO_2) levels have increased by 30% in the last three centuries as a result of increased deforestation and fossil fuel combustion (Chapin III *et al*., 2000; Conti & Díaz, 2013). In savannas, rising atmospheric CO_2 levels have been reported to cause increased woody density at the expense of C_4 grasses (Bond & Parr, 2010; Kulmatiski & Beard, 2013; Smit & Prins, 2015). Dominant grass species in savanna systems tend to follow the C_4 photosynthetic pathway (Shorrocks, 2007). These grasses have evolved under low atmospheric CO_2. With increased CO_2 they may potentially lose their competitive edge over their temperate competitors (Bond & Parr, 2010; Parr *et al*., 2014). This shift in life form dominance is predicted to continue and intensify with increasing CO_2 concentrations (Smit & Prins, 2015). The ecological and conservation implications of these shifts have not yet been adequately addressed (Bond & Parr, 2010).

Herbaceous layers are functionally important in savanna ecosystems providing, among others, primary production as forage for herbivores (Scholes & Walker, 1993; Bailey & Scholes, 1997; Khomo & Rogers, 2005), organic litter for increased water infiltration, soil stability and nutrient cycling (Walker *et al*., 1981; Moretto *et al*., 2001) and fuel for fires (Skarpe, 1992; Bond, 1997; Govender *et al*., 2006; Van Wilgen *et al*., 2011).

2.4 Herbaceous layer dynamics

2.4.1 Forb-grass co-occurrence

While many studies report on the relationship between trees and herbaceous layers (Walker *et al*., 1981; Belsky *et al*., 1989; Jeltsch *et al*., 1998; Jeltsch *et al*., 2000; Sankaran *et al*., 2004; Belay & Moe, 2012), emphasis is generally placed on the grassy component (Muoghalu, 1996). However, the herbaceous layer consists not only of different grass species, but also herbaceous dicotyledonous species, non-graminoid monocots and geophytes, often collectively termed as forbs (Scholes, 1987; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015). Rangeland research in South Africa has largely been driven by agriculture rather than conservation, and therefore management planning and decisions are often based on dominant grass species (Uys, 2006; Trollope *et al.*, 2014). Consequently, the biology, heterogeneity and function of the forb component in current savanna ecological models remains weakly represented and poorly understood (Uys, 2006; Siebert & Scogings, 2015).

Studies reporting on savanna vegetation dynamics and response to grazing and fire are abundant (Scholes, 1987; Skarpe, 1991; Skarpe, 1992; Milchunas & Lauenroth, 1993; Fynn & O'Connor, 1999; Illius & O'Connor, 1999; Archibald *et al.,* 2005; Archibald, 2008; Savadogo *et al.*, 2008; Tessema *et al.*, 2011; Koerner & Collins, 2013; Guo *et al.*, 2016; Tessema *et al.*, 2016). However, it seems that forbs have largely been overlooked in such ecological studies and are often lumped into a non-grass category, rarely further subdivided based on functional attributes such as palatability or life history (Uys, 2006; Scott-Shaw & Morris, 2015).

Palatable perennial grass dynamics are closely related to, among others, rainfall variability (Buitenwerf *et al.*, 2011; O'Connor, 2015), showing increased abundance in years with above-average rainfall and decreased abundance in years with below-average rainfall (O'Connor, 2015; Tessema *et al.*, 2016). Annual grasses and both annual and perennial forbs have been reported to be favoured by drought episodes in semi-arid savannas of southern Africa (O'Connor, 1998; Buitenwerf *et al.*, 2011). Sustained heavy grazing with no rest in such systems is generally presumed to favour annual grasses, unpalatable perennial grasses and both annual and perennial forbs at the expense of palatable perennial grasses (Milchunas & Lauenroth, 1993; Lavorel *et al.*, 1997; Fynn & O'Connor, 2000; Buitenwerf *et al.*, 2011; O'Connor, 2015; Yé *et al.*, 2015; Guo *et al.*, 2016; Tessema *et al.*, 2016). Low intensity surface fires early in the dry season have been reported to have positive effects on grasses with an annual life history at the expense of perennial grass species (Govender *et al.*, 2006; Shorrocks, 2007; Savadogo *et al.*, 2008; Trollope *et al.*, 2014; Fensham *et al.*, 2015). Forb cover tends to be negatively affected by fire alone, whilst the combined effect of grazing and fire has been reported to promote forb cover (Koerner & Collins, 2013).

Increased atmospheric CO_2 levels may favour plants with a C_3 photosynthetic pathway (including trees and forbs) (Bond & Parr, 2010; Wang *et al.*, 2013). The associated increase in woody cover in savannas will potentially lead to a reduction in grass biomass (Smit & Prins, 2015), and is widely thought to subsequently cause decreases in plant diversity and richness (Price & Morgan, 2008; Kulmatiski & Beard, 2013). However, various studies in savanna ecology, especially in nutrient-rich environments, have reported on higher herbaceous species richness and diversity when standing biomass levels are low (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Van Coller & Siebert, 2015). Often considered a subdominant life form, the morphology, life history and ecophysiology of forbs differ from that of dominant C_4 grasses, this possibly attributing to their success as reflected by their density and biomass production (Turner & Knapp, 1996). Although grasses generally make up the bulk of above-ground biomass in savanna systems (Scholes and Walker, 1993; Scott-Shaw and Morris, 2014), it is the forb component that contributes substantially to the richness and diversity of these systems (Uys, 2006; Trollope *et al.*, 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015). For example, forbs make up 1194 of the 1421 taxa in the KNP, whilst Uys (2006) encountered 3-5 forb taxa for every one grass and sedge across a range of South Africa's rangelands. Considering this, the forb component of the herbaceous layer may become increasingly important when trying to determine and understand the consequences of increased atmospheric CO_2 levels.

2.4.2 Functions of grasses in savanna systems

Grasses belong to the Poaceae family, and can be considered the most important plant family on earth (Van Oudtshoorn, 2015). The distribution of mammalian herbivores is correlated with a rise in dominance and diversity of grasses (Scholes *et al.*, 2003). Grasses are fierce competitors for water and nitrogen, and can generally not be outcompeted by woody plants below-ground (Skarpe, 1992). However, increased tree growth may suppress grasses which may be outcompeted for resources such as light (Scholes & Archer, 1997).

Food source

At high levels of productivity, grasses are usually the primary life form in the herbaceous layer, since they are tall, fast-growing and can out-compete other species of smaller stature for resources such as light, water and nutrients (Grime, 1973; Jacobs & Naiman, 2008; Van Coller & Siebert, 2015). Grasses contributed approximately 80 % of the herbaceous layer production at Nylsvley – semi-arid to mesic savanna on the highveld (Scholes & Walker, 1993).

Palatable perennial grasses are an important source of forage stability to grazers in semi-arid savanna systems (O'Connor, 2015), and are considered important for livestock production (Uys, 2006; Trollope *et al.*, 2014). Many herbivores such as the Cape buffalo (*Syncerus caffer*), hippopotamus (*Hippopotamus amphibius*), blue wildebeest (*Connochaetes taurinus*), white rhinoceros (*Ceratotherium simum*) and plains zebra (*Equus quagga*) are inherently dependent on grass as a source of food (Van Oudtshoorn, 2006; Waldram *et al.*, 2008; Treydte *et al.*, 2013). Many grass species such as *Sporobolus nitens* and *Urochloa mosambicensis* are considered important lawn-grass species (Archibald, 2008; Waldram *et al.*, 2008). Grazing lawns are important components of savanna ecosystems (Archibald, 2008) and are created and maintained by continuous grazing of large–and meso-herbivores in the same area, leading not only to increased supply, but also enhanced quality and digestibility of forage (McNaughton, 1984; Archibald *et al.*, 2005; Verweij *et al.*, 2006; Hempson *et al.*, 2014).

Fuel for fire

Grass biomass is the source of fuel in fire-prone African savanna ecosystems (Skarpe, 1992; Bond, 1997; Govender *et al.*, 2006; Van Wilgen *et al.*, 2011). Fire is a key agent that shapes many terrestrial landscapes as it removes large quantities of plant biomass, which in turn creates nutrient fluxes that contribute to ecological rejuvenating qualities (Van Wilgen *et al.*, 2003; Farina, 2007; Higgins *et al.*, 2007). Fire, a significant evolutionary force and worldwide phenomenon, has been part of ecosystems for millions of years, shaping global biome distribution and ecological properties, maintaining structure and function of fire-prone communities and strongly affecting savanna vegetation dynamics and the carbon cycle (Baker, 1992; Bond & Keeley, 2005; Bond *et al.*, 2005; Bowman *et al.*, 2009; Staver *et al.*, 2009).

Regrowth of grasses after fires is short, palatable and nutritious, attracting animals into burnt areas (Gureja & Owen-Smith, 2002; Archibald *et al.*, 2005; Van Oudtshoorn, 2006). Two long-term consequences of this 'magnet-effect' are suggested by Archibald *et al.* (2005). Firstly, that when there are few fires it would lead to the development of patches of intensively utilized grassland and the invasion and spread of grazing-tolerant lawn grasses. Secondly, where fires are frequent, intensively utilized patches would not persist and tall, fast-growing, but highly flammable grasses intolerant of grazing would become dominant.

Stabilizing and protecting soil

Perhaps the most important, yet least recognized function of grasses is their role in protecting and stabilizing soil (Van Oudtshoorn, 2015). Grasses, perennial species in particular, not only protect the soil against wind and water erosion (Skarpe, 1991; Van Oudtshoorn, 2006), but also from excessive water evaporation through shading the surface (Rowntree *et al*., 2004). After heavy rain, sediments get caught by obstacles such as grass tufts, causing them to become an important sight for the germination of seeds (Scholes *et al*., 2003). Grass cover reduces the generation and speed of runoff, which in turn reduces soil erosion (Mekuria *et al*., 2007). Decomposition is an important process in ecosystem functioning, since it is a major determinant of nutrient cycling (Moretto *et al*., 2001). Litter is a source of organic matter and nutrients during decomposition, and helps maintain soil fertility (Koukoura *et al*., 2003). An ungrazed grass sward becomes moribund over time (Trollope, 2011), which promotes litter fall with various beneficial effects (Walker *et al*., 1981). Decomposition of litter helps maintain system productivity through regulating the availability of nutrients for plant growth (Koukoura *et al*., 2003; Li *et al*., 2011).

Assessing range condition

Key grass species can be used to determine habitat condition and to monitor the effect of different management practices and functional attributes such as burning, development of watering points, forage production potential of the grass sward and the resistance to soil erosion (Trollope *et al*., 1989; Trollope, 1990; Van Oudtshoorn, 2006).

2.4.3 Functions of forbs in savanna systems

Forbs represent various plant families and are an important component of semi-arid African savanna systems (Kallah *et al*., 2000; Van Oudtshoorn, 2015), particularly following episodes of disturbance, such as herbivory or drought (Scholes, 1987). Although more research is still needed to study the function of forbs in ecologically important systems such as nutrient-rich sodic zones (Siebert & Scogings, 2015), some of the more general functions will be discussed below.

Food source

At the end of the dry season, when little green foliage is available, robust forbs are an important source of forage for herbivores (Owen-Smith, 1994; Kallah *et al*., 2000). Forbs are considered scarce and nutritious forage resources (Odadi *et al*., 2013), and may constitute an important component of ungulate diets at certain times of the year (Scholes, 1987). Forbs have been reported to comprise between 50 % and 80 % of the wet-season diets of savanna mesoherbivores such as the steenbok (*Raphicerus campestris*), impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*) respectively (Du Toit, 1988; Codron *et al*., 2007; Van der Merwe & Marshal, 2012). Megaherbivores such as the white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*) and elephant (*Loxodonta africana*) also consume forbs, especially in the winter (Owen-Smith & Novellie, 1982; Young *et al*., 2005; Kraai, 2010; Malan *et al*., 2012; Landman *et al*., 2013). Siebert and Scogings (2015) reported on the browsing intensity of herbaceous forbs across a semi-arid savanna catenal sequence, and concluded that forbs were more intensely utilized and browsed in the nutrient-rich sodic zone. Forbs are widely used as supplementary forage in livestock production in semi-arid and sub-humid savanna regions of West Africa (Kallah *et al*., 2000).

Species diversity

Forbs contribute significantly to the total species richness of herbaceous layers in savanna and grassland systems (Turner & Knapp, 1996; Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Trollope *et al*., 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015; Van Oudtshoorn, 2015). Family diversity of forbs in African savannas is remarkable (Uys, 2006; Bond & Parr, 2010). In the Kruger National Park, forbs contribute 84 % to the diversity of the herbaceous layer, and make up 1194 of the 1421 herbaceous taxa (Trollope *et al*., 2014).

Nutrient cycling

Many forbs belong to the Fabaceae family, and can therefore promote nitrogen fixation, enriching the soil with this essential nutrient (Van Oudtshoorn, 2015). Siebert and Scogings (2015) reported that one-third of all browsed species in the dystrophic uplands of a semi-arid catenal sequence, belonged to the Fabaceae family. Although the eutrophic sodic bottomlands revealed higher browsing, the density of browsed forbs in the sodic zone was not higher than in the dystrophic crest community, suggesting that the high richness of browsed species in the uplands are a result of the high numbers of N-fixing species (Siebert & Scogings, 2015). Furthermore, forbs, as a functional group, perform better with improved soil conditions such as increased nutrient availability associated with sub-canopy habitats (Singh *et al*., 2008; Linstädter *et al*., 2016), as well as increased soil Nitrogen and moisture content (Turner & Knapp, 1996).

Significant features

Forbs are considered better adapted to shaded microenvironments than grasses, and can therefore persist under dense woody canopies and high grass biomass (Belsky, 1987; Turner & Knapp, 1996; Mlambo *et al*., 2005; Kahi *et al*., 2009). Considering the predicted increase in woody vegetation due to local drivers such as land use change (e.g., heavy grazing or fire suppression), and global drivers such as increased CO_2 (Wigley *et al*., 2010; Buitenwerf *et al*., 2012), shade-tolerant forb species may become a favoured life form under woody densification. Factors leading to increased nutrient availability in soil such as woody canopy effects (e.g., increased availability of water and nutrients in lowland environments (Jacobs *et al*., 2007)) and herbivore presence (e.g., mammalian herbivores promote the conservation of nutrients near the soil surface, hence reducing the leaching of nutrients (Skarpe, 1992)), may furthermore enhance forb performance, since forbs have been shown to make better use of improved soil conditions such as increased nutrient and water availability (Turner & Knapp, 1996; Singh *et al*., 2008; Linstädter *et al*., 2016). Forbs are known to be prominent and especially well adapted to conditions after fire (Van Oudtshoorn, 2015). This rapid resprouting after fire could be attributed to the occurrence of underground storage organs (Uys, 2006; Bond & Parr, 2010). However, long-term annual burning has been reported to reduce forb abundance and diversity (Turner & Knapp, 1996). As sodic patches generally exhibit low standing biomass, fire effects on sodic patch dynamics are unknown (Alard, 2010). Furthermore, impacts and extent of fire is strongly affected by soil nutrients (Archibald & Hempson, 2016). Bond (2005) suggested that nutrient-poor soils would tend to reduce mammalian herbivory, in turn favouring fire. Herbivores would therefore dominate in nutrient-rich patches, and fire in nutrient-poor patches (Bond, 2005). In accordance, Van Coller *et al*. (2013) suggested that fire is considered a secondary driver of herbaceous dynamics in a nutrient-rich semi-arid sodic savanna. The occurrence of bare soil as a result of herbivore presence often facilitates colonization by forb species with rosette and prostrates growth forms, which are associated with high grazing pressure, enhancing species diversity (Burkepile *et al*., 2016). Forbs have furthermore been reported to exhibit a diversity of morphologies, regeneration strategies and eco-physiological attributes, enhancing their resilience to different environmental conditions (Turner & Knapp, 1996; Lavorel *et al*., 1999). Many forbs are symbiotically associated with specific insect species, and support highly specialised faunal pollinator systems (Uys, 2006; Van Oudtshoorn, 2015).

Assessing range condition

Previous research has shown that understanding the dynamics and function of the forb component is essential for the management of the floral diversity of semi-arid African rangelands (Uys, 2006). Forbs should therefore be included in assessments of the response of vegetation to disturbances, and could be used as indicator species for indexing the effect of grazing on forb assemblages (Scott-Shaw & Morris, 2015).

2.4.4 Drivers of herbaceous layer dynamics

Herbaceous layers interact strongly with the biotic (i.e., herbivory) and abiotic (i.e., fire and water availability) top-down controls of semi-arid savanna distribution, structure and function (Scholes & Walker, 1993; Bergström & Skarpe, 1999; Augustine, 2003; Sankaran *et al*., 2008; Buitenwerf *et al*., 2011; Belay & Moe, 2012; Bufford & Gaoue, 2015; Yu & D’Odorico, 2015).

Herbivory

Herbivory is considered a primary driver of herbaceous vegetation dynamics in sodic patches of African savanna systems (Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Van Coller & Siebert, 2015). Herbivores are important disturbance agents, increasing the spatial and physical heterogeneity of ecosystems through creating grazing patches, wallows and game paths (Olff & Ritchie, 1998; Adler *et al*., 2001; Jacobs & Naiman, 2008; Van Der Waal *et al*., 2011; Angassa, 2014). High densities of herbivores create positive feedback effects in which trampling, excretion and defoliation contribute to the nutritive state of vegetation (Grant & Scholes, 2006; Archibald *et al*., 2008; Siebert & Scogings, 2015). Herbivores generally enhance herbaceous species diversity and richness through the suppression of biomass levels and the reduction of herbaceous competition, allowing more species to coexist (Bakker *et al*., 2003; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Van Coller & Siebert, 2015). Moreover, species richness has been reported to increase under high grazing pressure in nutrient-rich ecosystems, possibly because species are less inhibited by resource availability and therefore have a greater capacity for regrowth after grazing (Proulx & Mazumder, 1998). African elephants (*Loxodonta africana*) in particular can induce landscape-scale changes which generally favour grasses over trees (Asner & Levick, 2012; Pellegrini *et al*., 2017). They are therefore considered important ecosystem engineers in savannas, maintaining open wooded grasslands (Pringle, 2008).

Conversely, herbivore exclusion causes the system to homogenize as a result of fewer disturbances (Jacobs & Naiman, 2008; Van Coller & Siebert, 2015). The associated increase in biomass levels in the absence of herbivores leads to a competitive exclusion effect (Grime, 1973; Milchunas *et al*., 1988; DeForest *et al*., 2001), where tall, fast-growing species such as tufted perennial grasses tend to overtop and out-compete forbs of lower stature for resources such as water, light and nutrients (Jacobs & Naiman, 2008). This negatively impacts species richness and diversity, since forbs, rather than grasses, contribute significantly to the diversity and richness of savanna systems (Uys, 2006). In a recent study Van Coller and Siebert (2015) examined above-ground herbaceous biomass and species diversity relationships in sodic patches of a semi-arid riparian ecosystem in a conservation area. They concluded that herbaceous species richness and diversity peaks at 1300 kg ha^{-1}, which is considered intermediate for the sodic zone.

In many regions native herbivores are being replaced by single species domestic livestock (Koerner *et al*., 2014). A known effect of elephant loss is increased woody biomass (Pellegrini *et al*., 2017). However, resolving effects of elephants on African landscapes remains challenging due to a lack of long-term experiments able to manipulate elephants (Van Langevelde *et al*., 2003; Asner & Levick, 2012; Pellegrini *et al*., 2017). Although recognizing that declines in herbivore numbers will impact savanna habitats (Daskin *et al*., 2016), comparative studies that focus particularly on the implications of such losses together with increased variations in fire regimes and rainfall are lacking (Koerner *et al*., 2014). Small-scale experiments able to manipulate the presence/absence of certain large mammalian herbivores over longer time scales are therefore essential in ecological research (Hooper *et al*., 2005; Daskin *et al*., 2016; Pellegrini *et al*., 2017), enabling a better understanding of the effects of herbivores on herbaceous vegetation. This thesis provides a basis for this, exploring herbaceous vegetation dynamics in a system where herbivores are partially (elephant exclosure) and totally (LMH exclosure) lost.

Fire

Fire incidences are a common phenomenon in African savanna ecosystems (Van Wilgen *et al*., 2003). Interactions between fire, grasses and trees in savanna systems are relatively well studied (Van Wilgen *et al*., 2003; Archibald *et al*., 2005; Bond & Keeley, 2005; Govender *et al*., 2006; Pellegrini *et al*., 2017; Veldhuis *et al*., 2017). Fire is considered an important factor in determining the structure and composition of African savanna ecosystems (Du Toit, 2003; Archibald *et al*., 2005; Bond & Keeley, 2005; Govender *et al*., 2006; Higgins *et al*., 2007; Sankaran *et al*., 2008). Fire effects on vegetation depend on various components of the fire regime, such as intensity, frequency and season of burning (Enslin *et al*., 2000). Depending on the fire regime fires can replace trees with shrublands or grasslands (Bond *et al*., 2005). Furthermore, fires occurring over smaller areas of nutrient-rich grazing lawns may promote the heterogeneity of herbaceous vegetation (Archibald *et al*., 2005; Staver *et al*., 2009; Grant *et al*., 2011). Low biomass levels of sparely vegetated sodic patches are considered insufficient to support fire (Levick & Rogers, 2008), possibly attributing to the lack of prominent response patterns of herbaceous vegetation, and fire being considered a secondary driver of herbaceous vegetation dynamics in nutrient-rich sodic patches (Van Coller *et al*., 2013)

Loss of fire from savanna systems is known to cause increased woody biomass and canopy cover, leading to the formation of dense woodlands (Van Wilgen *et al*., 2003; Dohn *et al*., 2017; Li & Waller, 2017). Increased woody cover generally leads to decreased herbaceous diversity and production (Fuhlendorf & Smeins, 1997). However, woody plant canopies enhance microsite conditions by increasing nutrient concentrations through litter deposition (Ludwig *et al*., 2004a). Forbs have been reported to perform better with improved soil conditions (Linstädter *et al*., 2016). Moreover, recent studies have revealed that forbs are tolerant to shaded, sub-canopy habitats (Singh *et al*., 2008; Linstädter *et al*., 2016). This might suggest a facilitative effect between trees and forbs and that forbs, which contribute significantly to savanna herbaceous diversity (Turner & Knapp, 1996; Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Trollope *et al*., 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015; Van Oudtshoorn, 2015), could be more important than previously acknowledged, especially with respect to diversity in systems where fire is lost. Many forbs have fire stimulated flowering, with many species flowering in the first season after a burn (Bond & Zaloumis., 2016). Although recent studies have started to acknowledge forbs and their responses to fire as a noteworthy component of savanna ecology (Koerner & Collins, 2013; Van Coller *et al*. 2013; Fensham *et al*., 2015; Burkepile *et al*., 2017), fire effects on the forb component of savanna herbaceous layers still remain unclear necessitating further exploration over longer time periods (Van Coller, 2014).

Natural fire regimes in savannas have undergone considerable alterations, ranging from complete suppression of fire to changes in seasonality and therefore frequency (Smith *et al*., 2012; Koerner *et al*. 2014). Furthermore, many smaller reserves in Africa do not possess fire management records, and therefore do not maintain prescribed burning (Buitenwerf *et al*., 2011). Understanding the implication of the loss of fire from systems of which the distribution, function, and structure are determined by it, should therefore receive attention.

Climate variability

Savannas are generally associated with strong seasonality and variability in rainfall (Tolsma *et al*., 1987; Fynn & O’Connor, 2000; Mucina & Rutherford, 2006). Global climate change is expected to cause increased frequency of extreme drought events and rainfall variability (Du Toit & Cumming, 1999; Batisani & Yarnal, 2010; Van Wilgen *et al*., 2016). Droughts are a general occurrence in South Africa’s arid and semi-arid rangelands, which may have serious ecological and economic impacts (Vetter, 2009). Severe drought generally leads to the deterioration of perennial species within herbaceous layers (Scholes *et al*., 2003). Palatable perennial grasses are particularly sensitive and closely related to rainfall variability (Scholes *et al*., 2003; Buitenwerf *et al*., 2011; O’Connor, 2015). Drought can lead to changes in grass species composition (Scholes *et al*., 2003), since perennial grasses generally tend to show significant increases with above-average rainfall, and decreases with below-average rainfall (O’Connor, 2015; Tessema *et al*., 2016). However, these rainfall effects on grass composition are moderated by soil properties (e.g., water-holding capacity and fertility) where sandy soil is less prone to compositional changes in perennial grasses than heavy textured soil (O’Connor, 2015). High grazing pressure in combination with below-average rainfall may lead to increased mortality of desirable perennial grass species (Scholes *et al*., 2003; O’Connor, 1998; Fynn & O’Connor, 2000; Buitenwerf *et al*., 2011; Fensham *et al*., 2015). Decreased production of grasses as a result of drought and soil moisture limitations, may lead to higher light availability to forbs in the following years (Turner & Knapp, 1996). Forbs have been shown to respond strongly to small-scale changes in the environment (Shackleton, 2000; Lettow *et al*., 2014). Drought episodes and heavy grazing tend to favour annual and perennial forb abundances in semi-arid savanna systems (Fynn & O’Connor, 2000;

Buitenwerf *et al*., 2011). Similarly to disturbances such as herbivory and fire, drought may either positively or negatively affect species richness, depending on whether dominant, or uncommon species are most affected (Wilson & Tilman, 2002). Drought events, even in the absence of overgrazing, have been reported to cause loss of floristic diversity in grasslands (Du Toit & Cumming, 1999). Understanding how richness and diversity of herbaceous life forms respond to drought is becoming progressively important, since continued global climate change portrays an increased frequency of extreme droughts for African savannas (Du Toit & Cumming, 1999; Batisani & Yarnal, 2010; Van Wilgen *et al*., 2016). Elevated levels of CO_2 may favour forbs over grasses (Bond & Parr, 2010), and forbs contribute considerably to savanna and grassland herbaceous diversity and richness (Turner & Knapp, 1996; Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Trollope *et al*., 2014; Siebert & Scogings, 2015; Van Oudtshoorn, 2015). Investigating the response of, specifically the forb component of the herbaceous layer in a nutrient-rich savanna system, to drier conditions should therefore be an important goal. Understanding how forb richness and diversity respond to such conditions may have important implications for the future management of natural systems.

2.5 Community ecology of herbaceous layers

Community ecology of the herbaceous layer is dependent on interactive mechanisms involving the abovementioned (section 2.4.4) drivers at different spatial scales (Skarpe, 1992). System function and processes rely on the species present (i.e., on its species composition) (Tilman, 2001), as well as the biodiversity (McCann, 2000; Eisenhauer & Schäder, 2011; Loreau & de Mazancourt, 2013) and productivity (Koukoura *et al*., 2003; Li *et al*., 2011) of that particular system.

2.5.1 Community composition

Shifts in herbaceous composition will alter the quantity and quality of available forage to herbivores, which may furthermore indirectly affect herbivore abundances (Veblen *et al*., 2016). Measures of such floristic changes in composition may provide insight into the ecological processes underlying these changes in vegetation (Clarke *et al*., 2005). Fire and herbivory are two major drivers of changes in herbaceous vegetation composition (O’Connor, 1994; Archibald *et al*., 2005; Masunga *et al.*, 2013; Angassa, 2014; Burkepile *et al*., 2017). Changes in climatic conditions, such as drought episodes, also lead to compositional shifts in herbaceous layers of savanna ecosystems (Fynn & O'Connor, 2000; Jacobs & Naiman, 2008; Zebro *et al*., 2016). Although it is recognized that these environmental drivers affect herbaceous vegetation composition, their effects remain dynamic and may be more severe under certain conditions (Fynn & O'Connor, 2000; Adler *et al*., 2001; Burns *et al*., 2009). Compositional shifts in herbaceous vegetation of a nutrient-rich semi-arid savanna system showed less distinct changes when large herbivores were removed from the system, whilst exposure to herbivores led to significant changes in herbaceous composition (Van Coller, 2014). Fire was suggested to have little effects on herbaceous composition in the same system (Van Coller, 2014). Considering a functional trait-based approach, disturbances may act as filters that either allow or exclude species with certain functional attributes to establish and persist in a local community (Grime, 1998; Van Der Plas *et al*., 2012), thereby driving changes in trait assemblages. Species which lack traits for persisting under certain environmental conditions are therefore removed or filtered out from the system (Díaz *et al*., 1998).

2.5.2 Biodiversity

Biological diversity research remains a central theme in community ecology (Magurran, 1988; Pärtel *et al*., 2011), although the definition thereof is almost as variable as diversity itself (Peet, 1974; Redford & Richter, 1999; Oksanen & Pietarinen, 2004; Kotschy, 2013). This seems sensible, since biodiversity is a multifaceted, scale-dependent property in space and time (Magurran, 1988; Willis & Whittaker, 2002; Townsend *et al*., 2003; Worm & Duffy, 2003; Kotschy, 2013). Biodiversity can broadly be defined as the variety and variability of living organisms at various levels and ecological systems in which they live (Levine & Miller, 1994; Guyer & Richards, 1996; Rawls, 2004). Biodiversity exists at various levels of complexity, which includes genetic-, species- , functional, landscape- and ecosystem diversity (Begon *et al*., 2006). Ecosystem diversity represents the variety of ecosystems in a region (Levine & Miller, 1994). Genetic diversity refers to the heritable variation among individuals of the same species (Levine & Miller, 1994; Begon *et al*., 2006). The taxonomic diversity of species in a community is referred to as species diversity, and can be distinguished within communities (alpha (α) diversity), between communities (beta (β) diversity) and between landscapes (gamma (γ) diversity) (Levine & Miller, 1994; Begon *et* *al*., 2006). Species diversity is the main constituent of biodiversity (Zhang *et al*., 2012). Functional diversity refers to the components of biodiversity that influence the functioning of a system (Tilman, 2001). This thesis will address alpha diversity at the plant species and-functional levels respectively.

Biodiversity quantification

Although species richness (S) show distinct patterns and remains an important measure in describing and comparing communities (Lande, 1996; Kotschy, 2013; Van Coller & Siebert, 2015), significant aspects of community structure are neglected when communities are simply described in terms of the number of species present (Begon *et al*., 2006). Information such as whether certain species are rare and others are common, as well as the evenness in distribution of species' abundances are overlooked when referring to species richness alone (Begon *et al*., 2006). Various indices are used to characterize the diversity of a sample by a single number (Botha, 2017). Margalef's species richness index (d) is sensitive to sample size (Warwick & Clarke, 1995) and focuses mainly on the number of species in a sample. Pielou's evenness (J'), also sensitive to sample size and known as equitability, is higher when the abundances of species in the sample are as equal as possible to the population (Kricher, 1972). Heterogeneity indices, i.e., Simpson's index of diversity (Ď) and Shannon-Wiener diversity index (H') accounts for both species richness and evenness. Simpson's index of diversity acknowledges both the abundance patterns and richness of species (Begon *et al*., 2006) and essentially measures the variance in species abundance distribution (Magurran, 2004), whilst Shannon-Wiener diversity index is sensitive to both species richness and the number of individuals (abundance) per species (Keller, 2002).

The recent shift in ecology from only knowing the number of species in a system, to a trait-based understanding of the nature of species, has led to renewed interest in diversity-stability relationships (Johnson *et al*., 1996; Loreau & Behera, 1999; Cornelissen *et al*., 2003; Cadotte *et al*., 2011; Kotschy, 2013). Functional trait-based approaches are becoming increasingly useful and popular in the quantification of functioning of large species assemblages, since plant functional traits are considered good surrogates of ecosystem function (Díaz & Cabido, 2001; Lavorel & Granier, 2002; Díaz *et al*., 2007; Violle *et al*., 2007; Biswas & Mallik, 2010; Kotschy, 2013; Tahmasebi *et al*., 2017). Functional traits include morphological, physiological and phenological traits which affect growth, reproduction and survival, and therefore ultimately individual performance of species (Violle *et al.*, 2007). It is neither possible, nor desirable to denote all aspects of functional diversity within a single number. Mason *et al*. (2005) and Mouillot *et al*. (2005) identified three components of functional diversity derived from the components of species diversity, namely functional evenness, functional richness and functional divergence. Identifying these separate properties allows for a more detailed examination of their relationship with system function (Mason *et al.*, 2005). Functional richness can be defined as the number of different traits in an assemblage (Mouillot *et al.*, 2005; Kotschy, 2013), and therefore measures how different species are and is thus a measure of disparity. Functional evenness refers to the distribution of trait abundance in a community, and will be optimal when the distribution of the abundance of a trait is constant (Mouillot *et al.*, 2005). Functional divergence or diversity refers to the degree of differences in niche space within a community and how it maximises diversity of functional traits, i.e., a community with high functional divergence has a high degree of niche differentiation and inherently higher diversity of traits (Mason *et al.*, 2005; Mouillot *et al.*, 2005).

Importance of biodiversity

"Biological diversity is the key to the maintenance of the world as we know it." – Edward O. Wilson

Biodiversity is a necessary driver of ecosystem stability, functionality and sustainability in the face of environmental changes (McCann, 2000; Eisenhauer & Schäder, 2011; Loreau & de Mazancourt, 2013). The notion that increased diversity leads to increased community stability has a long history in ecology (De Grandpré & Bergeron, 1997; McCann, 2000; Tilman *et al.*, 2006; Ives & Carpenter, 2007; Eisenhauer & Schäder, 2011; Loreau & de Mazancourt, 2013). A firm patron of this idea was Charles Elton who argued that simpler communities are more prone to be easily upset than richer ones, i.e., more subject to unfavourable variations in populations and vulnerable to invasions (McCann, 2000). Ecologists need to understand how loss or addition of species would influence ecosystem stability and function in the face of biodiversity loss and high rates of invasions (De Grandpré & Bergeron, 1997; McCann, 2000; Eisenhauer & Schäder, 2011). The diversity-stability hypothesis (Elton, 1958) states that increased diversity leads to increased ecosystem stability.

Biodiversity regulates many aspects of ecosystem stability (Eisenhauer & Schäder, 2011) such as temporal stability (Tilman *et al.*, 2006); spatial stability (Weigelt *et al.*, 2008);

resistance against disturbance (Tilman & Downing; 1994; Mulder *et al*., 2001); increased invasion resistance (Fargione & Tilman, 2005; De Paula *et al*., 2010) and resilience (Tilman & Downing, 1994; De Paula *et al*., 2010). Various mechanisms underlie this positive relationship between diversity and stability (Eisenhauer & Schäder, 2011). For instance, (i) more diverse communities have various life strategies that respond differently to environmental disturbance, ensuring system stability (Tilman *et al*., 2006; Eisenhauer & Schäder, 2011); (ii) communities with higher diversity are characterized by complementary resource usage in time and space (Eisenhauer & Schäder, 2011) and (iii) increased diversity leads to increased primary productivity, since there is a better chance that more productive species would be present at higher diversity (Tilman, 1999).

Many studies support the diversity-stability hypothesis (Tilman, 1996; McCann, 2000; Cadotte *et al*., 2012; Kuiters *et al*., 2013; Loreau & de Mazancourt, 2013). However, new insights show that although this may be true for some systems, it may not be true for others (Johnson *et al*., 1996). Despite being an important and widely studied subject in ecology (De Grandpré & Bergeron, 1997; McCann, 2000; Tilman, 2006; Ives & Carpenter, 2007; Eisenhauer & Schäder, 2011; Loreau & de Mazancourt, 2013), the underlying mechanisms of this relationship remain controversial and poorly understood (Kennedy *et al*., 2003; Loreau & de Mazancourt, 2013). One such mechanism is known as the insurance hypothesis (Yachi & Loreau, 1999; Valone & Barber, 2008) which states that increased biodiversity insures ecosystems against declines in their functioning when environmental conditions fluctuate (Yachi & Loreau, 1999; Chappin III *et al*., 2000; Cadotte *et al*., 2012). Diversity therefore has a stabilising effect on ecosystem properties (Loreau & De Mazancourt., 2013).

2.5.3 Productivity

In savanna ecosystems, primary production, or the total amount of organic material produced by plants (Van Oudtshoorn, 2015), is determined and influenced by various abiotic factors such as rain (Scholes, 1987; Hopcraft *et al*., 2009), atmospheric CO_2 (Zhu & Southworth, 2013) soil nutrients and fire (Jensen *et al*., 2001; Masunga *et al*., 2013), and biotic factors such as herbivory (Hopcraft *et al*., 2009). Changes in productivity can be used to predict patterns in species–and functional richness and diversity, where least and most productive systems generally reveal lower richness and diversity and systems with intermediate productivity revealing the highest species richness and diversity (Grime, 1973; Gough *et al*., 1994; Guo & Berry, 1998; DeForest *et al*., 2001; Oba *et al*., 2001; Bhattarai *et al*., 2004; Michalet *et al*., 2006; Biswas & Malik, 2010). Furthermore, changes in productivity can be linked to functional traits, whereas with high levels of environmental stress or disturbance and low levels of productivity, only a few species are able to survive and tolerate such extreme conditions (Grime, 1973; Milchunas *et al*., 1988; DeForest *et al*., 2001) because of the traits that they possess. Species that do not have the necessary trait to allow them to survive in these conditions are filtered from the system (Díaz *et al*., 1998). Similarly, high levels of productivity would also favour species with a competitive advantage (e.g. species with traits such as erect, leafy growth forms, and tufted graminoids with high leaf production).

2.6 Linking patterns in herbaceous dynamics to ecosystem resilience

The term resilience refers to a measure of a system's ability to adapt to disturbance by exploiting fluxes, while still continuing to persist and maintain key functions, components and interactions through time, providing essential goods and services (Walker *et al*., 1981; Holling, 1973; Walker, 1992; Kotschy, 2013). Ecosystems generally show remarkable resilience in the face of many natural disturbances, however, little is known about how changes in species composition and abundance would affect system resilience (Kotschy, 2013). Biodiversity is thought to enhance resilience through two important properties, namely i) response disparity or the provisioning of various options for response to change and disturbance (Chillo *et al.*, 2011; Kotschy, 2013; Leslie & McCabe, 2013), and ii) redundancy or similarities in ecological functioning of species (Kotschy, 2013). Ecologists are increasingly recognizing the importance of the inclusion of species functional diversity and a trait-based causal view of community diversity in understanding the effects of disturbance on diversity (Biswas & Mallik, 2010; Cadotte *et al*., 2011; Chillo *et al*., 2011; Hanke *et al*., 2014). However, exploring patterns in species richness and diversity remain essential to understand ecosystem resilience (Okullo & Moe, 2012), and can therefore not simply be disregarded (Grime, 1998).

Vegetation states, or the ability of a system to absorb and adjust to environmental fluctuations without reorganization into a new state, in ecosystems are controlled by resilience (Gillson & Ekblom, 2009), and more resilient systems are more resistant to disturbances (Tilman & Downing, 1994; Walker, 1995) and invasions by alien species (Chambers *et al*., 2014). Consequently, it is important for managers to obtain information concerning resilience so that ecosystem-based management can be implemented and flexibility and resilience of ecosystems can be promoted (Walker, 1995). This is especially true for sodic plant communities which are considered potentially stressful environments (Scogings *et al*., 2013; Siebert & Scogings, 2015) sought after by large herbivores which acquire essential nutrients from the more palatable and nutritious vegetation growing there (Bailey & Scholes, 1997; Tarasoff *et al*., 2007; Jacobs & Naiman, 2008; Scogings, 2011; Scogings *et al*., 2013; Siebert & Scogings, 2015). Because sodic vegetation is considered rich in nutrients, sparsely vegetated sodic patches are associated with overgrazing (Bailey & Scholes, 1997; Khomo & Rogers, 2005; Jacobs & Naiman, 2008; Alard, 2010; Van Coller *et al*., 2013). The resilience of sodic vegetation to this over–utilization is poorly understood and explored. This thesis attempts to address this shortcoming by exploring the community ecology of the herbaceous layer of a nutrient-rich semi-arid savanna ecosystem.

2.7 Summary

Fire, herbivory and climatic variability are major drivers of savanna ecosystem structure, function and distribution. Although the severity and frequency of these drivers on vegetation dynamics have received ample attention from ecologists, potential implications of losing these drivers from savanna ecosystems on vegetation dynamics and structure under increasing rainfall variability are less appreciated. Moreover, these effects on herbaceous layer dynamics and co-occurrence of forbs and grasses in a semi-arid nutrient-rich savanna community remain largely unexplored. Considering the potential importance of forbs in system function, this thesis will aim to provide a better understanding of the interactions between abovementioned drivers or their loss and herbaceous life form dynamics under rainfall variability.

Chapter 3

Study Area

3.1 General ecology of the Dry Sodic Savanna of the Nkuhlu exclosures

3.1.1 Locality

The study was conducted in the Dry Sodic Savanna plant community of the Nkuhlu exclosures, a large-scale, long-term exclusion experiment situated on the northern bank of the perennial Sabie River (24°58′S, 31°46′E), approximately 18 km downstream from Skukuza in the Kruger National Park (KNP), South Africa (Siebert & Eckhardt, 2008) (Figure 3.1).

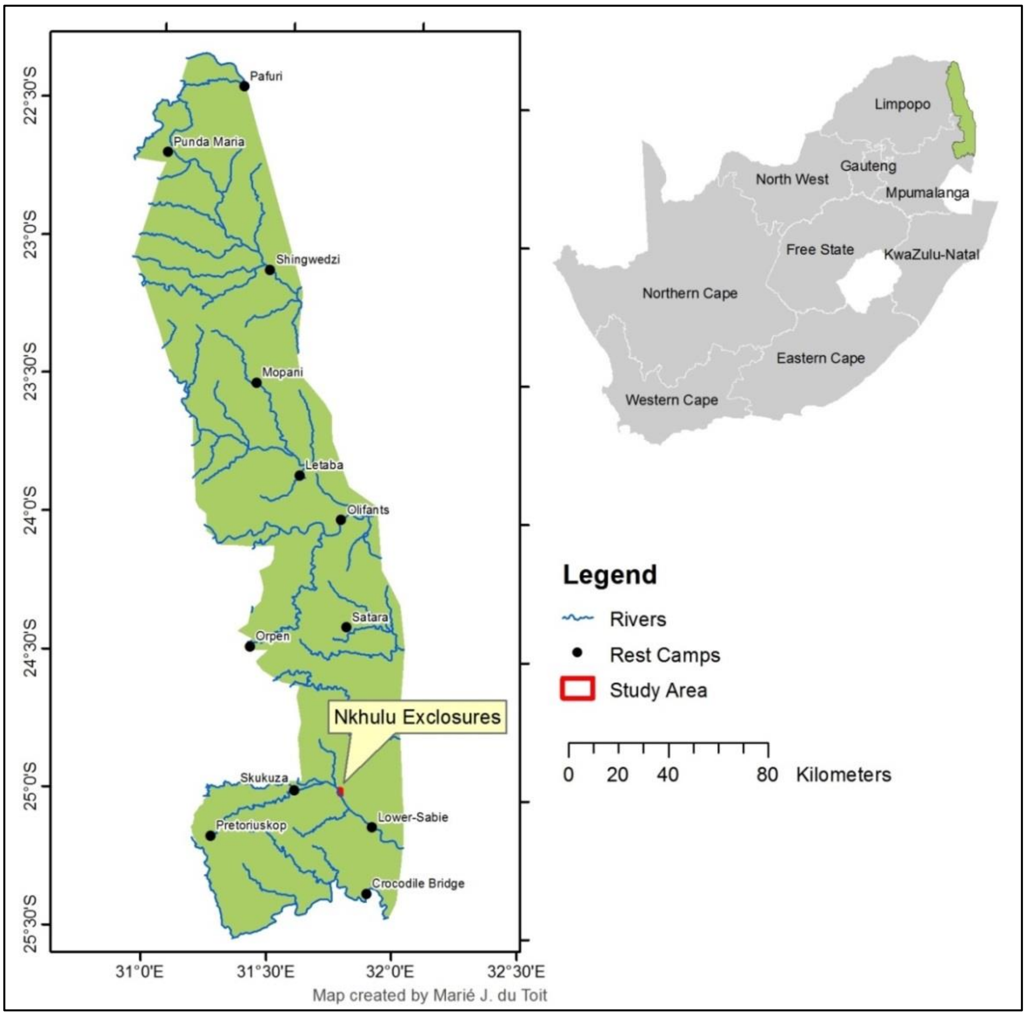


Figure 3.1. Map of Kruger National Park showing the position of the Nkuhlu exclosures, as well as an inset map of South Africa indicating position of the KNP.

