

Herbaceous plant diversity responses to various treatments of fire and herbivory in sodic patches of a semi-arid riparian ecosystem

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Abstract

Understanding relationships between large herbivores and plant species diversity in dynamic riparian zones, and more specifically sodic zones, is critical to biodiversity conservation. Sodic patches form an integral part of savanna ecosystems because of the ecosystem services and functions they provide, i.e. accumulation of nutrients, provision of open spaces for predator vigilance and formation of wet season wallowing points. Furthermore, these key resource areas sustain body condition for dry season survival and support reproduction through nutritional benefits, making them ‘nutrient hotspots.’

The Nkuhlu research exclosures in the Kruger National Park (KNP) provide a unique opportunity to investigate spatial and temporal heterogeneity patterns within riparian zones, and how these patterns are affected by fire and herbivory. A monitoring project was initiated to answer questions pertaining to the dynamics of the herbaceous layer and was aimed at determining (a) whether there exists meaningful variance in herbaceous plant species richness and diversity across different treatments of fire and herbivory in the ecologically sensitive sodic zone, (b) if temporal shifts in plant species composition and diversity occurs, (c) whether an increase in herbaceous biomass, an artifact of herbivory and fire exclusion, suppresses herbaceous plant species diversity and richness, and (d) whether there exists a significant relationship between herbaceous biomass and species richness/diversity. The Nkuhlu exclosures consist of three herbivory treatments, each divided into a fire and no-fire treatment, hence six treatment combinations overall. Herbivory treatments consisted of, (1) a partially fenced area designed to specifically exclude elephants (giraffes are also excluded due to body size), (2) an open, unfenced area and (3) a fully fenced area, designed to exclude all herbivores larger than a hare. Herbaceous vegetation was sampled in two 1 m² circular sub-plots in the eastern and western corners of each of the 82 fixed plots. Biomass of each plot was estimated with a Disc Pasture Meter (DPM) by sampling ten points diagonally within each plot. DPM-readings were converted to kg/ha according to latest conversions for the Lowveld Savanna.

Species richness and biomass showed significant variance across treatments for the 2010 dataset, whereas no significant variation in herbaceous species diversity was perceived. Combined treatment of fire absence and herbivore presence contributed to higher forb species richness in the sodic zone. Biomass was significantly higher in fully fenced areas where herbivores were excluded, opposed to the open and partially fenced areas. Although no significant variation was recorded for diversity across treatments, lowest diversity was recorded in the absence of all herbivores, especially in combination with fire treatment. After nine years of herbivory exclusion, diversity of herbaceous species varied significantly. Herbaceous species composition changed over time in areas exposed to

herbivory, while composition of fully fenced treatments did not reveal change. A hump-shaped relationship exists between herbaceous species richness/diversity and field biomass, at least for areas with biomass levels not exceeding 2500 kg/ha. Herbivores are therefore considered essential in sustaining herbaceous plant species richness and system heterogeneity in the sodic zone, since herbaceous species richness/diversity was higher in herbivore presence and herbaceous species composition changed over time in areas exposed to herbivory. Although statistically non-significant, fire seems to suppress species richness.

Conservation implications: This study could be used as framework to advance and develop science-based management strategies for, at least, the sodic zones of the KNP. Research in these exclosures contributes to our understanding of these landscapes and benefit ecosystem conservation planning. It also provides valuable long-term data for key ecological processes.

Key words: *fire; herbivory; sodic zone; nutrient hotspots; species richness; species diversity; biomass; riparian zone*

Opsomming

Biodiversiteitsbewaring noodsaak dat die interaksie tussen groot herbivore en diversiteit van plantspesies bestudeer en verstaan word, veral met betrekking tot dinamiese rivieroewersones en meer spesifiek die natriumhoudende ('sodic') areas. Natriumhoudende gebiede maak 'n belangrike deel uit van savanna-ekosisteme omdat hierdie gebiede essensiële ekosisteedienste lewer, soos die vaslegging van nutriënte, voorsiening van oop ruimtes vir predator/prooi waaksaamheid en die vorming van modder poele gedurende die nat seisoen. Hierdie voedingstofryke areas onderhou verder diere se liggaamskondisie gedurende droë seisoene en bevorder voortplantingsukses d.m.v. voordele verkry vanaf nutriëntryke plantegroei, wat daartoe lei dat hierdie areas bekend staan as 'nutriëntbrandpunte'.