3.1.2. Climate

Since semi-arid savannas are water-limited systems (Walker *et al*., 1981; Scholes, 1987), patterns in soil moisture, water availability and ultimately climate are of the main determinants of savanna distribution and structure (Scholes & Walker, 1993; Scholes & Archer, 1997; Sankaran *et al*., 2004, Shorrocks, 2007). A characteristic feature of savanna climate is the variation between hot, occasionally wet growth seasons from October to April, and warm, dry, non-growing seasons (Scholes *et al*., 2003; Venter *et al*., 2003; Scogings *et al*., 2012).

3.1.2.1 Rainfall

Semi-arid savannas are associated with and adapted to highly variable rainfall and water limitations across temporal and spatial scales (Scholes, 1987; Baudena & Rietkerk, 2013). Rainfall is concentrated in five to seven months, whilst the remainder of the year is associated with high temperatures and water-stress (Scholes, 1987). The south and central parts of the KNP, also the area in which the Nkuhlu exclosures are located, falls into the Lowveld bushveld zone with a rainfall of approximately 500 – 700 mm per year (Figure 3.2) and potential evaporation of 6 mm per day in October (Venter *et al*., 2003).

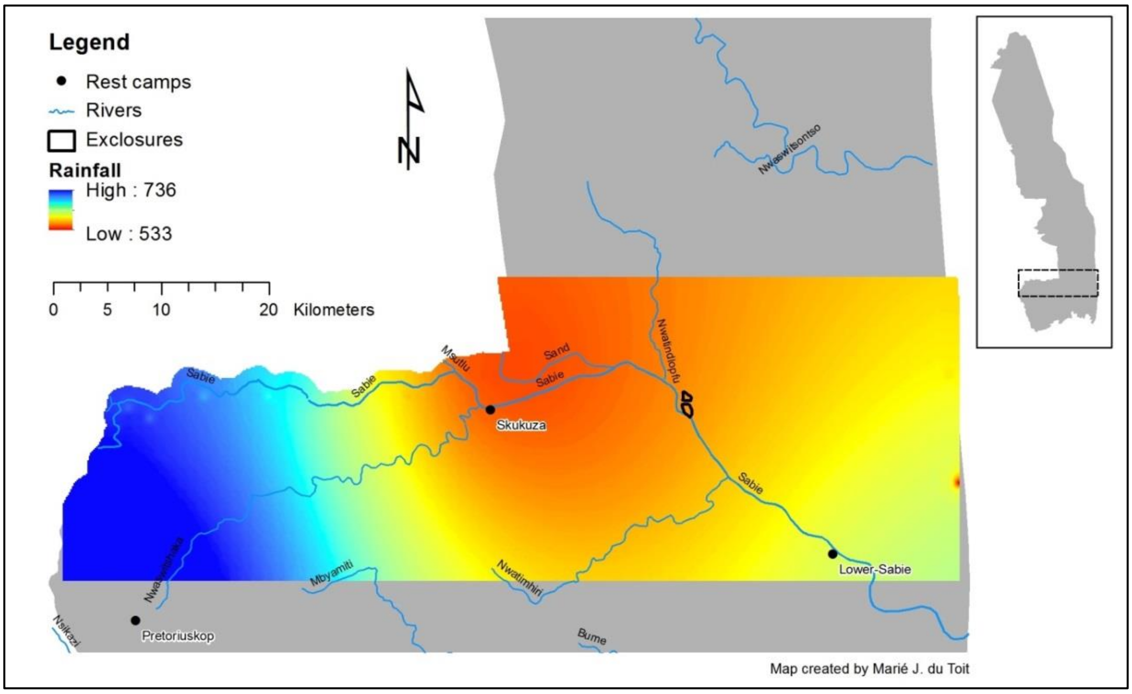


Figure 3.2. Rainfall map of the southern parts of the KNP in which the Nkuhlu exclosures are situated.

The long-term mean annual rainfall measured at Skukuza, 30 km west of Nkuhlu, is ~550 mm (Figure 3.3) (Scogings *et al.*, 2015). Rainfall of 100 mm below this average are considered dry savanna regions (Scholes & Archer, 1997), and was therefore considered a proxy for drought conditions in this particular study area.

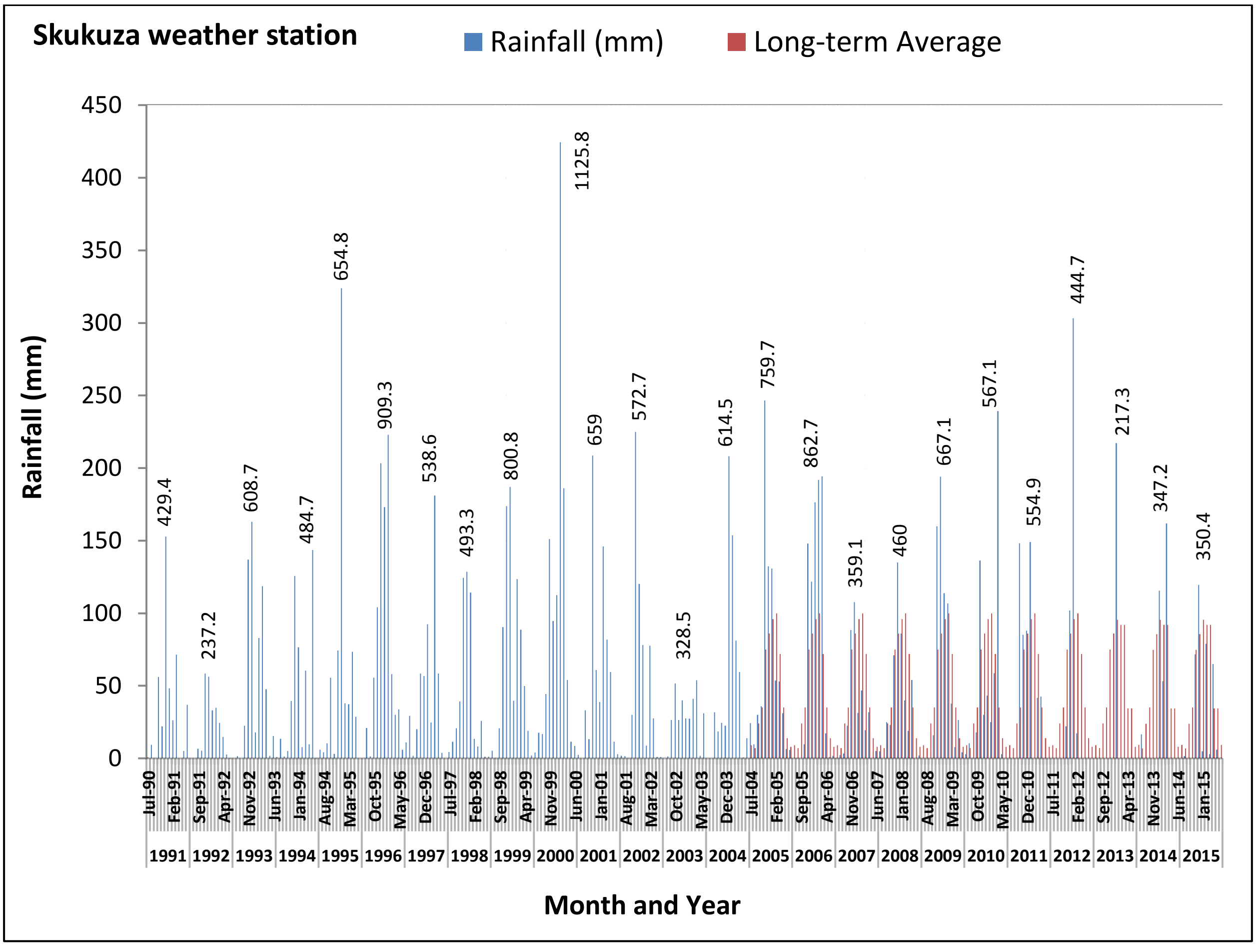


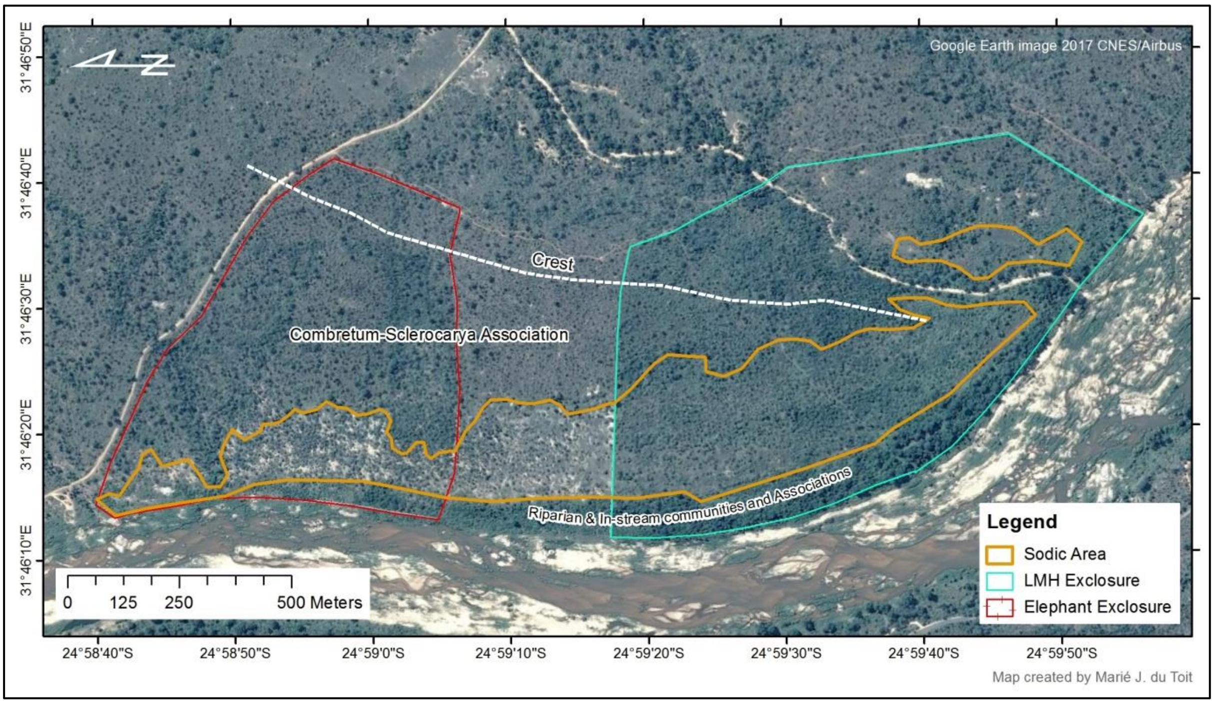
Figure 3.3. Monthly rainfall at Skukuza from 1991 to 2015, including long-term averages. Total annual rainfall (in mm) (July-June) is shown above each year (Kruger National Park Meteorological Records). Long-term mean annual rainfall is ~ 550 mm

3.1.2.2 Temperature

The study area has a general climate pattern of hot summers and mild winters (Venter *et al.*, 2003). The mean daily temperature is 21.9 °C, ranging from 5.6 ºC mean minimum in winter to a mean maximum of 32.6 ºC in the summer months (Siebert & Eckhardt, 2008; Scogings *et al.*, 2012).

3.1.3 Topography

The Dry Sodic Savanna is associated with footslopes of undulating granitic landscapes ranging between 200 m and 230 m above sea level (Dye & Walker, 1980; Venter, 1990; Grant & Scholes, 2006; Alard, 2010; Scogings *et al.*, 2011). Sodic patches are located in the bottomlands at the foot slopes of a typical granitic landscape, close to drainage lines (Figure 3.4) (Bailey & Scholes, 1997; Khomo & Rogers, 2005). Soil moisture and nutrient levels are affected by this altitudinal positioning since water, cations and anions are transported to the bottomlands (Bailey & Scholes, 1997). The main source of water is the perennial Sabie River, with no nearby artificial waterholes, although, zoogenic waterholes created by elephant, buffalo and warthog form Seasonal Pan communities throughout the exclosures (Siebert & Eckhardt, 2008).



Map created by Marié J. du Toit

Figure 3.4. Aerial view of the vegetation zones in the Nkuhlu research exclosures.

3.1.4 Geology and soil

Sodic patches are typically characterized by sodium-rich duplex soil (Dye & Walker, 1980; Siebert & Eckhardt, 2008). The majority of the Dry Sodic Savanna community is underlain with the Montagu soil form (Mu (Figure 3.5)) (Siebert & Eckhardt, 2008). The duplex structure consists of a shallow (< 15 cm), coarsely textured sandy loam A-horizon, supporting most plant life, overlying a B-horizon of almost impervious calcium-rich heavy clay, often leading to vegetation mortality and the limitation of rooting of woody species (Khomo & Rogers, 2005; Grant & Scholes, 2006; Siebert & Eckhardt, 2008; Alard, 2010; Siebert & Scogings, 2015).

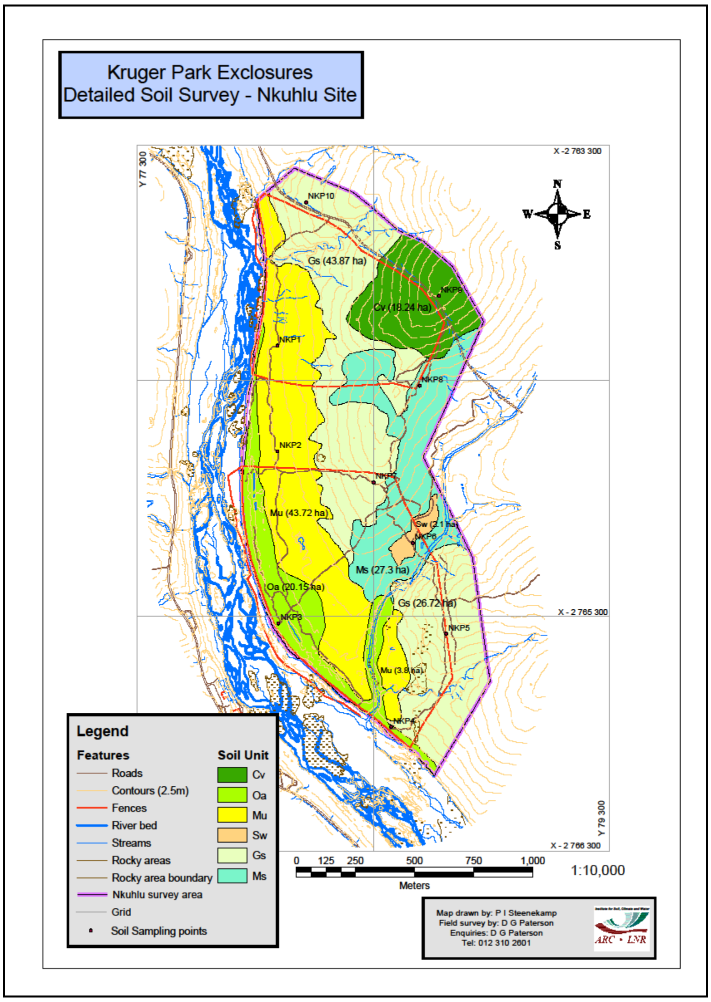


Figure 3.5. Soil map of the Nkuhlu research exclosures.

(This figure by Siebert, F. and Eckhardt, H.C., is licensed under the Creative Commons Attribution Licence. It was first published in *Koedoe* under the title ‘The vegetation and floristics of the Nkuhlu Exclosures, Kruger National Park’. The original version of the article can be found here: http://www.koedoe.co.za/index.php/koedoe/article/view/138/738)

Deep, duplex soil contains dispersed clay with a low infiltration capacity and high concentrations of nitrogen, phosphorus, and sodium (Dye & Walker, 1980; Khomo & Rogers, 2005). Sodic soil is associated with reduced hydraulic conductivity as a result of the hyper-accumulation of exchangeable sodium and is prominent in landscapes derived from sodium releasing parent material such as granite (Khomo & Rogers, 2005) (Figure 3.6). Soil is considered ‘sodic’ when high concentrations of soluble salts prevail, which are dominated by sodium, the pH is greater than 8.5, and electrical conductivity is less than 4.0 dS / m (Tarasoff *et al*., 2007). The level of sodium in soil is often reported as the sodium adsorption ratio (SAR). The SAR of sodic soil is above 13, and causes poor physical soil conditions (Davis *et al.*, 2012).

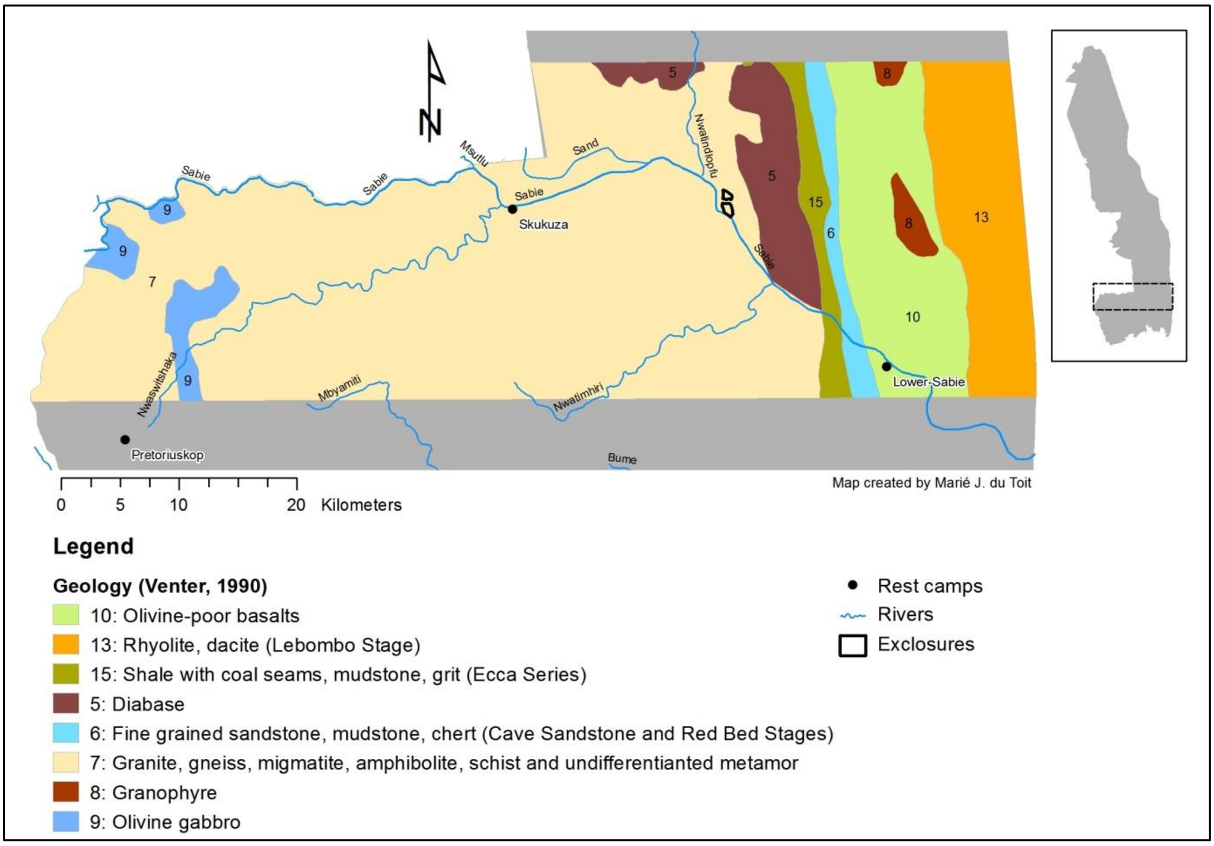


Figure 3.6. Map of underlying geology of southern parts of the KNP.

3.1.5 Vegetation

The Nkuhlu exclosures research site is located within the Granite Lowveld vegetation unit (SVI 3) of the Savanna Biome (Mucina & Rutherford, 2006). Vegetation is described as the *Sporobolus nitens–Euclea divinorum* Dry Sodic Savanna plant community (Figure 3.7) (Siebert & Eckhardt, 2008). The relatively continuous herbaceous layer is dominated by forb species such as *Abutilon austro-africanum*, *Portulaca kermesina* and *Ocimum americanum*, whilst dominant grasses include *Chloris virgata*, *Enteropogon monostachyus* and *Sporobolus nitens* (Siebert & Eckhardt, 2008). The discontinuous woody component is dominated by *Vachellia* (*Acacia*) *grandicornuta*, *Euclea divinorum*, *Spirostachys africana* and *Pappea capensis* (Grant & Scholes, 2006; Scogings, 2011). Vegetation growing on sodic soil is considered more palatable than crest vegetation by herbivores, particularly grazers and mixed feeders (Scogings 2011; Siebert & Scogings 2015). Sodic zones are considered nutrient hotspots (Grant & Scholes, 2006; Van Coller *et al*., 2013; Van Coller & Siebert, 2015) and are favoured by large herbivores which acquire essential nutrients from the more palatable and nutritious vegetation growing there (Bailey & Scholes, 1997; Tarasoff *et al*., 2007; Jacobs & Naiman, 2008; Scogings, 2011; Scogings *et al*., 2013; Siebert & Scogings, 2015).

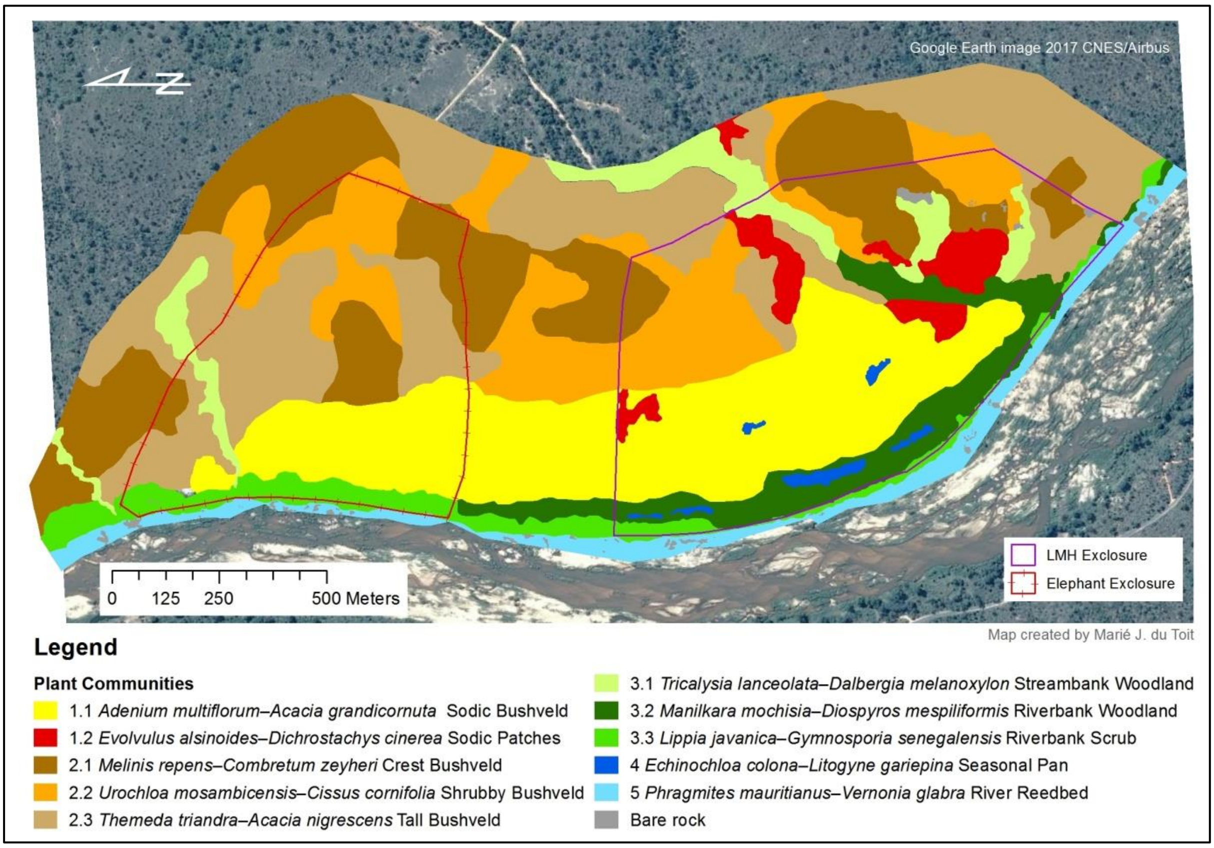


Figure 3.7. Vegetation map of the Nkuhlu research exclosure site.

(This figure by Siebert, F. and Eckhardt, H.C., is licensed under the Creative Commons Attribution Licence. It was first published in *Koedoe* under the title 'The vegetation and floristics of the Nkuhlu Exclosures, Kruger National Park'. The original version of the article can be found here: http://www.koedoe.co.za/index.php/koedoe/article/view/138/738)

3.1.6 Fauna

Large mammalian herbivores residing in the study site include browsers: (giraffe (*Giraffa camelopardalis*), black rhino (*Diceros bicornis*), bushbuck (*Tragelaphus sylvaticus*) and the greater kudu (*Tragelaphus strepsiceros*)); grazers: (Cape buffalo (*Syncerus caffer*), hippopotamus (*Hippopotamus amphibius*), blue wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*)) and mixed–or intermediate feeders: (impala (*Aepyceros melampus*), African elephant (*Loxodonta africana*), Grey Duiker (*Sylvicarpa grimmia*) and steenbok (*Raphicerus campestris*)) (Scogings *et al*., 2012). Trampling, excretion and defoliation by these large mammalian herbivores are thought to maintain vegetation growing on sodic soil in a nutritious vegetative state (Grant & Scholes, 2006; Scogings *et al*., 2012). Abovementioned information is based upon census data for the larger grid, as well as personal observations made in the field since census data specifically for the exclosures is unavailable.

Chapter 4

Materials and Methods

4.1 Overview

This chapter describes survey methods that were followed to collect floristic and trait data, as well as the statistical analyses that were applied for which results are presented in chapters 5-8. The experimental layout of the Nkuhlu exclosures is discussed, although small variation to the design will be highlighted and elaborated upon in the respective chapters.

4.2 Background

The primary mandate of South African National Parks (SANParks) is the conservation of South Africa's biodiversity, landscapes and associated heritage sites (Van Wilgen *et al.*, 2011). Research and ecosystem conservation is therefore two of its core activities (O'Keefe & Alard, 2002). In conjunction with a team of international scientists, SANParks constructed large exclosures in 2001 to study the effects of fire and herbivory on spatial and temporal heterogeneity patterns of vegetation (O'Keefe & Alard, 2002). The exclosures provide ecologists with the opportunity to conduct numerous ecological studies focusing on different life forms and plant communities, as well as cross-catenal vegetation patterns. Herbaceous vegetation studies include, among others, testing the relationship between herbaceous species diversity and aboveground biomass of a nutrient-rich sodic zone (Van Coller & Siebert, 2015); the effect of fire and herbivory on the species richness and diversity of the sodic herbaceous layer (Van Coller *et al.*, 2013; Van Coller, 2014) and testing the browsing intensity on herbaceous forbs across a semi-arid savanna catenal sequence (Siebert & Scogings, 2015).

4.3 Experimental design and sampling

The Nkuhlu exclosures comprise 139 ha of semi-arid savanna in the riparian zone of the Sabie River which is divided into three large scale experimental exclusion treatments. These treatments were designed to include a fire and no-fire treatment (Figure 4.1). One exclusion treatment was designed to specifically exclude elephants (giraffes are also excluded due to their body size), but not other large mammalian herbivores (LMH), and therefore represented an area with intermediate grazing pressure (O'Keefe & Alard, 2002) (Figure 4.1 (a)). A second treatment excluded all herbivores larger than a hare and represented an area with low grazing pressure (rested) (Figure 4.1 (c)). The two exclusion treatments were separated by an unfenced area which allowed movement of all LMH, and hence represented an area with high grazing pressure (no rest) (Figure 4.1 (b)).

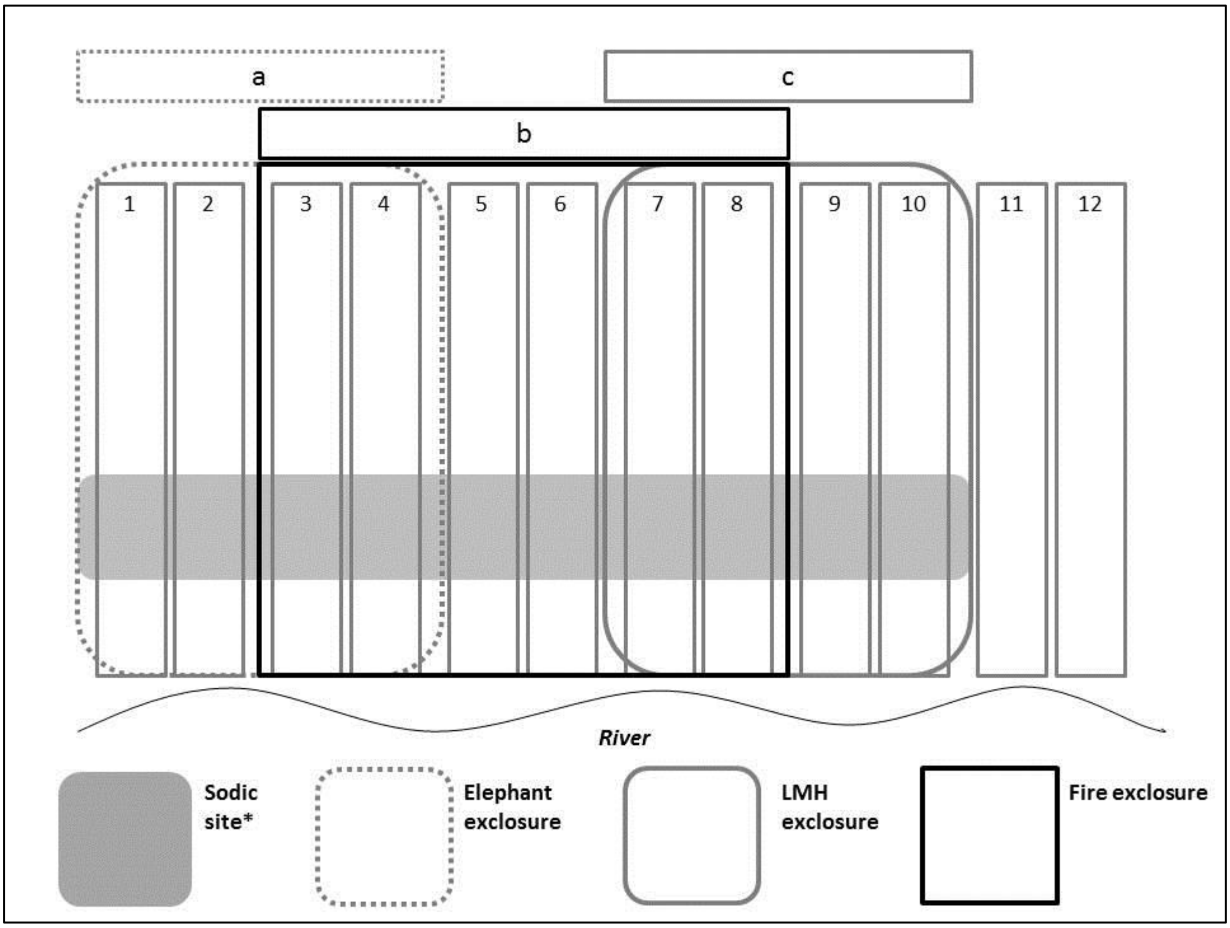


Figure 4.1. Experimental layout of 12 transects within six fire and herbivory treatments in the Nkuhlu exclosures. Data from transects 11 and 12 were omitted from analyses in this study due to the absence of typical sodic soils (Adapted from Van Coller & Siebert (2015)). *Study area relevant to this particular study.

a, b, & c represents the different systems relevant to this thesis: (a) system without elephants (intermediate grazing pressure); (b) system without fire; (c) system without LMH (low grazing pressure).

4.3.1 Floristic sampling

Floristic sampling conformed to the guidelines stipulated in O’Keefe & Alard (2002) and was conducted during the rainy season when plant cover was at its maximum and most plant species were present. Sodic vegetation did not extend into the fire-exposed site where all herbivores are present, and therefore data from transects 11 and 12 were not considered for floristic analyses (Figure 4.1). Fire treatment in the exclosures was established in 2002 (Govender, 2016). Fires occurred in October 2002, August 2007 and June 2012 and were dependent on the occurrence of fire in the larger Kruger National Park (KNP) burn blocks (fire management units) in which the exclosures are situated (Van Coller *et al*., 2013; Van Coller & Siebert, 2015).

Two permanent transects (Figure 4.1) with varying numbers of fixed 10 m x 20 m plots (Figure 4.2), with longest sides running parallel to the river channel, were laid out within each treatment of fire and herbivory. To identify the plots that were representative of the sodic plant community, positions of transects and plots were plotted on the vegetation map of the Nkuhlu exclosures (Siebert & Eckhardt, 2008). Data from 82 fixed plots were sampled in the sodic community. Detailed sampling of herbaceous vegetation was done within two 1 m^2 circular subplots nested at the corners of each 200 m^2 fixed plot, which added up to 164 x 1m^2 in total. Subplots were placed in the eastern (upland downstream) and western (river upstream) corners of each fixed plot (Figure 4.2) (O’Keefe & Alard, 2002). All herbaceous individuals (forbs and grasses) rooted within the circle were counted and identified up to species level conforming to Germishuizen and Meyer (2003). Above-ground rooted clonal structures were counted as individuals. Sampling was conducted in 2002 when the experiment started. Effects of the respective treatments on the 2002 data set were therefore assumed to be negligible. Sampling was repeated in 2010 (i.e., 3 years after a recorded fire incident and 8 years after herbivore exclusion) and again in 2015 (i.e., 3 years after a second fire incident and 13 years after herbivore exclusion).

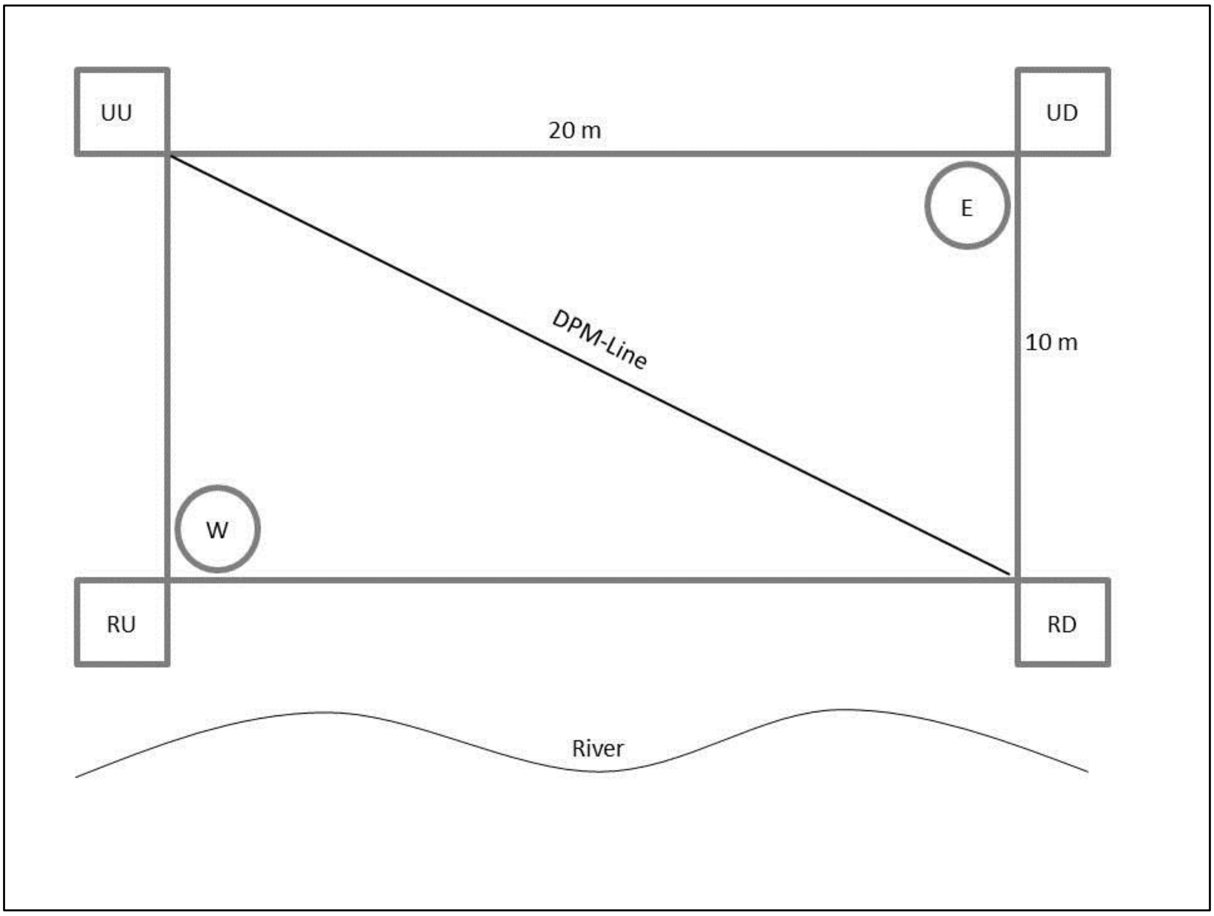


Figure 4.2. Illustration of the position of paired 1 m^2 subplots (W & E) and the diagonal sampling line for disc pasure meter (DPM) readings within a fixed plot. Corners of plots are permanently marked with metal droppers, representing different positions parallel to the Sabie River. Corners: UU = upland-upstream, UD = upland-downstream, RU = river-upstream, RD = river-downstream, E = eastern subplot, W = western subplot (Adapted from Van Coller & Siebert (2015)).

4.3.2 Herbaceous biomass sampling

Above-ground biomass was estimated by taking ten readings with a Lowveld Savanna-calibrated disc pasture meter (DPM) along the diagonal of the fixed 10 m x 20 m plot (Figure 4.2) (Van Coller *et al*., 2013) (Please see Zambatis *et al*., 2006 for a brief explanation on the calibration of the instrument, as well as additional references). DPM–readings were then converted to kilograms per hectare in accordance with the latest biomass conversions for the Lowveld Savanna (Zambatis *et al*., 2006).

4.3.3 Trait selection and sampling

Traits were limited to a number of soft traits (i.e., easily measurable traits for large numbers of species) which were good correlates with the selected functions and hard traits (i.e., traits that are more difficult to measure) (Walker & Langridge, 2002; Cornelissen *et al*., 2003). Traits were identified with particular focus on their potential contribution to the functioning of a nutrient-rich system, as well as their ability to promote the success of herbaceous species which are subjected to fire and herbivory. Traits were assigned to species using various sources in literature including field guides (Van Wyk & Malan, 1998; Van Wyk, 2000; Cornelissen *et al*., 2003; Van Oudtshoorn, 2006; Manning, 2009; Van der Walt, 2009; Kirby, 2013) and various Floras (Germishuizen & Meyer, 2003; Hyde *et al*., 2015; JSTOR, 2016)

Ten traits that capture nutrient cycling, provision of food to animals, primary production and response to damage were recorded for each plant taxa (Table 4.1). Because this study considers three major disturbances in savanna systems, i.e., fire, herbivory and rainfall variability, response to damage was included as a response function (Table 4.1). This response function describes the responses of species to particular types of disturbances as determined by plant functional traits (Kotschy, 2013).

Table 4.1. Effect–and response functions and the traits used to represent them.

Effect functions	**Functional traits**
Nutrient cycling	Specific Leaf Area, Nitrogen-fixing ability
Provision of food to animals	Growth form, Palatability, Flowering phenology, Life history
Primary production	Growth form, Life form
Response functions	**Functional traits**
Response to damage	Clonality, Life form, Life history, Specific Leaf Area, Spinescence

The choice of effect–and response functions and the corresponding trait sets will be elaborated upon in the following sections:

Nutrient cycling

Vegetation growing in nutrient-rich environments generally exhibit traits which further enhances the nutritive state of that community (Lavorel & Garnier, 2002).

Specific leaf area (SLA)

Specific leaf area (SLA) (Table 4.2) is a trait associated with resource economy (Castro *et al*., 2010) and useful to indicate where a species is located on the resource economic spectrum (Kotschy, 2013). SLA is also an indicator of how rapidly a plant can allocate resources to growth, and strongly correlates with leaf nitrogen (N) and phosphorus (P) concentrations (Wright *et al*., 2004).

Specific leaf area measurements were made for 25 herbaceous species following the technique used by Kotschy (2013). Values for the remaining species were obtained from a database compiled for a Ph.D. thesis (courtesy of Kotschy (2013)) SLA was calculated by measuring the projected area of fresh, relatively young leaves from adult plants, with as little as possible damage from pathogens or herbivores, after which leaves were dried and weighed (Cornelissen *et al*., 2003). Leaf area was measured using a Canon CanoScan LiDE 110 Photo scanner together with Leaf Area Measurement software (version 1.3, A.P. Askew, University of Sheffield, June 2003). Images were scanned at 600 dpi using the 'black and white' output mode, no scaling options, and default brightness, contrast and threshold settings. Scanned leaves were labeled and dried in an oven at 30° C for 48 hours. Leaves were then weighed using an OHAUS Scout ^{tm} Pro scale. SLA values of two leaves per individual (5 individuals per species) were averaged to give a mean value per species (Kotschy, 2013). SLA values were considered high when >10 $mm.mg^{-1}$.

Nitrogen-fixating ability

The nutrient uptake strategy of macronutrients, especially N and P, and the efficiency thereof is important for the growth of plants, and their position in ecosystems varying in nutrient availability (Cornelissen *et al*., 2003). Even though there are many other adaptations by plants for the uptake of nutrients, i.e., relations with various types of mycorrhizal fungi and hairy root clusters (Cornelissen *et al*., 2003), the nitrogen-fixing ability of species is the main strategy that is included in this study, since abundant published information was available. It is, however, important to acknowledge, and include, where possible, the other modes of nutrient uptake, such as mycorrhizal fungi and root parasitism (Kotschy, 2013).

Nitrogen-fixing ability was recorded as a binary trait (i.e., N-fixing ability present or absent) (Table 4.2). Information was primarily obtained through field guides (Van Wyk & Malan, 1998; Van Wyk, 2000; Van Oudtshoorn, 2006; Manning, 2009; Van der Walt, 2009; Kirby, 2013) Floras (Germishuizen & Meyer, 2003; Hyde *et al*., 2015; JSTOR, 2016) and other literature (Naisbitt *et al*., 1992; Sprent *et al*., 2013).

Provision of food to animals

This function is perhaps one of the most important in nutrient-rich sodic savannas, since sodic vegetation is preferentially consumed by large herbivores (Bailey & Scholes, 1997) which acquire essential nutrients from the more palatable and nutritious vegetation growing there (Bailey & Scholes, 1997; Tarasoff *et al*., 2007; Jacobs & Naiman, 2008; Scogings, 2011; Scogings *et al*., 2013; Siebert & Scogings, 2015).

Growth form

The accessibility of species to herbivores is affected by their growth form (Kotschy, 2013). Grazing tends to favour small-statured and prostrate species over taller and more erect species (Lavorel *et al*., 1997; Díaz *et al*., 2007; Anderson & Hoffman, 2011), and stoloniferous and rosette growth forms over tussock growth forms (Díaz *et al*., 2007; Anderson & Hoffman, 2011; Rutherford & Powrie, 2011; Hempson *et al*., 2014).

Each species was assigned to one of seven growth form categories (Table 4.2) according to Floras and field guides (Cornelissen *et al*., 2003; Germishuizen & Meyer, 2003; Van Oudtshoorn, 2006). Please refer to Table B.1., Appendix B, for a detailed list of definitions and visual illustrations of the various growth forms.

Palatability

Species with high forage potential produce material that is suitable and available for the consumption by herbivores (Van Oudtshoorn, 2015). These species may vary in palatability and preference, since herbivores may prefer some species over others to acquire essential nutrients and minerals for growth and reproduction (Bailey & Scholes, 1997; Tarasoff *et al*., 2007; Jacobs & Naiman, 2008; Scogings, 2011; Scogings *et al*., 2013; Siebert & Scogings, 2015; Van Oudtshoorn, 2015). Preference by herbivores is an indication of leaf palatability, and can also indicate various underlying leaf–quality traits (Pérez–Harguindeguy *et al.*, 2013). Utilization by herbivores generally benefit species with high forage potential in various ways, i.e., promoted seed dispersal, better germination of seeds after passing through the digestive system of herbivores, enrichment of the soil as a result of urine and dung, stimulated growth because of increased light availability and sustained lower biomass levels for promoted richness and diversity (Jacobs & Naiman, 2008; Van Coller & Siebert, 2015; Van Oudtshoorn, 2015). The main morphological plant parts utilized by herbivores are the leaves (Van Oudtshoorn, 2015). Although plants with high forage potential are essential in ecosystems, all species are equally important to the ecology of a system and fulfil other important functions such as protecting the soil against erosion when the area is over-utilized (Skarpe, 1991; Van Oudtshoorn, 2006; Van Oudtshoorn, 2015).

Palatability was recorded as a categorical trait (Table 4.2). Species were assigned to three categories of palatability based on literature and field guides (Van Wyk & Malan, 1998; Van Wyk, 2000; Manning, 2009; Van der Walt, 2009; Kirby, 2013; Van Oudtshoorn, 2015; Siebert & Scogings, 2015).

Flowering phenology

Flowering phenology is an essential aspect of the ecology of plants, and can influence community assemblage, the relative abundance of species and also their presence or absence (Craine *et al.*, 2011). Phenological traits such as flowering season also determine the availability of species as a food source for animals (Kotschy, 2013), since overlapping of flowering times can affect aspects such as canopy development, which inherently affects competition for resources (Cleland *et al.*, 2006; Craine *et al.*, 2011).

Flowering phenology was considered a categorical trait (Table 4.2). Information for this trait was obtained from field guides, as well as herbarium specimens (Van Wyk & Malan, 1998; Van Wyk, 2000; Manning, 2009; Van der Walt, 2009; Kirby, 2013).

Life history

Sustained grazing favours annual grass species and forbs, at the expense of palatable perennial grass species (Skarpe, 1991; Skarpe, 1992; Milchunas & Lauenroth, 1993; Fynn & O'Connor, 1999; Illius & O'Connor, 1999; Savadogo *et al.*, 2008; Tessema *et al.*, 2011;

Koerner & Collins, 2013). Plants with a short life span are usually associated with species that show high investment in fast growth and photosynthesis (Díaz *et al*., 1998).

Species were assigned to two categories of life span (i.e., annual or perennial) (Table 4.2). Annual species complete their life cycle within one growing season and then dies after numerous seeds have been produced to secure future generations (Pérez-Harguindeguy *et al*., 2013). Perennial species generally survive at least three growing seasons (Pérez-Harguindeguy *et al*., 2013). Biennial species were included under annual species, since they respond similarly to annuals in semi-arid and arid ecosystems (Van Staden, 2016).

Primary production

Primary production is defined as the total volume of organic material produced by plants (Van Oudtshoorn, 2015). Primary production in savannas is determined and influenced by various biotic and abiotic factors such as rain (Scholes, 1987; Hopcraft *et al*., 2009), atmospheric CO_2 (Zhu & Southworth, 2013), fire (Jensen *et al*., 2001; Masunga *et al*., 2013) and herbivory (Hopcraft *et al*., 2009). Growth form (previously described) may be associated with maximising plant production (Pérez-Harguindeguy *et al*., 2013).

Life form

Similarly to growth form, the life form of a species may contribute to its primary production (Pérez-Harguindeguy *et al*., 2013). Species were categorized based on representing herbaceous life forms of plants, i.e., forbs or grasses (Germishuizen & Meyer, 2003) (Table 4.2). Each species was then further assigned to one of five categories originally described by Raunkiaer (1934). Raunkiaer selected varying degrees of adaptation and response in the positioning of perennating buds of species growing in various environments (Smith, 1913; Kent & Coker, 1994; Begon *et al*., 2006). The position of perennating tissue allows us to understand the likelihood of plant survival when subjected to unpredictable disturbances such as periodic grazing and fire, as well as harsher climatic conditions such as droughts (Cornelissen *et al*., 2003).

Species were assigned to categories using relevant literature, Floras and field guides (Smith, 1913; Cornelissen *et al*., 2003; Germishuizen & Meyer, 2003). All climbers were categorized as 'phanerophytes' (Greek *phanero*, 'visible'; *phyte*, 'plant' (Begon *et al*., 2006)), or herbaceous perennials growing taller than 20 cm with perennating buds emerging from aerial parts of the plant (Kent & Coker, 1994; Cornelissen *et al*., 2003). Herbaceous perennial species growing 10 to 20 cm tall with perennating buds emerging from aerial parts close to the ground were classified as ‘chamaephytes’ (*chamaephytes*: ‘on the ground plants’ (Begon *et al*., 2006)) (Kent & Coker, 1994; Cornelissen et al., 2003; Kotschy, 2013). All annual species or plants that die after seed production and complete their life cycle in one year were assigned to the ‘therophyte’ (*therophytes*: ‘summer plants’ (Begon *et al*., 2006)) category (Kent & Coker, 1994; Cornelissen *et al*., 2003; Kotschy, 2013). Species forming buds at or in the soil surface, and which die back in unfavourable conditions were classified as ‘hemicryptophytes’ (*hemicryptophytes*: ‘half hidden plants’ (Begon *et al*., 2006)) (Kent & Coker, 1994; Cornelissen *et al*., 2003; Kotschy, 2013). Plant species with buds or shoot apices which survive unfavourable conditions below the ground were categorized as cryptophytes (*cryptophytes*: ‘hidden plants’ (Begon *et al*., 2006)) (Kent & Coker, 1994; Cornelissen *et al*., 2003).

Response to damage

Vegetation growing on sodic soil is particularly susceptible to herbivory, since forage is nutrient-rich and favoured by herbivores (Bailey & Scholes, 1997; Tarasoff *et al*., 2007; Jacobs & Naiman, 2008; Scogings, 2011; Scogings *et al*., 2013; Siebert & Scogings, 2015).

Spinescence

Nutrient-rich savannas exhibit physical defences against herbivory, opposed to nutrient-poor areas dominated by broad-leafed vegetation, which are chemically protected from herbivory (Scholes *et al*., 2003). One such physical defence and response to grazing is spinescence (Anderson & Hoffman, 2011). Spinescence, collectively used to describe any form of spine, thorn or prickle is considered a mechanical defence which contributes to anti-herbivore defence (Cornelissen *et al*., 2003; Anderson & Hoffman, 2011; Alves-Silva & Del-Claro, 2016). Spines are defined as a modified sharp-pointed leaf, leaf part or stipule; thorns are woody, hard modified twigs; spiny bracts are modified leafs; and a prickle is modified epidermis seen as a sharp–pointed outgrowth (Cornelissen *et al*., 2003; Hanley *et al*., 2007; Pérez-Harguindeguy *et al*., 2013). Although spines are generally known as an anti-herbivore defence mechanism, they provide many additional functions, such as reducing heat or drought stress (Cornelissen *et al*., 2003), structurally assisting climbing plants and providing other plants protection from herbivores (Cornelissen *et al.*, 2003; Hanley *et al.*, 2007). Spinescence is generally a prevalent feature when there are many herbivores present in the system, and is considered an efficient defence mechanism mainly for large mammalian herbivores (Cooper & Owen-Smith, 1986; Hanley *et al.*, 2007; Kotschy, 2013).

Spinescence was recorded as a binary trait (Table 4.2) with either no spines and /thorns present (absent) and spines and/or thorns present (present). Information for this trait was obtained primarily from observations of species in the field, as well as from herbarium specimens.

Clonal ability

Clonality or the ability of a species to reproduce vegetatively by producing aboveground ramets or units and expanding horizontally (Cornelissen *et al.*, 2003), and gives plants a competitive edge and ability to exploit nutrient-rich patches (Pérez-Harguindeguy *et al.*, 2013).

Herbaceous species were categorized into one of four categories based on Cornelissen *et al*. (2003) and Pérez-Harguindeguy *et al*. (2013). Species with no clonal organs were classified as ‘non-clonal’, while other species were categorized as ‘clonal aboveground’ when stolons are formed, ‘clonal below ground’ when rhizomes, tubers, bulb or corms were present, and lastly clonal above and below ground.

A summary of the selected traits together with trait categories, units, definitions of traits and the relevance of the traits to this study with supporting literature is presented in Table 4.2.

Table 4.2 Selected plant traits with a description of the trait categories, units, definitions of traits and relevance of traits to this study.

Trait	**Trait categories and code score**	**Trait units**	**Definition of trait**	**Motivation for inclusion in this study**	**References**
Life form	1 = Forb 2 = Graminoid	Categorical	Main life forms of plants, i.e., grasses and forbs	Response to disturbance	Germishuizen & Meyer (2003); Lavorel *et al*. (1997)
Specific Leaf Area (SLA)	1 = < 10 2 = 10-20 3 = 30-40 4 = > 40 5 = Unspecified	Categorical	One-sided area of a fresh leaf divided by its oven-dry mass (mm^2mg^{-1})	Response to damage	Garnier *et al*. (2001); Cornelissen *et al*. (2003); Pérez-Harguindeguy *et al*. (2013)
Growth form	1 = Erect leafy 2 = Tufted graminoid 3 = Prostrate 4 = Climber 5 = Creeping graminoid 6 = Shrub 7 = Rosette	Categorical	Mainly determined by canopy structure and height	Plant strategy and adaptations in response to shifts in climate, disturbance and response to damage	Lavorel *et al*. (1997); Cornelissen *et al*. (2003); Germishuizen & Meyer (2003); Van Oudtshoorn (2006); Pérez-Harguindeguy *et al*. (2013)
Raunkiaer's life form	1 = Chamaephyte 2 = Therophyte	Categorical	The height above ground of the perennating buds (i.e., plants from which growth commences	Response to damage, disturbance and climatic	Kent & Coker (1994); Cornelissen *et al*. (2003); Begon *et al*. (2006); Kotschy (2013); Pérez-

	3 = Hemicryptophyte 4 = Cryptophyte 5 = Phanerophyte		in the next favourable growing season) of plant species	conditions	Harguindeguy *et al*. (2013)
Life history	1 = Annual 2 = Perennial	Categorical	The time period from establishment until no live part remains	Response to damage and disturbance	Cornelissen *et al*. (2003); Lavorel *et al*. (1997); Kotschy (2013); Pérez-Harguindeguy *et al*. (2013)
Palatability	1 = Low 2 = Moderate 3 = Good	Categorical	The amount of nutrients in vegetation, also influencing palatability	Provision of food to herbivores	Van Wyk & Malan (1998); Van Wyk (2000); Manning (2009); Van der Walt (2009); Kirby (2013); Van Oudtshoorn (2015); Siebert & Scogings (2015)
Spinescence	0 = Absent 1 = Present	Binary	The degree to which a plant is defended by thorns, spines and/or prickles	Anti-herbivore defence; response to disturbance	Cornelissen *et al*. (2003); Scholes *et al*. (2003); Pérez-Harguindeguy *et al*. (2013); Alves-Silva & Del-Claro (2016)
Flowering phenology	1 = All year 2 = Spring-Autumn 3 = Summer-Autumn 4 = Spring-Summer 5 = Summer-Winter 6 = Summer	Categorical	The timing of flowering	Response to changes in climatic conditions	Craine *et al*. (2011); Geldenhuys (2011)

	7 = Winter-Autumn 8 = Unspecified 9 = Autumn 10 = Spring-Winter 11 = Spring 12 = Summer-Spring				
Clonal ability	1 = Non-clonal 2 = Clonal above-ground 3 = Clonal below-ground 4 = Clonal above and below ground	Categorical	The ability of a plant to reproduce vegetatively	Response to damage; competitive vigour; persistence after disturbance	Cornelissen *et al*. (2003); Pérez-Harguindeguy *et al*. (2013); Kotschy (2013)
Nitrogen-fixing ability	0 = Absent 1 = Present	Binary	The ability of plants to convert atmospheric nitrogen (N_2) to NH_3 which can be used by plants	Nutrient cycling; plant growth	Naisbitt *et al*. (1992); Cornelissen *et al*. (2003); Sprent *et al* (2013); Van Oudtshoorn (2015)

4.4 Data preparation

Two separate data matrices were compiled and consolidated in Excel (Windows 2010). The first data matrix consisted of quantitative floristic (i.e., species and individual counts) data for the herbaceous layer for each transect, across all treatments for the sodic plots. The second matrix composed of the functional trait data for each herbaceous species in the sodic zone. Data were formatted to be imported into PRIMER 6, Statistica and SPSS software packages respectively. Herbarium specimens of unknown species were collected during field sampling and sent to the National Herbarium, South African National Biodiversity Institute (SANBI) in Pretoria for identification.

4.5 Data analysis: Chapters 5 and 6

Similar statistical methods that were applied in chapters 5 (Interactive effects of herbivory, fire and rainfall variability on herbaceous diversity and life form abundance in a system wihout elephants) and 6 (Interactive effects of herbivory and rainfall variability on herbaceous diversity and life form abundance in system without fire) are outlined in this section.

Species diversity

For species diversity analyses, the 2001 data set was not included to avoid sampling bias effects, as it was sampled by a different group of field ecologists. A species abundance-plot matrix of the 2010 and 2015 floristic data was compiled in Excel (Windows 2010). Diversity metrics (total species (S) and Simpson's index of diversity (1-Lambda)) were calculated using PRIMER 6 software (Clarke & Gorley, 2006). Since these metrics display different aspects of diversity, they were used in combination to provide a full overview of herbaceous species richness and diversity patterns. Species richness and Simpson's index of diversity was calculated separately for grasses and forbs across fire and herbivore treatments.

Species richness is defined as the number of species present in a defined area (Begon *et al.*, 2006). In this study species richness was considered as the total species (S), i.e., the mean number of species per circular nested sub-plot (1 m^2). Species diversity was calculated for the plots with the Simpson's index of diversity (1-Lambda). Simpson's index of diversity is considered a robust and meaningful diversity index, also known as a dominance or evenness measure, since it is weighted towards the most abundant species in the sample and less sensitive to species richness (Magurran, 2004). Simpson's index of diversity essentially measures the variance in species abundance distribution (Magurran, 2004). The index was calculated according to the following equation:

$$\mathbf{1 - \Sigma\ (N_i * (N_i - 1) / N * (N - 1))}$$

Whereby **N** is the mean total of individuals per plot and **N_i** represents the number of individuals in the i^{th} species (Peet, 1974).

Total species (species richness) (for system without fire) and species diversity data (for both systems) were not normally distributed (Kolmogorov-Smirnov test; $p < 0.001$; Shapiro-Wilk test; $p < 0.001$). To stabilize variance within diversity data, analyses were undertaken on Ln-transformed data. Variables that were transformed were appropriately back-transformed to generate visual representations of Hierarchical Linear Modelling results.

Simpson's diversity index values exhibited a substantial proportion of zero values, even after Ln-transformation. To account for this zero-inflation, a class of two-part distribution hurdle model was fitted to the data (Fletcher *et al*., 2005), in which (a) binary presence (varying levels of abundance)/absence (zeros) data and (b) positive log-abundance values were separately modelled using cross-tabulations and Chi-square tests.

Life form abundances and functional group dominance

Frequency measures (%) were used to identify herbaceous species most commonly observed across fire and herbivore treatments and sampling years (2001, 2010 and 2015 data were used). Frequency is considered a stable variable for the abundance of an individual species (O'Connor, 2015).

Each dominant herbaceous species was assigned to a functional group based on life form (forb or grass) and life history (perennial or annual) according to Germishuizen & Meyer (2003), and to a broad forage classification (palatable or unpalatable) based on Van Oudtshoorn (2006; 2009) and Fish *et al*. (2015) for grasses and Siebert & Scogings (2015) for forbs. Life form, life history and palatability groupings are commonly used in savanna vegetation studies as it reflects differences in important grazing variables such as forage production and forage quality (Buitenwerf *et al*., 2011). As a measure of functional response to various combinations of herbivory, fire and rainfall variability, we used mean abundance values of species within respective functional groups, rather than standing biomass (Fensham *et al*., 2015; O'Connor, 2015). Abundances of life forms were used as a proxy for dominance of one life form over the other.

Since rangeland assessments in savanna systems are largely based on dominant palatable perennial grass species (Uys, 2006; Kioko *et al*., 2012; Treydte *et al*., 2013; Trollope *et al*., 2014), abundances within this functional group were furthermore independently compared with abundances of annual grasses, perennial and annual forbs and unpalatable perennial grasses, which are referred to in this study as the presumed 'unfavourable' functional groups.

Statistical analyses

Prior to detailed statistical analyses, normality of the data sets were tested by plotting the distribution of richness, diversity and abundance data between different treatments and sampling years on histograms, Q-Q plots and the application of Kolmogorov-Smirnov and Shapiro-Wilk normality tests. The Kolmogorov-Smirnov normality test is sensitive to differences in both the location and shape of the empirical cumulative distribution functions (CDF) (Sokal & Rohlf, 1995). Empirical distribution function tests compare the empirical distribution function, which is estimated based on data from the CDF of normal distribution to assess whether there is a good agreement between them (Razali & Wah, 2011). The Shapiro-Wilk test is considered a highly effective test for all sample sizes and distribution types (Razali & Wah, 2011). Variance within richness, diversity and abundance data was stabilised through Ln-transformations. Variables that were transformed were appropriately back-transformed to generate visual representations of HLM results.

A four-way ANOVA type Hierarchical Linear Model (HLM) was applied to the data in SPSS (Version 24) (Hancock & Mueller, 2010) to investigate interaction effects of time, fire and herbivory on variation in forb and grass richness, diversity and abundance data. Significance levels for analysis were set at the standard significance level of $p < 0.05$, enabling confident conclusions made from statistical results (Lindgren & Sullivan, 2001). The covariance structure for the HLM was defined as unstructured and therefore incorporated random effects and heterogeneity of variance across repeated measures, allowing for more precise conclusions about treatment effects and generalization of inferences to other times, places and species (Bolker *et al*., 2009; Woltman *et al*., 2012; Gili *et al*., 2013). This hierarchical model is a special type of generalized linear mixed model (GLMM) which caters for a repeated measures design, which applies to this particular study since the response variable of each subject was observed at multiple points in time (Davis, 2002).

The nested data structure comprised of four hierarchical levels, which included 1 m^2 subplots within 200 m^2 fixed plots nested in transects that were established within treatments of herbivory and fire. To account for the nestedness of transects within treatments, the sampled plots were specified as subjects (ID) with life form, year, fire and herbivory as the interactive effects.

Significant differences in forb and grass richness, diversity and life form–and functional group abundances in response to year, fire and herbivory were further tested using effect sizes (Cohen's *d*). Effect sizes were interpreted as: (a) small effect: $d < 0.4$, (b) medium effect: $d = 0.4 – 0.6$ and (c) large effect $d \geq 0.7$ (Cohen, 1988; Ellis & Steyn, 2003). Effect sizes were calculated according to the following equation:

$$\boldsymbol{d} = \frac{|\bar{x}i - \bar{x}j|}{\sqrt{\boldsymbol{MSE}}} \textbf{ For } \boldsymbol{i \neq j}$$

Whereby **MSE** is the mean square error and $\bar{\mathbf{x}}_{\boldsymbol{i}}$ is the sample mean of the i^{th} group.

(Only large effect sizes will be presented on visual representations).

4.6 Data analysis: Chapters 7 and 8

Similar statistical methods that were applied in chapters 7 (Drought-tolerant herbaceous community composition and function in a fire-exposed system without elephants) and 8 (Drought-tolerant herbaceous community composition and function in a system without fire) are outlined in this section. A short description of different analyses performed to reach chapter objectives will be mentioned in each results chapter respectively for easy reference.

Floristic composition structure

Non-Metric Multi-Dimensional Scaling (NMDS) analyses were used to explore herbaceous species assemblages among fire and herbivore treatments. These analyses were performed using Bray-Curtis similarity and square root transformations of species abundances. Bray-

Curtis similarity distance measures are recommended for ordinations and also match Permutational Multivariate Analysis of Variance (PERMANOVA) settings (Linstädter *et al*., 2016). NMDS is an unrestricted ordination technique for the evaluation of relationships among sampling locations (Bliss *et al*., 2017). NMDS ordinations are based on species space measures and plots similar sites closer together and dissimilar sites further apart (Gaines & Gratton, 2010). NMDS ordinations were compiled using PRIMER 6 software (Clarke & Gorley, 2006). Results were presented as two-dimensional plots. NMDS stress functions indicate a good fit or match between two data points (Kent & Coker, 1994). Stress values can be interpreted as follows: (a) a stress value of < 0.05 gives an excellent representation with no prospect of misinterpretation; (b) stress values of < 0.1 corresponds to a good ordination; (c) stress of < 0.2 gives a potentially good and useful two-dimensional picture; (d) stress > 0.3 can be considered poor and difficult to interpret and should be treated with a great deal of scepticism (Clarke & Warwick, 2001).

To corroborate visual representations, Permutational Multivariate Analysis of Variance (PERMANOVA; permutations = 999; type III sums of squares) was applied in PRIMER 6 to test for significant differences in floristic composition among herbivore and fire treatments. PERMANOVA is suitable for abundance data, since response data within complex experimental designs are analysed based on permutations of dissimilarity matrices to make analyses distribution free (Hunter, 2017). Permutation analysis of variance does therefore not require specific assumptions for normality (Linstädter *et al*., 2016). To distinguish between significantly different treatments, pairwise comparisons of PERMANOVA analyses were conducted.

Similarity Percentage Analysis (SIMPER) was applied to the data in Paleontological Statistics software (PAST) (Hammer *et al*., 2001) to explore which taxa contributed most to differences in composition between fire and herbivore treatments (Clarke, 1993). SIMPER determines and compares the contribution of each species or trait to the similarity (Hunter, 2017).

Trait diversity patterns

A trait abundance-plot matrix was compiled by multiplying a trait-species matrix (with presence and absence data) with the species-abundance matrix using the MMult function in Microsoft Excel. The dataset containing abundances of traits with corresponding plots was used to calculate diversity indices for plant traits in PRIMER 6 software (Clarke & Gorley, 2006; Hanke *et al.*, 2014). Diversity analyses were conducted to indicate trait richness, Margalef's species richness, Pielou's evenness, Shannon-Wiener diversity index and Simpson's index of diversity. Diversity analyses were performed separately for each of the systems investigated in this thesis. To test whether trait differences of the respective life forms had underlying effects on the patterns revealed for the entire herbaceous layer, the entire herbaceous layer was analysed after which analyses were performed on forbs and grasses respectively.

Statistical analyses

Diversity data for both systems were tested for normality and homogeneity of variance by means of histograms, probability plots, Levene's–and Shapiro Wilk tests.

Hierarchical Linear Model (HLM) analyses were performed on the data using a three-way ANOVA with random effects model to investigate overall significant differences in trait index values between fire and herbivory treatments, as well as significant variance in index values between herbaceous life forms in response to fire and herbivory in a system without elephants. The covariance structure of the HLM was specified as unstructured.

In the data set representing an ecosystem without fire (Chapter 8), herbivore transects were considered confounding variables (i.e., variables which affect both independent and dependent variables) with the type of herbivore treatment, and therefore a HLM could not be fitted to the data. Two-way Analysis of Variance (ANOVA) analyses were applied to the data to test the overall effects of herbivore treatment on herbaceous trait diversity measures. A two-way ANOVA was furthermore applied to data from the system without fire to determine significant differences in forb and grass trait richness and diversity index values between various herbivore treatments. Significant differences in forb and grass trait diversity index values in response to fire and herbivory were further tested by means Cohen's d of effect sizes (please refer to section 4.5 for description). Significance levels for analysis were set at the standard significance level of $p < 0.05$, enabling confident conclusions made from statistical results (Lindgren & Sullivan, 2001). HLM and ANOVA analyses were performed in SPSS (Version 24) (Hancock & Mueller, 2010).

Identification of functional groups

One hundred and twenty-six herbaceous species were investigated for ten functional traits (Table 4.2). A data matrix of species (rows) and traits (columns) was constructed in which each trait was given a numerical score (binary or categorical) as listed in Table 4.2. Trait selection and sampling were done according to the procedures described in section 4.3.3. Trait categories were defined according to cited literature in Table 4.2.

A hierarchical agglomerative clustering analysis with an Unweighted Pair Group Method with Arithmetic Mean (UPGMA)-clustering algorithm and Gower distance measure was used in PRIMER 6 software (Clarke & Gorley, 2006) to group plant species based on their trait scores (Botha *et al.*, 2017). The Gower distance measure was used as it is appropriate for mixed data types (binary and categorical) (Gower, 1971; Podani, 1999; Bota-Dukát, 2005; Kotschy, 2013; Botha *et al.*, 2017). The cluster analysis was combined with a Similarity Profile (SIMPROF) test which is considered an objective method for identifying significant groupings (Botha *et al.*, 2017). Results from the cluster analysis were used to perform multivariate analyses of species trait data with Principal Co-ordinate Analysis (PCoA) in Paleontological Statistics software (PAST) (Hammer *et al.*, 2001; Geldenhuys, 2011; Van Staden, 2016). Similarly to the cluster analysis, Gower similarity was selected as distance measure for multivariate analyses. PCoA is considered an improved analysis over Principal Component Analysis (PCA) which allows a wide array of distance measures, which include both binary and categorical data types (Geldenhuys, 2011). A PCoA was conducted on all species and traits to investigate groupings which were interpreted as functional groups. Functional groups produced by PCoA were studied in detail for trait attributes.

Functional assemblages of fire and herbivore treatments

Using the MMult function in Microsoft Excel, a functional group-plot matrix was compiled by multiplying a functional group-species matrix (with presence and absence data) with the species-abundance matrix. Furthermore, a treatment-plot matrix was compiled in Microsoft Excel, in which herbivore and fire treatments were given binary scores which were then used as environmental data (Van Staden, 2016).

Patterns in functional assemblages of herbivore and fire treatments were analysed with Canoco for Windows version 4.5 (Ter Braak & Šmilauer, 2002). Detrended Correspondence Analysis (DCA) with detrending segments was performed on functional group-plot matrices for both systems to detect the length of the gradient (Lepš & Šmilauer, 2003). Gradient length in DCA estimates community heterogeneity and indicates which ordination technique will best suit the data (Lepš & Šmilauer, 2003). A gradient length larger than 4.0 is indicative of unimodal, heterogeneous data, whilst a gradient length < 4.0 reveals linearly distributed data (Lepš & Šmilauer, 2003, Van Staden, 2016). When the gradient length exceeds 4.0, unimodal methods (CA (Correspondence Analysis) or CCA (Canonical Correspondence Analysis)) should be used, whilst linear data should be analysed using Principal Component Analysis (PCA) and Redundancy Analysis (RDA) (Lepš & Šmilauer, 2003).

Principal Component Analysis (PCA) was applied to the data set of the system without elephants to provide a summary of community variation (Ter Braak & Šmilauer, 2002), and Redundancy Analysis (RDA) was applied to quantify the effect of herbivore and fire treatments on functional group assemblage. Correspondence Analysis (CA), an example of a direct gradient analysis (Ter Braak & Šmilauer, 2002) was used to summarise relationships between functional groups and herbivore treatments, whilst Canonical Correspondence Analysis (CCA) was applied to the data set of the system without fire in Canoco for Windows version 4.5 (Ter Braak & Šmilauer, 2002) to evaluate patterns in variation in functional group assemblage and demonstrate principal relationships between functional groups and herbivore treatments (Kent & Coker, 1992). Eigenvalues for each ordination is presented in the supplementary tables in the appendices of the respective results chapters. Eigenvalues represent the relative contribution (%) of each component to the explanation of the total variation in the data (Kent & Coker, 1994). Each component has one eigenvalue, with the size of the value directly indicative of the importance of that component in total data variation (Kent & Coker, 1994).

4.7 Summary

A layout summarizing the various elements (i.e., species diversity and richness, life form and functional group dominance, species composition and trait richness, evenness and diversity), data (i.e., 2001, 2010 and 2015), treatments and statistical methods considered in each results chapter is presented in Figure 4.3.

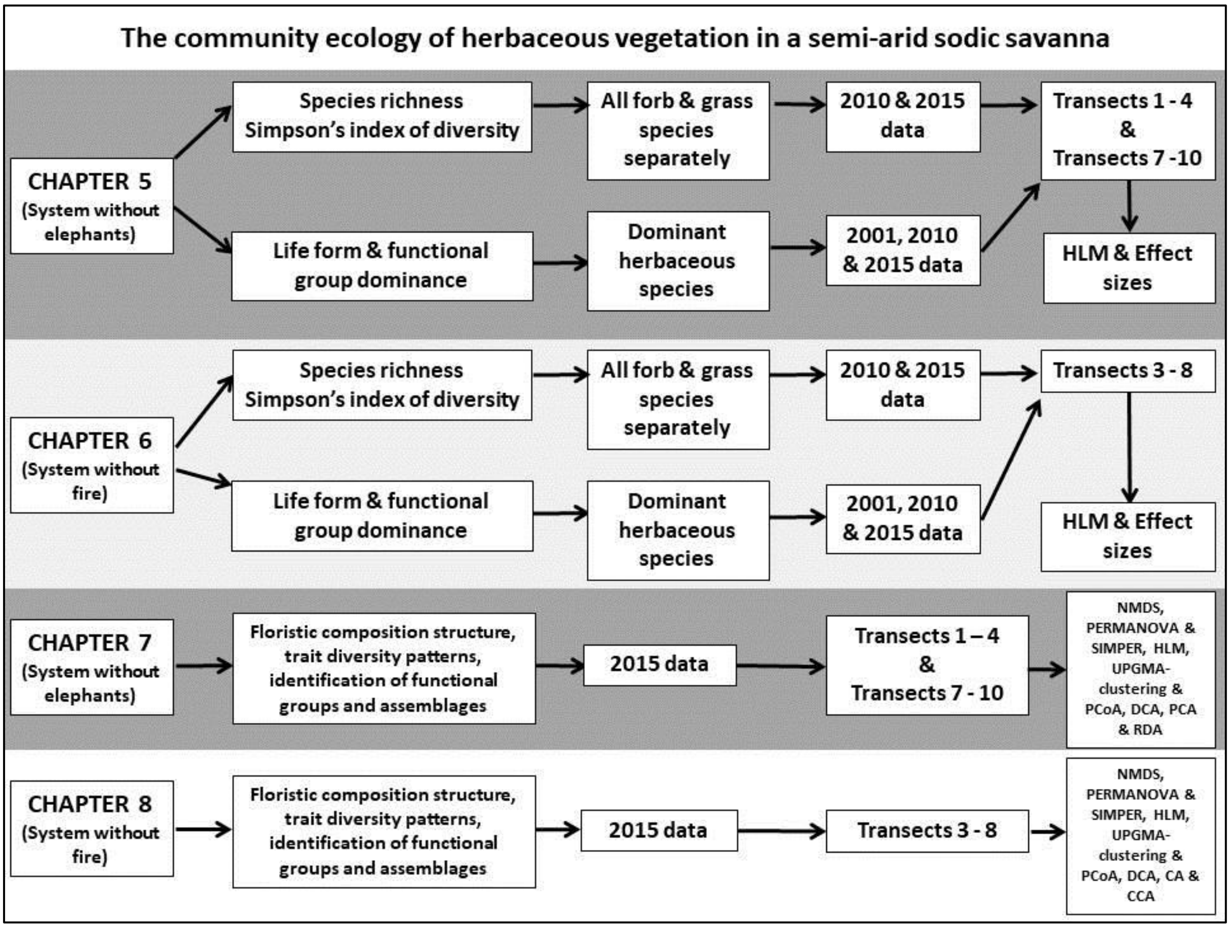


Figure 4.3. The layout of results chapters summarizing various systems elements, data, treatments and statistical methods considered.

Chapter 5

Interactive effects of herbivory, fire and rainfall variability on herbaceous diversity and life form abundance in a system without elephants

5.1 Introduction

Effects of large mammalian herbivores (LMH) as major drivers of vegetation structure, function, and dynamics contribute to some of the core focus areas in savanna ecology (Savadogo *et al.*, 2008; Asner *et al.*, 2009; Burns *et al.*, 2009). Nevertheless, studies concentrating on possible implications of their loss from these systems under rainfall variability are less sufficient. Large mammalian herbivore (LMH) populations in African savannas have declined by more than 50 % in the last several decades (Daskin *et al.*, 2016). These declines are not exclusive to unprotected areas, and management within many protected areas in Africa is faced with the challenge of preventing LMH declines (Robson *et al.*, 2016). Herbaceous species richness in this study area has been shown to decline as a result of herbivore exclusion (Jacobs & Naiman, 2008; Van Coller *et al*. 2013; Van Coller & Siebert 2015). This phenomenon, however, was revealed only when the complete herbaceous layer was considered (i.e., forbs and grasses that could potentially respond differently to disturbances were not separated) under mean rainfall conditions (~550 mm). Changes in global climate and the probable increased frequency of extreme droughts in African savannas (Du Toit & Cumming, 1999; Batisani & Yarnal, 2010; Van Wilgen *et al.*, 2016) prompted questions pertaining to whether such patterns will remain evident during below-average rainfall conditions. Furthermore, rainfall in the eastern parts of South Africa is becoming more variable, notably so in the Kruger National Park (Van Wilgen *et al.*, 2016). Since this study period included the most severe regional drought in 33 years (Swemmer, 2016), it provided the opportunity to test the effect of drought on herbaceous species richness and diversity patterns, as well as potential variations in herbaceous life form–and functional group abundances. Many LMH include forbs in their diet, particularly at certain times of the year when green forage is scarce (Owen-Smith & Novellie, 1982; Scholes, 1987; Du Toit, 1988; Young *et al.*, 2005; Kraai, 2010; Malan *et al.*, 2012; Van Der Merwe & Marshal 2012; Landman *et al.*, 2013; Koerner *et al.*, 2014; Burkepile *et al.*, 2017). Forbs are therefore considered a rare and nutritious resource (Odadi *et al.*, 2013). Despite their apparent functional importance, effects of grazing on forb diversity patterns remain understudied (Uys, 2006). Fire effects on vegetation are dynamic and dependent on the type of plant community and its interaction with ecological factors, including herbivory within that specific community (Savadogo *et al*., 2008). Considering herbaceous life forms in African savannas, low intensity surface fires early in the dry season favours annual grasses at the expense of perennial grass species (Sawadogo *et al*., 2005; Savadogo *et al*., 2008). Forb cover is reduced by fire alone (i.e., in absence of herbivores) (Koerner & Collins, 2013; Van Coller *et al*., 2013), but the combined effects of grazing and fire have been reported to promote forb cover (Koerner & Collins, 2013). Competitive exclusion effects and reduced grass and forb richness have been associated with exclusion of both herbivores and fire (Burkepile *et al*., 2016). Although fire is considered a secondary driver of herbaceous dynamics in sparsely vegetated nutrient-rich semi-arid sodic patches (Van Coller *et al*., 2013; Van Coller & Siebert, 2015), comparative studies focusing on the implications of fire loss on herbaceous vegetation dynamics and how these impacts change with grazing intensity and increased rainfall variability are lacking. This is particularly true when considering herbaceous life forms as separate functional entities. The species and functional response of herbaceous life forms to herbivory and fire has been less explored.

Therefore, the aim of this chapter was to investigate herbaceous responses to rainfall variability (particularly drier conditions) and combined effects of fire and herbivore presence or absence by:

1. Assessing patterns in forb and grass richness and diversity;
2. Evaluating differences in forb and grass abundances, and
3. Testing whether favourable range conditions (increased abundance of palatable perennial grasses) can be maintained in sodic patches of a semi-arid savanna ecosystem.

Anticipated variation in responses of herbaceous life forms was hypothesized to provide functional redundancy, i.e., when two or more life forms share similarities concerning a specific function in such a way that one life form can fully or partially compensate for another should it disappear or decline in abundance (Kotschy, 2013). It was predicted that combined effects of average rainfall, fire and herbivores will favour palatable perennial grasses, since indigenous African grasses are well adapted to withstand severe grazing (Scholes & Walker, 1993; Owen-Smith, 2013). It was furthermore hypothesized that unpalatable grasses and forbs will be more abundant with higher grazing pressure and drought, whilst the exclusion of herbivores and fire will favour palatable perennial grasses at the expense of other functional groups as a result of competitive exclusion effects (Van Coller & Siebert, 2015). Herbivory was expected to be the primary driver of herbaceous vegetation dynamics under variable rainfall conditions in this system. Herbivores maintain low aboveground biomass, as opposed to their exclusion, which causes increased biomass (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Van Coller & Siebert, 2015) (Figure C.1.; Appendix C). Consequently, fire was not expected to have significant effects on herbaceous species dynamics when herbivores are present. However, fire effects were anticipated to become more distinct in the absence of herbivores and the subsequent increase in aboveground biomass. Fire improves the quality of grazing for wildlife by reducing competition and removing moribund and undesirable grass material (Garnier & Dajoz, 2001; Trollope, 2011). It was therefore expected that fire effects in the absence of herbivores would enhance herbaceous species diversity and dominance of palatable grass species.

5.2 Material and Methods

Floristic data collected in transects 1-4 and 7-10 (refer to Figure 4.1 and 4.3) were used to address the aim and objectives of this chapter. Please refer to Chapter 4 (Materials and Methods, sections 4.3.1 and 4.5) for a detailed account of the floristic sampling and data analysis performed to obtain the following results.

Variations in Hierarchical Linear Modelling (HLM) together with statistical effect sizes were used to reach the three objectives of this chapter:

1. To reach the first objective, a three-way ANOVA type HLM was fitted to herbaceous diversity data (i.e., richness and diversity of forbs and grasses as a whole), where herbaceous species richness and diversity were the response variables and fire, herbivory and year were specified as the predictor variables. Life form was added as an additional predictor variable to test whether differences in diversity of the respective life forms had underlying effects on the patterns revealed for the entire herbaceous layer. Species richness and diversity were specified as the response variables and life form, fire, herbivory and year were specified as predictor variables in the four-way ANOVA type HLM.

2. The second objective was reached by performing Hierarchical Linear Model (HLM) analyses on abundance data using a four-way ANOVA with random effects model. Herbaceous species abundances within functional groups were specified as the response variable, whilst life form, fire, herbivory and year were the predictor variables in the model.
3. A four-way ANOVA type HLM with abundances of functional groups as the response variable and functional group, fire, herbivory and year as the predictor variables, was performed to reach the third objecive.

5.3 Results

5.3.1 Richness and diversity patterns

Herbaceous species richness revealed no significant response to herbivory, fire or year ($p > 0.05$; Table 5.1). Herbivory ($p < 0.001$; Table 5.1) and year ($p < 0.001$; Table 5.1), respectively, revealed to be significant predictors of herbaceous species richness. Sampling year was the only significant predictor of herbaceous species diversity ($p = 0.035$; Table 5.1).

Table 5.1. Summary of the three-way ANOVA type Hierarchical Linear Model (HLM) results for variance in herbaceous species richness and diversity with respect to year, fire and herbivory.

	Fixed effects						
	Year	**Fire**	**Herbivory**	**Year*Fire**	**Year*Herbivory**	**Fire*Herbivory**	**Year*Fire* Herbivory**
Herbaceous richness							
df	1	1	1	1	1	1	1
F	65.9	3.0	42.8	5.6	1.0	0.003	0.1
p	**< 0.001***	0.084	**< 0.001***	**0.019***	0.320	0.956	0.734
Herbaceous diversity							
df	1	1	1	1	1	1	1
F	4.5	0.5	1.5	0.3	1.6	1.0	0.3
p	**0.035***	0.484	0.218	0.596	0.210	0.311	0.600

Year, 2010 and 2015; *Fire*, present or absent; *Herbivory*, present or absent. Significant effects (at $p < 0.05$) indicated in bold with *.

There was an interaction between fire and year ($p = 0.019$; Table 5.1), such that the effect of drought was less severe in the burned site (Figure 5.1 (a)). Herbaceous species richness was significantly higher with herbivore presence ($p < 0.001$; Table 5.1; Figure 5.1 (b)). Overall, there was lower herbaceous species richness and diversity in the drought year (Figure 5.1 (c) and (d)).

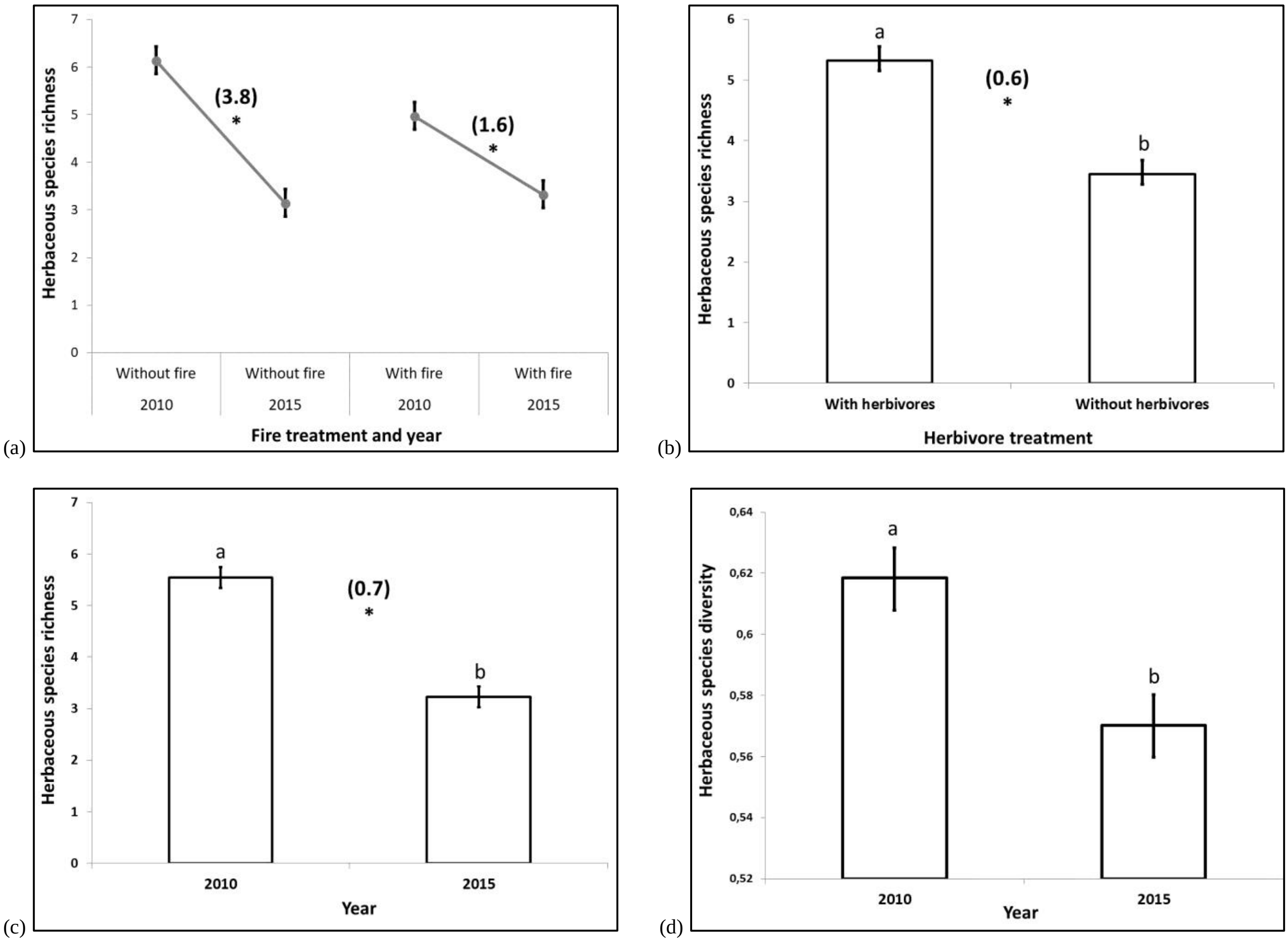


Figure 5.1. Mean (±SE) (a) herbaceous species richness over time and across fire treatments, (b) herbaceous species richness across herbivore treatments, (c) herbaceous species richness over time and (d) herbaceous species diversity over time. * indicates significant differences (at $d > 0.7$) in trait richness, whilst values in parenthesis indicate effect sizes. Significant differences (at $p < 0.05$) indicated by means of different letters.

Herbaceous life form was added as an additional fixed effect to determine whether variance in life form diversity had underlying effects on diversity patterns revealed for the complete herbaceous layer.

Table 5.2. Summary of the four-way ANOVA type Hierarchical Linear Model (HLM) results for variance in herbaceous species richness and diversity with respect to life form, year, fire and herbivory.

	Fixed effects							
	Life form	**Life from* Year**	**Life form* Fire**	**Life form* Herbivory**	**Life form* Year*Fire**	**Life from* Year* Herbivory**	**Life form* Fire*Year**	**Life form* Fire*Year* Herbivory**
Species richness								
df	1	1	1	1	1	1	1	1
F	453.8	69.3	0.3	38.6	1.3	3.5	0.1	0.1
p	**< 0.001***	**< 0.001***	0.559	**< 0.001***	0.254	0.062	0.799	0.777
Species diversity								
df	1	1	1	1	1	1	1	1
F	147.5	2.3	0.3	1.9	0.1	0.4	0.01	0.6
p	**< 0.001***	0.130	0.605	0.173	0.825	0.527	0.921	0.457

Life form, forb or grass; *Year*, 2010 and 2015; *Fire*, present or absent; *Herbivory*, present or absent. Significant effects (at $p < 0.05$) indicated in bold with *.