Die oprigting van die Nkuhlu-navorsingsuitsluitpersele in die Kruger Nasionale Park (KNP) het 'n geleentheid geskep om heterogeniteitspatrone oor ruimte en tyd binne rivieroewersones te bestudeer asook tot welke mate sodanige patrone deur vuur en herbivorie beïnvloed word. 'n Monitoringsprojek is geloods om spesifieke vrae rondom die dinamiek van kruidagtige spesies te beantwoord, naamlik (a) of daar 'n betekenisvolle variasie in die kruidagtige plante se spesierykheid en diversiteit is in die ekologies sensitiewe natriumhoudende ('sodic') sone van die Nkuhlu-uitsluitpersele oor verskillende vuur- en herbivoriebehandelings, (b) of daar verandering in die plantspesiesamestelling en diversiteit oor tyd intree, (c) of 'n toename in biomassa van die kruidagtige spesies, as gevolg van die uitsluiting van herbivorie en vuur, die spesiesrykheid en diversiteit van die kruidagtige spesies onderdruk en (d) of daar 'n betekenisvolle verhouding tussen kruidagtige plante se biomassa, spesierykheid en diversiteit is. Die Nkuhlu-uitsluitpersele bestaan uit drie herbivoorbehandelings, wat elk verder in 'n brand- en nie-brandbehandeling verdeel is, dus ses kombinasies van behandelings altesaam. Herbivoorbehandelings sluit in, (1) 'n gedeeltelik omheinde gebied wat olifante uitsluit (kameelperde word ook uitgesluit a.g.v. hul liggaamsgrootte), (2) 'n oop area en (3) 'n vol-omheinde area wat alle diere groter as 'n haas uitsluit. Plantopnames van die kruidagtige spesies is gedoen in sirkelvormige sub-plotte in onderskeidelik die oostelike en westelike hoeke van elk van die 82 permanente plotte. Die biomassa van elke plot is bepaal m.b.v. 'n weiveld-skyfmeter langs 'n diagonale lyn tussen die noordelike en suidelike hoeke van elke plot. Lesings is omgeskakel na kg/ha volgens die nuutste omskakelingstabel vir die Laeveld-Savanna.

Spesierykheid en biomassa het onderskeidelik betekenisvolle verskille t.o.v. die afsonderlike behandelings getoon. Geen betekenisvolle verskille was egter sigbaar in die diversiteit van kruidagtige spesies nie. Resultate het aangedui dat die gekombineerde behandeling van geen vuur met herbivorie

lei tot 'n hoër kruidagtige spesierykheid in die natriumhoudende sone van die Nkuhlu-uitsluitpersele. Biomassa is aansienlik hoër in die vol-omheinde areas, waar alle herbivore uitgesluit is, teenoor die oop en gedeeltelik omheinde areas. Hoewel geen betekenisvolle variasie getoon is vir spesiediversiteit oor verskillende behandelings nie, is die laagste diversiteit teenwoordig in die afwesigheid van alle herbivore, veral wanneer vuurbehandeling toegepas is. Na uitsluiting van herbivore vir nege jaar, het die diversiteit van die kruidlaag betekenisvol verander. Spesiesamestelling van die kruidlaag het verander oor tyd in gebiede blootgestel aan herbivorie, terwyl die samestelling van die vol-omheinde behandelings geen verandering getoon het nie. 'n Klokvormige verhouding is waargeneem tussen kruidagtige plant spesierykheid/diversiteit en biomassa vir areas met biomassa-vlakke wat nie 2500 kg/ha oorskry het nie. Op grond van hierdie studie kan herbivorie dus as noodsaaklik vir die handhawing van kruidagtige spesierykheid in die natriumhoudende sone van die Nkuhlu-uitsluitpersele in die KNP beskou word, omdat kruidagtige plante se spesierykheid/diversiteit hoër was in die teenwoordigheid van herbivore en die spesiesamestelling oor tyd verander het in areas blootgestel aan herbivorie. Vuur onderdruk die spesierykheid van die kruidagtige spesies in die Nkuhlu-uitsluitpersele in die KNP.

Bewaringsimplikasies: Die studie kan gebruik word as 'n raamwerk om wetenskap-gebaseerde bestuurstrategieë te bevorder en te ontwikkel vir ten minste die natriumhoudende sones van die KNP. Navorsing wat in hierdie uitsluitpersele gedoen word kan wetenskaplikes help om hierdie landskappe beter te verstaan en kan ook die beplanning van ekosisteembewaring van die KNP bevoordeel. Verder sal dit ook langtermyn inligting m.b.t. kern-ekologiese prosesse bied.

Sleutelwoorde: vuur; herbivorie; natriumhoudende ('sodic') sone; nutriëntbrandpunte ('hotspots'); spesierykheid; spesiediversiteit; biomassa; rivieroewersone

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Chapter 1

Introduction

1.1 Preamble

Savannas occupy approximately 20 % of the land surface of the world, making it one of the largest biomes, and unique among the terrestrial biomes in having no one single dominant plant growth form (Scholes, 1987; Smith *et al.*, 2012). There exists a dynamic coexistence where woody and herbaceous plants share dominance in structure and function, while these growth forms are mutually exclusive in other biomes (Scholes, 1987; Sankaran & Anderson, 2009; Smith *et al.*, 2012). Savannas are widely defined as strongly seasonal plant communities, having a relative continuous and sometimes dynamic herbaceous layer and a discontinuous woody component (Walker *et al.*, 1981; Knoop & Walker, 1985; Belsky *et al.*, 1989; Skarpe, 1991; Couteron & Kokou, 1997; Scholes & Archer, 1997; Sankaran *et al.*, 2008).