Species richness revealed no response to life form, fire, herbivory or year (Life form*Year*Fire*Herbivory F = 0.1, $p > 0.05$; Table 5.2). Nevertheless, life form (F = 453.8, $p < 0.001$; Table 5.2) is considered an important predictor of species richness, with forbs contributing significantly to species richness, irrespective of fire, sampling year or herbivore treatment (Figure 5.2 (a)). Drought had a much bigger negative effect on forb richness than it did on grass richness (F = 69.3, $p < 0.001$; Table 5.2; Figure 5.2 (b)). Moreover, herbivore treatment did not impact grass richness, but did significantly increase forb richness (F = 38.6, $p < 0.001$; Table 5.2; Figure 5.2 (c)).

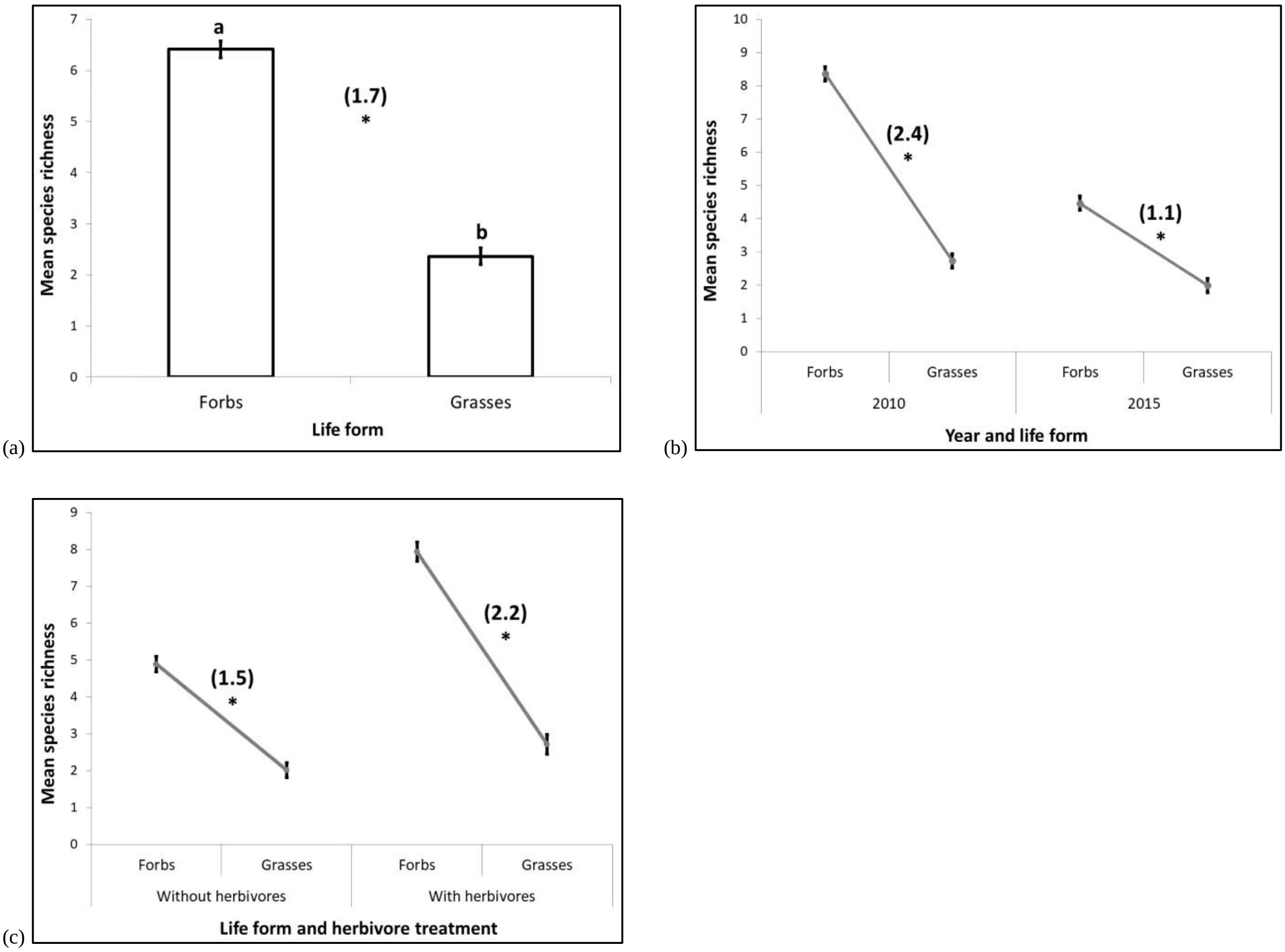


Figure 5.2. Comparisons of mean (±SE) forb and grass species richness (a) between herbaceous life forms, (b) over time and between herbaceous life forms and (c) across herbivore treatments and between life forms. * indicates significant differences (at $d \geq 0.7$), whilst values in parenthesis indicates effect sizes. Significant differences (at $p < 0.05$) in species richness indicated by means of different letters.

No significant responses were revealed by species diversity to life form, fire, herbivory or year (Life form*Year*Fire*Herbivory F = 0.6, $p > 0.05$; Table 5.2). However, life form (F = 147.5, $p < 0.001$; Table 5.2) is a significant predictor of species diversity, with forbs revealing significantly higher species diversity compared to grasses $d = 1.2$; Figure 5.3).

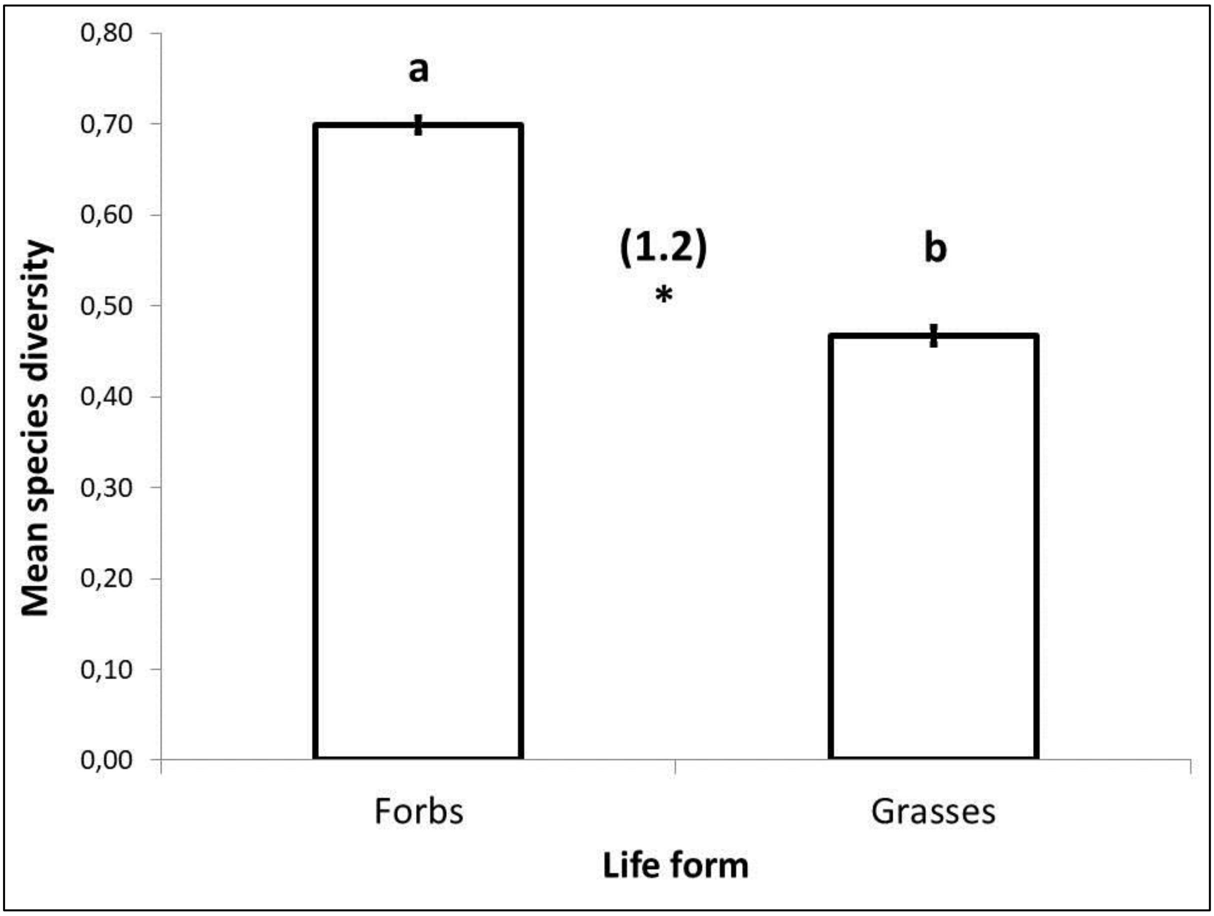


Figure 5.3. Comparisons of mean (±SE) forb and grass species diversity. * indicates significant differences (at $d \geq 0.7$), whilst values in parenthesis indicates effect sizes. Significant differences (at $p < 0.05$) in species richness indicated by means of different letters.

5.3.2 Life form–and functional group abundances

Of the 40 dominant herbaceous species, forbs represented 62.5 % (25 species of which 15 were palatable and 10 were unpalatable) whereas 15 species (37.5 %) were grasses of which nine were palatable and six unpalatable (See Table C.1.; Appendix C for a complete species list).

Life form abundances

Life form abundance variability was the greatest source of variation within all functional groups (Table 5.3). Nevertheless, life form showed no significant response to year, fire and herbivory (Life form*Year*Fire*Herbivory $p > 0.05$; Table 5.3) for any of the functional groups. These results suggest that forb and grass abundances varied significantly, irrespective of combined effects of herbivory, fire and different rainfall conditions (sampling year). Significant within-group variability (life form) across all plant functional groups (Life form fixed effect size of $p < 0.05$) lead us to further explore the conditions under which life form dominance varied. We therefore tested for significant differences between mean abundances of forbs and grasses under different rainfall conditions as well as in the presence or absence of herbivores and under conditions with or without fire. Results are presented per plant functional group.

Table 5.3. Summary of the four-way ANOVA type Hierarchical Linear Model (HLM) results for variance in abundances within herbaceous species functional groups with respect to life form, year, fire and herbivory.

	Fixed effects							
	Life form	**Life form* Year**	**Life form* Fire**	**Life form* Herbivory**	**Lifeform* Year*Fire**	**Life form* Year* Herbivory**	**Life form* Fire* Herbivory**	**Life form* Year*Fire* Herbivory**
Palatable Perennial Species								
df	1	2	1	1	2	2	1	2
F	16.59	4.81	0.55	4.56	0.03	0.15	0.04	0.04
p	**< 0.001***	**0.009***	0.460	**0.034***	0.968	0.860	0.846	0.964
Palatable Annual Species								
df	1	2	1	1	2	2	1	2
F	4.09	1.86	0.06	1.41	0.23	1.04	0.27	0.03
p	**0.001***	0.162	0.810	0.239	0.798	0.358	0.602	0.974
Unpalatable Perennial Species								
df	1	2	1	1	2	2	1	2
F	4.11	0.71	2.71	3.31	0.07	0.21	1.07	0.06
p	**0.046***	0.497	0.104	0.072	0.935	0.815	0.304	0.943
Unpalatable Annual Species								
df	1	2	1	1	2	2	1	2
F	8.14	0.98	0.81	2.31	0.41	0.59	0.01	0.49
p	**0.006***	0.382	0.372	0.134	0.669	0.556	0.939	0.614

Life form, forb or grass; *Year*, 2001, 2010 and 2015; *Fire*, present or absent; *Herbivory*, present or absent. Significant effects (at $p < 0.05$) indicated in bold with *. Results for distinct fixed effects (i.e., year, herbivory and fire) are not presented in the table, since they did not show significant effects on life form abundances.

Palatable perennials

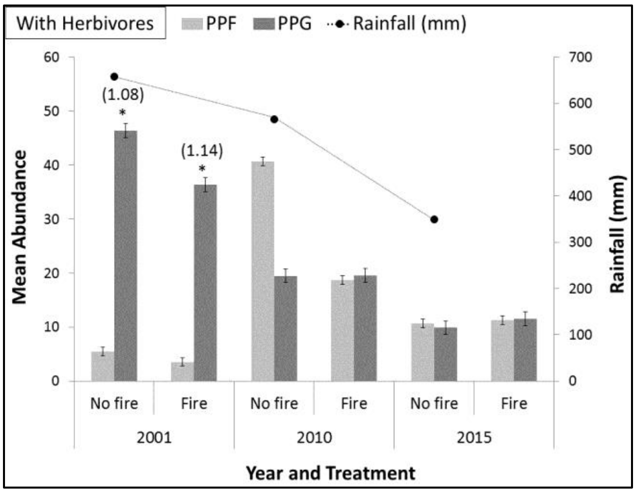
Overall, palatable perennial grass abundances were favoured by above-average rainfall (Table 5.3; Figure 5.4 (a) and (b)). The removal of herbivores furthermore favoured palatable perennial grasses ($p = 0.034$; Table 5.3), irrespective of rainfall (year). However, large effect sizes revealed that this effect was most significant in the presence of fire ($d > 0.9$; Figure 5.3 (b)).

Palatable annuals

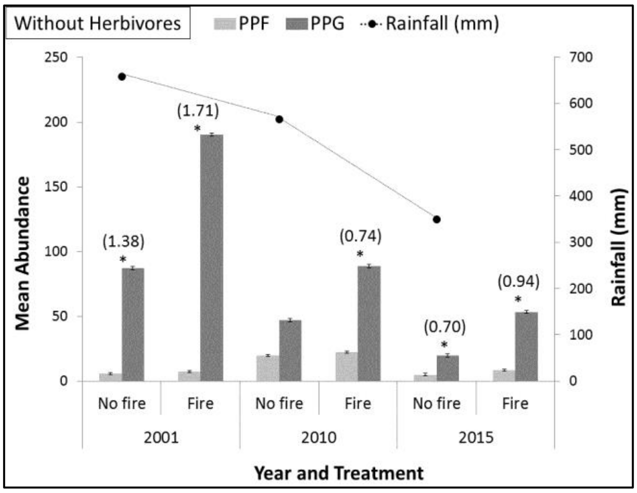
Irrespective of fire treatment, palatable annual forbs (PAF) dominated over palatable annual grasses (PAG) under average conditions (i.e., average rainfall and herbivore presence) (Figure 5.3 (c)). Although no significant herbivore effect was revealed ($p = 0.239$; Table 5.3), PAF also dominated over similar grass functional groups under herbivore exclusion (Figure 5.3 (d)). Fire did not seem to affect this forb dominated state, except in the drought year, where PAF and PAG abundances were less variable

Unpalatable perennials

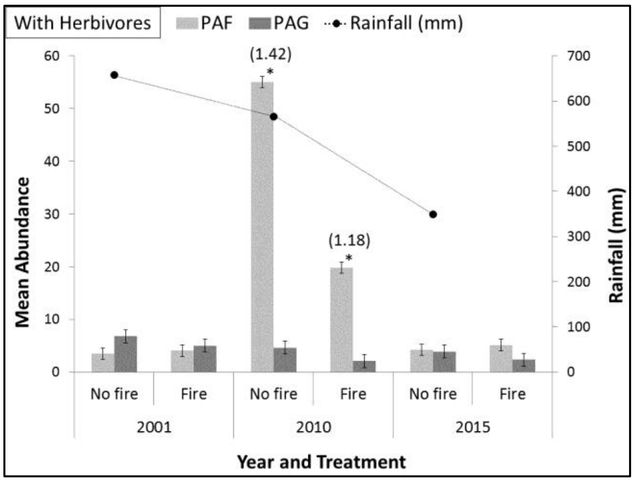
Life form abundances differed significantly within the unpalatable perennial herbaceous species functional group ($p < 0.05$; Table 5.3). Similarly to patterns found in the PAF functional group, fire did not affect an unpalatable perennial forb dominated state under average conditions (Figure 5.4 (e)). Shifts in dominance between forbs and grasses in the unpalatable perennial functional group were conspicuous under herbivore exclusion. UPF dominated in the burned sites of the above-averagel (2001) and average rainfall (2010) years (Figure 5.4 (f)). Conversely, in the drought year (2015), fire absence favoured UPG abundances significantly over UPF abundances ($d = 0.76$; Figure 5.4 (f)). Irrespective of rainfall, UPG abundances seemed to be higher in the unburned sites, whilst UPF abundances seemed to be enhanced by fire presence, although these patterns were not always statistically significant.


With Herbivores
PPF
PPG
Rainfall (mm)
Mean Abundance
Rainfall (mm)
0
10
20
30
40
50
60
0
100
200
300
400
500
600
700
(1.08)
*
(1.14)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

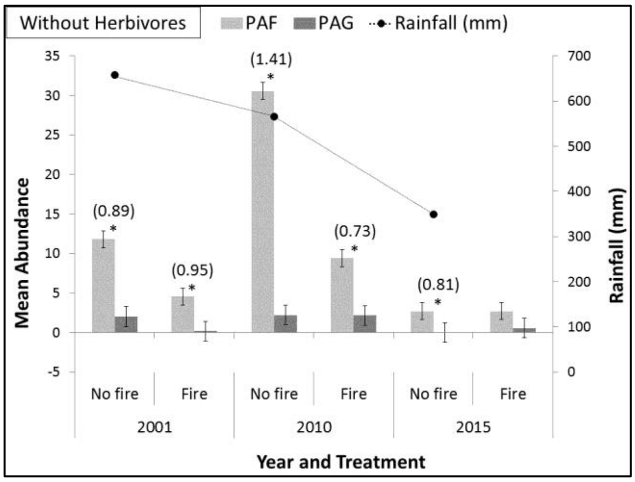
(a)


Without Herbivores
PPF
PPG
Rainfall (mm)
Mean Abundance
Rainfall (mm)
0
50
100
150
200
250
0
100
200
300
400
500
600
700
(1.38)
*
(1.71)
*
(0.74)
*
(0.70)
*
(0.94)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

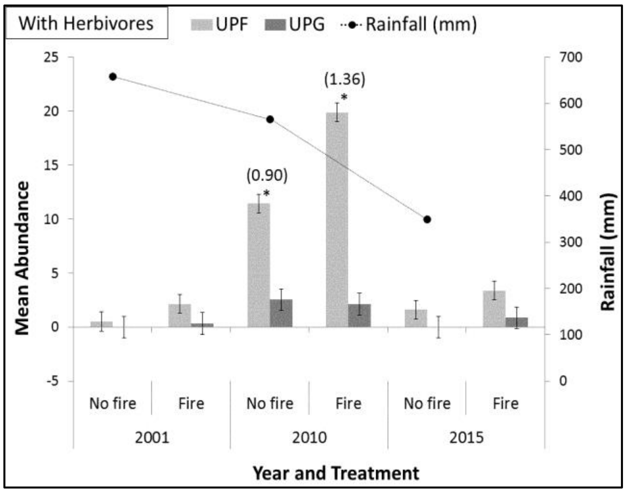
(b)


With Herbivores
PAF
PAG
Rainfall (mm)
Mean Abundance
Rainfall (mm)
0
10
20
30
40
50
60
0
100
200
300
400
500
600
700
(1.42)
*
(1.18)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

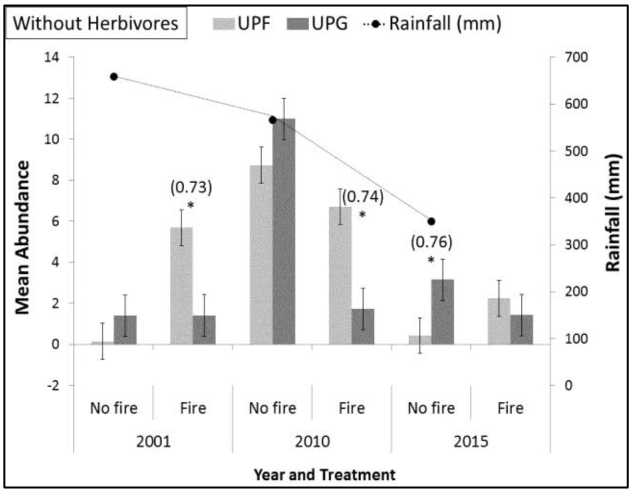
(c)


Without Herbivores
PAF
PAG
Rainfall (mm)
Mean Abundance
Rainfall (mm)
-5
0
5
10
15
20
25
30
35
0
100
200
300
400
500
600
700
(0.89)
*
(0.95)
*
(1.41)
*
(0.73)
*
(0.81)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

(d)


With Herbivores
UPF
UPG
Rainfall (mm)
Mean Abundance
Rainfall (mm)
-5
0
5
10
15
20
25
0
100
200
300
400
500
600
700
(0.90)
*
(1.36)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

(e)


Without Herbivores
UPF
UPG
Rainfall (mm)
Mean Abundance
Rainfall (mm)
-2
0
2
4
6
8
10
12
14
0
100
200
300
400
500
600
700
(0.73)
*
(0.74)
*
(0.76)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

(f)

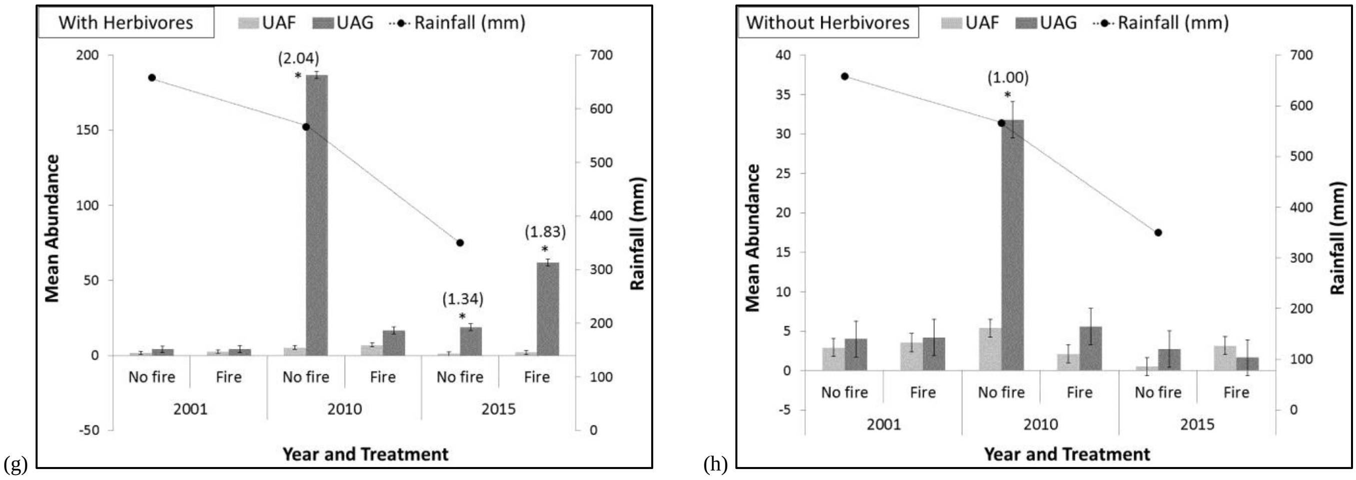


Figure 5.4. Mean (±SE) abundances of herbaceous forbs and grasses assigned to different functional groups in a system exposed to long-term herbivory, i.e., ‘With Herbivores’ (a, c, e, g) vs. abundances of forbs and grasses in a system where herbivores have been excluded for 14 years, i.e., ‘Without Herbivores’ (b, d, f, h) with their respective fire treatments. Total annual rainfall (mm) for each sampling year is depicted on the secondary vertical axis. *Significant variation between forb and grass abundances within similar plant functional groups and fire and herbivory treatments ($p < 0.05$; Table 5.6) and values in parenthesis indicate size effects.

PPF, Palatable perennial forbs; *PPG*, Palatable perennial grasses; *PAF*, Palatable annual forbs; *PAG*, Palatable annual grasses; *UPF*, Unpalatable perennial forbs; *UPG*, Unpalatable perennial grasses; *UAF*, Unpalatable annual forbs; *UAG*, Unpalatable annual grasses.

Unpalatable annuals

Unpalatable annual herbaceous species abundances varied significantly, irrespective of fire or herbivory treatment and sampling year (rainfall conditions) ($p < 0.05$; Table 5.3). Regardless of herbivore treatment, average rainfall and fire exclusion significantly enhanced unpalatable annual grass (UAG) abundances (Figure 5.4 (g) and (h)). Although no significant responses to herbivore treatment and year ($p = 0.556$; Table 5.3) were revealed, UAG abundances were significantly higher than unpalatable annual forbs in the drought year (Figure 5.4 (g)).

Palatable perennial grass dominance

Functional group abundances revealed no significant response to the interactive effects of year, fire and herbivory ($p > 0.05$; Table 5.4). Herbivory was, however, the only significant predictor of herbaceous functional group dominance (F = 3.92; $p = 0.004$; Table 5.4) suggesting the importance of palatable perennial grass (PPG) abundance variation in response to herbivore treatment. As expected, PPG abundances varied significantly against other functional groups (Functional groups; F = 20.75, $p < 0.001$; Table 5.4), which were explored independently to identify shifts in PPG dominance exposed to different treatments of herbivory and fire and rainfall variability.

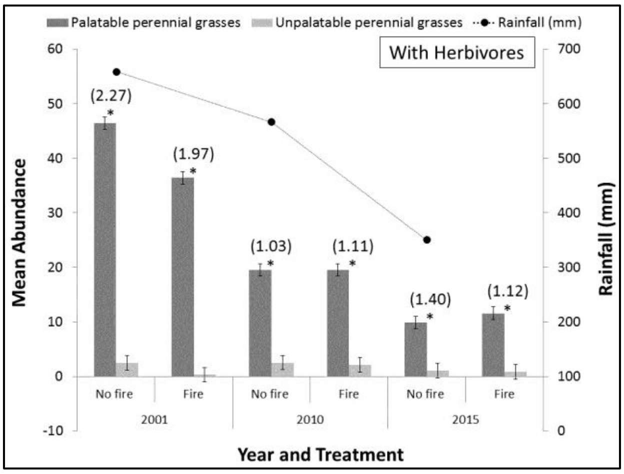
Table 5.4. Results for the four-way ANOVA type Hierarchical Linear Model (HLM) analysis of variance between herbaceous functional group abundances and year, fire and herbivory.

Fixed effects	**df**	**F**	***p***
Functional groups	4	20.75	**< 0.001***
Functional groups*Year	8	1.78	0.078
Functional groups*Fire	4	0.62	0.648
Functional groups*Herbivory	4	3.92	**0.004***
Functional groups*Year*Fire	8	0.12	0.999
Functional groups*Year*Herbivory	8	0.27	0.976
Functional groups*Fire*Herbivory	4	0.66	0.621
Functional groups*Year*Fire*Herbivory	8	0.13	0.998

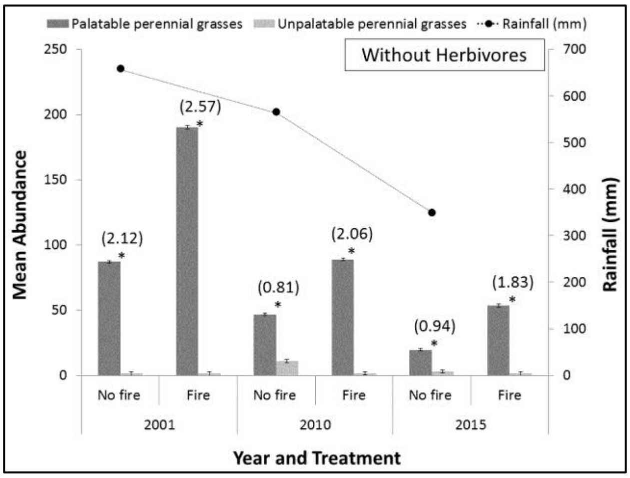
Functional groups, palatable perennial grass abundances compared to abundances of other functional groups, i.e., unpalatable perennial grasses, annual grasses, perennial forbs and annual forbs; *Year*, 2001, 2010 and 2015; *Fire*, present or absent; *Herbivory*, present of absent. Significant effects (at $p < 0.05$) indicated in bold with *. Results for distinct fixed effects (i.e., year, herbivory and fire) are not presented in the table, since they did not show significant effects on life form abundances (results available in supporting data).

Results obtained through independent comparison of means revealed that palatable perennial grasses dominated over all other functional groups in this ecosystem type, regardless of herbivore, fire and rainfall conditions (Figure 5.5), with the exception of perennial forbs when rainfall was average and fire was excluded (Figure 5.5 (e)).

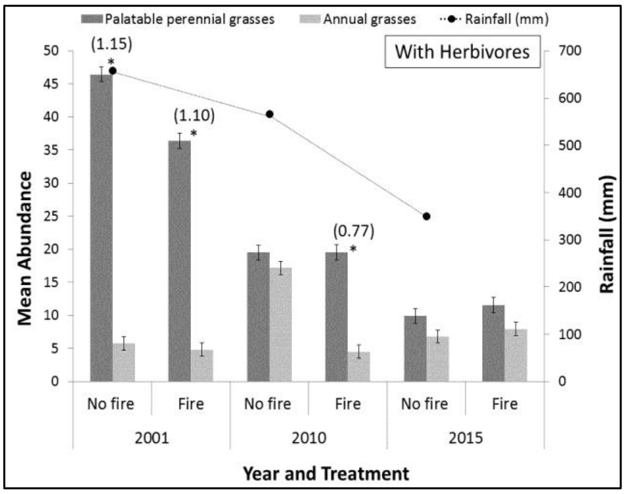
Despite revealing significant interactive effects with herbivory (Table 5.4), herbivore treatment did not affect the PPG dominated state (Figure 5.5 (a) and (b)). The weakest dominance of PPG over UPG was revealed in the unburned sites when rainfall was average (2010), both under long-term grazing (d = 1.03, Figure 5.5 (a)) and exclusion (d = 0.81, Figure 5.5 (b)). As would be expected PPG had the strongest dominance over UPG in the year with above-average rainfall, irrespective of fire or herbivore treatment (Figure 5.5 (a) and (b)).


Palatable perennial grasses
Unpalatable perennial grasses
Rainfall (mm)
With Herbivores
Mean Abundance
60
50
40
30
20
10
0
-10
Rainfall (mm)
700
600
500
400
300
200
100
0
(2.27)
*
(1.97)
*
(1.03)
*
(1.11)
*
(1.40)
*
(1.12)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

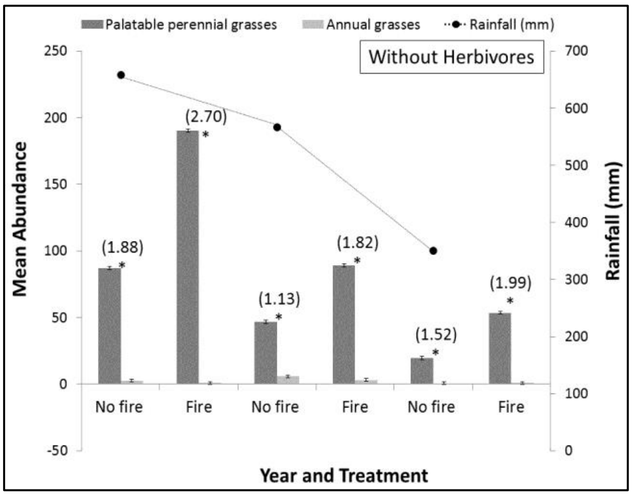
(a)


Palatable perennial grasses
Unpalatable perennial grasses
Rainfall (mm)
Without Herbivores
Mean Abundance
250
200
150
100
50
0
Rainfall (mm)
700
600
500
400
300
200
100
0
(2.12)
*
(2.57)
*
(0.81)
*
(2.06)
*
(0.94)
*
(1.83)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

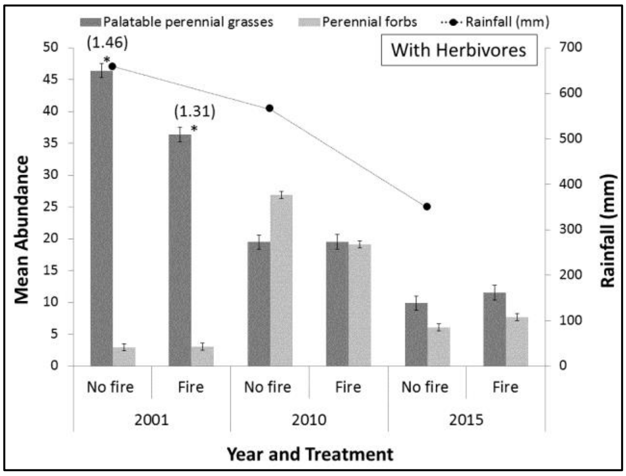
(b)


Palatable perennial grasses
Annual grasses
Rainfall (mm)
With Herbivores
Mean Abundance
50
45
40
35
30
25
20
15
10
5
0
Rainfall (mm)
700
600
500
400
300
200
100
0
(1.15)
*
(1.10)
*
(0.77)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

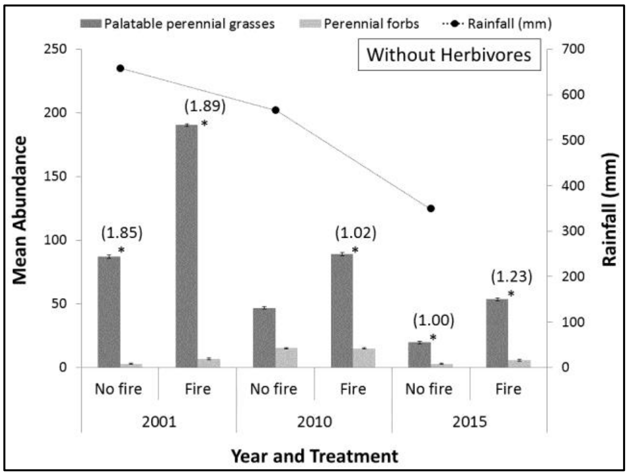
(c)


Palatable perennial grasses
Annual grasses
Rainfall (mm)
Without Herbivores
Mean Abundance
250
200
150
100
50
0
-50
Rainfall (mm)
700
600
500
400
300
200
100
0
(1.88)
*
(2.70)
*
(1.13)
*
(1.82)
*
(1.52)
*
(1.99)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

(d)


Palatable perennial grasses
Perennial forbs
Rainfall (mm)
With Herbivores
Mean Abundance
50
45
40
35
30
25
20
15
10
5
0
Rainfall (mm)
700
600
500
400
300
200
100
0
(1.46)
*
(1.31)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

(e)


Palatable perennial grasses
Perennial forbs
Rainfall (mm)
Without Herbivores
Mean Abundance
250
200
150
100
50
0
Rainfall (mm)
700
600
500
400
300
200
100
0
(1.85)
*
(1.89)
*
(1.02)
*
(1.00)
*
(1.23)
*
No fire
Fire
No fire
Fire
No fire
Fire
2001
2010
2015
Year and Treatment

(f)

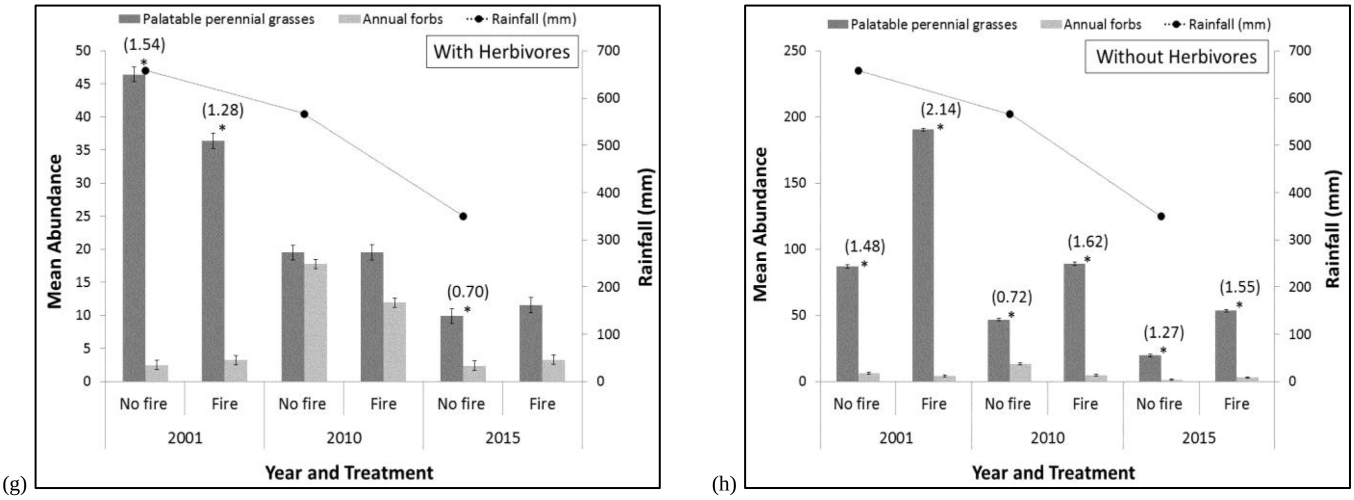


Figure 5.5. Mean (±SE) abundances of (a) palatable perennial grasses vs. unpalatable perennial grasses, (c) palatable perennial grasses vs. annual grasses, (e) palatable perennial grasses vs. perennial forbs and (g) palatable perennial grasses vs. annual forbs in a system exposed to long-term herbivory, i.e., ‘With Herbivores’; and (b) palatable perennial grasses vs. unpalatable perennial grasses, (d) palatable perennial grasses vs. annual grasses, (f) palatable perennial grasses vs. perennial forbs, (h) palatable perennial grasses vs. annual forbs in a system where herbivores have been excluded for fourteen years, i.e., ‘Without Herbivores’. Total annual rainfall (mm) for each sampling year is depicted on the secondary vertical axis. *Significant variation between herbaceous functional group abundances within similar treatments of fire and herbivory ($p < 0.05$; Table 5.10) and values in parenthesis indicate size effects.

Overall, PPG dominated consistently over annual grasses, particularly in ungrazed sites (Figure 5.5 (d)). Expectedly, PPG dominated in the above-average rainfall year (2001) in grazed sites (Figure 5.5 (c)). With average rainfall, however, the exclusion of fire seemed to allow annual grass abundances to increase, and PPG abundance was no longer significantly higher than annual grass abundances (Figure 5.5 (c)). With below-average rainfall (2015), PPG and annual grasses co-dominated in the herbivore exposed sites, suggesting that drought conditions did not favour annual grasses at the expense of perennial palatable grasses (Figure 5.5 (c)).

Above-average rainfall (2001) in grazed sites revealed the strongest and only dominance of PPG over perennial forbs ($d > 0.7$; Figure 5.5 (e)). With average (2010) and below-average (2015) rainfall, no significant dominance of one functional group over the other was revealed. Moreover, perennial forbs dominated over PPG with average rainfall in unburned sites (Figure 5.5 (e)). Equal conditions, but in the absence of herbivores also revealed the weakest dominance of PPG over perennial forbs (Figure 5.5 (f)), which suggests that perennial forbs become more competitive with PPG under fire exclusion and average rainfall. PPG was the dominant functional group in the remaining ungrazed sites (Figure 5.5 (f)).

As would be expected, PPG was the dominant functional group in the year with above-average rainfall in grazed and ungrazed sites (Figure 5.5 (g) and (h)). In the grazed sites, PPG dominance over annual forbs weakened under average rainfall conditions (2010), however, a combination of drought (2015) and fire exclusion favoured PPG abundance significantly ($d = 0.7$; Figure 5.5 (g)). In the ungrazed sites, palatable perennial grasses were significantly ($d > 0.7$) more abundant than annual forbs, irrespective of rainfall variability and fire treatment. However, this increased abundance of PPG was consistently stronger in the burned sites. The weakest dominance of PPG over annual forbs was also revealed during average rainfall conditions in the absence of fire treatment (Figure 5.5 (h)).

5.4 Discussion

Richness and diversity patterns

Similarly to results presented by Van Coller *et al.* (2013) herbaceous richness was significantly enhanced by herbivore presence. In agreement with Du Toit and Cumming (1999) drought had a negative effect on herbaceous species diversity and richness. Savanna forbs have evolved under particular disturbance regimes (Uys, 2006). Consistent with literature (e.g. Shackleton, 2000; Bond & Parr, 2010; Lettow *et al.*, 2014), forbs in this study showed dynamic responses to small-scale environmental heterogeneity. Our results showed that forb richness was favoured by exposure to long-term sustained grazing without rest which coincides with forb response to grazing in savanna systems (Scholes, 1987; Skarpe, 1991; Skarpe, 1992; Milchunas & Lauenroth, 1993; Fynn & O’Connor, 1999; Illius & O’Connor, 1999; Savadogo *et al.*, 2008; Tessema *et al.*, 2011; Koerner & Collins, 2013). Herbivores maintain low grass biomass levels reducing grass dominance and competition, in favour of forbs, thereby increasing species richness (Uys, 2006; Jacobs & Naiman, 2008; Burkepile *et al.*, 2016). Although forbs have been reported to tolerate frequent fire regimes in high rainfall montaine grasslands (Uys, 2006; Bond & Parr, 2010), forbs in the present study are favoured by the exclusion of fire treatment under average conditions (i.e., average rainfall and herbivore presence), similarly to results found by Turner and Knapp (1996). Nevertheless, forbs may take advantage of periods after burns before grasses re-establish

(Bond & Parr, 2010; Burkepile *et al*., 2016). Herbaceous forbs in savanna systems generally possess below-ground storage organs and other traits, enabling them to survive frequent burning and above-ground disturbances (Uys, 2006; Bond & Parr, 2010). These traits may enhance the resilience of forbs to changes in the environment caused by herbivory, fire and increased rainfall variability, and allow forbs to adapt, tolerate, persist and continue recruitment in such extreme environments (Uys, 2006; Van Der Merwe & Marshal, 2012).

Grass species richness also revealed significant interaction effects with environmental disturbances. Similarly to forbs, grass richness is favoured by average rainfall and fire exclusion, suggesting that the survival and growth rates of different grasses are higher in the absence of fire (Garnier & Dajoz, 2001). However, when it is dry and the biomass levels are low (Bergström & Skarpe, 1999; Mbatha & Ward, 2010), burning promotes grass species richness. Enhanced nutritional quality of grass and associated open spaces for enhanced predator vigilance after a fire generally creates favoured patches by attracting herbivores to burnt areas (Gureja & Owen-Smith, 2002; Archibald *et al*., 2005). Fire and grazing therefore promotes system heterogeneity, allowing the establishment of species-rich communities, by reducing competition (Jacobs & Naiman, 2008; Masunga *et al*., 2013).

Forbs dominated the richness and diversity of the herbaceous layer, which corresponds with various studies in grassland and savanna ecosystems (e.g. Uys, 2006; Bond & Parr, 2010; Axmanová *et al*., 2012; Koerner *et al*., 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015). Forbs are considered to be more adapted to shaded microenvironments than grasses (Uys, 2006; Kahi *et al*., 2009; Bond & Parr, 2010), attributing to their successful contribution to the richness of the herbaceous layer under average rainfall, when herbaceous biomass is high in herbivore absence. Moreover, forbs are persistent during dry conditions (Kallah *et al*., 2000; Van Der Merwe & Marshal, 2012), justifying their dominance in richness and diversity in the drier sampling year. Herbaceous richness and diversity was still dominated by forbs with long-term sustained grazing without rest, reinforcing their adaptability to aboveground disturbances, possibly due to belowground storage organs and other traits (Uys, 2006). Grazing by LMH furthermore maintained low biomass levels, preventing grasses from outcompeting forbs of a lower stature for resources such as light, water and nutrients, consequently enhancing richness and diversity (Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Burkepile *et al*., 2016).

Results suggested that forbs still proved more species rich and diverse after 14 years of LMH removal from the system, which is contradictory to patterns that would generally be expected (Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; La Pierre *et al*., 2015;

Van Coller & Siebert, 2015). A possible explanation for these patterns could be the increased tree cover associated with herbivore exclusion (Levick & Rogers, 2007) favouring forbs which are considered more shade tolerant than grasses (Uys *et al*., 2004; Uys, 2006; Kahi *et al*., 2009; Bond & Parr, 2010). Richness and diversity patterns suggest that forbs in this system are notably competitive and resilient to environmental conditions that are usually thought to cause decreased richness and diversity (i.e., high biomass levels in the absence of herbivores) (Jacobs & Naiman, 2008; Van Coller & Siebert, 2015). In accordance with the majority of studies concerning herbaceous forbs (e.g. Uys *et al*., 2004; Uys, 2006; Kahi *et al*., 2009; Bond & Parr, 2010), it is furthermore suggested that herbaceous forbs in the sodic zone is particularly resilient to higher biomass levels and the subsequent effects of shading under moribund grass swards.

Life form–and functional group abundances

Similar to other studies, the herbaceous layer responded dynamically to grazing, fire and rainfall variability (Muoghalu 1996; Hendrickson & Olson 2006; O’Connor 2015). Dynamic patterns in forb-grass dominance were revealed, irrespective of function (e.g., annual/perennial or palatability) when these distinct herbaceous components were separated.

Rainfall conditions and herbivory were the only two variables which showed a significant interaction with forb and grass abundance variance, although only within the palatable perennial functional group. In terms of range condition, this functional group is particularly valuable, especially palatable perennial grasses which are generally considered an important and stable source of forage to livestock and grazers in savanna systems (Uys, 2006; Trollope *et al*., 2014, O’Connor, 2015). Significant interactive effects of herbivory and rainfall variability on herbaceous life form abundances are consistent with previous studies reporting that range condition (in systems without direct human interference) is controlled by rainfall variability and herbivory and less so by fire (O’Connor, 1995; O’Connor, 1998; Buitenwerf *et al*., 2011; O’Connor, 2015). The impacts and extent of fire, however, is strongly affected by soil nutrients (Archibald & Hempson, 2016). For example, as suggested by Bond (2005), nutrient-poor soils would tend to reduce mammalian herbivory, in turn causing increased biomass which would favour fire (Van Wilgen *et al*., 2003). Herbivores would therefore dominate in nutrient-rich patches, such as the sodic zone, and fire in nutrient-poor patches (Bond, 2005). One would therefore expect that fire would become a more significant top-down control in the dystrophic upland crests, although fire effects on different landscape positions within semi-arid catenal sequences remain less known (Alard, 2010).

Palatable perennial grass abundances were enhanced by above-average rainfall conditions in this semi-arid savanna system, which is consistent with various ecological studies reporting on herbaceous vegetation dynamics in savanna systems (e.g., Buitenwerf *et al*. 2011; Fensham *et al*., 2015; O'Connor 2015; Guo *et al*., 2016; Tessema *et al*. 2016). During wetter conditions, palatable perennial grasses overtop, shade out and outcompete forb species of a lower stature for resources such as water, light and nutrients (Jacobs & Naiman 2008; Savadogo *et al*. 2008; Bond & Parr 2010; Van Coller *et al*. 2013). Under average and below-average rainfall conditions and sustained long-term grazing pressure, palatable perennial forbs and grasses co-dominated the herbaceous layer. Considering that a large component of LMH in African savannas are mixed feeders that feed on both grasses and forbs in the herbaceous layer (Koerner *et al*., 2014), palatable perennial forbs are suggested to provide trait-based redundancy to the sodic system. Forbs can, furthermore, also be considered an important source of forage stability during stressed conditions, such as a combination of drought and sustained long-term grazing pressure.

Forbs dominated over grasses during average environmental conditions (i.e., average rainfall and herbivore presence) in the palatable annual plant functional group, irrespective of fire. Decreased abundances of palatable annual grasses may suggest that herbivores prefer palatable annual grass species over palatable annual forb species. Another possible explanation for higher palatable annual forb abundances may be the notion that forbs are relatively unaffected by disturbance regimes (Uys *et al*., 2004), they rather respond indirectly to changes in dominant grass abundance (Koerner & Collins, 2014). Although the appearance of annual herbaceous species in semi-arid ecosystems is very sporadic (Scholes, 1990), our results suggest that forbs can maintain forage provision when abundances of other palatable plant species become low. The exclusion of herbivores, irrespective of rainfall or fire treatment, favoured palatable annual forbs over grasses. Herbivore exclusion generally leads to increased herbaceous biomass (Jacobs & Naiman 2008; Van Coller *et al*. 2013; Van Coller and Siebert 2015) and hence increases shading effects on understorey vegetation, however, forbs have been shown to be more shade-tolerant than grasses (Ludwig *et al*. 2004). Forbs can therefore persist under dense canopies and high grass biomass (Mlambo *et al*. 2005; Kahi *et al*. 2009), possibly attributing to higher forb abundances.

Unpalatable perennial forb abundances were consistently higher than unpalatable perennial grasses under long-term sustained grazing and were favoured by average rainfall conditions. Forbs may be able to withstand long-term sustained grazing through their adaptability to aboveground disturbances, possibly due to belowground storage organs and other traits (Uys, 2006). Functional traits which allow forbs to persist under such stressful conditions therefore needs to be further explored. Fire strengthened this dominance of forbs, both in the presence and absence of herbivores, which is consistent with Fensham *et al*. (2015). The inverse responses of herbaceous functional groups to fire suggest that life forms alone provide limited understanding of savanna herbaceous dynamics. For instance, under sustained grazing, unpalatable perennial forbs dominated over grasses, irrespective of fire treatment, whereas palatable perennial forbs were more sensitive to fire. However, palatable perennial grasses provide redundancy to forbs when exposed to fire, irrespective of herbivory. This finding may have strong management implications, given that managers are able to manipulate a disturbance such as fire (Uys 2006). Considering typical semi-arid savanna conditions, i.e. average rainfall and long-term exposure to herbivory, forbs either dominated over or co-dominated with grasses, irrespective of fire treatment, life history and palatability, with the exception of unpalatable annual grasses and palatable perennial grasses in fire presence. However, unpalatable annual grasses are more resilient than forbs since they dominated across all treatments of herbivory, fire and rainfall variability.

Although nutrient-rich sodic patches are generally considered as overgrazed, trampled, eroded and degraded systems (Bailey & Scholes 1997; Khomo & Rogers 2005; Grant & Scholes 2006; Van Coller *et al* 2013), the grass sward did not show shifts from palatable perennial grasses to unpalatable perennial grasses as would be expected after long-term sustained grazing and below-average rainfall conditions (Skarpe 1991; O’Connor 2015). Persistent dominance of palatable perennial grasses over unpalatable perennial grasses under sustained grazing suggests that sodic patches are particularly resilient to sustained grazing impacts, especially considering that they are regularly utilized by herbivores (Scogings 2011; Siebert & Scogings 2015). Similar to findings by Verdoodt *et al.* (2010), palatable perennial grasses dominated the fenced treatment. Increased abundance in this functional group can be ascribed to the competitive exclusion effect (Grime 1973) where tall, fast growing grasses tend to out-compete other species of lower stature for resources such as light, water and nutrients (Jacobs & Naiman 2008). Although fire is considered a secondary driver of herbaceous dynamics in sodic patches of a semi-arid savanna (Van Coller *et al*. 2013), fire presence had strong positive effects on palatable perennial grass abundance in the absence of herbivores. These results are in accord with Garnier & Dajoz (2001) and Trollope (2011) which stated that fire removes moribund and undesirable grass material, to inherently reduce competition while improving quality of grazing for wildlife.

Rainfall variability best explained the dominance of palatable perennial grasses (PPG) over perceived undesirable functional groups as the strongest dominance of PPG was revealed during above-average rainfall conditions, whereas average and below-average rainfall lead to weaker dominance by PPG. These findings are in accordance with Buitenwerf *et al*. (2011); O'Connor (2015) and Tessema *et al.* (2016). Research and management on rangelands often focus on understanding and managing the conditions that are responsible for shifts from palatable perennial grass species to unpalatable species (Skarpe 1991; Bergström & Skarpe 1999). Results presented here indicate that, according to general range condition assessments, i.e. dominance of palatable perennial grasses (O'Connor 2015), conditions in the sodic zone are not degraded.

5.5 Conclusion

Herbaceous life forms revealed dynamic patterns of response to fire, herbivory, and rainfall variability. Palatable forbs provide redundancy to semi-arid sodic patches, by providing forage to herbivores when palatable grasses decrease in abundance.

This study did not support previous findings that conditions such as drought, fire and sustained herbivory, favour alleged unfavourable functional groups at the expense of palatable perennial grasses. Sodic patches are considered resilient to the sustained use by herbivores since there were no clear indications of any degradation to the herbaceous plant community (i.e., palatable perennial grasses remained the dominant functional group, irrespective of herbivore or fire treatment or rainfall). Palatable perennial functional groups provide forage stability in such systems.

Although herbivore presence (irrespective of fire presence or absence) enhanced herbaceous species richness, inter-annual variation in rainfall seemed to be the most important driver of herbaceous layer dynamics in this system. Consistent with patterns of soil moisture and water availability in semi-arid systems, results presented indicated that below-average rainfall negatively affects both forb and grass species richness. Rangeland managers are therefore posed with future challenges to find ways to mitigate the ecological impact of droughts. Despite lower richness during drier conditions, the sodic zone maintained a character of palatable perennial grasses when rainfall was below-average.

The response of forb and grass richness to fire is subject to rainfall. The interaction between fire and rainfall is valuable in areas where fire treatment can be manipulated to obtain optimal herbaceous richness. Life form dominance within functional groups varied with fire treatment, particularly within the palatable perennial functional group in herbivore absence. Although not showing significant interaction effects, fire presence seemed to enhance abundances of palatable perennial grasses in the absence of herbivores, thereby improving forage for wildlife. Considering that more frequent droughts are predicted for semi-arid systems due to global climate change, results presented here provides important insights into the responses of herbaceous life forms to such conditions.

Forb species contributed most to the diversity and richness of the sodic herbaceous layer, irrespective of rainfall variability, and the presence or absence of fire and/or herbivory. Forbs are therefore considered a resilient life form, able to adapt to various extreme conditions. Herbaceous forbs in the sodic system are suggested to have particular plant traits enabling them to adapt and colonize in such extreme environments. Further studies that relate plant traits to disturbance tolerance and how these traits change across environmental gradients are however anticipated to better our understanding of their function in savanna systems. When studying fire effects on herbaceous vegetation, life form alone is not sufficient, since herbaceous life forms respond dynamically to fire presence or absence. Researchers should include other functional attributes such as palatability and life history, which reveals more comprehensive patterns of response. Palatable perennial forbs co-dominate the herbaceous layer with palatable perennial grasses under average and dry conditions. Palatable perennial forbs are therefore considered functionally important during these conditions. Forbs, particularly palatable annual species, are furthermore considered resilient to sustained utilization by herbivores, as well as increased biomass in their absence. Unpalatable perennial forbs are adapted to sustained herbivore presence. Since our knowledge pertaining to the functionality of forbs in savanna systems remains limited, results presented here provide evidence of a dynamic coexistence between forbs and grasses in a nutrient-rich setting. However, functional traits of forbs and how they relate to various disturbances in savannas need to be further explored.

Lastly, results presented here suggest that herbaceous vegetation response patterns remain dynamic in the absence of elephants. Herbivores other than elephants are therefore able to drive herbaceous species dynamics.

Chapter 6

Herbaceous responses to herbivory and rainfall variability in a semi-arid savanna a system without fire

6.1 Introduction

Elephants (*Loxodonta africana*) are considered dominant herbivores and ecological engineers in many African savanna ecosystems (Holdo, 2007; Kohi *et al*., 2011; Hempson *et al*., 2015). However, from 2010 – 2012, 6.8 % (i.e., 100 000) of Africa's elephants were claimed annually by poaching (Robson *et al*., 2016). Although elephants dominate the biomass in the KNP, understanding the effects of changes, especially such drastic decreases, in elephant population densities on vegetation dynamics is of particular importance for the sustainable management of protected areas (Holdo, 2007; Holdo *et al*., 2009). Experiments able to manipulate the long-term presence or absence of certain large mammalian herbivores (LMH), particularly elephants, are considered important for ecological research in savanna systems (Hooper *et al*. 2005; Daskin *et al*. 2016). Despite the knowledge that elephants include forbs and grasses in their diet, the effect of elephants, and more pressingly, their exclusion, on herbaceous layers under varying rainfall conditions remains understudied (Young *et al*., 2005).

The aim of this chapter was to explore herbaceous responses to rainfall variability and herbivore presence or absence (including elephant effects) by:

1. Assessing patterns in forb and grass richness and diversity;
2. Evaluating differences in forb and grass abundances, and
3. Testing whether favourable range conditions (increased abundance of palatable perennial grasses) can be maintained in a nutrient-rich semi-arid savanna ecosystem without fire as an ecological driver.

As suggested by Bond (2005), herbivores would dominate as a top-down controlling agent in nutrient-rich patches, and fire in nutrient-poor patches when mammalian herbivory is reduced. Accordingly, it was expected that herbivory would become the strongest top-down controlling agent of herbaceous layer dynamics when fire is lost from nutrient-rich sodic savanna ecosystems. However, Buitenwerf *et al*. (2011) suggested that rainfall variability is the main driver of herbaceous dynamics in semi-arid savanna systems, although there were no clear topo-edaphic gradients in their study sites. Herbaceous diversity was hypothesized to be highest in herbivore presence (irrespective of elephant) (Jacobs & Naiman, 2008). Species and functional response patterns similar to those found in Chapter 5 were expected for this fire-excluded system, although particular elephant exclusion effects are presented here. Elephants are considered ecosystem engineers, and can alter vegetation structure and composition (Kohi *et al*., 2011). They are capable of shifting landscapes from dense woodlands to open savannas (Pellegrini *et al*., 2017), potentially enhancing resource heterogeneity in the system (Levick *et al*., 2009). Elephants were, therefore, expected to enhance herbaceous species diversity, and, through increased system heterogeneity allow functionally different grasses and forbs to coexist. Since elephants include both grasses and forbs in their diet (Young *et al*., 2005), elephants, or their exclusion, were furthermore expected to affect life form dominance.

6.2 Material and Methods

Floristic data collected in transects 3-8 (refer to Figure 4.1 and 4.3) were used to address the aim and objectives of this chapter. Please refer to Chapter 4 (Materials and Methods, sections 4.3.1 and 4.5) for a detailed account of the floristic sampling and data analysis performed to obtain the following results.

Variations in Hierarchical Linear Modelling (HLM) together with statistical effect sizes were used to reach the three objectives of this chapter:

1. To reach the first objective, a two-way ANOVA type HLM was fitted to herbaceous diversity data (i.e., richness and diversity of forbs and grasses as a whole), where herbaceous species richness and diversity were the response variables and herbivory and year were specified as the predictor variables. Life form was added as an additional predictor variable to test whether differences in diversity of the respective life forms had underlying effects on the patterns revealed for the entire herbaceous layer. Species richness and diversity were once again specified as the response variables and life form, herbivory and year were specified as predictor variables in the three-way ANOVA type HLM.

2. The second objective was reached by performing Hierarchical Linear Model (HLM) analyses on abundance data using a three-way ANOVA with random effects model. Herbaceous species abundances within functional groups were specified as the response variable, whilst life form, herbivory and year were the predictor variables in the model.
3. A three-way ANOVA type HLM with abundances of functional groups as the response variable and functional group, herbivory and year as the predictor variables, was performed to reach the third objecive.

6.3 Results

6.3.1 Richness and diversity patterns

Herbaceous species richness and diversity revealed no significant response to the interactive effects of herbivory and year ($p > 0.05$; Table 6.1). This suggests that herbivory and year (rainfall) revealed similar effects on herbaceous species richness and diversity. Stand-alone effects of year ($p < 0.001$; Table 6.1) and herbivory ($p < 0.001$; Table 6.1) on herbaceous species richness were, however, significant. Year was the only significant predictor of herbaceous species diversity ($p = 0.034$; Table 6.1).

Table 6.1. Summary of the two-way ANOVA type Hierarchical Linear Model (HLM) results for variance in herbaceous species richness and diversity with respect to year and herbivory.

	Fixed effects		
	Year	Herbivory	Year*Herbivory
Herbaceous species richness			
df	1	2	2
F	56.1	10.1	0.9
p	**< 0.001***	**< 0.001***	0.404
Herbaceous species diversity			
df	1	2	2
F	4.5	2.3	0.7
p	**0.034***	0.099	0.501

Year, 2010 or 2015; *Herbivory*, Present or absent. Significance (at $p < 0.05$) indicated with * and in bold.

Overall, herbaceous species richness and diversity was lower in the drought year (Figure 6.1 (a) and (c)). Expectedly, herbivore presence (irrespective of assemblage) significantly enhanced herbaceous species richness (Figure 6.1 (b); Table D.1.; Appendix D).

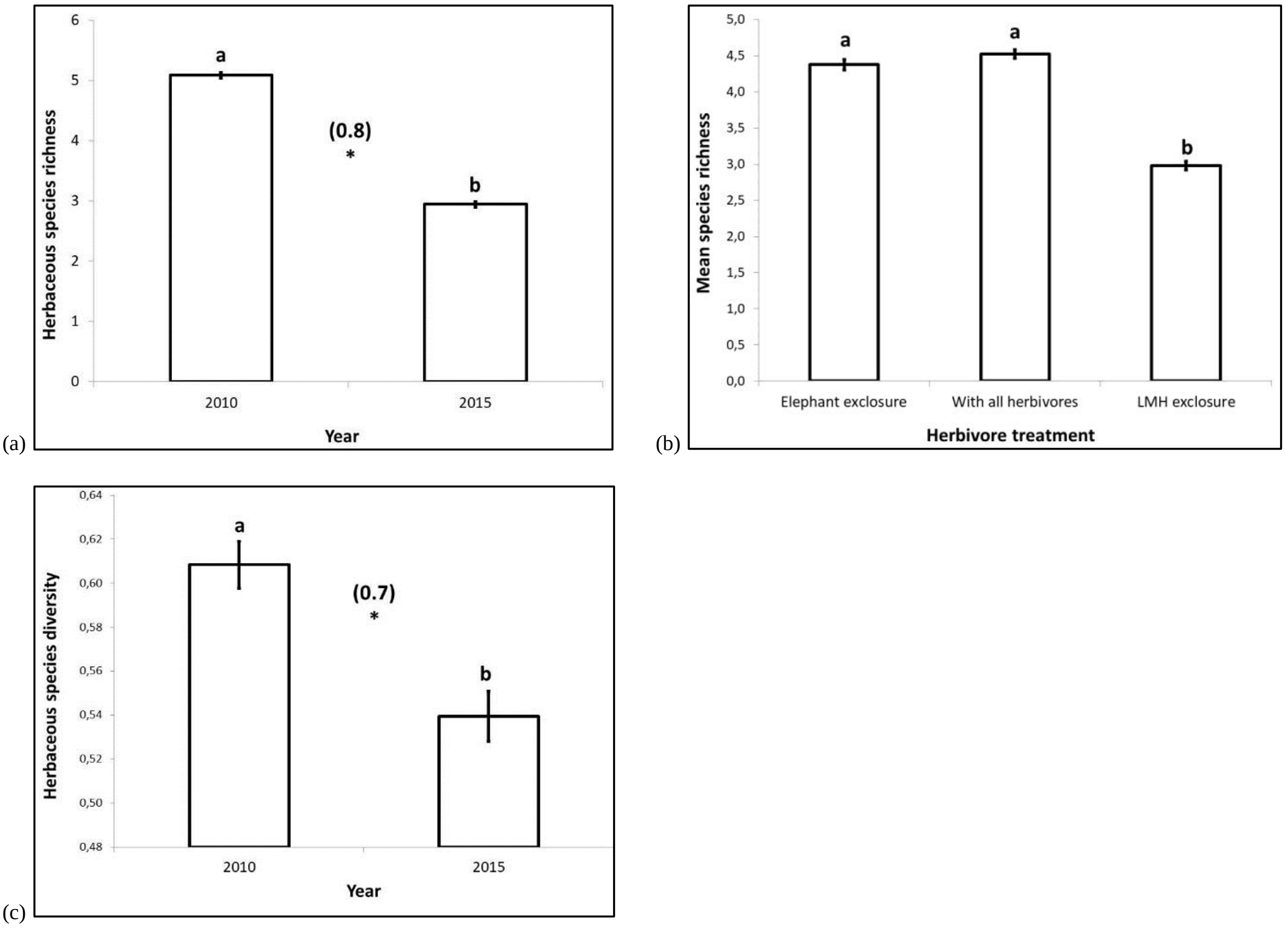


Figure 6.1. Mean (±SE) (a) herbaceous species richness over time, (b) herbaceous species richness across herbivore treatments and (c) herbaceous species diversity over time. * indicates significant differences (at $d > 0.7$) in trait richness, whilst values in parenthesis indicate effect sizes. Significant differences (at $p < 0.05$) indicated by means of different letters.

No significant interactive effects were revealed for species richness or diversity with life form, herbivory and year (Life form*Herbivory*Year $p > 0.05$; Table 6.2).

Table 6.2. Summary of the three-way ANOVA type Hierarchical Linear Model (HLM) results for variance in species richness and diversity with respect to life form, year and herbivory.

	Fixed effects			
	Life form	**Life form*Year**	**Life form*Herbivory**	**Life form*Herbivory*Year**
Herbaceous species richness				
Df	1	1	2	2
F	462.4	16.6	4.4	0.3
P	**< 0.001***	**< 0.001***	**0.013***	0.727
Herbaceous species diversity				
Df	1	1	2	2
F	224.5	0.1	1.3	0.6
P	**< 0.001***	0.714	0.279	0.534

Life form, forb or grass; *Year*, 2010 and 2015; *Herbivory*, present or absent. Significant effects (at $p < 0.05$) indicated in bold with *.

Overall, forb richness and diversity was significantly higher than grass richness and diversity (Figure 6.2 (a) and (d)). Drought had a bigger negative effect on forb species richness than it did on grass species richness (*p* < 0.001; Table 6.2; Figure 6.2 (b)). Moreover, the impact of herbivore loss was less severe on grass species richness, but did significantly decrease forb species richness (*p* = 0.013; Table 6.2; Figure 6.2 (c)).

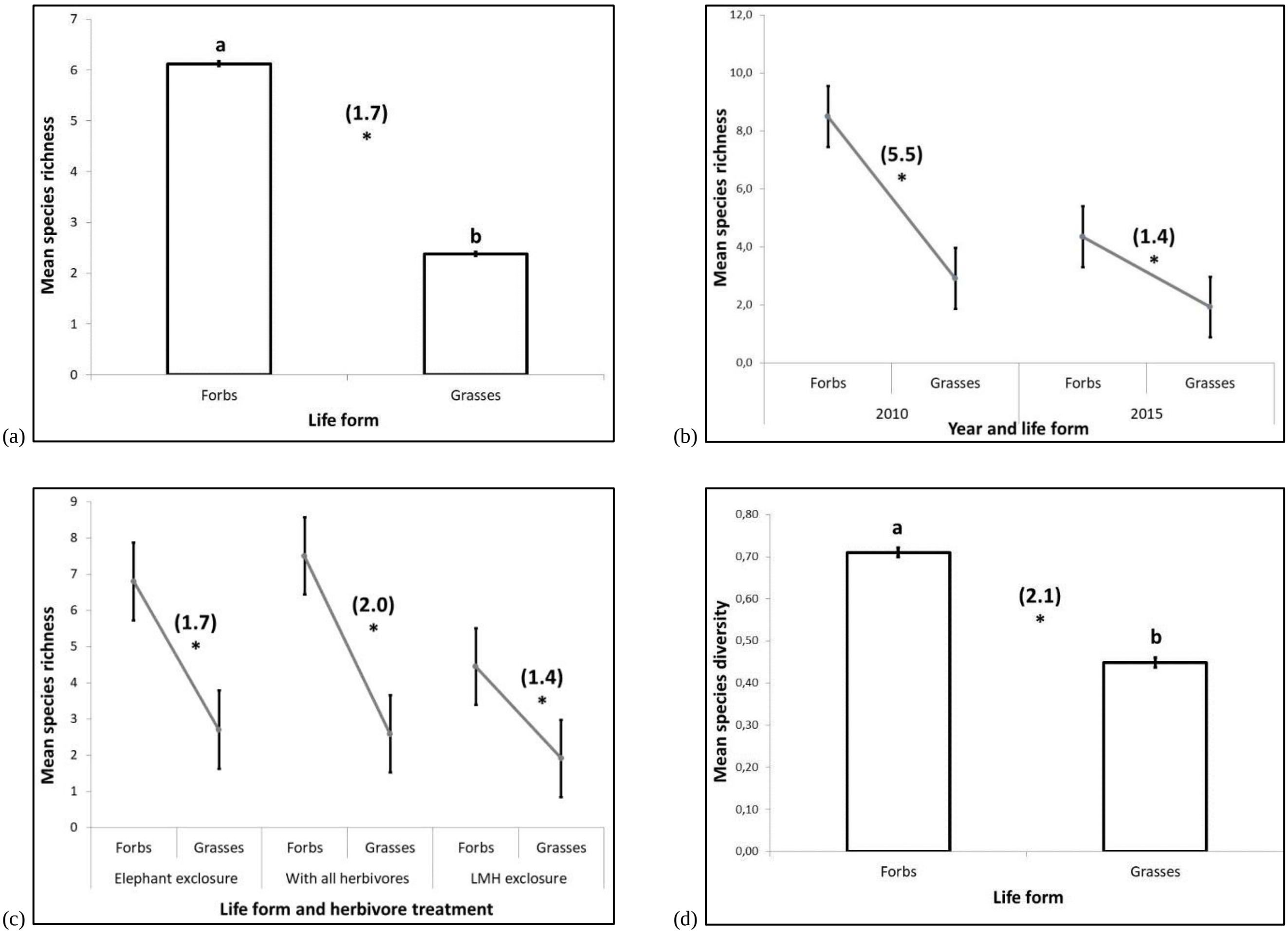


Figure 6.2. Comparisons of mean (±SE) species richness (a) between herbaceous life forms, (b) between herbaceous life forms over time, (c) between herbaceous life forms across herbivore treatments and (d) mean (±SE) species diversity between herbaceous life forms. * indicates significant differences (at $d > 0.7$), whilst values in parenthesis indicates effect sizes. Significant differences (at $p < 0.05$) in species richness indicated by means of different letters.

6.3.2 Life form–and functional group abundances

Of the 40 dominant herbaceous species (See Table C.1.; Appendix C for a complete species list) on which analysis were performed, forbs represented 62.5 % (25 species of which 15 were palatable and 10 were unpalatable) whereas 15 species (37.5 %) were grasses of which nine were palatable and six unpalatable.

Life form abundances

Variability in life form abundance was the greatest source of variation within all functional groups, except unpalatable perennial herbaceous species (Table 6.3). Irrespective of this, life form showed no significant interactive effects with year and herbivory (Life form*Year*Herbivory $p > 0.05$; Table 6.3) on any of the functional groups. Significant within-group variability (Life form) across functional groups (Life form fixed effect size of $p < 0.05$; Table 6.3) lead us to further explore the conditions under which life form dominance varied. We therefore tested for significant differences between mean abundances of forbs and grasses under different rainfall conditions as well as different assemblages of wild ungulate herbivores. Results are presented per plant functional group.

Palatable perennials

Herbaceous life form was the greatest source of variation in the palatable perennial functional group ($p = 0.002$; Table 6.3). As would be expected, significant differences between forb and grass abundances occurred mainly with above-average rainfall (2001), where palatable perennial grasses (PPG) were significantly more abundant than palatable perennial forbs (PPF) (Figure 6.3 (a)). Moreover, herbivore exclusion in above-average rainfall revealed the strongest dominance of grasses over forbs (Figure 6.3 (a)). Surprisingly, the only other dominance of PPG over PPF was in the drought year (2015) in sites exposed to all large mammalian herbivores (LMH) (Figure 6.3 (a)).

Table 6.3. Summary of the three-way ANOVA type Hierarchical Linear Model (HLM) results for variance in abundances within herbaceous species functional groups with respect to life form, year and herbivory.

	Fixed effects					
	Year	**Herbivory**	**Life form**	**Life form* Year**	**Life form* Year*Herbivory**	**Life form* Year*Herbivory**
Palatable Perennial Species						
df	2	2	1	2	2	4
F	1.6	0.4	10.0	2.7	1.0	0.3
p	0.206	0.686	**0.002***	0.073	0.364	0.880
Palatable Annual Species						
df	2	2	1	2	2	4
F	6.2	1.9	9.4	2.6	0.7	0.2
p	**0.004***	0.158	**0.003***	0.079	0.502	0.923
Unpalatable Perennial Species						
df	2	2	1	2	2	4
F	11.8	1.9	1.4	1.8	2.7	0.6
p	**< 0.001***	0.158	0.248	0.175	0.075	0.698
Unpalatable Annual Species						
df	2	2	1	2	2	4
F	8.4	1.7	9.3	1.5	0.6	0.1
p	**0.001***	0.197	**0.004***	0.235	0.577	0.991

Life form, forb or grass; *Year*, 2001, 2010 and 2015; *Herbivory*, elephant exclosure, with all herbivores or LMH exclosure. Significant effects (at $p < 0.05$) indicated in bold with *.

Palatable annuals

Life form ($p = 0.003$; Table 6.3) and year ($p = 0.004$; Table 6.3)) are considered significant predictors of palatable annual herbaceous species.

Overall the exclusion of LMH, irrespective of rainfall, favoured the dominance of palatable annual forbs (PAF) over palatable annual grasses (PAG) (Figure 6.3 (b)). Furthermore, significant dominance of PAF occurred with average rainfall, irrespective of herbivore treatment (Figure 6.3 (b)). However, the strongest dominance of PAF over PAG with average rainfall was revealed in the sites exposed to all LMH (Figure 6.3 (b)).

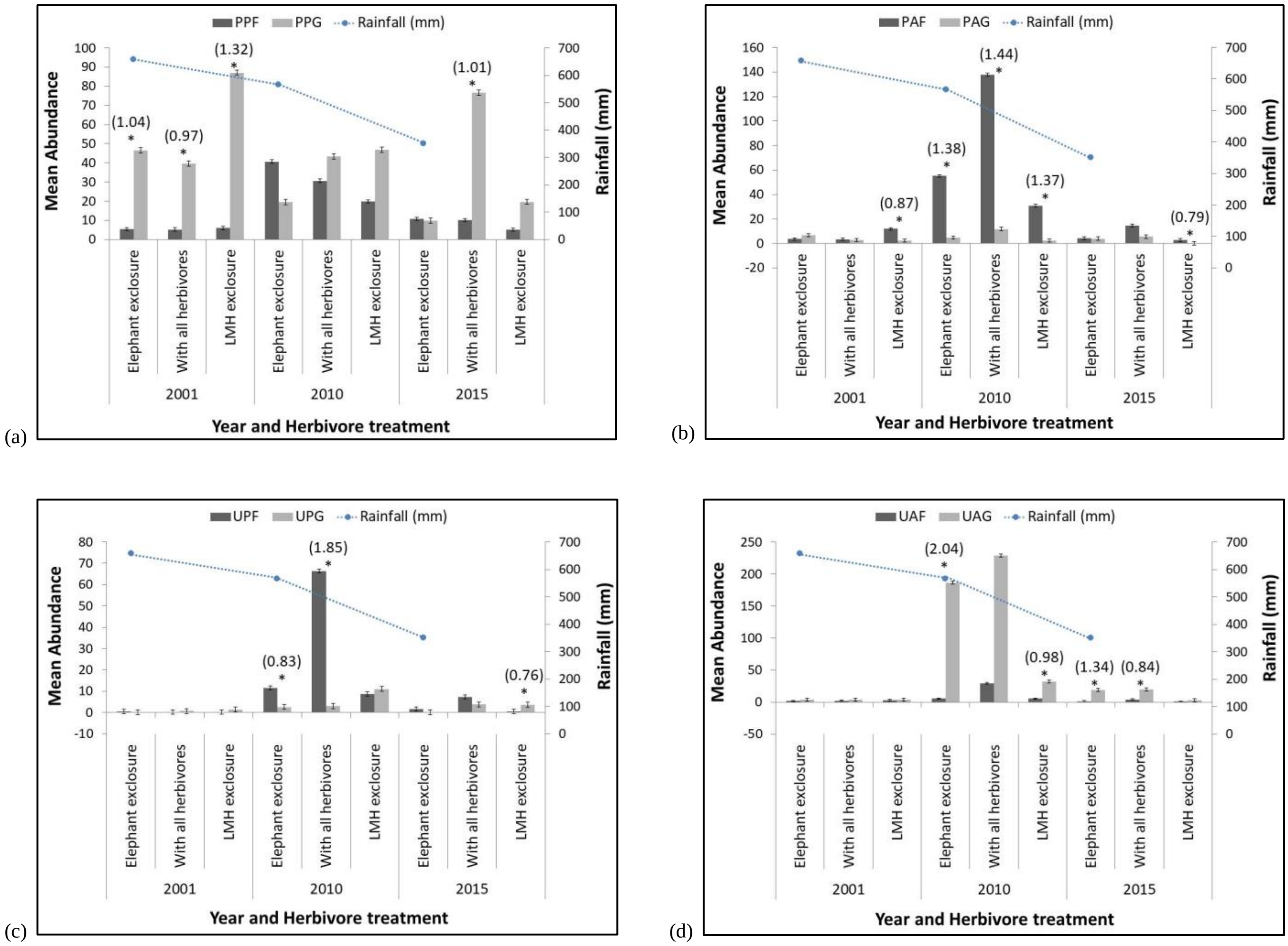


Figure 6.3. Mean (±SE) abundances of herbaceous forbs and grasses assigned to different functional groups exposed to various treatments of herbivory. *Significant variation between forb and grass abundances within similar plant functional groups and herbivory treatments ($p < 0.05$) and values in parenthesis indicate size effects.

Total annual rainfall (mm) for each sampling year is depicted on the secondary vertical axis. PPF, Palatable perennial forbs; PPG, Palatable perennial grasses; PAF, Palatable annual forbs; PAG, Palatable annual grasses; UPF, Unpalatable perennial forbs; UPG, Unpalatable perennial grasses; UAF, Unpalatable annual forbs; UAG, Unpalatable annual grasses.

Unpalatable perennials

Year was a significant predictor of unpalatable perennial herbaceous species' abundance ($p < 0.001$; Table 6.3). Average rainfall conditions (2010) and herbivore presence significantly favoured UPF over UPG. This significant effect was most distinct in the sites exposed to the complete assemblage of LMH (i.e., where no herbivores were excluded) ($d= 1.85$; Figure 6.3 (c)). A combination of drought and herbivore exclusion favoured dominance of UPG over UPF ($d = 0.76$; Figure 6.3 (c)).

Unpalatable annuals

Life form abundances varied significantly in the unpalatable annual functional group ($p = 0.004$; Table 6.3). Above-average rainfall (2001) did not seem to favour either unpalatable annual forbs (UAF) or unpalatable annual grasses (UAG) (Figure 6.3 (d)). Significant dominance of UAG over UAF occurred mainly in the year with average and below-average rainfall ($p = 0.004$; Table 6.3). Herbivore treatment did not seem to affect UAG dominance over UAF with average rainfall (Figure 6.6 (d)). However, the strongest dominance occurred in the elephant exclosure sites ($d = 2.04$; Figure 6.3 (d)). Herbivore presence in the drought year favoured dominance of UAG over UAF (Figure 6.3 (d)).

Palatable perennial grass dominance

Mean abundances of palatable perennial grasses (PPG) and abundances of the other functional groups perceived as being less desirable (i.e., unpalatable perennial grasses (UPG), annual grasses, perennial forbs and annual forbs) revealed no significant response to interactive effects of year and herbivory ($p > 0.05$; Table 6.4). However, within-group effects were significant, suggesting that functional group abundances differed significantly (Functional groups: $p < 0.001$; Table 6.4). Year is furthermore considered a significant predictor of variances between functional group abundances ($p < 0.001$; Table 6.4). Significant differences between functional group abundances in different herbivore treatments and sampling years were assessed and expressed by means of effect sizes (Cohen's d; Figure 6.4).

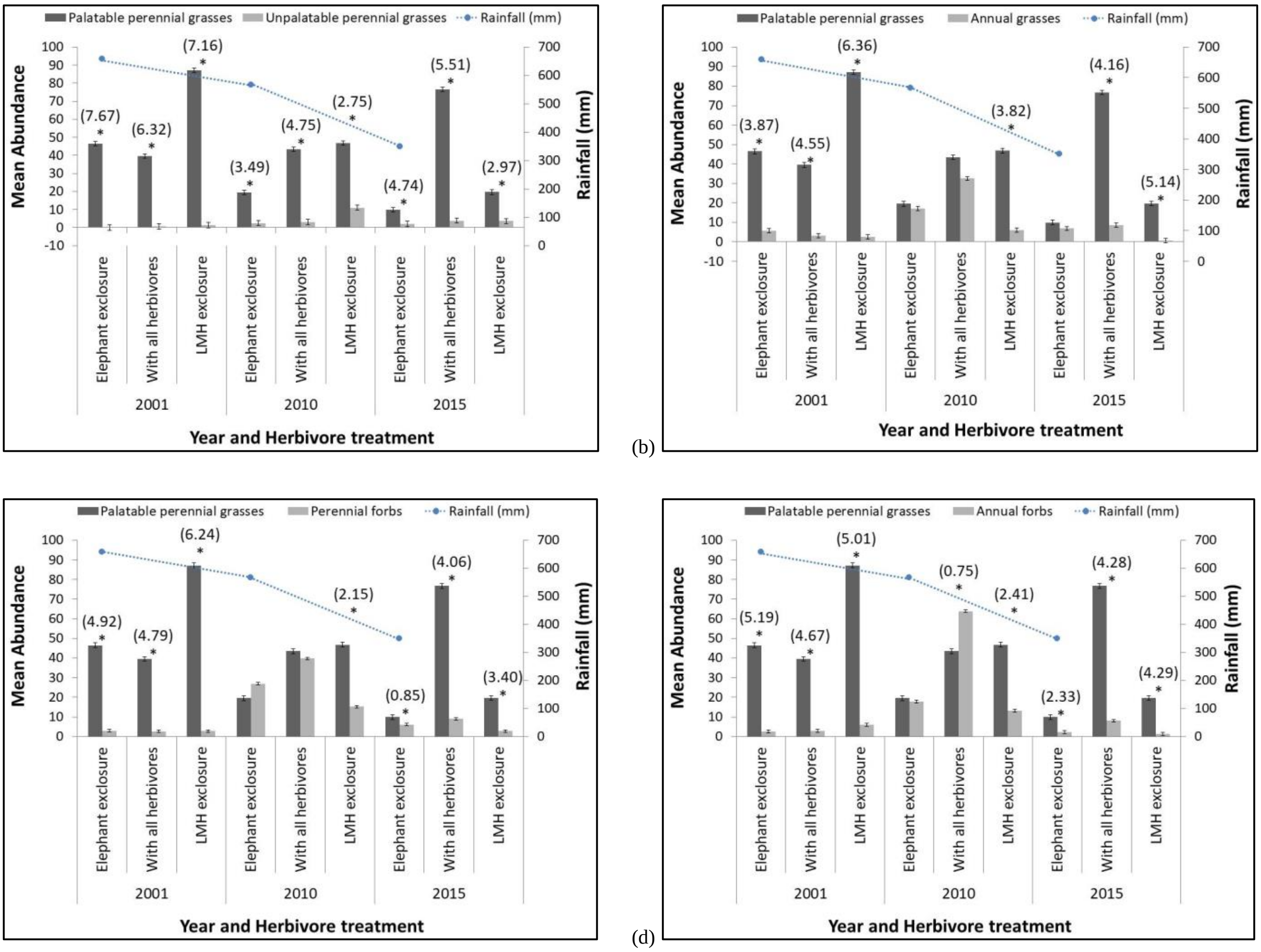
Table 6.4. Results for the three-way ANOVA type Hierarchical Linear Model (HLM) analysis of variance between herbaceous functional group abundances with respect to year and herbivory.

Fixed effects	**df**	**F**	***p***
Year	2	12.5	**< 0.001***
Herbivory	2	2.5	0.083
Functional groups	4	11.1	**< 0.001***
Functional groups*Year	8	1.6	0.133
Functional groups*Herbivory	8	1.1	0.331
Functional groups*Year*Herbivory	16	0.2	0.999

Functional groups, palatable perennial grass abundances compared to abundances of other functional groups, i.e., unpalatable perennial grasses, annual grasses, perennial forbs and annual forbs; *Year*, 2001, 2010 and 2015; *Herbivory*, elephant exclusion, with all herbivores or LMH exclusion. Significant effects (at $p < 0.05$) indicated in bold with *.

Independent comparisons of means revealed that palatable perennial grasses dominated over all other functional groups in this system, with the exception of perennial forbs with elephant exclusion (Figure 6.4 (c)) and annual forbs under the combined effects of average rainfall and exposure to all LMH (Figure 6.4 (d)).

Irrespective of the assemblage of LMH or whether herbivores were excluded from the system, PPG dominated over UPG in this system without fire (Figure 6.4 (a)), suggesting that this nutrient-rich sodic plant community is resilient to the loss of a major driver of savanna ecosystems, i.e., fire. As expected, strongest dominance of PPG ($d > 6$) was revealed with above-average rainfall in 2001 despite the level grazing pressure (i.e., low/none in the fully fenced sites, intermediate in the elephant exclosures and high in the sites open to all LMH) (Figure 6.4 (a)).



(a) (b) (c) (d)

Figure 6.4. Mean (±SE) abundances of (a) palatable perennial grasses *vs* unpalatable perennial grasses, (b) palatable perennial grasses *vs* annual grasses, (c) palatable perennial grasses *vs* perennial forbs and (d) palatable perennial grasses *vs* annual forbs in a system exposed to various treatments of herbivory at different times. *Significant variation between herbaceous functional group abundances within similar treatments of fire and herbivory ($p < 0.05$) and values in parenthesis indicate size effects.

Total annual rainfall (mm) for each sampling year is depicted on the secondary vertical axis.

Expectedly, PPG was the dominant functional group when compared to annual grasses in the above-average rainfall year (Figure 6.4 (b)). Similarly, herbivore exclusion favoured PPG dominance over annual grasses, irrespective of rainfall (Figure 6.4 (b)). Surprisingly, PPG still dominated over annual grasses during drought conditions when exposed to high grazing pressure (Figure 6.4 (b)).

Overall, above-average rainfall and LMH exclusion particularly favoured dominance of PPG over perennial forbs (Figure 6.4 (c)). Unexpectedly, PPG remained the dominant functional group in the drought year under herbivore presence (Figure 6.4 (c)).

Patterns in dominance of PPG over annual forbs were particularly strong with above-average rainfall in 2001 as revealed by large size effects ($d > 4$; Figure 6.4 (d)). However, when conditions were average for this system (i.e., average rainfall (2010) and all LMH present) the PPG functional group lost its dominance over annual forbs (Figure 6.4 (d)). As expected, the removal of LMH favoured PPG dominance over annual forbs (Figure 6.4 (d)). However, annual forbs did not dominate over PPG in the drought year when exposed to herbivores as would be expected in disturbed savanna ecosystems (Figure 6.4 (d)).

6.4 Discussion

Richness and diversity patterns

The most consistent patterns that were observed in this study were reductions in forb and grass species richness and diversity as a result of below-average rainfall. These results support other studies documenting decreases in species richness due to drought (Tilman & El Haddi, 1992; Venter *et al*., 2003; Copeland *et al*., 2016; Van Wilgen *et al*., 2016). Our results showed higher forb and grass species richness when exposed to herbivores which is consistent with literature reporting on patterns in herbaceous richness (e.g. Scholes 1987; Skarpe 1991; Skarpe 1992; Milchunas & Lauenroth 1993; Fynn & O’Connor 2000; Illius & O’Connor 1999; Jacobs & Naiman, 2008; Savadogo *et al*. 2008; Tessema *et al*. 2011; Koerner & Collins 2013; Van Coller *et al*., 2013).

Herbivores increase spatial and physical heterogeneity and are therefore important disturbance agents, especially in the absence of fire (Olff & Ritchie, 1998; Adler *et al*., 2001; Jacobs & Naiman, 2008; Van Der Waal *et al*., 2011; Angassa, 2012). Diversity and richness is generally enhanced by the presence of herbivores through the suppression of biomass levels and the reduction of herbaceous competition, allowing more species to coexist (Bakker *et al*., 2003; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Van Coller & Siebert, 2015). Moreover, species richness have been reported to increase under high grazing pressure in nutrient-rich ecosystems, possibly because species are less inhibited by resource availability and therefore have a greater capacity for regrowth after grazing (Proulx & Mazumder, 1998). Although non significant, elephant presence enhanced herbaceous species richness which is in accordance with various studies reporting on elephant effects (e.g., Pringle, 2008; Robson *et al*., 2016).