The single most important feature of savannas is the strong seasonality of rainfall (Scholes, 1987). Semi-arid, sub-tropical African savannas have two distinctive seasons, namely a hot, sporadically wet growth season, with the bulk of rainfall between October and April, and a warm, dry, non-growing season (Venter *et al.*, 2003; Scogings *et al.*, 2012). Annual rainfall patterns are clearly reflected in the vegetation, and the unique wet and dry cycles have a marked influence on grass cover, fire regimes, animal population dynamics and movements, and an increase of certain animal diseases (Venter *et al.*, 2003).

1.2 Herbivory and fire

In African savannas, disturbances such as fire, floods, climatic variability, nutrients and herbivory interact and may change the structure and diversity of landscapes in nature reserves, driving spatial and temporal heterogeneity (Baker, 1992; Van Wilgen *et al.*, 2003; Scogings *et al.*, 2012). Herbivory and fire are important ecosystem modifiers and agents of disturbance, often acting together, and have significantly contributed to determining the structure, dynamics and functioning of ecosystems throughout evolutionary history (Archibald *et al.*, 2005; Jacobs & Naiman, 2008; Levick & Rogers, 2008). Both fire and herbivory have been shown to influence vegetation composition,

annual above ground net primary productivity and nutrient cycling of semi-arid African savannas (O'Connor, 1994; Archibald *et al.*, 2005).

The savannas of Africa are inhabited by the Earth's richest and most magnificent large mammalian fauna and include more ungulate species than any other continent (Du Toit, 2003; Mucina & Rutherford, 2006). The dependence of herbivores on plants has many wide-ranging direct and indirect effects on plant communities and vegetation with which they are associated (Skarpe, 1991; Mucina & Rutherford, 2006; Scogings *et al.*, 2012). The most commonly observed reaction by herbaceous species upon intense grazing is a decrease in the palatable perennial species and in the total production and ground cover (Skarpe, 1991). Conversely, the removal of herbivores may cause an increase of grass biomass at the cost of forb species richness (Jacobs & Naiman, 2008).

Research on the effects of herbivory exclusion from semi-arid savannas and particularly riparian zones is surprisingly scarce (Jacobs & Naiman, 2008). In the Kruger National Park (KNP) uncertainty still prevails with respect to the scales and geographic locations at which the vegetation and ecosystem processes are impacted by large herbivores (Asner *et al.*, 2009). Elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), zebra (*Equus burchellii*) and many other ungulates cause marked structural changes in African landscapes, however, few studies have been done at a geographic scale that can establish the impact of herbivores on the overall diversity of the landscape (Asner *et al.*, 2009). Optimal sustainable usage of savanna rangelands can only be achieved through a better understanding of the dynamic interactions between herbivores, vegetation, fire and the physical environment (Skarpe, 1991).

Frequently recognized for driving savanna structure, function and dynamics, fire has undoubtedly been an important factor ever since the rise of the grass layer to dominance, and is used as a management tool to control bush encroachment (Mucina & Rutherford, 2006; Smith *et al.*, 2012). Southern African savannas have a strong seasonality of rainfall, allowing for plant material produced in the wet season to dry, accumulate and be burned in the dry season. Many savanna plants tend to recover well after the removal of plant material due to fire (Mucina & Rutherford, 2006). Depending on timing and intensity, fire can promote heterogeneity and productivity of vegetation, yet could also cause a decline in each, and therefore the effect of fire in savannas still remains uncertain (Bond & Keeley, 2005; Smith *et al.*, 2012).

The grazing lawns of East Africa does not occur in the KNP, yet vegetation of sodic patches and termite mounds are considered to be preferentially foraged by large herbivores (Naiman *et al.*, 2003; Grant & Scholes, 2006). Ecologically important sodic patches are often associated with footslopes of undulating granitic landscapes and are commonly referred to as ‘nutrient hotspots’ due to the production of high quality forage (Venter, 1990; Khomo & Rogers, 2005; Grant & Scholes, 2006; Van Coller *et al.*, 2013). These nutrient hotspots tend to form a chain of high quality forage patches in large conservation areas, providing large herbivores with sustained nutrition despite shifts in climatic patterns, i.e. drought (Grant & Scholes, 2006). Notwithstanding its ecological significance, sodic patches are often considered as desolate land due to its disturbed appearance and low aesthetic value (Khomo & Rogers, 2005) as a result of overgrazing, which in turn impacts on herbaceous species diversity, richness and biomass (Jacobs and Naiman, 2008). Areas such as these play a vital role in conservation and monitoring design, as it indicates core areas for monitoring programmes (Grant & Scholes, 2006).

The project forms part of a long-term monitoring project of the KNP (O’Keefe & Alard, 2002), and the research presented in this dissertation is primarily aimed at gaining insight on the effect of fire and herbivory on temporal and spatial heterogeneity patterns of the herbaceous layer within one of the most intriguing and ecologically important sodic zones in African savannas.