Forbs dominated the richness and diversity of the herbaceous layer which coincides with the findings of several studies in grassland and savanna ecosystems (Uys, 2006; Bond & Parr, 2010; Axmanová *et al*., 2012; Koerner *et al*., 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015). This dominance of forbs in herbaceous richness and diversity in both sampling years and across all herbivore treatments reinforces their potential functional importance in nutrient-rich ecosystems, as well as their resilience to extreme environmental conditions. Forbs respond dynamically to changes in the environment (Shackleton, 2000; Bond & Parr, 2010; Lettow *et al*., 2014). Contrary to what would be expected in the absence of LMH, which is a competitive exclusion effect of forbs by grasses (Grime, 1974; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; La Pierre *et al*., 2015), forb richness revealed to be higher than grass richness. Our results therefore agree with Uys *et al*. (2004), Uys (2006), Kahi *et al*. (2009) and Bond and Parr (2010) reporting that forbs are likely more adapted to shaded environments than grasses. Forbs are furthermore persistent during drier conditions (Kallah *et al*., 2000; Van Der Merwe & Marshal, 2012) and belowground storage organs and other traits allow them to adapt to aboveground disturbances (Uys, 2006). This may have strong management implications since extreme drought events are expected to become more frequent in savannas (Van Wilgen *et al*., 2016). However, further research on forbs and their functions is anticipated (Siebert & Scogings, 2015).

Life form–and functional group abundances

Increased palatable perennial grass abundance over other functional groups and life forms with above-average rainfall was a persistent pattern observed in life form–and functional group abundances. This is consistent with the findings of various studies reporting on herbaceous vegetation dynamics in semi-arid savanna systems (e.g. Jacobs & Naiman, 2008; Buitenwerf *et al*., 2011; O'Connor, 2015; Tessema *et al*., 2016).

Indigenous African grasses are well adapted to withstand severe grazing (Scholes & Walker, 1993; Owen-Smith, 2013). In support of this, our results revealed predominance of palatable perennial grasses over other functional groups when exposed to all LMH. Furthermore, palatable perennial grasses were more abundant under long-term heavy grazing wiothout rest (i.e., control sites) in combination with drought conditions, which contradicts general patterns found in semi-arid savanna systems (O’Connor & Pickett, 1992; O’Connor, 1995; O’Connor, 2015).

Palatable annual forbs were more abundant than palatable annual grasses during conditions of above-average rainfall and when herbivores were excluded from the system, regardless of rainfall. High rainfall and herbivore exclusion leads to increased biomass (Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Van Coller & Siebert, 2015). The increased abundance of palatable annual forbs over grasses suggests that this functional group is shade-tolerant and can persist under high grass biomass and dense canopies (Ludwig *et al*., 2004; Mlambo *et al*., 2005; Kahi *et al*., 2009). Similarly, palatable annual forbs were more abundant when exposed to herbivores when rainfall was average. Average rainfall and herbivore presence kept biomass levels low, possibly enhancing forb abundances through the reduction of competition effects for light, water and nutrients (Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Burkepile *et al*., 2016).

Abundances of unpalatable grasses and forbs did not respond positively to above-average rainfall conditions, suggesting that high abundances of palatable perennial grasses during such conditions possibly lead to the out-competition of unpalatable grasses and forbs (O’Connor & Pickett, 1992; O’Connor, 1995; Jacobs & Naiman, 2008; Buitenwerf *et al*., 2011; O’Connor, 2015; Tessema *et al*., 2016). Unpalatable perennial forbs were more abundant when exposed to herbivores with average rainfall. This finding might suggest that unpalatable perennial forbs are well adapted to withstand above-ground disturbances (Uys, 2006), more so than unpalatable perennial grasses. Herbivores exclusion and dry conditions favoured unpalatable perennial grasses over unpalatable perennial forbs.

Unpalatable annual grasses (UAG) are generally abundant in disturbed places (Van Oudtshoorn, 2006). Our results are consistent with this, since UAG were more abundant than unpalatable annual forbs (UAF) when exposed to herbivores. These results furthermore suggest that UAG are more tolerant to such disturbances than UAF. Similarly to unpalatable perennial forbs, unpalatable annual forbs (UAF) are less tolerant to shaded environments than unpalatable grasses. Unpalatable annual grasses were more abundant than unpalatable annual forbs with average rainfall and herbivore exclusion, suggesting that UAF are outcompeted for resources when biomass levels are high (Jacobs & Naiman, 2008).

In accordance with Verdoodt *et al.* (2010) and Eby *et al.* (2014), palatable perennial grasses became more abundant in the absence of grazing. Tall, fast growing palatable perennial grasses may therefore out-compete other functional groups of lower stature for resources, further attributing to the increased abundance of the palatable perennial grass functional group (Grime, 1973; Jacobs & Naiman, 2008). The change in vegetation under sustained heavy grazing and drought, i.e., from dominance in palatable perennial grasses to unpalatable perennial grasses (Skarpe, 1992; O'Connor & Pickett, 1992; O'Connor, 1995; O'Connor, 2015) did not prevail in this semi-arid savanna sodic zone. Increased abundance of palatable perennial grasses improves the condition of a sward in terms of cover and erosion (O'Connor, 2015). Under average conditions annual forbs were more abundant than palatable perennial grasses. Herbivores maintain lower levels of above-ground biomass (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Van Coller & Siebert, 2015) which may contribute to the increased abundance of annual forbs as a result of a reduction in competition for resources.

6.5 Conclusion

Herbaceous species richness was significantly higher with herbivore (including elephant) presence. Although non-significantly, elephant presence further enhanced species richness, since highest species richness was recorded in the presence of all LMH. LMH, including elephants, are suggested to be important drivers of species richness in nutrient-rich savanna systems, especially in systems without additional disturbances such as fire.

Similarly to a system without elephants, life form dominance in functional groups is dynamic in its response to herbivory (including elephants) and rainfall variability. Palatable perennial grasses are promoted by above-average rainfall in this nutrient-rich semi-arid savanna system. Unpalatable forbs and grasses do not respond positively to above-average rainfall. Predominance of palatable perennial grasses in the sward, irrespective of rainfall and elephant treatment, suggests that the sodic zone is ecologically well maintained. It can therefore be deduced that the nutrient rich sodic zone of the Nkuhlu exclosures is well adapted to withstand severe grazing, i.e., presence of all LMH including elephants. Palatable annual forbs are able to compete successfully for resources when compared to palatable annual grasses. Furthermore, annual forbs maintained a higher abundance when compared to palatable perennial grasses in the presence of all LMH. Annual forbs are therefore considered functionally important in this nutrient-rich system. Forbs, furthermore, dominated richness and diversity across all herbivore treatments and sampling years, which is indicative of their functional importance and resilience in a system exposed to the entire suite of LMH. Herbaceous community richness and diversity is therefore driven by forbs in this particular system. Further exploration of the function of forbs as a life form is therefore necessary for the successful understanding and management of systems such as this one.

Correspondent with conclusions drawn in chapter 5, herbivory had significant effects on herbaceous species richness, although, inter-annual rainfall variability is suggested to be the main driver of herbaceous dynamics.

Similarly to deductions in chapter 5, a consideration of life-history and palatability traits of herbaceous life forms in nutrient-rich patches would seem to hold some promise in determining the effects of grazing and rainfall variability in a semi-arid savanna system without fire disturbance. Through results presented in this chapter (and also results from chapter 5), the common perception that sodic savanna patches represents degraded ecosystems are being challenged.

Chapter 7

Drought-tolerant herbaceous community composition and function in a fire-exposed system without elephants

7.1 Introduction

Understanding relationships between species functional traits and the environment provides a framework for describing changes in vegetation response to environmental disturbances and constraints (Navarro *et al*., 2006). It may furthermore facilitate the development of predictive models of ecological community response (Wesuls *et al*., 2012). When considering trait comparisons, species with similar combinations of functional attributes (Navarro *et al*., 2006) that respond similarly to environmental disturbances (Lavorel *et al*., 1997) are defined as functional groups. Functional group classifications are valuable to ecological studies, and provide a framework for the description of functional traits and mechanisms underlying vegetation changes in natural ecosystems (McIntyre *et al*., 1999; Cornelissen *et al*., 2003; Navarro *et al*., 2006). Severe droughts in savanna ecosystems have been reported to alter herbaceous species composition and negatively affect perennial herbaceous species (Scholes *et al*., 2003), whilst favouring annual and perennial forb abundances (Fynn & O'Connor, 2000; Buitenwerf *et al*., 2011). Copeland *et al*. (2016) found no consistent effects of drought on functional diversity, however, Carmona *et al*. (2012) reported decreased functional diversity in grasslands with grazing and drought. Climatically extreme events such as episodic droughts, even in the absence of overgrazing, are reported to have deteriorating effects on floristic diversity in grasslands (Du Toit & Cumming, 1999). Tilman *et al*. (1997) identified a strong relationship between species composition and ecosystem processes, and suggested that factors influencing the composition of species are likely to affect ecosystem processes as well. It is widely accepted that the functioning of an ecosystem is dependent on the species present in that particular system (i.e., on its species composition) (Tilman, 2001), since the functional traits associated with plant communities control the variety of terrestrial ecosystem processes (De Deyn *et al*., 2008). Biotic (herbivore assemblages) and abiotic (fire and rainfall) factors act as filters that select for specific traits and functions from the species pool (Grime, 1998; Geldenhuys, 2011; Van Der Plas *et al*., 2012). Despite increased alterations in natural fire regimes (Koerner *et al*., 2014) and substantial declines in mammalian herbivore numbers, related consequences especially the effects on biodiversity and ecosystem function remain relatively unexplored (Jonsson *et al*., 2010; Zhang *et al*., 2012). Furthermore, specific information on the impacts of climate change (rainfall variability and droughts) on protected areas remains limited (Van Wilgen *et al*., 2016). Below-average rainfall in the 2015 sampling year provided opportunities to study and identify patterns in herbaceous vegetation response to an episodic drought with variations in fire and herbivore occurrence.

This chapter aimed to investigate herbaceous response patterns through assessing species assemblages, trait diversity and functional group assemblages in a nutrient-rich savanna ecosystem during an episodic drought. Specific objectives were to:

1. Identify herbaceous species that are able to withstand the combined effects of an episodic drought, and various fire and herbivore treatments;
2. Identify herbaceous trait diversity response patterns, and
3. Determine whether fire and herbivore treatments are characterised by distinctive sets of functional groups when exposed to an episodic drought event.

Similar to the expectations of chapter 5, herbivory was expected to be the primary driver of herbaceous vegetation dynamics on a functional level during an episodic drought event. Fire was not expected to have significant effects on herbaceous functional dynamics when herbivores are present and grass biomass levels are low (Figure E.1.; Appendix E). However, fire effects on herbaceous functional dynamics and composition were anticipated to become more distinct in herbivore absence and the consequent increase in aboveground biomass.

7.2 Materials and Methods

A full description of the methodological approach is presented in Chapter 4 (Materials and Methods). Only the 2015 dataset was analysed to reach the various objectives of this chapter (Figure 4.3). Floristic sampling (section 4.3.1) and floristic composition structure analyses (section 4.6), as well as the selection and sampling of plant functional traits (section 4.3.3) and trait data analyses (section 4.6) has relevance to this specific results chapter.

- Non-Metric Multi-Dimensional Scaling (NMDS) ordination combined with Permutational Analysis of Variance (PERMANOVA) and Similarity Percentage Analysis (SIMPER) were performed on the 2015 floristic data to address objective 1;

- A two-way ANOVA type Hierarchical Linear Model (HLM) was applied to trait diversity data sampled in 2015 to reach objective 2,
- To identify and summarize community variation in functional groups and to further quantify the effects of herbivore and fire treatments on functional group assemblage (objective 3), Unweighted Pair Group Method with Arithmetic Mean (UPGMA)-clustering analysis, Principal Co-ordinate Analysis (PCoA), Detrended Correspondence Analysis (DCA), Principal Component Analysis (PCA) and Redundancy Analysis (RDA) were applied to functional group data across herbivore and fire treatments.

7.3 Results

7.3.1 Floristic composition structure

Results from the Non-Metric Multidimensional Scaling ordination revealed clustering according to herbivore presence or absence (Figure 7.1).

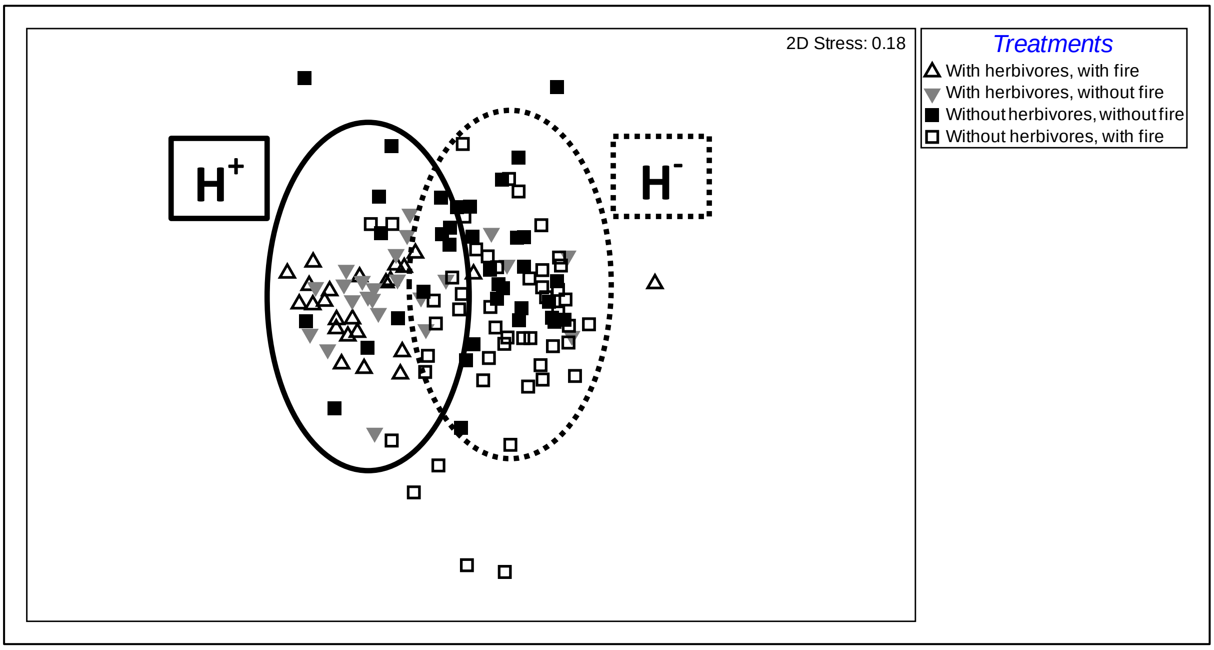


Figure 7.1. Non-Metric Multidimensional Scaling (NMDS) ordination of herbaceous species assemblages across all combinations of herbivory and fire treatments (Bray Curtis resemblance on square root-transformed species abundance data).

H^+, with herbivores, excluding elephant; H^-, without all LMH

Clustering in a two-dimensional space was corroborated by Permutational Multivariate Analysis of Variance (PERMANOVA: df = 3, Pseudo-F = 7.18, $p = 0.001$) which indicated significant differences in floristic composition between treatments. Pairwise comparisons conducted between fire and herbivore treatments indicated significant differences in species composition between herbivore treatments with similar fire treatment (Table E.1.; Appendix E). Overlapping of plots in a two-dimensional space suggests limited effects of fire on floristic composition in a herbivore-exposed, nutrient rich savanna system (Figure 8.1), which was further confirmed by pairwise comparisons ($p > 0.05$; Table E.1.; Appendix E). However, species composition differed significantly between herbivore exclosure plots, suggesting that fire becomes a significant driver of species composition when herbivores are lost from this system (PERMANOVA, $p = 0.002$; Table E.1.; Appendix E).

Fourteen herbaceous species each contributed more than 2 % to the variation between fire and herbivore treatments according to the SIMPER Analysis (Clarke, 1993), of which seven represented forb species (*Achyranthes aspera*, *Barleria prionitis*, *Blepharis innocua*, *Blepharis integrifolia*, *Justicia protracta*, *Kyphocarpa angustifolia*, *Ruellia cordata*). The remaining seven were grass species (*Aristida congesta*, *Cynodon dactylon*, *Dactyloctenium aegyptium*, *Enteropogon macrostachyus*, *Panicum maximum*, *Sporobolus nitens* and *Urochloa mosambicensis* (Table E.2.; Appendix E).

When considering the different herbivore treatments with fire (i.e., herbivore and fire effects), main differences in floristic composition were driven by various grasses which included *A. congesta*, *C. dactylon*, *D. aegyptium*, *E. macrostachyus*, *P. maximum* and *S. nitens*, and forbs which included *B. prionitis*, *B. innocua*, *B. integrifolia*, *K. angustifolia* and *R. cordata*.

As would be expected, exclusion of large herbivores, but presence of fire filtered out herbaceous species unable to compete under high biomass and fire. Alternatively, species adapted to these conditions were more abundant. An example of such a species that was benefited by fire presence, but herbivore absence, was the highly palatable, decreaser sub-climax species *P. maximum* (Table E.3.; Appendix E). Similarly, *C. dactylon* was favoured by herbivore exclusion and fire (Table E.3.; Appendix E), suggesting that fire removes moribund plant material, allowing this short growing species to be able to compete successfully in this system. Increased abundance of *B. prionitis* in herbivore absence and fire presence (Table E.3.; Appendix E) could be attributable to the family it belongs (i.e., Acanthaceae) since species that belong to this family are known to resprout after fire. Grass species associated with disturbed areas dominated the herbivore and fire exposed plots. These plots were characterised by the annual, pioneer grass species *Aristida congesta* and *D. aegyptium*, as well as *E. macrostachyus* which is a palatable, perennial decreaser sub-climax or climax grass that was expected to grow in disturbed places such as in the presence of fire and herbivory. As expected *S. nitens*, which is generally considered an unpalatable grass, but an important lawn-grass species in this system, was also abundant in disturbed plots. Dominance of *R. cordata*, *K. angustifolia*, *B. innocua* and *B. integrifolia* in herbivore and fire exposed plots could be attributable to their families (Acanthaceae and Amaranthaceae) since species belonging to these families resprout after fire.

Considering herbivore treatments without fire (i.e., herbivore effect), differences in herbaceous species composition were mainly driven by *B. integrifolia*, *B. innocua*, *Justicia protracta*, *K. angustifolia*, *A. aspera* and *R. cordata*. Some grass species remained dominant (*D. aegyptium*, *P. maximum E. macrostachyus* and *S. nitens*), suggesting that fire did not affect their abundances in this system. *U. mosambicensis* became more dominant in herbivore and fire absence, whilst *P. maximum* remained dominant (Table E.3.; Appendix E). Similar to grass species, certain forbs remained dominant when subjected to herbivore presence and fire absence (*B. innocua*, *B. integrifolia*, *K. angustifolia* and *R. cordata*). However, *A. aspera* and *J. protracta* became more abundant in fire absence.

7.3.2 Trait diversity patterns

Measures of herbaceous trait diversity revealed no significant interaction effects with herbivory or fire, nor any stand-alone effects ($p > 0.05$; Table 7.1).

Table 7.1. Results from the two-way ANOVA type Hierarchical Linear Modelling (HLM) indicating overall differences in herbaceous trait diversity measures across fire and herbivore treatments.

		Richness	**Margalef's richness**	**Pielou's evenness**	**Shannon's diversity**	**Simpson's diversity**
Herbivory	df	1	1	1	1	1
	F	1.15	0.05	2.59	0.15	1.0
	p	0.283	0.829	1.000	1.000	0.325
Fire	df	1	58562	1	1	1
	F	0.03	0.001	0.328	0.05	1.3
	p	0.865	0.978	1.000	1.000	0.262
Herbivory*Fire	df	1	1	1	1	1
	F	0.02	0.02	0.334	0.04	1.5
	P	0.896	0.891	1.000	1.000	0.217

Separate analyses of herbaceous life forms revealed that life form trait richness (including Margalef's richness index) differed significantly, irrespective of fire or herbivore treatment ($p < 0.001$; Table 7.2; Figure 7.2 (a & b)). Pielou's evenness trait index values revealed a significant interaction effect between herbivory, fire and life form (Herbivory*Fire*Life form $p = 0.002$; Table 7.2). Shannon's trait diversity revealed no interaction effects across herbivore and fire treatments ($p > 0.05$; Table 7.2), although life form, irrespective of herbivory and fire, varied significantly ($p < 0.001$; Table 7.2). Furthermore, herbivory (i.e., presence *vs.* absence) significantly affected herbaceous trait diversity, irrespective of life form or fire treatment ($p = 0.019$; Table 7.2).

Table 7.2. Summary of the three-way ANOVA type Hierarchical Linear Model (HLM) results for variance in trait diversity measures with respect to life form, fire and herbivory.

	Fixed effects					
	Herbivory	**Fire**	**Life form**	**Herbivory*Life form**	**Fire*Life form**	**Herbivory*Fire*Life form**
Trait richness						
df	1	1	1	1	1	1
F	8.2	0.2	112.8	3.2	0.6	1.7
p	1.000	1.000	**<0.001***	0.074	0.438	0.195
Margalef's richness index						
df	1	1	1	1	1	1
F	0.02	0.001	109.5	0.2	0.001	1.9
p	1.000	1.000	**<0.001***	0.648	0.973	0.163
Pielou's evenness						
df	1	1	1	1	1	1
F	6.2	11.2	0.008	4.9	11.8	10.2
p	1.000	1.000	0.930	**0.027***	**0.001***	**0.002***
Shannon's diversity index						
df	1	1	1	1	1	1
F	5.6	0.4	19.9	0.000	0.002	0.4
p	**0.019***	0.527	**<0.001***	0.996	0.962	0.536

Mean trait richness (Figure 7.2 (a)) and Margalef’s richness index (Figure 7.2 (b)) was significantly higher in forbs than in grasses. This, however, was expected, since forbs represent substantially more families than grasses do.

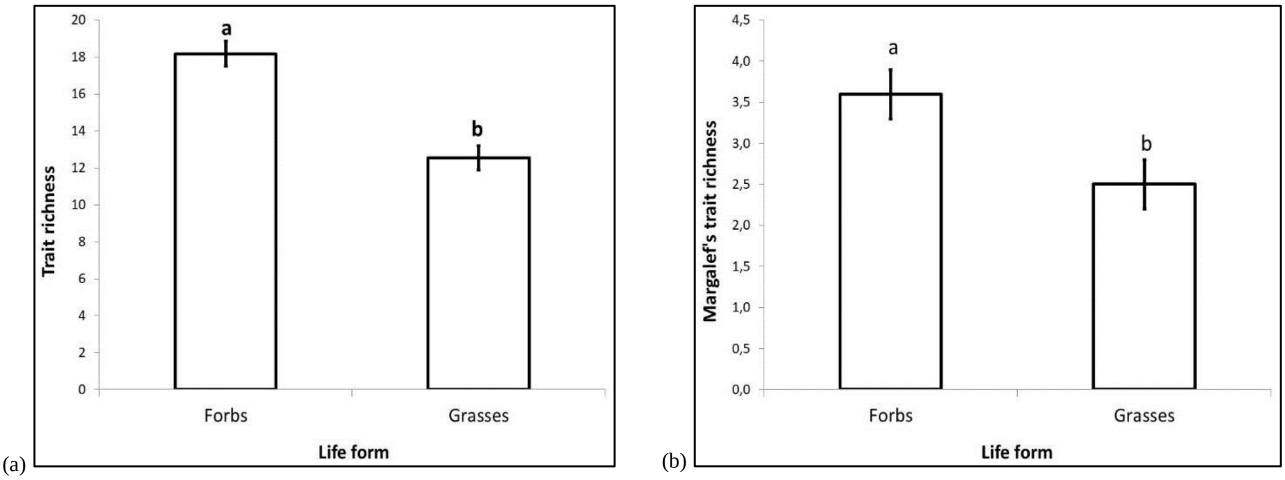


Figure 7.2. Comparisons of mean (±SE) (a) trait richness and (b) Margalef’s trait richness of herbaceous forbs and grasses. Significant differences (at $p < 0.05$) in trait richness and Margalef’s trait richness indicated by means of different letters.

The significant three-way interaction revealed for Pielou’s trait evenness with herbivory, fire and life form ($p = 0.002$; Table 7.2) suggests that herbivory, fire and life form type significantly affects trait evenness. Significant interactions between life form with herbivory ($p = 0.027$; Table 7.2) and life form with fire ($p = 0.001$; Table 7.2) suggests that herbaceous life form type significantly affects the response of the system to herbivory and fire respectively. When all important drivers (herbivores and fire) were excluded, forb trait evenness was significantly higher than grass trait evenness (Figure 7.3).

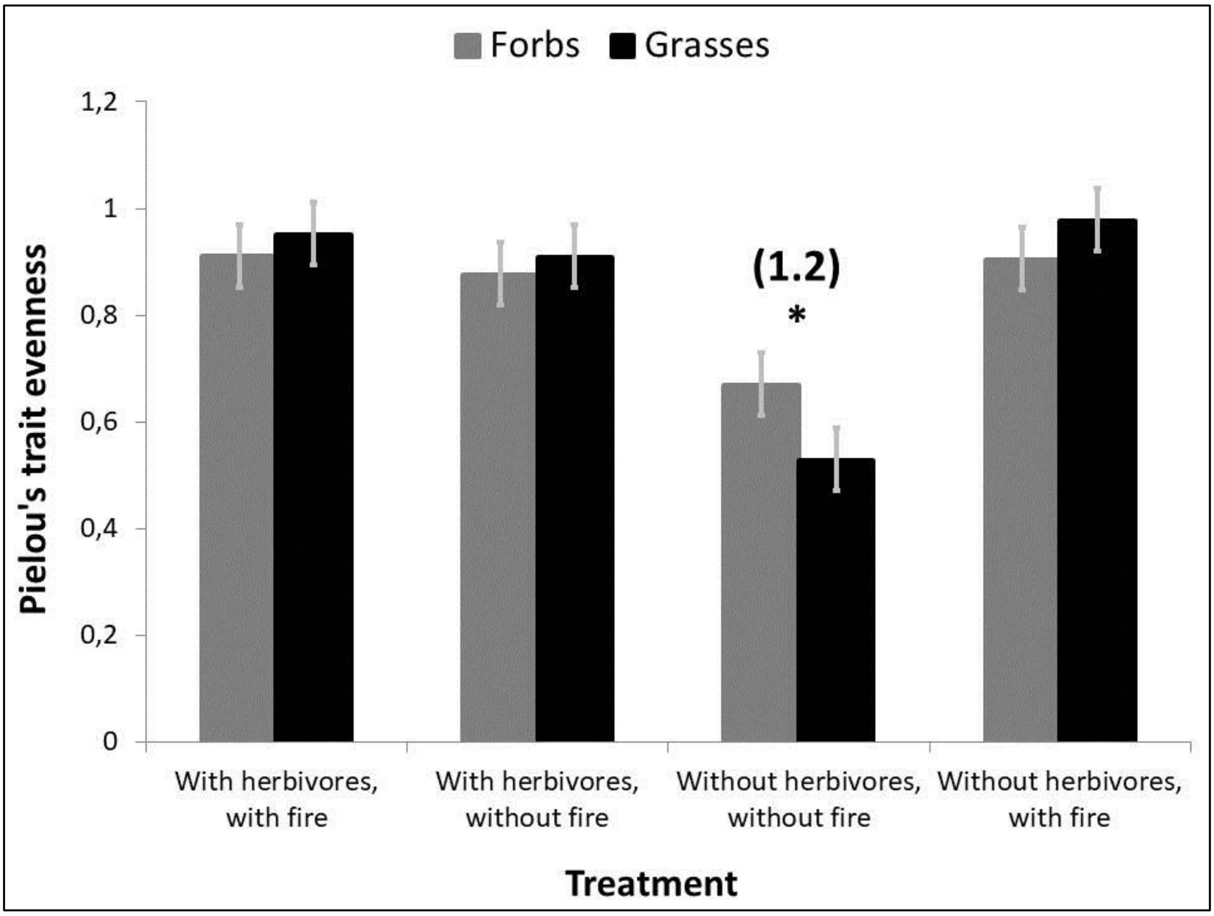


Figure 7.3. Comparisons of mean (±SE) Pielou's evenness for traits of herbaceous forbs and grasses across fire and herbivore treatments. * indicates significant differences (at $d > 0.7$) in trait evenness, whilst values in parenthesis indicate effect sizes.

As expected, forbs were significantly more diverse in traits than grasses (Figure 7.4 (a)). Herbivore presence significantly enhanced trait diversity (Figure 7.4 (b)). No significant effects were obtained through Simpson's diversity indices applied to trait data ($p > 0.05$).

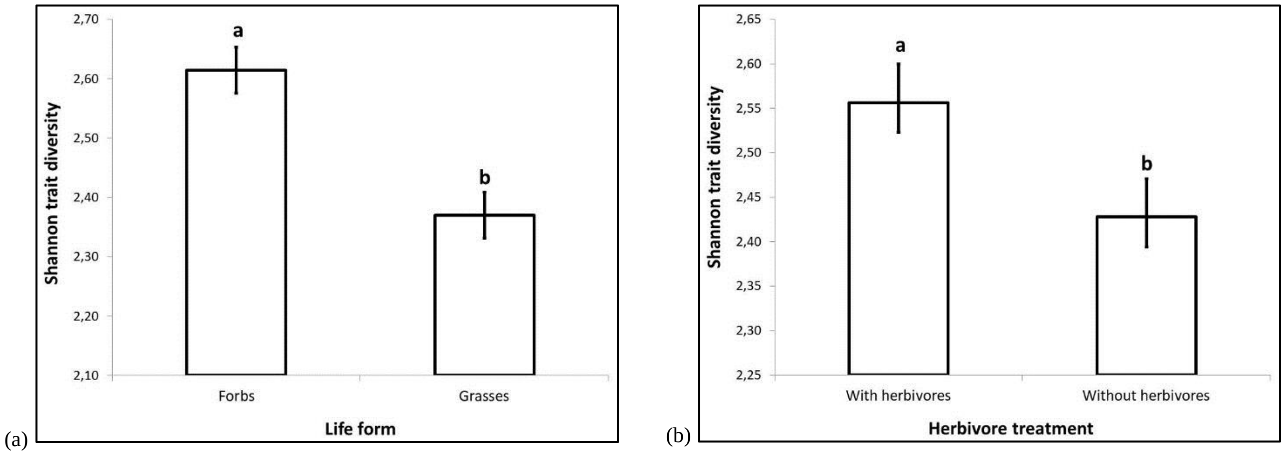


Figure 7.4. Comparisons of mean (±SE) Shannon trait diversity between (a) herbaceous forbs and grasses and (b) herbivore treatments. Significant differences (at $p < 0.05$) in Shannon trait diversity are indicated by means of different letters.

7.3.3 Identification of functional groups (FG)

In the PCoA of ten plant traits herbaceous species formed clusters that were strongly linked to life history and palatability traits (Figure 7.5). Across the ordination plane, the groups were identifiable as annual spinescent N-fixing forbs with moderate palatability (FG I) leading into annual spinescent forbs with low palatability (FG II), annual erect leafy or prostrate forbs with moderate to high palatability (FG III), annual erect leafy forbs with low palatability (FG IV), annual tufted graminoids with moderate palatability (FG V) and annual tufted graminoids with low palatability (FG VI). On the left side of the ordination, groups were identifiable as perennial tufted graminoids with low palatability (FG VII), perennial tufted graminoids with high palatability (FG VIII), perennial erect leafy forbs with low palatability (FG IX), perennial forbs with moderate to high palatability (FG X), perennial spinescent and N-fixing forbs with moderate palatability (FG XI), perennial spinescent and N-fixing forbs with high palatability (FG XII) and lastly, perennial forb climbers with low palatability (FG XIII).

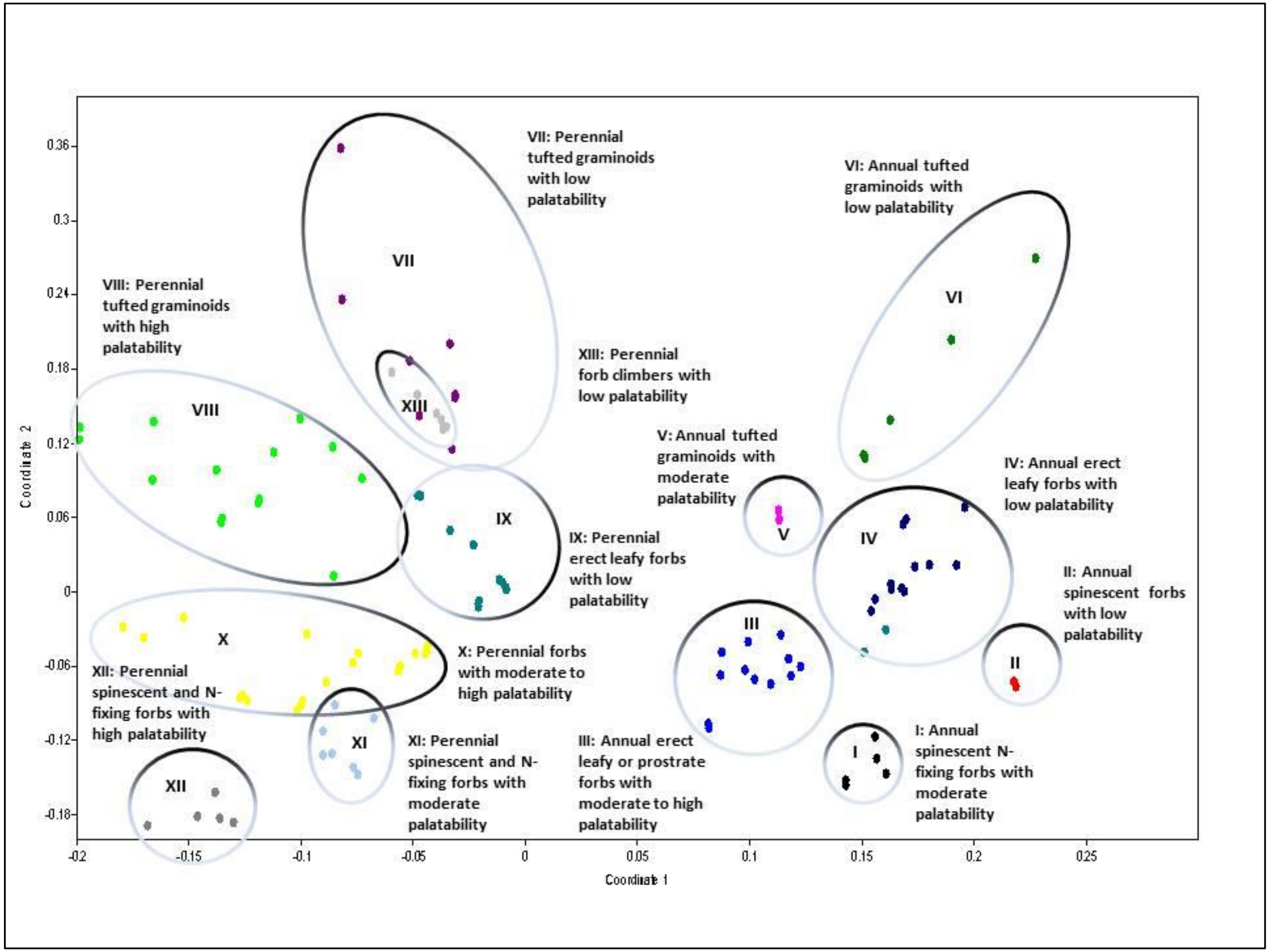


Figure 7.5. Principal Co-ordinate Analysis (PCoA) scatter diagram of 126 sodic herbaceous species for a set of ten plant traits. Roman numerals denote the number of each functional group.

Trait attributes for each of the functional groups were investigated in detail (Table 7.3). The traits "specific leaf area, flowering season and clonality" were omitted for the purpose of this table, since scores for these traits showed no clear patterns. Results were accordingly summarised by describing characteristic features of each functional group.

- **Functional Group I – Annual spinescent N-fixing forbs with moderate palatability**

This group was distinguished as annual spinescent N-fixing forbs with moderate palatability and consisted of five species (Table 7.3). All five forb species were categorised as therophytes with an erect leafy growth form.

- **Functional Group II – Annual spinescent forbs with low palatability**

The second functional group consisted of two annual, and therefore therophytic, spinescent and unpalatable forb species without the ability to fix nitrogen (Table 7.3).

- **Functional Group III – Annual erect leafy and prostrate forbs with moderate to high palatability**

Consisting of 14 annual forb species, the therophytic Raunkiaer life form characterised this functional group (Table 7.3). Prostrate (46 %) and erect leafy (54 %) growing species without the presence of spinescence or nitrogen fixing ability furthermore characterised this functional group. 46 % of species were identified as being moderately palatable, whilst the remaining 54 % were considered highly palatable.

- **Functional Group IV – Annual erect leafy forbs with low palatability**

The fourth functional group was dominated by erect leafy growing, unpalatable forb species (Table 7.3). Some perennial forbs were more closely related to species in this functional group (as can be seen on Figure 7.5) and were therefore included in this group. This might suggest that life form and palatability had an overriding effect on all other functional traits, since these forb species grouped with unpalatable perennial forbs, irrespective of life history.

- **Functional Group V – Annual tufted graminoids with moderate palatability**

Group V comprised of three moderately palatable therophytic tufted graminoids (Table 7.3).

- **Functional Group VI – Annual tufted graminoids with low palatability**

This group was dominated by annual (therophytes) unpalatable tufted graminoid species Table 7.3).

- **Functional Group VII – Perennial tufted graminoids with low palatability**

This group was characterised by both perennial grasses and forbs with low palatability scores. Forbs comprised 64 %, whilst grasses contributed the remaining 36 %. Species with a tufted graminoid growth form contributed 64 % of the species, whilst 36 % of species were climbers. None of the species in group VII had the ability to fix nitrogen or had any spines. (Table 7.3).

- **Functional Group VIII – Perennial tufted graminoids with high palatability**

Perennial, palatable tufted graminoids with hemicryptophytic life form was typical of this functional group (Table 7.3).

- **Functional Group IX – Perennial erect leafy forbs with low palatability**

Fifteen unpalatable forb species comprised this functional group (Table 7.3). Dominant growth forms included erect leafy and chamaephytes. Nitrogen fixing abilities and spinescent traits are absent from this group.

- **Functional Group X – Perennial forbs with moderate to high palatability**

Twenty-eight erect leafy perennial forbs with chamaephytic life form comprised this functional group (Table 7.3). Palatability of species ranged from moderate (61 %) to high (39 %).

- **Functional Group XI – Perennial spinescent and N-fixing forbs with moderate palatability**

This group was characterised by perennial forb species with moderate palatability (Table 7.3). Some of these forb species furthermore had the ability to fix nitrogen (29 %), whilst others were spinescent (71 %).

❖ Functional Group XII – Perennial spinescent and N-fixing forbs with high palatability

Palatable perennial forbs comprised this functional group (Table 7.3). All forbs grew erect leafy, whilst 40 % were N-fixers and 60 % were spinescent.

❖ Functional Group XIII – Perennial forb climbers with low palatability

This group consisted of perennial phenrophetic forb species categorised with the growth form ‘climber’ (Table 7.3). The clustering of this group close to the perennial tufted graminoids with low palatability (FG VII) suggests that life history and palatability traits once again portrayed overriding effects over growth form traits.

Table 7.3. Detailed descriptions of functional groups identified by PCoA (Figure 7.5).

	Group I	**Group II**	**Group III**	**Group IV**	**Group V**	**Group VI**	**Group VII**	**Group VIII**	**Group IX**	**Group X**	**Group XI**	**Group XII**	**Group XIII**
Number of species	5	2	14	13	3	5	8	15	15	28	7	5	6
Life form	Forb	Forb	Forb	Forb	Graminoid	Graminoid	Graminoid	Graminoid	Forb	Forb	Forb	Forb	Forb
Growth form	Erect leafy	Erect leafy	Erect leafy, prostrate	Erect leafy	Tufted graminoid	Tufted graminoid	Tufted graminoid	Tufted graminoid	Erect leafy	Erect leafy	Erect leafy	Erect leafy	Climber
Life form (Raunkiaer)	Therophyte	Therophyte	Therophyte	Therophyte	Therophyte	Therophyte	Hemicryptophyte	Hemicryptophyte	Chamaephyte	Chamaephyte	Chamaephyte	Chamaephyte	Phanerophyte
Life span	Annual	Annual	Annual	Annual	Annual	Annual	Perennial	Perennial	Perennial	Perennial	Perennial	Perennial	Perennial
Palatability	Moderate	Low	Moderate to high	Low	Moderate	Low	Low	High	Low	Moderate to high	Moderate	High	Low
Spinescence	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present	Present	Absent
Nitrogen fixing ability	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present	Present	Absent

Traits were assigned to herbaceous species by referring to various field guides, Floras and manuscripts cited in the Materials and Methods chapter (Chapter 4 (section 4.3.3 and Table 4.2).

7.3.4 Functional group assemblages of herbivore and fire treatments

Detrended Correspondence Analysis (DCA) revealed a linear distribution of functional group data across fire and herbivore treatments (gradient lengths < 4; Table E.4.; Appendix E). Principal Component Analysis (PCA) together with Redundancy Analysis (RDA) was therefore applied to functional group data (Lepš & Šmilauer, 2003).

The first two PCA axes (Principal Components) explained 62.4 % (0.403 + 0.221) of the variability in functional group data (Figure 7.6 (a)). The first Principal Component (Axis 1) was mainly correlated with herbivory (herbivore exclusion to the left and herbivore exposure to the right), and explained the largest proportion of variance (40.3 %; Figure 7.6 (a)). Neither the PCA, nor the RDA revealed any clear representation of fire treatments (Figure 7.6 (a & b)). This suggests that the second principal component (Axis 2) may be related to another environmental variable that was not necessarily tested for in this study. Functional groups with palatability traits correlated along the Y-axis (moderately to highly palatable functional groups towards the top and functional groups with low palatability towards the bottom of the ordination) (Figure 7.6 (a)), suggesting a soil nutrient gradient.

FG VII, FG VIII and FG XII were equally explained by both principal components with FG VIII (perennial tufted graminoids with high palatability) correlating strongly with herbivore exclusion and FG VII (perennial tufted graminoids with low palatability) and XII (perennial spinescent and N-fixing forbs with high palatability) correlating strongly with herbivore exposure (Figure 7.6 (a)). FG III (annual erect leafy or prostrate forbs with moderate to high palatability) correlated the most strongly with herbivore exposure (Figure 7.6 (a)). FG VI (annual tufted graminoids with low palatability) and IV (annual erect leafy forbs with low palatability) correlated with herbivore exposure, although these correlations were weak (as could be seen from short vector lengths) (Figure 7.6 (a)). Similarly, a correlation (although weak) was revealed between herbivore exclusion and FG IX (perennial erect leafy forbs with low palatability) (Figure 7.6 (a)).

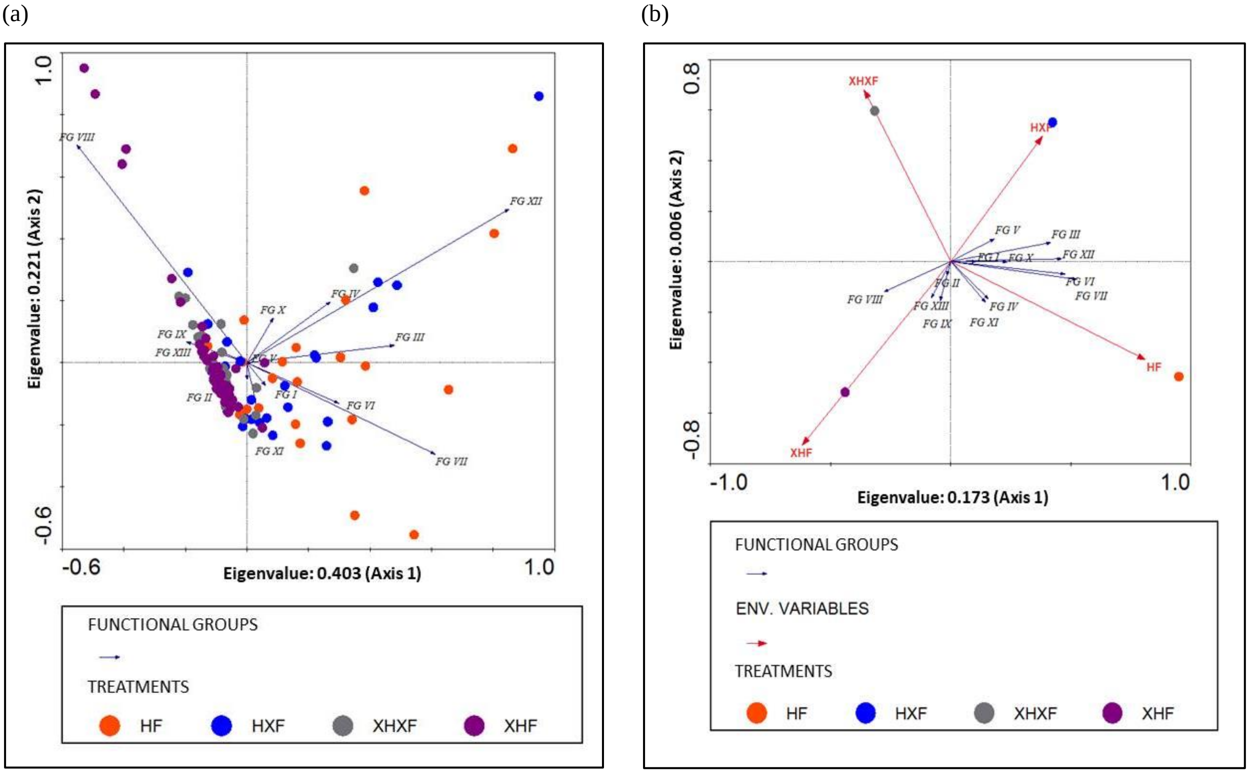


Figure 7.6. (a) Principal Component Analysis (PCA) and (b) Redundancy Analysis (RDA) of functional group data with herbivore and fire treatments.

FG, Functional group; *HF*, With herbivores, with fire; *HXF*, With herbivores, without fire; *XHXF*, Without herbivores, without fire; *XHF*, Without herbivores, with fire. (Refer to Tables E.5 and E.6 (Appendix E) for supplementary statistics)

7.4 Discussion

Results revealed that, during an episodic drought event herbivore treatment exerts a stronger effect on herbaceous species assemblages than fire. In accordance with Levick and Rogers (2008), our results suggest that vegetation in sodic patches, especially during droughts, are too sparse to support fire. Nevertheless, fire becomes a significant driver of species composition with the exclusion of all LMH and inherent accumulation of herbaceous biomass (Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Van Coller & Siebert, 2015) and fuel loads for fire (Belsky, 1995; Higgins *et al*., 2000).

In accordance with Van der Plas *et al*. (2013) herbivory, or the exclusion thereof, has strong filtering effects on herbaceous species. As would be expected grass species generally associated with disturbed areas (e.g., *S. nitens*, *D. aegyptium*, *A. congesta*, and *E. macrostachyus* (Van der Plas *et al*., 2013, Van Oudtshoorn, 2009)) were abundant in herbivore exposed plots. However, the annual grass species *A. congesta* was more abundant on burnt plots, which coincides with Ludwig *et al*. (1999) reporting that annual grasses are not disadvantaged by dry season fires. This may cause annual grasses, such as *A. congesta*, to be resilient and provide a competitive edge under sustained grazing, drought and fire. Furthermore, *A. congesta* is a pioneer species, which colonizes open and disturbed spaces (Van Oudtshoorn, 2015). Although pioneer species, such as *A. congesta* generally have low grazing value, they are important stabilizers of soil and therefore enhance the establishment of other grass species (Van Oudtshoorn, 2015), and may therefore be functionally important. *S. nitens* and *E. macrostachyus* have hemicryptophytic life forms (i.e., perennating buds at or in the soil surface which die back in unfavourable conditions (Cornelissen *et al*., 2003; Begon *et al*., 2006; Kotschy, 2013), which may enhance their survival under sustained herbivory.

Various forb species (e.g., *B. innocua*, *B. integrifolia*, *K. angustifolia* and *R. cordata*) were dominant in herbivore exposed plots. However, *B. prionitis* occurred only in fire and herbivore exposed plots. This forb belongs to the Acanthaceae family which is known to have thick woody seed-holding structures that open in response to fire (Baskin & Baskin, 2014). Forb species dominating herbivore exposed plots, with the exception of *K. angustifolia*, are classified as chamaephytes, with perennating buds growing close to the ground (Raunkiaer, 1934; Lansberg *et al*., 1999; Cornelissen *et al*., 2003; Begon *et al*., 2006). Because their perennating buds are situated close to the surface of the ground, they are protected from disturbances and may therefore persist under extreme conditions such as sustained grazing, and in the case of *B. prionitis*, in combination with fire (Smith, 1913). These results suggest that forb species, particularly palatable forb species, are structurally adapted to high grazing pressure by mammalian hebrivores. They will, therefore, be able to contribute to trait richness and diversity, and also enhance trait-based redundancy of herbaceous layers in these high stress conditions. *K. angustifolia* is common in most areas (Van der Walt, 2009), attributing to its persistence both with and without fire. Forb species *A. aspera* and *J. protracta* were more abundant with the exclusion of fire. Both *A. aspera* and *J. protracta* (Siebert & Scogings, 2015) are palatable and browsed in this system, and increased abundance in fire absence suggests that they are not resilient to the combined effects of being browsed and subjected to fire.

Grazing abandonment favoured the abundance of the tufted graminoids *U. mosambicensis* and *P. maximum* which is known to tolerate shaded conditions (Van Oudtshoorn, 2009), such as when herbivores are excluded, and woody and herbaceous biomass increases (Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Van Coller & Siebert, 2015). *C. dactylon* was favoured by herbivore absence, but fire presence, suggesting fire tolerance and resilience to disturbance (Van Oudtshoorn, 2009).

The lack of significant interaction effects of herbivory and fire on the overall functional trait diversity patterns of the herbaceous layer is consistent with the conclusions drawn by Biswas and Mallik (2010), who noted that life form responses strengthens disturbance effects. Results from this study support these findings, since life form type had a significant effect on most functional diversity trait measures. Although widely accepted that forbs contribute significantly to the species diversity of herbaceous layers in savanna and grassland systems (Turner & Knapp, 1996; Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Trollope *et al*., 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015; Van Oudtshoorn, 2015; Burkepile *et al*., 2017), plant functional diversity analyses suggest that their ecological significance is not limited to species richness alone, but also to the richness and diversity of functional traits. While the function of forbs in nutrient-rich semi-arid savannas remains less explored (Siebert & Scogings, 2015), results presented here suggest that the forb component is important for the functioning of these systems through the significant contribution of this herbaceous life form to trait richness and diversity (i.e., grasslands without forbs, would not be grasslands as we know them).

Trait evenness is considered a useful tool for measuring the effects of disturbance on ecosystems (Hanke *et al*., 2014). Results presented here corroborate this statement, with Pielou’s trait evenness being the only index showing significant interactions with herbivory, fire and herbaceous life form. Removal of fire and herbivory from a disturbance-maintained savanna system significantly affects trait evenness, which could lead to loss of ecological function through changes is ecosystem structure, function and biodiversity (Waldram *et al*., 2008; Asner *et al*., 2009). However, increased forb trait evenness in the absence of herbivory and fire suggests trait-based redundancy and hence enhanced ecosystem insurance provided by a particular suite of forb traits (Yachi & Loreau, 1999; Chappin III *et al*., 2000; Cadotte *et al*., 2012).

Herbaceous layers in savanna systems are characterised by forb-grass mixtures (Scholes, 1987). Consequently, when grouping herbaceous vegetation, life form (forb or grass) is an important category to include. Maximum life span is indicative of population persistence and strongly linked to environmental disturbance (Pérez-Harguindeguy *et al*., 2013). Life history attributes correlates strongly with patterns in grazing intensity (Skarpe, 1991; Skarpe, 1992; Milchunas & Lauenroth, 1993; Fynn & O’Connor, 1999; Illius & O’Connor, 1999; Savadogo *et al*., 2008; Tessema *et al*., 2011; Koerner & Collins, 2013) and results presented here reinforce the importance of this functional trait in herbivore driven systems. In a typical granitic savanna landscape, sodic bottomlands produce more palatable forage than upland crests, particularly for grazers and mixed feeders (Scogings 2011; Siebert & Scogings 2015). Palatability is considered a useful attribute to consider when classifying herbaceous vegetation, especially in nutrient-rich systems. Although generally associated with nutrient-poor ecosystems (Cornelissen *et al*., 2003), N-fixing ability revealed to be important in the grouping of herbaceous vegetation. As the height and positioning of vegetation foliage is an indication of adaptations and responses to grazing by different herbivores (Cornelissen *et al*., 2003; Peréz-Harguindeguy *et al*., 2013), it was expected that the growth form of herbaceous species would play an important part in their grouping, especially in this primarily herbivore-driven herbaceous layer. Our results did not meet this expectation, with plant functional traits forming clusters strongly linked to life history and palatability traits. Palatability and life history traits furthermore revealed overriding effects on traits related to herbaceous growth form.

Herbivory explains the largest proportion of variation in herbaceous functional group data which corroborates studies suggesting that herbivory is the primary driver of herbaceous vegetation dynamics in sodic patches (Jacobs & Naiman, 2008; Van Coller *et al*., 2013). The presence or absence of fire during an episodic drought was not clearly delineated in any of the multivariate analyses, indicating that, similarly to species diversity patterns (Van Coller *et al*., 2013), fire is a secondary driver of herbaceous functional assemblages in this nutrient hotspot.

Palatability is generally associated with increased soil nutrient content (Hobbie, 1992). The second principal component of the PCA is therefore suggested to correlate with soil nutrients, showing functional groups with increased palatability along the Y-axis (from bottom to top). Correlations of forb functional groups towards the top of the DCA ordination could possibly be ascribed to enhanced performance by forbs in nutrient-rich systems (Linstädter *et al*., 2016). However, these observations need to be confirmed through further studies, since soil nutrients were not tested for in this particular study.

Herbivores enhance system heterogeneity and therefore species diversity (Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Koerner *et al*., 2014), possibly attributing to the greater variation of functional groups correlated with herbivore exposed plots. Results from this study therefore suggest that herbivores are functionally important by enhancing functional group heterogeneity, and therefore functional diversity (e.g. Tomlinson *et al* (2016). The strong correlation between annual erect leafy or prostrate forbs with high palatability and herbivore exposed plots was both expected and unexpected, considering that sustained grazing and drought generally favours annual (Milchunas & Lauenroth, 1993; Lavorel *et al.,* 1997; O'Connor, 1998; Fynn & O'Connor, 2000; Buitenwerf *et al.,* 2011; O'Connor, 2015; Yé *et al.*, 2015; Guo *et al.*, 2016; Tessema *et al.*, 2016) and prostrate growing (Cornelissen *et al.*, 2003; Peco *et al.*, 2005) species over erect leafy species. Despite annual species generally being favoured by sustained heavy grazing without rest and drought (Fynn & O'Connor, 2000; Buitenwerf *et al.*, 2011), perennial spinescent and N-fixing forbs with high palatability correlated strongly with herbivore exposure. Regardless of being associated with nutrient-poor ecosystem types (Cornelissen *et al.*, 2003), forbs with N-fixing ability still correlated strongly with herbivore exposed plots in this nutrient-rich system. Species subjected to long-term herbivory generally develop defence strategies such as spinescence (Cooper & Owen-Smith, 1986; Alves-Silva & Del Claro, 2016), which might explain the strong correlation of spinescent forbs with herbivore exposed plots. Unpalatable species are usually associated with constant grazing in savannas (Skarpe, 1992). Persistence of palatable forbs under these conditions suggests resilience of this herbaceous life form to sustained grazing, and also functional redundancy through providing forage to herbivores under dry conditions. As would be expected perennial tufted graminoids with low palatability revealed strong correlations with sustained herbivore exposure, whilst palatable perennial tufted graminoids correlated strongly with herbivore exclusion (e.g., Skarpe, 1992; Milchunas & Lauenroth, 1993; Lavorel *et al.*, 1997; O'Connor, 1998; Fynn & O'Connor, 2000; Buitenwerf *et al.*, 2011; O'Connor, 2015; Yé *et al.*, 2015; Guo *et al.*, 2016; Tessema *et al.*, 2016).

7.5 Conclusion

This chapter identified drought-tolerant herbaceous species and their respective functions in a nutrient-rich semi-arid savanna ecosystem and their responses to long-term exposure or exclusion of wild ungulate herbivory and fire. Fire and herbivory remain important drivers of herbaceous species composition, although the effect of fire on species composition in this system is dependent on the presence or absence of herbivores. When herbivores are removed from the system, fire effects on species composition become significant. This might be attributable to significant increases in herbaceous biomass (Figure E.1.; Appendix E) with the removal of herbivores, providing sufficient fuel to carry fires, therefore revealing significant patterns.

In the analysis of herbaceous functional diversity patterns, it is important to treat forbs and grasses as separate functional entities so as not to fail in identifying significant disturbance effects. Trait richness and diversity is a function of herbaceous forbs rather than grasses. Forbs are considered ecologically significant by contributing functionally (i.e., provisioning of palatable forage to LMH) to semi-arid nutrient-rich herbaceous layers, particularly during episodic droughts. Trait evenness is considered an important measure of functional diversity patterns in this sodic system. Life form, fire and herbivory can interact to affect functional trait evenness. When herbivores and fire are lost from the system, forb trait evenness is higher than grass trait evenness. This suggests that forbs are more resilient to the loss of savanna drivers, since forb trait dominance is evenly distributed, insuring the system against declines in function. Conversely, grasses are not considered resilient to the loss of fire and herbivores, at least at a trait-based level, since only a few functional traits dominate. Grasses therefore do not enhance system insurance when all drivers are lost.

Important herbaceous functional traits to consider when studying the functional level responses of semi-arid nutrient-rich savanna systems include life form, life history, palatability, spinescence, N-fixing ability and growth form. Nevertheless, in grouping of herbaceous species, life history and palatability traits tend to override some of the abovementioned functional traits, suggesting that these two traits are most important. Herbivory is considered a major determinant and driver of herbaceous functional group distribution in sodic patches of semi-arid savanna. Herbivores furthermore enhance functional group heterogeneity, and are considered important for system function. Fire is considered a secondary driver of herbaceous functional assemblages during an episodic drought in this nutrient hotspot. Correlations of functional groups along the second principal component (i.e., palatability) suggest a soil nutrient gradient.

Chapter 8

Drought-tolerant herbaceous community composition and function in an elephant-exposed system without fire

8.1 Introduction

Large-scale effects of elephants on savanna vegetation structure and function are widely recognized (Pringle, 2008; Robson *et al*., 2016). Less well appreciated, however, are their potential effects on vegetation at smaller scales (i.e., increasing trait heterogeneity of herbaceous species). Studies investigating the frequency and severity of drivers such as herbivores on vegetation dynamics are abundant. However, studies that aim to understand community-level implications of the loss of herbivory from savanna systems are less prevalent (Daskin *et al*., 2016). Considering increased losses of native herbivores to single-species domestic livestock (Koerner *et al*., 2014; Daskin *et al*., 2016), and the probable increased frequency of droughts (Van Wilgen *et al*., 2016) in savannas, empirical studies able to tease out functional-level interactions between savanna vegetation and sustained herbivore exposure or exclusion under dry environmental conditions are critical. Herbivores increase species diversity by reducing competitive effects between species allowing more species that are functionally different to coexist (Jacobs & Naiman, 2008; Savadogo *et al*., 2008), thereby enhancing functional diversity (Tomlinson *et al*., 2016). Elephants enhance system heterogeneity and species diversity (Robson *et al*., 2016). It was therefore expected that herbivore exclusion will cause decreased functional diversity, whilst treatments exposed to all LMH (including elephants) will reveal the highest functional diversity.

This chapter aimed to investigate functional-level responses of herbaceous vegetation to various intensities of herbivory in a system from which fire was excluded. Objectives of this chapter included to:

1. Identify herbaceous species able to persist under combined effects of an episodic drought, and various herbivore treatments;
2. Investigate functional trait diversity response patterns, and
3. Determine whether herbivore treatments are characterised by distinctive sets of functional groups during an episodic drought.

In the absence of fire, a strong herbivore effect on herbaceous species composition and function was expected. Elephants were anticipated to have a strong filtering effect on herbaceous species functional traits, since elephants tend to uproot grasses and forbs.

8.2 Materials and Methods

Floristic sampling, trait selection and trait sampling was done according to the procedures described in sections 4.3.1 and 4.3.3 (Chapter 4 Materials and Methods). Statistical analyses relevant to this chapter are described in section 4.6.

- Non-Metric Multi-Dimensional Scaling (NMDS) ordination together with Permutational Analysis of Variance (PERMANOVA) and Similarity Percentage Analysis (SIMPER) were performed on floristic data to achieve objective 1;
- Herbivore transects were considered confounding variables (i.e., variables which affect both independent and dependent variables) with the type of herbivore treatment, and Hierarchical Linear Modelling (HLM) could not be fitted to the data. Two-way Analysis of Variance (ANOVA) was applied to the data to test the overall effects of herbivore treatment on herbaceous trait diversity measures (objective 2), and
- To identify and summarise community variation in functional groups and to further quantify the effect of herbivore treatments on functional group assemblage (objective 3), Unweighted Pair Group Method with Arithmetic Mean (UPGMA)-clustering analysis, Principal Co-ordinate Analysis (PCoA), Detrended Correspondence Analysis (DCA), Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) were applied to functional group data across herbivore and fire treatments.

8.3 Results

8.3.1 Floristic composition structure

Permutational Multivariate Analysis of Variance (PERMANOVA) revealed significant differences in plant species composition between herbivore treatments (df = 2, Pseudo F = 5.6, $p = 0.001$). Pairwise comparisons conducted between herbivore treatments revealed that species composition of plots exposed to herbivores (with all herbivores and elephant exclosure) differed significantly from large mammalian herbivore (LMH) exclosure plots

(Figure 8.1; Table F.1.; Appendix F). Herbivore exposed plots did not differ significantly in species composition (*p* > 0.05; Table F.1.; Appendix F), suggesting that elephants did not affect herbaceous species composition.

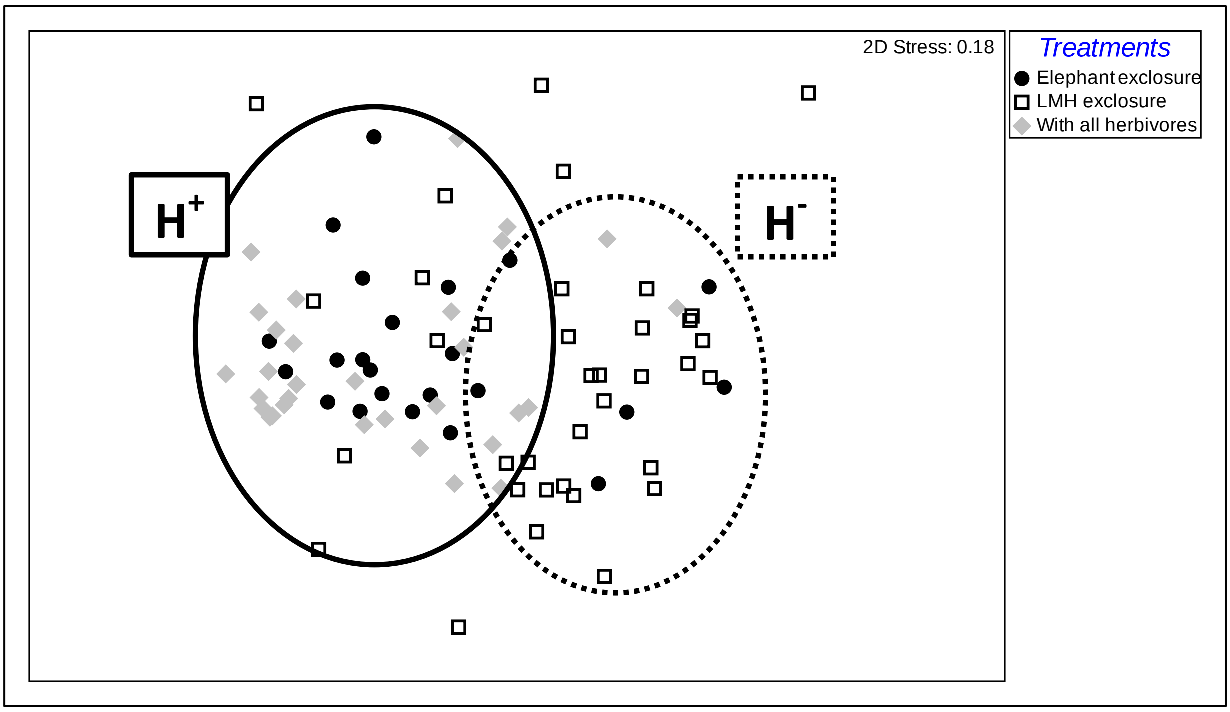


Figure 8.1. Non-Metric Multidimensional Scaling (NMDS) plot of between herbivore treatment resemblances (Bray Curtis, square root-transformed species abundance data).

H^{+}, With herbivores, including elephants; H^{-}, Without all LMH

Similarity Percentage Analysis (SIMPER) analysis revealed thirteen herbaceous species which contributed more than 2 % to the dissimilarity between herbivore treatments (Clarke, 1993). Six of these species represented forbs (*Achyranthes aspera*, *Blepharis innocua*, *Blepharis integrifolia*, *Justicia protracta*, *Kyphocarpa angustifolia* and *Ruellia cordata*) The remaining seven were grass species (*Cynodon dactylon*, *Dactyloctenium aegyptium*, *Enteropogon macrostachyus*, *Enteropogon monostachyus*, *Panicum maximum*, *Sporobolus nitens* and *Urochloa mosambicensis* (Table F.2.; Appendix F).

Similar to results found in the system without elephants (Chapter 7), *P. maximum* and *U. mosambicensis* were abundant with the complete exclusion of all LMH (Table F.3.; Appendix F. Exclusion of elephants, but allowing movement of all other LMH favoured abundances of grass species generally associated with disturbed areas (*D. aegyptium*, *E. monostachyus* and *S. nitens*). All of the forb species responsible for driving changes between herbivore treatments (*A. aspera*, *B. innocua*, *B. integrifolia*, *J. protracta*, *K. angustifolia* and *R. cordata*) were abundant in herbivore presence (excluding elephants).

Differences in forb assemblage between plots accessible to all LMH and LMH exclosure plots were mainly driven by the herbivory-tolerant prostrate growing palatable forb species such as *B. integrifolia* and *R. cordata,* which are consistent with results presented in chapter 7. Grass species generally associated with disturbed areas *D. aegyptium*, *S. nitens, C dactylon* and *E. macrostachyus* were abundant when subjected to the complete assemblage of LMH (with all herbivores), reinforcing the resistance of these species to sustained herbivory.

8.3.2 Trait diversity patterns

Significant variation in trait richness (excluding Margalef's richness index) was revealed across herbivore treatments ($p < 0.001$; Table 8.1). None of the remaining trait diversity indices revealed significant variation across herbivore treatments ($p > 0.05$; Table 8.1).

Table 8.1. Two-way ANOVA results of mean plant functional trait diversity measures across herbivore treatments.

Response	**Source**	***df***	**SS**	**MS**	**F**	***p***
Trait richness	Herbivory	2	484.7	242.3	10.3	**<0.001***
Margalef's richness index	Herbivory	2	0.051	0.0025	0.04	0.958
Pielou's trait evenness index	Herbivory	2	0.040	0.020	2.1	0.134
Shannon's trait diversity index	Herbivory	2	0.344	0.172	1.5	0.222
Simpson's trait diversity	Herbivory	2	0.022	0.011	1.2	0.314

Treatments exposed to long-term herbivory (irrespective of elephant presence) were more trait rich than the treatment from which all LMH were excluded (Figure 8.2; Table F.4.; Appendix F).

Figure 8.2. Comparisons of mean (±SE) trait richness across herbivore treatments. Significant differences (at $d < 0.7$) in trait richness are indicated by means of different letters.

Separate analyses of life forms revealed no significant interactions ($p > 0.05$; Table 8.2). Trait diversity measures (except Simpson's index of trait diversity) differed significantly between life forms (Table 8.2). Trait richness (excluding Margalef's richness) and Pielou's trait evenness varied significantly with herbivore treatment, irrespective of life form ($p < 0.05$; Table 8.2).

Table 8.2. Results from two-way ANOVA analyses indicating variations in mean plant functional trait diversity index values with respect to herbivore treatment and herbaceous life form. Significant variation (at $p < 0.05$) indicated in bold and with *.

Response	**Source**	***df***	**SS**	**MS**	**F**	***p***
Trait richness	Herbivory	2	592.9	296.5	15.0	**<0.001***
	Life form	1	1815.8	42.6	91.9	**<0.001***
	Herbivory*Life form	2	106.8	53.4	2.7	0.070
Margalef's trait richness	Herbivory	2	0.581	0.291	0.5	0.628
	Life form	1	67.6	67.1	108.6	**<0.001***
	Herbivory*Life form	2	2.3	1.1	1.8	0.165
Pielou's trait evenness	Herbivory	2	0.157	0.078	7.4	**0.001***
	Life form	1	0.062	0.062	5.8	**0.017***
	Herbivory*Life form	2	0.000	0.000	0.023	0.977
Shannon-Wiener trait diversity index	Herbivory	2	0.448	0.224	1.4	0.253
	Life form	1	3.531	1.879	21.851	**<0.001***
	Herbivory*Life form	2	0.141	0.070	0.44	0.648
Simpson's index of diversity	Herbivory	2	0.028	0.014	0.76	0.469
	Life form	1	0.051	0.226	2.78	0.097
	Herbivory*Life form	2	0.011	0.005	0.29	0.750

Forbs contributed significantly to trait richness, irrespective of herbivore presence or absence (Figure 8.3).

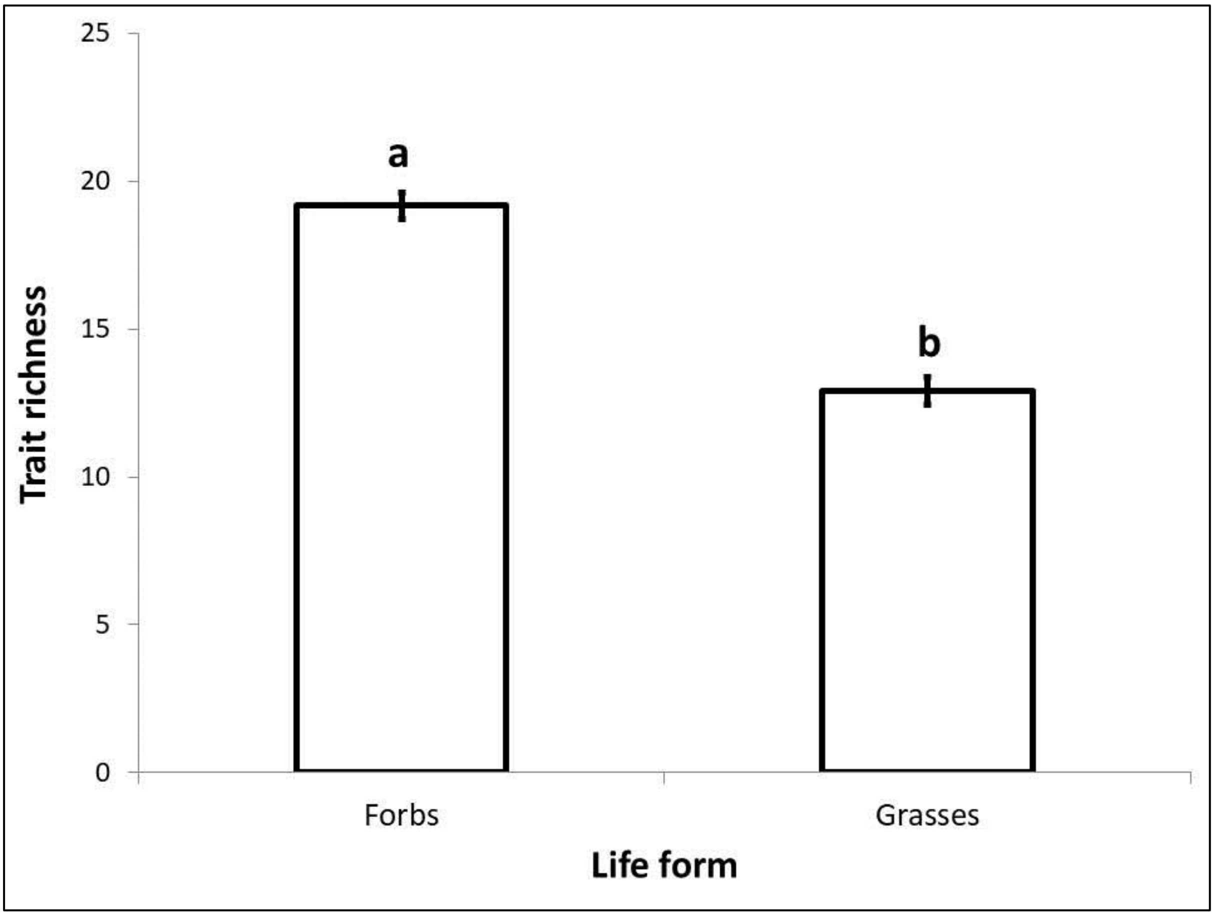


Figure 8.3. Comparisons of mean (±SE) trait richness between herbaceous life forms. Significant differences (at $p < 0.05$ and $d > 0.7$) in trait richness are indicated by means of different letters.

Forbs contributed significantly to functional trait richness (Margalef's trait richness) and diversity (Shannon's trait diversity) (Figure 8.4 (a) and (b)).

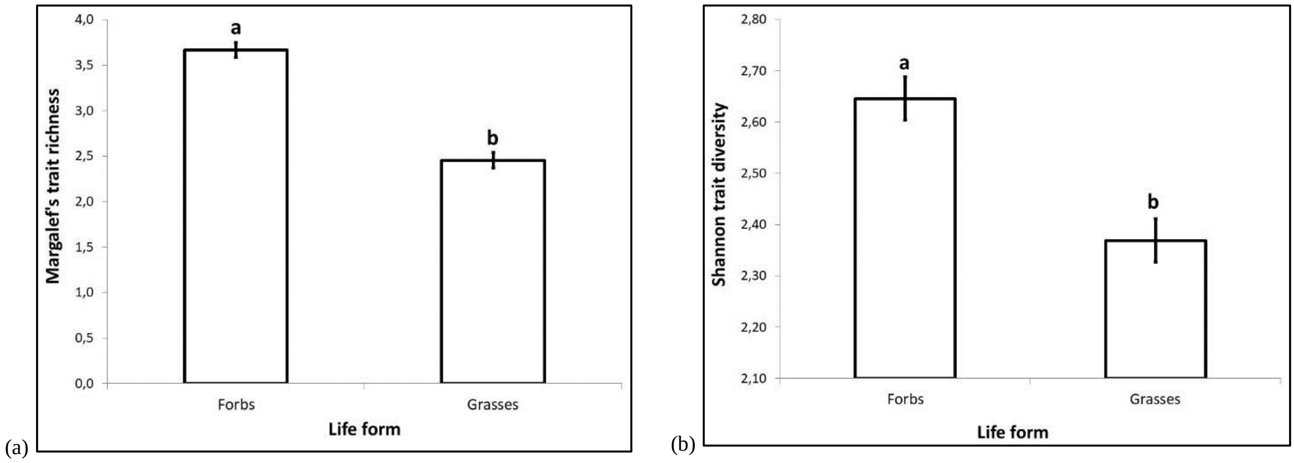


Figure 8.4. Mean (±SE) (a) Margalef's trait richness and (b) Shannon's trait diversity between herbaceous life forms. Significant differences (at $p < 0.05$ and $d > 0.7$) are indicated by means of different letters.

Trait evenness varied significantly between the LMH exclosure plots and elephant exclosure plots (Figure 8.5 (a); Table F.5.; Appendix F) with trait evenness being significantly higher in LMH exclosure plots. This suggests that herbivores other than elephants suppress trait evenness, and that only certain functional traits dominate in their presence. Trait evenness did not differ significantly between plots exposed to all herbivores and LMH exclosure plots (Figure 8.5 (a); Table F.5.; Appendix F). When considering evenness of traits and herbaceous life forms, irrespective of herbivore treatment, trait evenness in grasses was significantly higher than in forbs (Figure 8.5 (b)).

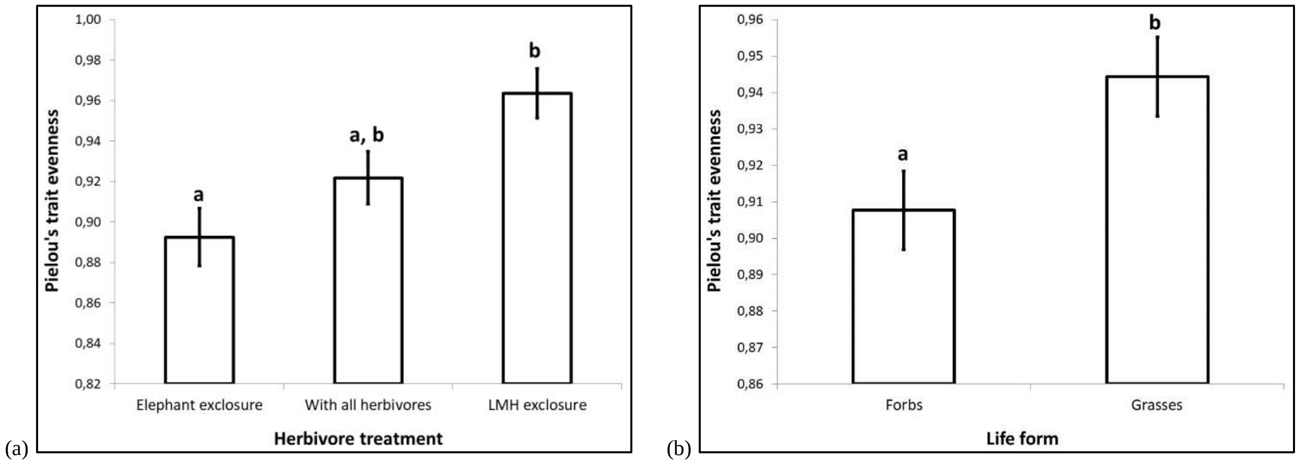


Figure 8.5. Comparisons of mean (±SE) Pielou's trait evenness (a) across herbivore treatments and (b) between herbaceous life forms. Significant differences (at $p < 0.05$ and $d > 0.7$) in trait richness are indicated by means of different letters.

8.3.3 Identification of functional groups (FG)

Functional groups were identified according to the method described in Chapter 4 (section 4.6 (Identification of functional groups)). The complete representation of results is presented in the previous results chapter (Chapter 7, section 7.3.3). A summary of the functional groups is presented in Table 8.3 for ease of reference.

Table 8.3. Summary of functional groups relevant to this study and their definitions.

Functional group	**Definition**
I	Annual spinescent N-fixing forbs with moderate palatability
II	Annual spinescent forbs with low palatability
III	Annual erect leafy and prostrate forbs with moderate to high palatability
IV	Annual erect leafy forbs with low palatability
V	Annual tufted graminoids with moderate palatability
VI	Annual tufted graminoids with low palatability
VII	Perennial tufted graminoids and forb climbers with low palatability
VIII	Perennial tufted graminoids with high palatability
IX	Perennial erect leafy forbs with low palatability
X	Perennial forbs with moderate to high palatability
XI	Perennial spinescent and N-fixing forbs with moderate palatability
XII	Perennial spinescent and N-fixing forbs with high palatability
XIII	Perennial forb climbers with low palatability

8.3.4 Functional group assemblages of herbivore treatments

Distribution of functional group data across herbivore treatments were unimodal as revealed by a Detrended Correspondence Analysis (DCA) gradient length of > 4 (Table F.6.; Appendix F). Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) were therefore performed on functional group data across herbivore treatments (Lepš & Šmilauer, 2003).

The correspondence analysis (CA) of functional group data showed that LMH exclosure plots formed a cluster separate from herbivore exposed plots, although some overlap was present (Figure 8.6 (a)). FG XIII and, similarly to results obtained in Chapter 7, FG VIII correlated strongly with the LMH exclosure plots (Figure 8.6 (a)). Herbivore exposed plots (H+E-

(elephant exclosure) and E+H+ (with all herbivores)) showed some overlap (Figure 8.6 (a)). The CA revealed no clear patterns in functional group assemblage, however, the majority of functional groups correlate with herbivore exposed plots (Figure 8.6 (a)). This suggests that elephants do not affect functional group assemblage in this system. An 'arch effect' was observed in the CA (Figure 8.6 (a)). This arch is produced when the second axis is a quadratic distortion of the first, and may contain important secondary gradients from emerging (Kent & Coker, 1994). To compensate for this, canonical correspondence analysis (CCA) was applied to the functional group and herbivore treatment data (Figure 8.6 (b)).

Although the two axes of the CCA did not explain sufficient variation in functional group data (19.9 %, Figure 8.6 (b)), functional groups correlated strongly herbivore treatments (Table F.8., Appendix F). Perennial tufted graminoids with high palatability (FG VIII) was once again strongly correlated with the LMH exclosure plots, as well as FG IX (perennial erect leafy forbs with low palatability) (Figure 8.6 (b)).

Removal of elephants revealed a strong correlation with FG VI (annual tufted graminoids with low palatability), and moderate correlations with FG XI (perennial spinsecent and N-fixing forbs with moderate palatability), FG III (annual erect leafy or prostrate forbs with moderate to high palatability) and FG XII (perennial spinescent and N-fixing forbs with high palatability) (Figure 8.6 (b)).

FG I (annual spinescent N-fixing forbs with moderate palatability) and FG IV (annual erect leafy forbs with low palatability) correlated strongly with exposure to all LMH, whilst FG II (annual spinescent forbs with low palatability) and FG VII (perennial tufted graminoids with low palatability) revealed a moderate correration with the same treatment (Figure 8.6 (b)).

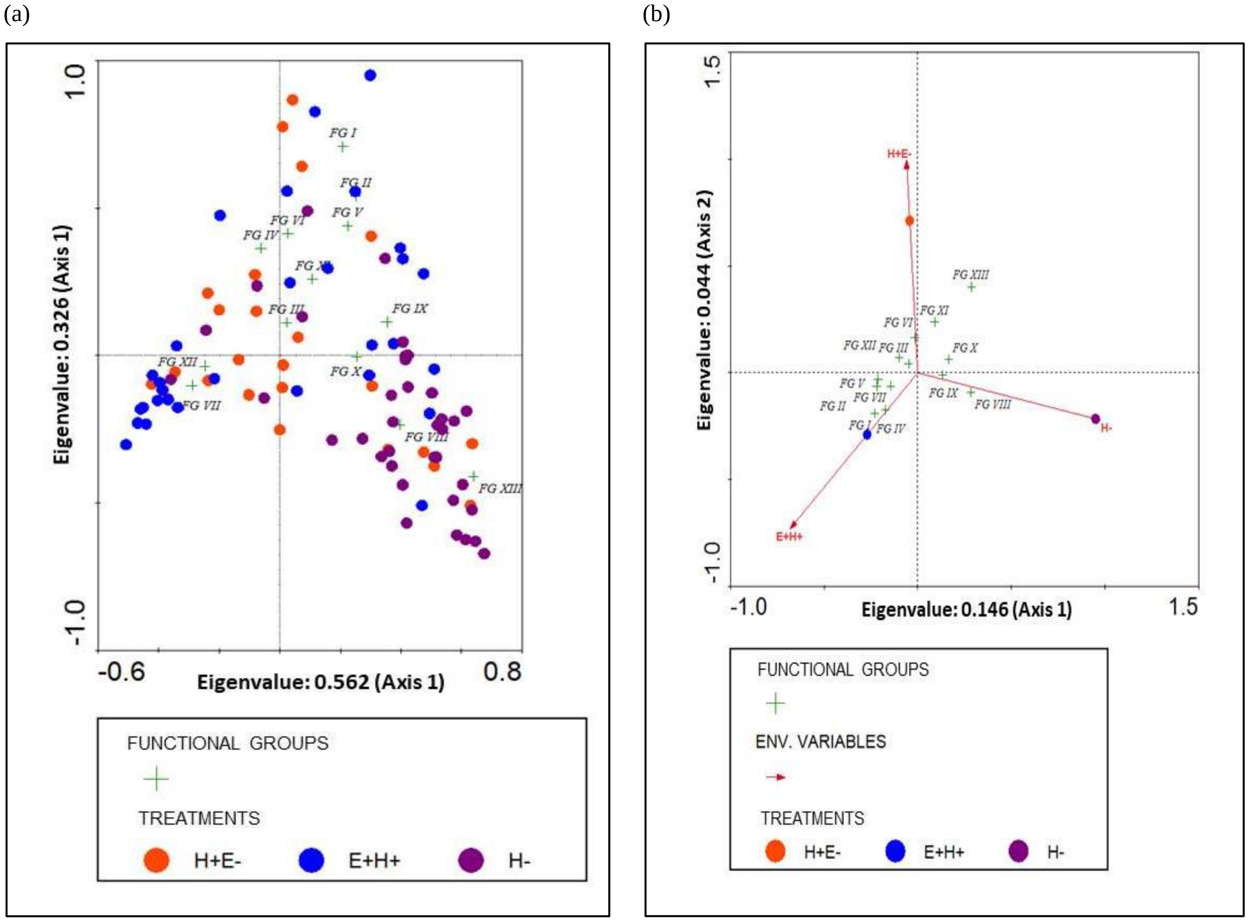


Figure 8.6. (a) Correpsondence analysis (CA) of functional group data with herbivore treatments and (b) Canonical Correpsondence Analysis (CCA) biplot of functional group data in conjunction with herbivore treatments.

FG, Functional Group; *H+E-*, Elephant exclosure; *E+H+*, All LMH present; *H-*, LMH exclosure.

8.4 Discussion

Floristic composition differed significantly between herbivore exposed plots and LMH exclosure plots. The absence of herbivores is suggested to have a filtering effect on herbaceous species in a system without fire. Specific herbivore treatment either allowed species to enter and persist in an environment, or filtered them from the system if they did not possess necessary traits (Grime, 1998; Díaz *et al*., 1999; Van Der Plas *et al*., 2012) attributing to shifts in species composition. Similar grass species (e.g. *D. aegyptium*, *E. monostachyus*, *E. macrostachyus*, *C. dactylon* and *S. nitens*) which generally occur in disturbed areas (Van Oudtshoorn, 2006), were dominant in the herbivore exposed plots (both with and without elephants). *C. dactylon*, which is a stoloniferous, creeping graminoid, occurred only in the plots accessible to all herbivores. This species generally grows in disturbed places, but is considered nutritious forage and can enhance soil stability (Van Oudtshoorn, 2006). Similar to the findings of Siebert and Scogings (2015), *Blepharis integrifolia*, a prostrate growing, palatable forb species was abundant in the plots accessible to all LMH. This forb species has been reported to form continuous forb ground cover or 'browsing lawns' when utilized (Siebert & Scogings, 2015). *R. cordata* was furthermore abundant when exposed to the full complement of herbivores. Persistence of *B. integrifolia* and *R. cordata,* which are both considered palatable, during extreme conditions such as intensive grazing and drought events suggests that these forb species are functionally important in sodic patches of a semi-arid savanna system, and may enhance system resilience, particularly with respect to forage stability. More forb species were dominant in elephant absence than in their presence. This may be attributable either to elephants including forbs in their diet, and therefore consuming many of the forb species, especially during dry conditions (e.g. Owen-Smith & Novellie, 1982; Young *et al*., 2005; Kraai, 2010; Malan *et al*., 2012; Landman *et al*., 2013; Koerner *et al*., 2014), or forbs sensitivity to grazing (Scott-Shaw & Morris, 2015). As would be expected, palatable perennial tufted grasses *P. maximum* and *U. mosambicensis* which grow in shaded environments (Van Oudtshoorn, 2006) dominated LMH exclosure plots.

Elephants enhance habitat heterogeneity and therefore abundance and richness of other species (Pringle, 2008; Kohi *et al*., 2011). Unlike the system without elephants, trait richness differed significantly across herbivore treatments in a system excluded from fire. This suggests that elephants enhance heterogeneity and dynamics of trait diversity patterns in this nutrient-rich system without fire. As expected, functional trait richness was lowest in the absence of herbivores (Burns *et al*., 2009; Koerner *et al*., 2014; Tomlinson *et al*., 2016). Similarly to results found by Díaz and Cabido (2001), loss of herbivores will ultimately lead to reduced functional trait variation. Herbivore presence significantly enhanced trait richness and diversity, although the complete assemblage of herbivores revealed the highest trait richness. This is contrary to findings from Biswas and Malik (2010) who found highest functional richness and diversity at intermediate levels of disturbance. Results suggest that the herbaceous layer of the sodic zone is resilient to utilization by the complete suite of herbivores under which the system has evolved under evolutionary time.