1.3 Rationale

Fire and herbivory are important driving forces of ecosystem functioning and interact strongly with rainfall unpredictability and prolonged droughts (Du Toit, 2003), and are vitally important for the maintenance and conservation of African savanna ecosystems (Govender *et al.*, 2006; Jacobs & Naiman, 2008). These two dominant mediators of vegetation change in the KNP have normally been investigated individually, and therefore little research is available on the interaction between the two, and even more, the impact on herbaceous biomass dynamics (Archibald *et al.*, 2005; Jacobs & Naiman, 2008).

Floods of February 2000 on the eastern seaboard of southern Africa caused widespread removal of riverine vegetation and altered the channel habitat considerably (Parsons *et al.*, 2005). The floods provided a unique research opportunity in which the long-term development and recovery of riverine ecosystems, after a major disturbance, could be characterized. South African National Parks (SANParks), together with a team of international scientists have constructed large exclosures to

study the effects of fire and herbivory on the transformation of spatial and temporal heterogeneity patterns of vegetation in a semi-arid African savanna. Exclosures, in their basic form, are fenced areas designed to keep animals out. At each locality (Nkuhlu and Letaba) a pair of exclosures was erected to limit the accessibility of herbivores.

The knowledge gained will contribute towards both local and international understanding of the floristic trends and patterns of herbaceous species dynamics in the KNP. This study is envisaged to provide a better understanding of semi-arid riparian ecosystem responses, particularly the ecologically important sodic zone to herbivory and fire, and will directly benefit and feed into the ecosystem conservation planning and science-based management strategies, to fit the adaptive management approach of SANParks.

1.4 Objectives

The main aim of this study is to unravel the effects that fire and herbivory, as important ecosystem drivers, have on spatial and temporal heterogeneity patterns within the herbaceous layer of sodic plant communities along riparian zones.

Specific objectives of this study of the sodic zone were to:

- ❖ Calculate, compare and assess species richness and diversity of herbaceous vegetation across different treatments of fire and herbivory;
- ❖ Test for significant temporal changes in plant species composition and diversity patterns between 2001 and 2010;
- ❖ Test whether herbaceous biomass suppresses herbaceous plant species diversity and richness;
- ❖ Interpret the relationship between herbaceous biomass and species richness and diversity.

1.5 Hypotheses

Broad hypothesis: Herbaceous plant species diversity and richness varies significantly across different treatments of fire and herbivory in the sodic zone of a semi-arid riparian ecosystem.

Hypothesis 1: Fire plays a secondary role to herbivory in maintaining plant species diversity, richness and evenness in semi-arid riparian ecosystems.

Hypothesis 2: Highest species richness and diversity is supported at intermediate levels of disturbance.

Hypothesis 3: Herbaceous plant richness, diversity and composition changes over time and across fire and herbivory treatments.

Hypothesis 4: Over time, the relationship between herbaceous species richness and field biomass for the sodic zone follows the ‘hump-shaped’ model.

1.6 Format of study

This dissertation conforms to the guidelines set for a standard dissertation at the North-West University¹. It encompasses eight chapters, of which one was prepared, submitted and accepted as manuscript by a scientific journal (Chapter 5). The structure of these chapters necessitated that certain methods were included in the results chapters for easy reference. Cited research is included as a single list of references at the end of the dissertation.

Chapter 2: Literature Review

An in-depth examination of the existing literature is provided in this chapter. It provides a backdrop on semi-arid savannas, fire and herbivory as ecosystem drivers and possible response models to relate herbaceous biomass and species richness. It lastly stresses the importance of long-term monitoring in the KNP, since ecological processes, i.e. how herbaceous vegetation reacts upon disturbances such as fire and herbivory, do not occur rapidly.

Chapter 3: Study Area

This chapter presents a detailed account of the study area and provides more information regarding relevant components such as location, exclosure layout, climate, rainfall, soil types, dominant species, topography and history.

Chapter 4: Materials and Methods

The general methodology followed to acquire floristic data for this study, along with specific methods of importance, i.e. preparation of data is thoroughly described. Since one of the chapters has already been published, and others have been prepared for submission to scientific journals, methods that are specific have been included in relevant chapters.

¹See section 2.1 of the manual for Post Graduate Studies (www.nwu.ac.za/library/documents/manualpostgrad.pdf)

Results and Discussion

Chapter 5: Sodic species diversity turnover between treatments

Floristic analyses were undertaken to determine whether herbaceous plant species diversity varies significantly across different treatments of fire and herbivory along the sodic zone of the semi-arid riparian ecosystem. This chapter has been published in *Koedoe: African Protected Area Conservation and Science* (Van Coller *et al.*, 2013). Even though herbaceous species diversity showed clear patterns, no significant variation or differences could be detected across treatments, inferring that monitoring over a larger time scale under similar conditions was required to support these preliminary results. The next chapter explored the temporal (nine years) effects of fire and herbivory on herbaceous species composition and diversity.