In accordance with Biswas and Mallik (2010) and results presented in the previous chapter, analysing functional variables for each herbaceous life form respecively revealed significant effects of herbivory – effects that were hidden when the entire herbaceous layer was analysed. However, Simpson's index of trait diversity did not explain much of the variation in herbaceous trait diversity patterns, suggesting that the variance in trait abundance distribution is not significant in this system. Although forbs are known to contribute significantly to species diversity in savanna systems (Turner & Knapp, 1996; Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Trollope *et al*., 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015; Van Oudtshoorn, 2015; Burkepile *et al*., 2017), results presented in this chapter suggest that trait richness and diversity is also a function of the forb component in a system exposed to various herbivore treatments, excluding fire, which is consistent with results revealed for the system without elephants.

Although the richness of functional traits was low with exclusion of all LMH, the evenness in distribution of these traits was high, suggesting a dissimilar response when richness and evenness is compared (in accord with Svensson *et al*., 2012). Functional evenness generally shows a continuous decline with increasing disturbance intensity (Mouillot *et al*., 2013). However, trait evenness was lowest in elephant exclosure plots, suggesting that herbivores other than elephants suppress trait evenness, and therefore exert a strong filtering effect on herbaceous traits leading to clustered occurrence of species with certain functional traits (Mouillot *et al*., 2013). Trait evenness in grasses was significantly higher than forb trait evenness. This may suggest that the balance between competitive interaction and trait filtering lead to progressive decreases in forb evenness (Mouillot *et al*., 2013). Decreased evenness could furthermore be explained by functional redundancy among grazing tolerant species which enhances functional dominance and decreases evenness (Díaz & Cabido, 2001; Hanke *et al*., 2014).

Functional group assemblage was sensitive to herbivory (Hanke *et al*., 2014). As expected, low palatability functional groups were associated with exposure to all herbivores (Skarpe, 1992; Milchunas & Lauenroth, 1993; Lavorel *et al*., 1997; Fynn & O'Connor, 2000; Buitenwerf *et al*., 2011; O'Connor, 2015; Yé *et al*., 2015; Guo *et al*., 2016; Tessema *et al*., 2016). However, persistence of forbs with moderate palatability (annual spinescent N-fixing forbs) is suggested to provide forage stability during these extreme conditions. Herbivore exclusion favoured palatable perennial tufted graminoids which is expected in savanna systems (Skarpe, 1992; O'Connor, 2015). Elephant exclosure plots correlated with functional groups consisting of forbs with moderately to high palatability. The removal of elephants and fire from savanna systems causes increased woody biomass (Bond & Keeley, 2005; Bond *et al*., 2005; Young *et al*., 2005; Levick & Rogers, 2007) and therefore increased shaded microenvironments and nutrient concentrations through litter deposition (Ludwig *et al*., 2004a). Considering recent studies that reported enhanced shade-tolerance and better performance by forbs in nutrient-rich systems (e.g. Singh *et al*., 2008; Linstädter *et al*., 2016), our results suggest a facilitative effect of trees on forbs, particularly palatable forbs.

8.5 Conclusion

Similarly to conclusions drawn in chapter 7, herbivore presence, irrespective of elephants, drives herbaceous species composition shifts in this semi-arid savanna nutrient hotspot. Palatable species considered resilient to drought and sustained exposure to herbivores include grasses (*D. aegyptium*, *E. macrostachyus*, *E. monostachyus*, *C. dactylon* and *S. nitens*) and forbs (*A. aspera*, *B. innocua*, *B. integrifolia*, *J. protracta*, *K. angustifolia* and *R. cordata*). These species are furthermore considered important sources of insurance, which are able to maintain system functions during episodic droughts and herbivore utilisation. *C. dactylon*, *B. integrifolia* and *R. cordata* are considered particularly resilient to extreme environments, by being the only dominant grass and forb species in the plots exposed to all LMH.

The presence of elephants enhances dynamics in trait richness patterns with exclusion of fire. Although considered important ecological drivers at larger scales, elephants are considered important drivers of heterogeneity at smaller scales (e.g. trait level). These findings, however, need to be further investigated. Highest trait richness was revealed in the presence of all herbivores, suggesting that this sodic system is resilient to the complete suite of herbivores under which it developed, and that optimal functioning can occur under these conditions. When analysing functional trait level responses to herbivores in nutrient-rich semi-arid savannas, it is important to acknowledge herbaceous life forms as separate functional entities. By doing so, various patterns are revealed that would otherwise (when analysing the entire herbaceous layer) be overlooked. Simpson's index of trait diversity is not considered a useful diversity index when analysing functional diversity of herbaceous traits. However, it may become useful when analysing long-term data, instead of point-in-time data such as the data presented in this particular chapter. Forbs are considered functionally important by contributing significantly to trait richness and diversity. Trait richness and evenness are negatively correlated in this particular system. LMH other than elephant are suggested to suppress trait evenness, since lowest evenness in traits was revealed in the elephant exclosure plots. They therefore exert strong filtering effects on herbaceous species functional traits. Herbaceous functional group assemblage is sensitive to herbivory. Herbivore treatments are characterised by certain functional groups. A particularly interesting finding was the correlation between palatable forbs species and the removal of both fire and elephants.

Chapter 9

Conclusions and Synthesis

9.1 Summary of research

This thesis studied the community ecology of herbaceous vegetation in semi-arid nutrient-rich sodic patches in response to important drivers of savanna structure and function. Analysis therefore included patterns in species–and functional diversity, herbaceous life form abundance, pre-identified functional group abundance, floristic composition structure and functional group assemblages across various fire and herbivore treatments under varying rainfall conditions. Some of the most important findings are summarized below:

Similar response patterns that were observed in both management systems when considering herbaceous species diversity patterns, and life form–and functional group abundance dynamics (Chapters 5 & 6) are listed below:

- The drought of 2015 negatively affected herbaceous species richness and diversity – irrespective of herbivore and fire presence or absence.
- Despite these effects and unlike other findings (e.g., O'Connor, 1993), the herbaceous layer did not represent a degraded state with palatable perennial grasses remaining the dominant herbaceous functional group, irrespective of fire and herbivore treatment or rainfall variability.
- Inter-annual rainfall variability, rather than herbivores, is suggested to be the primary driver of herbaceous species dynamics in this nutrient-rich ecosystem.
- The presence of herbivores (irrespective of elephants) significantly enhanced herbaceous species richness.
- Herbaceous life forms revealed dynamic patterns of response to herbivory and rainfall variability and less so to fire.
- Forbs contributed significantly to diversity and richness, irrespective of rainfall, herbivory and fire.
- Forbs promote ecosystem resilience of nutrient-rich patches of a semi-arid savanna.

- Sodic patches of the Nkuhlu exclosures are resilient to withstand drought and intensive utilization by LMH.

9.1.1 Chapter 5:

- Fire presence or absence seems to drive dynamic shifts in forb-grass dominance within herbaceous plant functional groups. Particularly in herbivore absence, where fire presence favoured abundances of palatable perennial grasses.
- Palatable perennial forbs co-dominate the herbaceous layer during average and drought conditions, suggesting that herbaceous forbs are functionally more important than previously acknowledged.

9.1.2 Chapter 6:

- The presence of elephants enhances herbaceous species richness.
- Annual forbs are suggested to be strong competitors in this system, particularly during average conditions (i.e., average rainfall and herbivore presence).

Similar response patterns that were observed in both management systems when considering herbaceous species composition, trait diversity response patterns and functional group assemblage during an episodic drought (Chapters 7 & 8) are listed below:

- Herbivory significantly affected herbaceous species composition.
- Herbaceous life forms should be acknowledged as separate entities when analysing functional level responses of herbaceous layers.
- Forbs contributed significantly to functional trait diversity and richness.
- Simpson's index of trait diversity is not considered a valuable diversity index when analyzing functional diversity response patterns.

- Significant response patterns revealed in trait evenness suggests that this diversity measure is important to consider when analysing functional level responses of herbaceous vegetation to herbivory and fire.
- Herbivore treatments were characterised by certain functional groups, suggesting that herbivory is a primary driver of herbaceous functional group assemblage during drought conditions.
- Life form, life history, palatability, spinescence, N-fixing ability and growth form were considered important functional traits when studying the function of nutrient-rich herbaceous layers.
- Life history and palatability traits seemed to override other functional traits in some instances.

9.1.3 Chapter 7

- Fire effects on herbaceous species composition were subject to herbivore presence or absence.
- *Blepharis innocua*, *B. integrifolia*, *Kyphocarpa angustifolia* and *Ruellia cordata* are considered resilient forb species in this system, and therefore functionally important in the face of changing environments.
- *Dactyloctenium aegyptium*, *Enteropogon macrostachyus* and *Sporobolus nitens* were resilient to drought and sustained exposure to herbivores and fire.
- These herbaceous species are considered to provide the sodic system with insurance against declines in system function during drought episodes.
- Forb trait evenness was higher than grass trait evenness when both drivers (i.e., fire and herbivory) were lost from the system, confirming forb resilience to fluctuations in the ecosystem.
- Fire is considered a secondary driver of functional group assemblage in this nutrient-rich semi-arid savanna system.

9.1.4 Chapter 8

- *Cynodon dactylon*, *Blepharis integrifolia* and *Ruellia cordata* are considered functionally important species in the sodics when facing increased drought with sustained herbivore pressure.
- Elephants enhanced trait richness dynamics, and could be considered important drivers of heterogeneity at smaller scales (e.g. trait level).
- Highest trait richness was recorded in the presence of all LMH, reinforcing the resilience of the sodic zone to drought and intensive utilisation by herbivores.
- Results suggest a facilitative effect between woody and forb life forms when elephants and fire is lost from this system, however, further studies are necessary to confirm these observations.

9.2 Synthesis

- Fire effects on herbaceous vegetation dynamics are dependent on rainfall and herbivore presence or absence. Stronger fire effects are obtained when herbivores are absent, and biomass levels are higher.
- Both herbaceous species richness and trait richness were higher in the presence of elephants, suggesting that elephants have positive effects at smaller scales in nutrient-rich savanna ecosystems.
- Loss of herbivores from this nutrient-rich ecosystem negatively affects herbaceous vegetation diversity, both on a species and functional level.
- Herbaceous species diversity is not maintained under drought conditions. However, this particular sodic system seems to be resilient to drought effects by still maintaining a character of palatable perennial grasses under below-average rainfall.

Herbivores were found to enhance herbaceous richness at both species and functional levels. Resulting from this, the **first (secondary) hypothesis** stating that herbivore presence will enhance taxonomic and functional diversity is accepted. These positive effects on diversity patterns were irrespective of elephant presence or absence. The loss of elephants from the sodic system is therefore not thought to negatively affect herbaceous species diversity and

richness since the remaining LMH are able to sustain species diversity, however, the loss of all LMH would have detrimental effects on herbaceous species diversity. Herbivores (with or without elephants) are furthermore considered primary drivers of herbaceous species composition and functional group assemblage and heterogeneity in this sodic community.
Richness and diversity of the herbaceous layer was largely a function of forbs, regardless of herbivore treatment, fire presence or absence and rainfall. The ecological importance of forbs is not limited to taxonomic diversity, but results showed that forbs also contribute significantly to the functional richness and diversity of this herbaceous layer. From this, our **second (secondary) hypothesis** that forbs will contribute most to taxonomic and functional diversity is accepted. Forbs are therefore considered important for the functioning of this sodic community. Despite being overlooked in many ecological studies, our results reinforce the importance of savanna forb species, and furthermore illustrate their resilience to environmental drivers and variations within them.

Herbaceous life forms responded dynamically to herbivory and rainfall variability, suggesting a forb-grass coexistence that is driven by the abovementioned ecological drivers. Interactions between herbaceous life forms have received little attention in past ecological studies which largely focus on tree-grass coexistence. Results presented here, however, indicates the necessity to further explore the dynamics within herbaceous life forms of savanna systems. Functional level responses furthermore indicated that herbaceous life forms reveal dynamic trait diversity patterns. Future studies should therefore acknowledge that forbs and grasses are separate functional entities, and analyses should be performed on these life forms separately as to not overlook response patterns. Without exception, results revealed that drought conditions negatively affect herbaceous species diversity and richness, irrespective of herbivore assemblage (i.e., elephant exclusion, LMH exclusion or presence of all LMH) and fire presence or absence. These results indicate that probable increases of extreme drought events in savannas due to global climate change, will inevitably affect herbaceous layer diversity patterns, especially in nutrient-rich ecosystems. Nevertheless, this study revealed some potentially positive interactions and responses in the face of these adverse prospects. For example, palatable perennial grasses remained the dominant functional group over other, alleged unfavourable functional groups during drought conditions, regardless of fire or herbivore treatment. The **third (secondary) hypothesis** is therefore rejected, since palatable perennial grasses dominated over all other functional groups irrespective of rainfall, fire treatment or herbivore assemblage. Despite being considered overgrazed, trampled, eroded and degraded systems, the dominance of palatable perennial grasses in this system is an indication that herbaceous layers of nutrient-rich sodic patches do not show signs of degradation. Similar results with respect to palatable perennial grass dominance for both the system without elephants and the system without fire, are indicative of the resilience of this herbaceous layer to changes in herbivore assemblage (i.e., elephant loss and LMH loss) as well as fire regime (i.e., loss of fire).

Life form dominance within particular functional groups varied with fire treatment. Fire effects on herbaceous species composition are subject to herbivore presence or absence. Fire is therefore considered a secondary driver of herbaceous vegetation dynamics and composition, by being dependent on other ecological drivers for its effects, confirming the **fourth (secondary) hypothesis**. Fire may, however, still affect woody biomass, which in turn affects herbaceous vegetation. Further studies are necessary to tease out possible facilitative effects between woody and forb life forms.

To conclude, results obtained through this thesis confirmed that herbaceous community structure and function of small-scale nutrient-rich semi-arid savanna ecosystems are shaped by varying interaction effects of fire, herbivory and rainfall variability. However, understanding herbaceous community ecology is largely based upon knowledge of potential hidden effects, such as life form variance, particulalry acknowledging that forbs and grasses do not necessarily respond equally to common environmental stressors at both species and functional level.

9.3 Conservation–and management implications and future research

Findings from this thesis add to our understanding of the effects of fire, herbivory and rainfall variability on herbaceous layers, particularly its forb component. Moreover, this study could be used as a framework to advance and develop science-based management strategies of herbaceous layers in nutrient-rich sodic patches. However, further comparable research on the relatively unexplored coexistence between herbaceous life forms in other nutrient-rich ecosysems under different management regimes, as well as nutrient-poor savanna ecosystems and across different land-use types including agricultural rangelands, is likely to broaden our current understanding of savanna vegetation dynamics. Furthermore, studies that link woody and herbaceous data are necessary to disentangle potential plant-plant interactions, e.g., increased woody biomass in elephant absence, and how these interactions will affect herbaceous life forms. Results presented in this thesis suggest a facilitative effect between increased woody biomass in the absence of fire and elephant and palatable forbs. However, tree-forb-grass coexistence data are necessary to confirm these preliminary observations. Lastly, the results suggest that functional groups correlate along a soil nutrient gradient. However, further studies that specifically analyse soil nutrient content are necessary to confirm this preliminary observation.

We have shown that herbivores enhance herbaceous richness at both species and functional levels. Therefore the removal or loss of large mammalian herbivores from these nutrient-rich sodic patches may alter herbaceous layer functioning, by decreasing species and functional richness. Conversely, herbivore presence is a main driver of species and functional richness and diversity. Managers therefore need to pay careful attention to the management of large mammalian herbivore populations in sodic patches, as our results clearly illutrate the potential consequences of a decline in animal numbers. In this study, what is considered a realtively short time scale (i.e., ~15 years) of herbivore loss, has already revealed some significant changes in functional trait composition. Examples of this include the dominance of non-spinescent, erect leafy and climbing species in ungrazed sites. Many species in this community are, therefore, dependent on herbivory for their success, and would be lost from the system should herbivores be lost or excluded. This might suggest that many species have already vanished from other parts of Africa where LMH communities have been lost. Drought events will inevitably affect herbaceous layer diversity patterns, however, further studies are anticipated to determine post-drought patterns in herbaceous richness and diversity at species and functional levels. Such future studies will help us understand the recovery time of ecological systems, and whether certain species were excluded by the drought, or persisted. Finally, our results emphasize the need to include the forb component of herbaceous layers in savanna management models, since they are both taxonomically and functionally important.

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Appendix A: List of abbreviations relevant to this thesis

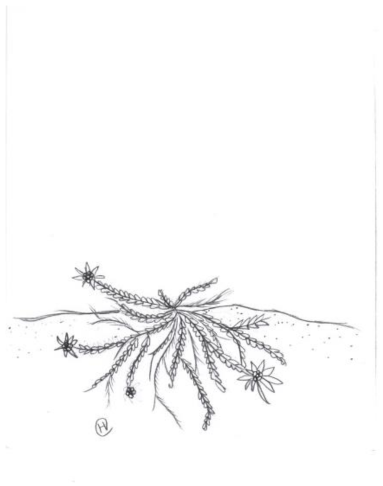
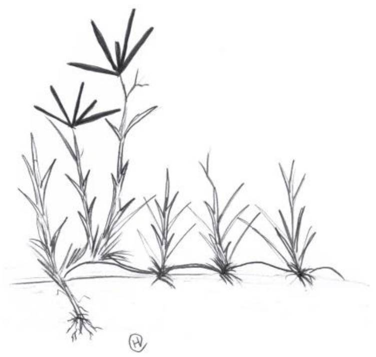
Table A.1. List of abbreviations used throughout the thesis with their meaning.

Abbreviation	**Meaning**
KNP	Kruger National Park
LMH	Large mammalian herbivore(s)
IDH	Intermediate Disturbance Hypothesis
SANParks	South African National Parks
SLA	Specific Leaf Area
HLM	Hierarchical Linear Model(ling)
NMDS	Non-Metric Multidimensional Scaling
PERMANOVA	Permutational Multivariate Analysis of Variance
SIMPER	Similarity Percentage Analysis
PAST	Paleontological Statistics software
ANOVA	Analysis of Variance
PCoA	Principal Co-ordinate Analysis
DCA	Detrended Correspondence Analysis
CA	Correspondence Analysis
CCA	Canonical Correspondence Analysis
RDA	Redundancy Analysis
PPG	Palatable perennial grass(es)
PPF	Palatable perennial forb(s)
PAG	Palatable annual grass(es)
PAF	Palatable annual forb(s)
UPG	Unpalatable perennial grass(es)
UPF	Unpalatable perennial forb(s)
UAG	Unpalatable annual grass(es)
UAF	Unpalatable annual forb(s)

Appendix B: Supplementary tables relating to Chapter 4

Table B.1. Definitions and visual representations of various growth forms referred to in this study.

Growth form	**Definition used in this study**	**Information source**	**Illustration** (Illustrations created by Helga van Coller)
Erect leafy	Species growing erect with leaves concentrated in the middle and/or top parts.	Cornelissen *et al*. (2003)	
Tufted graminoid	Contained many perennial grasses and some sedges forming prominent tufts with leaves concentrated and sprouting from a basal meristem.	Cornelissen *et al*. (2003) & Pérez–Harguindeguy *et al*. (2013)	

Prostrate	❖ Species described as being ‘prostrate’ or ‘procumbent’ or ‘decumbent’ in literature. ❖ Plants growing horizontally at ground level.	Van Wyk & Malan (1998); Van Wyk (2000); Cornelissen *et al*. (2003); Manning (2009); Van der Walt (2009); Kirby (2013); Pérez–Harguindeguy *et al*. (2013)	
Climber	Plants rooted in the soil but use, at least initially, external substrates for support for upward growth and leaf positioning.	Cornelissen *et al*. (2003) & Pérez–Harguindeguy *et al*. (2013)	
Creeping graminoid	Grass species forming roots at the nodes of trailing stems (stolons or runners).	Van Oudtshoorn (2006)	

Dwarf shrub	Included to accommodate *Lantana rugosa*, however, herbaceous shrubs such as species in the genera *Abutilon*, *Tephrosia* and *Indigofera* were placed in the 'erect leafy' category.	Kotschy (2013)	
Rosettes	Species with leaves concentrated very close to the soil surface.	Pérez–Harguindeguy *et al*. (2013)	

Appendix C: Supplementary tables relating to Chapter 5

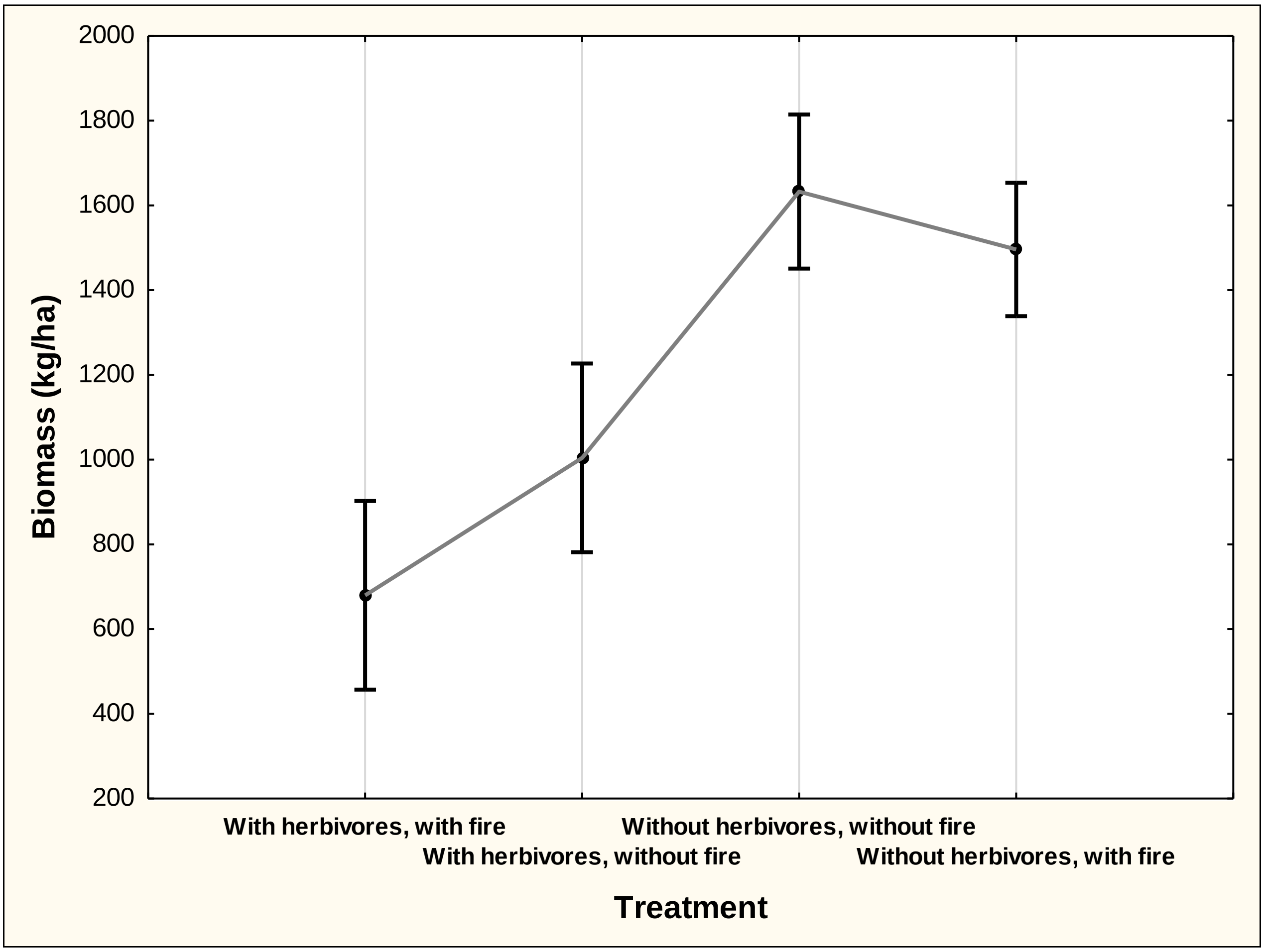


Figure C.1. Mean biomass (kg/ha) across fire and herbivore treatments.

Table C.1. Abundances of dominant species for each herbaceous plant functional group over sampling years.

	With herbivores, with fire			**With herbivores, without fire**			**With all herbivores**			**Without herbivores, without fire**			**Without herbivores, with fire**		
	2015	**2010**	**2001**	**2015**	**2010**	**2001**	**2015**	**2010**	**2001**	**2015**	**2010**	**2001**	**2015**	**2010**	**2001**
Palatable Perennial Forbs (PPF)															
*Achyranthes aspera** L.	14	72	0	13	230	5	23	496	0	12	122	0	20	76	32
Aizoon canariense L.	1	0	0	0	192	0	1	3	0	0	0	0	0	0	0
Barleria prionitis L.	0	1	2	1	3	1	0	3	2	14	77	7	61	73	13
Blepharis innocua C.B. Clarke	42	17	0	39	7	21	11	14	0	4	2	0	19	17	0
*Blepharis integrifolia (*L.f.) E.Mey. ex Schinz	277	280	78	215	146	39	365	235	140	38	19	35	1	0	12
Commelina africana L.	34	14	0	9	9	0	11	27	4	24	28	16	6	15	7
Hypertelis bowkeriana Sond.	0	6	0	0	196	0	0	1	0	0	8	0	0	51	0
Justicia flava (Vahl) Vahl	14	51	10	8	14	10	9	83	31	0	45	51	8	45	50
Justicia protracta (Nees) T.Anderson	5	28	35	31	29	22	14	54	50	0	10	35	25	52	7
Ruellia cordata Thunb.	67	76	40	66	84	46	75	137	24	68	202	26	76	208	78
Palatable Perennial Grasses (PPG)															
Cynodon dactylon (L.) Pers.	0	0	0	0	0	0	87	0	0	0	1	0	214	227	208
Enteropogon macrostachyus (A.Rich.) Benth.	37	14	48	33	55	105	76	25	19	46	120	117	36	30	33
Panicum maximum Jacq.	4	40	95	23	63	103	37	65	227	115	246	170	202	303	484
Sporobolus nitens Stent	329	329	1193	186	503	837	547	931	614	13	19	639	32	48	736
Urochloa mosambicensis (Hack.) Dandy	4	17	12	0	1	25	19	107	38	48	208	410	8	55	100
Palatable Annual Forbs (PAF)															
Acalypha indica L.	2	58	0	3	42	0	17	190	0	1	16	43	4	40	3
Commelina benghalensis L.	8	28	35	5	12	38	32	101	14	5	36	37	11	57	36
Kyphocarpa angustifolia (Moq.) Lopr.	54	143	30	33	190	46	34	92	14	5	26	103	11	25	35

Portulaca quadrifida L.	2	1	0	0	152	0	2	348	0	4	36	0	0	0	0
Trianthema salsoloides Fenzl ex Oliv.	1	7	2	4	33	0	13	80	6	1	49	1	0	1	0
Palatable Annual Grasses (PAG)															
Brachiaria deflexa (Schumach.) C.E.Hubb. ex Robyns	1	0	0	2	1	0	23	51	0	0	8	0	5	33	0
Dactyloctenium aegyptium (L.) Willd.	63	14	80	189	56	118	71	50	224	0	11	84	0	2	1
Echinochloa colona (L.) Link	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0
Urochloa panicoides P.Beauv.	0	5	15	0	8	30	0	0	0	0	0	0	0	0	0
Unpalatable Perennial Forbs (UPF)															
Abutilon austro-africanum Hochr.	7	20	8	9	22	3	6	23	2	0	10	1	11	9	11
Alternanthera pungens Humb., Bonpl. & Kunth*	9	20	0	3	223	0	8	497	0	0	0	0	0	0	9
Bulbostylis burchellii (Ficalho & Hiern) C.B.Clarke	1	46	33	0	0	0	17	228	0	0	34	0	0	9	55
Cyperus indecorus Kunth	9	11	0	0	0	0	31	4	0	5	18	0	5	12	0
Phyllanthus asperulatus Hutch.	0	15	0	2	57	1	0	101	0	0	11	0	4	20	1
Unpalatable Perennial Grasses (UPG)															
Aristida bipartita (Nees) Trin. & Rupr.	0	0	0	0	0	0	0	0	0	0	0	0	6	10	0
Chloris virgata Sw.	11	93	2	0	155	0	23	269	0	12	53	32	0	0	0
Oropetium capense Stapf	0	0	0	0	0	0	22	0	0	22	95	0	0	0	0
Pogonarthria squarrosa (Roem. & Schult.) Pilg.	0	0	0	0	0	0	0	0	7	0	3	0	4	4	33
Unpalatable Annual Forbs (UAF)															
Abutilon guineense (K.Schum.) Baker f. & Exell	1	4	0	0	1	0	0	0	0	0	0	0	0	0	0
Acanthospermum hispidum DC.*	0	0	0	0	0	0	14	257	0	0	0	0	12	0	1
Evolvulus alsinoides (L.) L.	8	106	16	14	90	2	10	85	11	1	33	45	3	21	21
Ocimum americanum L.	12	60	30	2	17	23	23	582	37	1	27	19	7	0	43
Pavonia senegalensis (Cav.) Leistner	0	0	0	0	2	1	0	1	0	1	10	0	2	12	0

Unpalatable Annual Grasses (UAG)															
Aristida congesta L. Roem & Schult.	103	314	28	21	124	25	13	276	20	1	42	24	6	42	26
Tragus berteronianus Schult.	37	0	0	17	281	0	31	190	0	6	24	0	0	0	0

Forage value of forb species was allocated according to Siebert & Scogings (2015), while the forage value of grass species follows Van Oudtshoorn (2006).

* Alien species

** Although classified by Van Oudtshoorn (2006) as a tufted graminoid having a low grazing value, *Sporobolus nitens* is an important and palatable grazing-lawn grass species (rhizomatous) in savanna systems (Archibald et al. 2005; Archibald 2008).

Appendix D: Supplementary tables relating to Chapter 6

Table D.1. Effect sizes of HLM results for comparisons between herbivore treatments and herbaceous richness. Significant effect sizes at $d \geq 0.7$ indicated with * and in bold.

Treatments compared		Forb richness
Elephant exclosure	LMH exclosure	**6.7***
With all herbivores	LMH exclosure	**2.7***
With all herbivores	Elephant exclosure	0.3

Appendix E: Supplementary tables relating to Chapter 7

Table E.1. Pairwise comparisons of PERMANOVA analysis indicating significance of differences between fire and herbivore treatments.

Treatment	**With herbivores, with fire**	**With herbivores, without fire**	**Without herbivores, without fire**	**Without herbivores, with fire**
With herbivores, with fire	---	---	---	---
With herbivores, without fire	0.063	---	---	---
Without herbivores, without fire	**0.001***	**0.001***	---	---
Without herbivores, with fire	**0.001***	**0.001***	**0.002***	---

Bold * indicates significance at $p < 0.05$ as determined by Monte Carlo tests.

Table E.2. Results for similarity percentage analyses (SIMPER) indicating specific herbaceous species contributing > 2 % to compositional differences across herbivore and fire treatments.

Species	**Life form**	**Across all treatments**		**With herbivores, with fire *vs* Without herbivores, with fire**		**With herbivores, without fire *vs* Without herbivores, without fire**	
		Av dis.	Cont. (%)	Av dis.	Cont. (%)	Av dis.	Cont. (%)
Overall		90.4	---	95.2	---	91.5	---
Sporobolus nitens	Grass	11.9	13.2	17.0	17.8	13.8	15.1
Blepharis integrifolia	Forb	9.9	11.0	13.2	13.8	12.7	13.9
Panicum maximum	Grass	8.4	9.3	6.5	6.8	7.3	8.0
Ruellia cordata	Forb	6.2	6.9	5.1	5.4	6.4	7.0
Enteropogon macrostachyus	Grass	4.0	4.5	3.0	3.2	4.4	4.9
Aristida congesta	Grass	3.4	3.7	6.6	7.0	---	---
Cynodon dactylon	Grass	3.2	3.6	4.1	4.3	---	---
Blepharis innocua	Forb	2.8	3.1	3.5	3.6	3.1	3.4
Barleria prionitis	Forb	2.5	2.7	2.1	2.2	---	---
Kyphocarpa angustifolia	Forb	2.4	2.6	3.5	3.7	2.2	2.4
Dactyloctenium aegyptium	Grass	2.3	2.5	2.6	2.7	3.2	3.5
Justicia protracta	Forb	1.9	2.1	---	---	3.1	3.4
Urochloa mosambicensis	Grass	1.9	2.1	---	---	2.6	2.8
Achyranthes aspera	Forb	1.8	2.0	---	---	1.9	2.1

Av.dis., Average dissimilarity; Cont. (%), Contribution %; Distance/Similarity measure: Bray-Curtis.

Table E.3. Summary of similarity percentage analyses (SIMPER) indicating mean abundances of species across fire and herbivore treatments.

Species	**Life form**	**With herbivores, with fire *vs* Without herbivores, with fire**		**With herbivores, without fire *vs* Without herbivores, without fire**	
		Mean abundance (H^+F^+)	Mean abundance (H^-F^+)	Mean abundance (H^+F^-)	Mean abundance (H^-F^-)
Achyranthes aspera	Forb	---	---	0.5	0.3
Aristida congesta	Grass	4.3	0.1	---	---
Barleria prionitis	Forb	0	1.3	---	---
Blepharis innocua	Forb	1.8	0.4	1.6	0.1
Blepharis integrifolia	Forb	11.5	0.02	9.0	1.1
Cynodon dactylon	Grass	0	4.5	---	---
Dactyloctenium aegyptium	Grass	2.6	0	7.9	0
Enteropogon macrostachyus	Grass	1.5	0.8	1.4	1.3
Justicia protracta	Forb	---	---	1.3	0
Kyphocarpa angustifolia	Forb	2.3	0.2	1.4	0.1
Panicum maximum	Grass	0.2	4.2	1.0	3.2
Ruellia cordata	Forb	2.8	1.6	2.8	1.9
Sporobolus nitens	Grass	13.7	0.7	7.8	0.4
Urochloa mosambicensis	Grass	---	---	0	1.3

H^+, with herbivores; F^+, with fire; H^-, without herbivores; F^-, without fire.

Table E.4. Detrended Correspondence Analysis (DCA) eigenvalues and gradient lengths.

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.728	0.358	0.217	0.156
Lengths of gradient	3.513	3.073	2.418	2.097
Cumulative percentage variance of functional group data	22.7	33.9	40.6	45.5
Sum of all eigenvalues	**3.208**			

Table E.5. Principal Component Analysis (PCA) eigenvalues and cumulative variance.

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.403	0.221	0.180	0.086
Cumulative percentage variance of functional group data	40.3	62.4	80.4	88.9
Sum of all eigenvalues	**1.000**			

Table E.6. Redundancy Analysis (RDA) eigenvalues, functional group-environment correlations and cumulative variance.

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.173	0.006	0.002	0.263
Functional group environment correlations	0.677	0.193	0.135	0.000
Cumulative percentage variance				
of functional group data	17.3	17.9	18.0	44.3
of species environment relation	95.9	99.1	100.0	0.0
Sum of all eigenvalues	**1.000**			
Sum of all canonical eigenvalues	**0.180**			

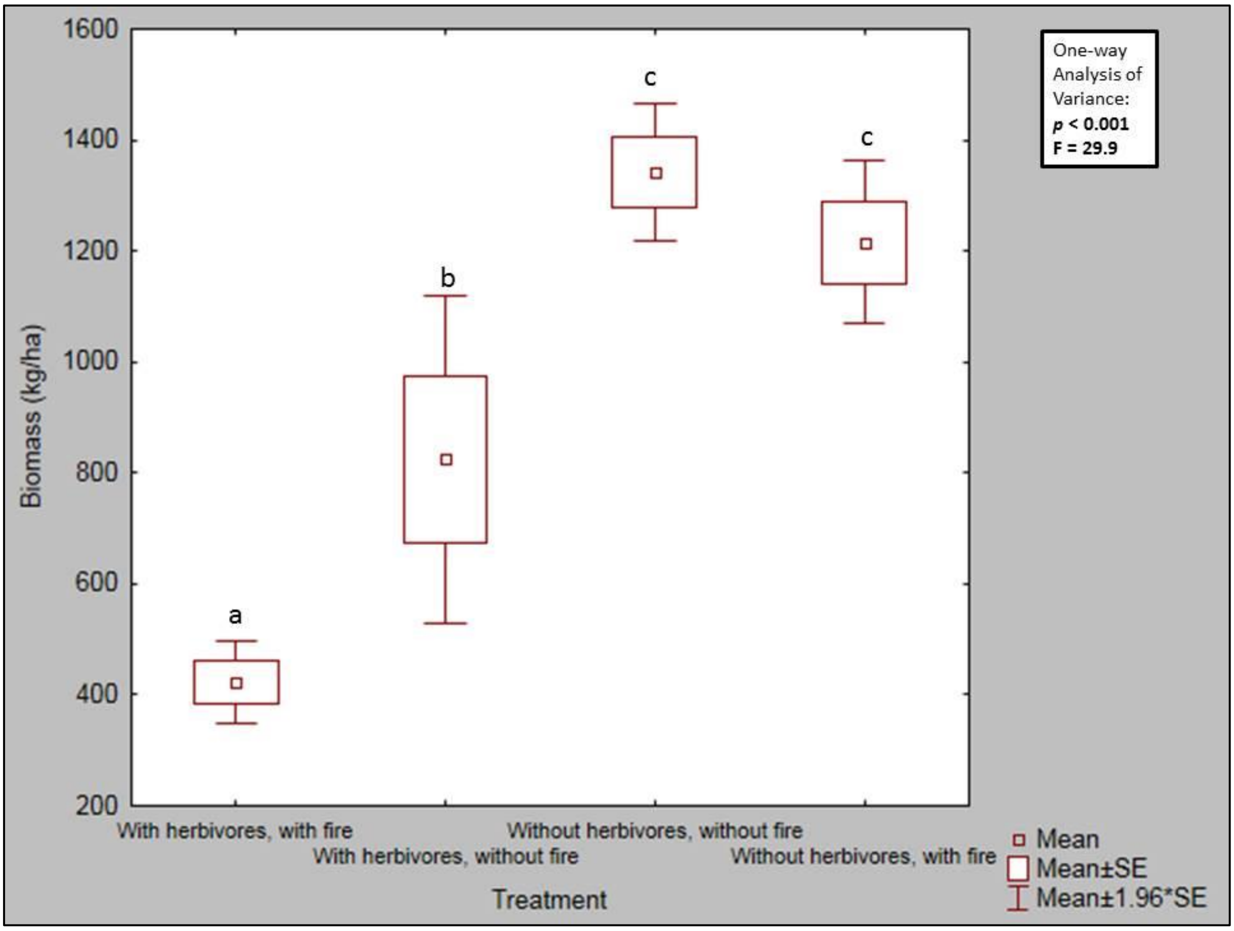


Figure E.1. Mean (±SE) herbaceous biomass across herbivore and fire treatments in a below-average rainfall year.

Appendix F: Supplementary table relating to Chapter 8

Table F.1. Pairwise comparisons of PERMANOVA analysis indicating significance of differences in floristic composition between herbivore treatments.

Treatment	**Elephant exclosure**	**With all herbivores**	**LMH exclosure**
Elephant exclosure	---	---	---
With all herbivores	0.056	---	---
LMH exclosure	**0.001***	**0.001***	---

Bold * indicates significance at $p < 0.05$ as determined by Monte Carlo tests.

Table F.2. Results for similarity percentage analyses (SIMPER) indicating specific herbaceous species contributing > 2 % to compositional differences between herbivore treatments.

Species	**Life form**	**Across all treatments**		**Elephant exclosure *vs* LMH exclosure**		**With all herbivores *vs.* LMH exclosure**	
		Av dis.	Cont. (%)	Av dis.	Cont. (%)	Av dis.	Cont. (%)
Overall		89.8	---	91.5	---	93	---
Sporobolus nitens	Grass	16.4	18.2	13.8	15.1	18.4	19.8
Blepharis integrifolia	Forb	12.9	14.4	12.7	14.0	12.8	13.8
Panicum maximum	Grass	5.3	5.9	7.3	7.9	5.8	6.2
Ruellia cordata	Forb	5.0	5.6	6.4	7.0	4.7	5.1
Enteropogon macrostachyus	Grass	4.4	4.9	4.4	4.9	4.8	5.2
Dactyloctenium aegyptium	Grass	3.4	3.8	3.2	3.5	2.6	2.8
Urochloa mosambicensis	Grass	2.1	2.3	2.6	2.8	2.6	2.8
Justicia protracta	Forb	1.8	2.0	3.1	3.4	---	---
Kyphocarpa angustifolia	Forb	1.8	2.0	2.2	2.4	---	---
Blepharis innocua	Forb	1.8	2.0	3.1	3.4	---	---
Achyranthes aspera	Forb	1.6	1.8	1.9	2.1	---	---
Cynodon dactylon	Grass	1.3	1.4	---	---	1.9	2.1
Enteropogon monostachyus	Grass	1.0	1.1	2.1	2.3	---	---

Av.dis., Average dissimilarity; Cont. (%), Contribution %; Distance/Similarity measure: Bray-Curtis.

Table F.3. Summary of similarity percentage analyses (SIMPER) indicating mean abundances of species across herbivore treatments.

Species	**Life form**	**Elephant exclusion *vs* LMH exclusion**		**With all herbivores *vs* LMH exclusion**	
		Mean abundance (E^{-})	Mean abundance (LMH^{-})	Mean abundance (Open)	Mean abundance (LMH^{-})
Achyranthes aspera	Forb	0.5	0.3	---	---
Blepharis innocua	Forb	1.6	0.1	---	---
Blepharis integrifolia	Forb	9.0	1.2	11.4	1.1
Cynodon dactylon	Grass	---	---	2.7	0
Dactyloctenium aegyptium	Grass	7.9	0	2.2	0
Enteropogon macrostachyus	Grass	1.4	1.3	2.4	1.3
Enteropogon monostachyus	Grass	1.1	0	---	---
Justicia protracta	Forb	1.3	0	---	---
Kyphocarpa angustifolia	Forb	1.4	0.1	---	---
Panicum maximum	Grass	1.0	3.2	1.2	3.2
Ruellia cordata	Forb	2.8	1.9	2.3	1.9
Sporobolus nitens	Grass	7.8	0.4	17.1	0.4
Urochloa mosambicensis	Grass	0	1.3	0.6	1.3

E^{-}, Elephant exclusion; H^{-}, LMH exclusion.

Table F.4. Effect sizes of Two-Way Analysis of Variance results for comparisons between herbivore treatments and trait diversity index values. Significant effect sizes at $d \geq 0.7$ indicated with * and in bold.

Treatments compared		Trait richness	Margalef's richness index	Pielou's evenness	Shannon-Wiener diversity index	Simpson's index of diversity
Elephant exclosure	LMH exclosure	**0.8***	0.1	0.5	0.1	0.3
With all herbivores	LMH exclosure	**1.0***	0.1	0.2	0.4	0.03
With all herbivores	Elephant exclosure	0.2	0.1	0.3	0.3	0.4

Table F.5. Effect sizes of Two-Way Analysis of Variance results for comparisons between herbivore treatments and Pielou's trait evenness. Significant effect sizes at *d* ≥ 0.7 indicated with * and in bold.

Treatments compared		Trait evenness
Elephant exclosure	LMH exclosure	**0.7***
With all herbivores	LMH exclosure	0.3
With all herbivores	Elephant exclosure	0.3

Table F.6. Detrended Correspondence Analysis (DCA) eigenvalues and gradient lengths.

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.679	0.444	0.218	0.139
Lengths of gradient	3.363	5.836	2.195	2.007
Cumulative percentage variance of functional group data	21.8	36.1	43.1	47.5
Sum of all eigenvalues	**3.116**			

Table F.7. Correspondence Analysis (CA) eigenvalues and cumulative percentage variance of functional group data.

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.562	0.326	0.249	0.225
Cumulative percentage variance of functional group data	24.4	38.6	49.4	59.2
Sum of all eigenvalues	**2.302**			

Table F.8. Canonical Correspondence Analysis (CCA) eigenvalues and cumulative percentage variance.

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.146	0.044	0.472	0.285
Functional group environment correlations	0.547	0.455	0.000	0.000
Cumulative percentage variance				
of functional group data	6.3	8.2	28.7	41.1
of species environment relation	76.9	100	0.0	0.0
Sum of all eigenvalues	**2.302**			
Sum of all canonical eigenvalues	**0.189**			