Chapter 6: Temporal shifts in plant species composition and diversity in the sodic zone

This chapter attends to the statistical description and analysis of the temporal effect of fire and herbivory on herbaceous plant species diversity and richness across different fire and herbivory treatments, comparing results from 2001 and 2010.

Chapter 7: Relationship between field biomass and herbaceous species richness and diversity

Since the presence of herbivores cause changes in the herbaceous species composition and biomass, this chapter determines the response patterns of herbaceous species richness/diversity upon varying levels of biomass, and also provides visual representations of these relationships.

Chapter 8: Conclusion

Critical findings from chapters 5 to 7 are presented, and the contribution towards our existing knowledge about fire and herbivory is articulated. The effects that these drivers have on the structure and function of African savanna ecosystems, particularly ecologically sensitive sodic zones, are explored. It also presents some recommendations for future reference.

Chapter 2

Literature Review

2.1 Semi-arid savannas

Savannas occupy about 20 % of the land surface of the world, and approximately 40 % of Africa (Scholes & Walker, 1993). In South Africa, savannas represent 33 % of land area, with many people depending on the associated ecosystem services for their livelihood (Higgins *et al.*, 1999; Van Wilgen *et al.*, 2000; Mucina & Rutherford, 2006). Savanna is a term that has been widely used and variously defined, yet there is no general consensus on the precise definition of savannas (Scholes & Walker, 1993; Scholes & Archer, 1997). This study is exclusively concerned with semi-arid savannas in southern Africa, and will for the sake of brevity be referred to as savannas.

Savannas can generally be described as strongly seasonal and water-limited 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; Belsky *et al.*, 1989; Skarpe, 1991; Couteron & Kokou, 1997; Scholes & Archer, 1997; Sankaran *et al.*, 2008). Therefore, the ecology of savannas is neither that of a forest, nor that of grassland, and the complex interactions between the woody and herbaceous components give this vegetation a character of its own (Scholes & Walker, 1993). Some characteristics of semi-arid savannas include diversity and biomass of large mammals, especially antelope, frequent occurrence of fire, with a high ratio of below to above-ground biomass and generally being overgrazed and encroached on by bush (Walker *et al.*, 1981; Scholes, 1987; Scholes & Walker, 1993). Savanna distribution, structure and function are primarily determined by water availability, nutrient availability, fire and herbivory (Scholes & Walker, 1993; Bergström & Skarpe, 1999; Augustine, 2003; Sankaran *et al.*, 2008; Belay & Moe, 2012).

2.1.1 Climate

Savanna distribution is ultimately determined by climate, since climate primarily determines and effects the role of fire and herbivory in ecosystems (Scholes & Walker, 1993; Bond & Keeley, 2005; Bond *et al.*, 2005; Augustine & McNaughton, 2006). Savannas occur in hot regions and have strong seasonality of precipitation (with wet, hot summers and mild, dry winter periods) and no or usually low occurrence of frost (Teague & Smit, 1992; Scholes & Walker, 1993; Venter *et al.*, 2003; Mucina

& Rutherford, 2006). Prolonged hot dry seasons allow for frequent, hot fires that are necessary for the maintenance of the tree-grass mixture (Scholes & Walker, 1993; Higgins *et al.*, 2000; Sankaran *et al.*, 2004). Most of the savanna area in South Africa has a distinct dry season and receives less than 50 mm of rain in each of the months of June, July and August (Scholes, 1987; Mucina & Rutherford, 2006). The bulk of the rainfall falls between October and April (Venter *et al.*, 2003; Scogings *et al.*, 2012). Annual primary production in semi-arid savannas strongly correlates with annual precipitation, which has a mean value in the range 250-700 mm (Scholes, 1987). The mean annual temperature exceeds 20 °C, while the mean minimum of the coldest month exceeds 5 °C (Scholes, 1987; Scogings *et al.*, 2012). Rainfall of semi-arid savannas is highly variable (Belay & Moe, 2012) over space and time and complex interactions with the variability in precipitation and other factors such as herbivory and soil nutrients (Augustine, 2003; Augustine & McNaughton, 2006) drive changes in vegetation dynamics, i.e. production and species composition (Fynn & O'Connor, 2000).

2.1.2 Soil

Soil conditions are to a large extent considered the key factors which determine and control savanna type, and both biotic and abiotic diversity in the savanna ecosystem, at any given point (Venter, 1986; Scholes & Walker, 1993; Venter *et al.*, 2003). Since the early 1970's knowledge pertaining to the distribution and properties of soil has increased significantly, and it is now known that the relationship between soil and vegetation in the drier regions with intermediate rainfall, such as savannas, is much closer than in regions with high rainfall (Scholes & Walker, 1993; Venter *et al.*, 2003; Mucina & Rutherford, 2006). African savanna vegetation is underlain with various soil types. This is attributed to the interaction of varied parent material with weathering regimes of different durations and intensities (Venter, 1986; Scholes & Walker, 1993; Venter *et al.*, 2003). The generally low content of organic matter in savanna soils can be attributed to the high temperatures, causing organic matter to decompose at high rates (Scholes & Walker, 1993). Local influences of soil properties, i.e. texture, moisture level, nutrient status and spatial and temporal variability, may have a marked influence on the pattern and type of tree-grass coexistence in an area (Scholes & Archer, 1997; Jeltsch *et al.*, 2000; Van Wilgen *et al.*, 2003; Sankaran *et al.*, 2004; Mucina & Rutherford, 2006). For instance, archaean granite and gneiss weather into sandy soil in the uplands and clayey soil with high sodium content in the lowlands (Venter *et al.*, 2003; Grant & Scholes, 2006; Mucina & Rutherford, 2006; Siebert & Eckhardt, 2008). Through the understanding of savanna soil properties and distribution, an understanding of further savanna ecosystem features and processes become possible (Venter *et al.*, 2003).

2.1.3 Vegetation structure and growth forms

A combination of different life-forms, i.e. forbs, grasses, shrubs and trees (Sankaran *et al.*, 2008; Belay & Moe, 2012), together with highly variable wet and dry seasons over time and space (Augustine, 2003), distinguish savanna structure and function from that of other biomes (Scholes & Archer, 1997; Bergström & Skarpe, 1999). Most savannas have a relatively continuous, often grass-dominated, herbaceous layer, and a significant but discontinuous woody plant layer above (Scholes, 1987; Belsky *et al.*, 1989; Skarpe, 1991; O'Connor, 1996; Mucina & Rutherford, 2006). The woody layer can be divided into a shrub and tree layer, or alternatively a regenerative and mature plant layer (Scholes, 1987). The non-graminoid component of the herbaceous layer, i.e. forbs, makes out a third growth form in savannas and may be prominent at times, particularly following episodes of disturbance, such as herbivory or drought (Scholes, 1987). It may constitute an important component of ungulate diets at certain times of the year (Scholes, 1987).

Water is the main limiting growth factor in drier areas, and a physical factor such as soil determines the rainfall efficiency and ultimately vegetation composition (Bergström & Skarpe, 1999; Mucina & Rutherford, 2006). There is often a significant correlation between vegetation patterns and soil types as seen in the KNP (Venter *et al.*, 2003; Mucina & Rutherford, 2006).

2.1.4 Heterogeneity

The KNP falls within the Savanna Biome of southern Africa and is one of the few remaining natural areas where spatial heterogeneity and ecological responses still function unhindered over time and space (Foxcroft & Richardson, 2003; Pickett *et al.*, 2003). The savanna of the KNP possesses a diverse assemblage of igneous, sedimentary and, metamorphic rocks, and the diversity of parent materials weather into a large variety of soil types, supporting different plant communities and animal populations (Venter *et al.*, 2003). Heterogeneity is defined by Pickett *et al.* (2003) as the degree by which a set of factors differ from one another, yet a definition of this nature is not suitable for the complete understanding or management of a complex ecosystem such as the KNP (Pickett *et al.*, 2003). Savanna heterogeneity, which can be expressed as the variety of plant communities and habitat assemblages, is determined by variation in environmental factors such as topography, soil conditions, fire regimes, competition, rainfall, distribution of surface moisture and herbivory, and may change the structure and diversity of landscapes in nature reserves, driving spatial and temporal heterogeneity (Baker, 1992; Bergström & Skarpe, 1999; Van Wilgen *et al.*, 2003; Scogings *et al.*, 2012). Increased

heterogeneity leads to increased species richness as a result of niche differentiation, allowing for more species to inhabit the same site (Moquet *et al.*, 2002). Savannas are in general not regarded as extremely diverse ecosystems, but all biotic types do in many cases show species richness above the global average (Scholes & Walker, 1993). Heterogeneity is the main pattern of every landscape and is produced by different processes of which fragmentation and disturbance are particularly influential (Farina, 2007a). Heterogeneity is considered the source of biodiversity and drives ecosystem function, richness and productivity, and must therefore be the ultimate focus of ecological management and restoration (Pickett *et al.*, 2003).

The structure and composition of savannas are highly sensitive to changes in climate and land use (Sankaran *et al.*, 2008). Spatial patterns and relative abundance of vegetation are dictated by dynamic and complex interaction among geological substrates, variability of wet and dry cycles, the rich mega-fauna and the role of fire and these elements combined make the KNP an ideal setting to study heterogeneity and its role in savanna ecosystems (Pickett *et al.*, 2003).

Natural riparian zones are some of the most heterogeneous and complex terrestrial habitats on the planet, and differs from surrounding and upland habitats regarding moisture content, soil, microclimate, topography and vegetation structure and productivity (Naiman & Décamps, 1997; Pettit & Naiman, 2007a). Therefore, riparian zones are described as highly heterogeneous habitats in time and space, having complex disturbance regimes (Pettit & Naiman, 2007a). Worldwide, riparian zones are recognized as among the most important and threatened ecological resources with critical conservation concern (Sabo *et al.*, 2005; Bechtold & Naiman, 2006). They not only filter agricultural contaminants, but buffer landscapes against erosion, support high productivity and biodiversity, and serve as a landscape corridor which mediates the movement of organisms and aquatic-terrestrial exchanges (Hood & Naiman, 2000; Sabo *et al.*, 2005; Bechtold & Naiman, 2006; Jacobs & Naiman, 2008).

Sodic patches, another unique feature of many semi-arid toposequences, form as a result of sodium accumulation on footslopes of undulating granitic landscapes due to evapotranspiration and catena processes (Venter, 1990; Khomo & Rogers, 2005; Jacobs & Naiman, 2008). Sodic patches are described as a complex boundary, both in space and time, with upland vegetation (Dye & Walker, 1980; Khomo & Rogers, 2005). Distribution of these patches is worldwide, predominantly in the arid and semi-arid regions of North America, Australia and Africa (Khomo & Rogers, 2005). Sodic patches are referred to as 'nutrient hotspots' as they produce high quality forage (Khomo & Rogers, 2005; Grant & Scholes, 2006). Despite their ecological significance, sodic patches are often

considered as desolate land because of their disturbed appearance and low aesthetic value (Khomu & Rogers, 2005) caused by overgrazing, which in turn impacts on herbaceous species diversity, richness and biomass (Jacobs & Naiman, 2008). Areas such as sodic patches play a vital role in conservation and monitoring design, as it indicates core areas for monitoring programmes, that will help give accurate representations of resource availability to large herbivores (Grant & Scholes, 2006).

2.2 Fire as a driver of ecosystem heterogeneity

Many of South Africa's national parks are prone to fire, making it an important facet to take into consideration when it comes to biodiversity management of African savanna ecosystems (Bond, 1997; Govender *et al.*, 2006; Van Wilgen *et al.*, 2011). Fire is one of the key agents for shaping 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, 2007b; 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, the carbon cycle and climate (Baker, 1992; Bond & Keeley, 2005; Bond *et al.*, 2005; Bowman *et al.*, 2009; Staver *et al.*, 2009). Frequency, season, intensity and the type of fire is usually used to characterize fire regimes of fire-prone ecosystems, and the effect fire has on vegetation is dependent on the combined effects of these components (Enslin *et al.*, 2000; Govender *et al.*, 2006).

Unlike soil and rainfall, management of fire is both possible and necessary (Archibald *et al.*, 2005). Although fire is usually considered a disturbance, it differs from other disturbances, i.e. cyclones and floods, by feeding on complex organic materials, converting it to organic and mineral products (Bond & Keeley, 2005).

2.2.1 The evolution of fire management in the Kruger National Park

The KNP has a long history of fire management (Van Wilgen *et al.*, 2011). Over the past 75 years fire management in the KNP reflects the evolution of an understanding of the role of fire (Van Wilgen *et al.*, 2003).

After the park's proclamation in 1926, burning was occasional and limited until 1948 (Van Wilgen *et al.*, 2000). Prescribed burning was stopped between 1948 and 1956, and firebreaks were stationed to help control the spread of wildfires (Van Wilgen *et al.*, 2000). Veld-burning experiments were initiated in 1954 in four of the six major vegetation zones in the KNP, together with the development of an extensive network of firebreak roads, eventually leading to the park being divided into 400 burn blocks (fixed management areas) (Enslin *et al.*, 2000; Van Wilgen *et al.*, 2000; Mabunda *et al.*, 2003).

Prescribed burning took place for a period of 36 years between 1956 and 1992 (Van Wilgen *et al.*, 2003; Van Wilgen *et al.*, 2011). In the late 1980's a majority of managers supported the idea of wilderness ecosystem management and therefore a policy of natural fires was adopted in 1992 (Van Wilgen *et al.*, 2000; Van Wilgen *et al.*, 2003). According to this policy, all fires caused by lightning were allowed to burn freely, while all other fires were prevented, suppressed or contained (Van Wilgen *et al.*, 2003).

With the help of experimental burning plots in KNP, fire intensities have been recorded for more than two decades (Govender *et al.*, 2006). Three periods are recognized in the fire history of the Kruger: the time preceding 1956 where the KNP was protected from fire; the period from 1957 to 1991 where prescribed burning was actively practiced and the time from 1992 where only the natural ('lightning fires') were allowed to burn (Van Wilgen *et al.*, 2000).

In the early 1990's the KNP adopted a heterogeneity paradigm, with variability as the central concept (Mentis & Bailey, 1990; Rogers, 2003; Van Wilgen *et al.*, 2011). This approach coincided with the introduction of adaptive management in the KNP, seeking to diversify the range of fire intensities achieved in the management of fires (Govender *et al.*, 2006; Van Wilgen *et al.*, 2011). Currently the KNP's fire policy aims for the stimulation of a range of fire frequencies and intensities over space and time (Smit *et al.*, 2012).

2.2.2 Sources of fire variability in the Kruger National Park

Fires are highly variable in frequency, season and intensity, and no two fires are the same, yet can have significant effects on vegetation (Van Wilgen *et al.*, 2003; Govender *et al.*, 2006). Fires influence ecosystem dynamics and heterogeneity and are dependent on fuel and climate which vary over time and space, therefore fire cannot be considered alone (Van Wilgen *et al.*, 2003). Important

sources of variability include soil fertility, rainfall, herbivory levels and the variation in the conditions under which fires burn (Van Wilgen *et al.*, 2003). Fire frequency, intensity and season interact, and enable the coexistence of trees and grasses in savannas (Smit *et al.*, 2012). Variability in climatic conditions influence the conditions suitable for the initiation and spread of fires, while herbivores can cause a reduction in fuel loads and fire intensity, or may even prevent fires (Van Wilgen *et al.*, 2003).

Fuel loads are an important variable which contributes to fire intensity (Govender *et al.*, 2006), and can at any given time vary between zero and 10 000 kg/ha⁻¹. Fires will not carry when fuel loads are below 2 000 kg/ha⁻¹ (Van Wilgen *et al.*, 2003). In savanna ecosystems, grass fires occur as a result of build-up of herbaceous biomass in the wet season followed by an extended dry season leading to a continuous cover of fuel and sources of ignition, i.e. human and lightning (Higgins *et al.*, 2000).

In KNP variation in soil and soil fertility is mainly found between granite (nutrient poor) and basalt derived soils (nutrient rich). Areas occurring on granitic substrates, located closer to rivers, have more heterogeneous fire regimes (Smit *et al.*, 2012). Total annual rainfall can vary from < 200 to >800 mm in a given year. Overlapping of these sources of variation produces different quantities of grass fuels on different soil types (Van Wilgen *et al.*, 2003). Fuel build-up occurs more rapidly in nutrient-poor areas, since less palatable grasses tend to dominate the sward and grazing pressure tends to be lower, whereas areas with lower rainfall and higher soil fertility are dominated by more palatable grasses, leading to a reduction in fuel build-up as a result of higher grazing pressure and fire intensities are lower (Govender *et al.*, 2006). Fires occur less frequently in riparian zones as a result of patchiness of fuel loads and higher fuel moisture content (Smit *et al.*, 2012).

Fire and grazers are in direct competition for grass fuels, however the numbers of grazers fluctuate in response to rainfall (Van Wilgen *et al.*, 2003). Fire and grazing influence each other on a landscape scale, which makes it difficult to determine the effects of fire-grazing interactions on grass communities and very little is known about the interaction between these two agents of disturbance, however, large-scale foraging patterns are changed by fire, while grazers reduce fuel loads and alter the spread of fire in a landscape (Archibald *et al.*, 2005). When grazing density is low, grass biomass is incompletely consumed and builds up as fuel, resulting in widespread and hot dry-season fires which burn more area at a higher intensity (Belsky, 1995). These high intensity fires exterminate trees at the edge of woodlands, prevent woody regeneration and destroy bush thickets, consequently causing a reduction in woodlands and an increase in grasslands (Belsky, 1995). Conversely, when grazing populations expand, grass that would otherwise fuel fires would be consumed and the occurrence, intensity and frequency of fires are less (Van Wilgen *et al.*, 2003).

2.2.3 Fire as an ecosystem driver in African savannas

Fire is an important factor determining ecosystem structure and composition, but also influencing total biomass and the maintenance and conservation of African savanna ecosystems (Archibald *et al.*, 2005; Bond & Keeley, 2005; Govender *et al.*, 2006; Higgins *et al.*, 2007; Sankaran *et al.*, 2008). Fire is an evolutionary force and is one of the first methods that people used to shape their environment (Bond & Keeley, 2005). The fire regimes of fire-prone ecosystems are usually described with respect to their frequency, season, intensity and type of fire (Govender *et al.*, 2006). African savannas are characterized by low intensity surface fires that spread by fuels adjacent to the ground, such as grass layers or dead organic material below tree canopies (Scholes *et al.*, 2003; Bond & Keeley, 2005; Govender *et al.*, 2006). Structural changes caused by fire influences various other abiotic characteristics, such as the microclimate and distribution of resources, i.e. nutrients and moisture (Ludwig *et al.*, 2004; Higgins *et al.*, 2007). These changes in turn have remarkable effects on biodiversity since organisms respond to microclimate and resource availability, and are directly influenced by woodland structure (Higgins *et al.*, 2007).

The effect of fire on vegetation is dependent on the combined effects of the different components of the fire regime (Enslin *et al.*, 2000). Plant communities are affected by fires through the large-scale periodic removal of biomass and the delivery of, in some cases, lethal temperatures to plant material (Van Wilgen *et al.*, 2003). Depending on the frequency and severity, fires can replace trees with shrublands or grasslands (Bond *et al.*, 2004). Regrowth after fires is short, palatable and nutritious, attracting animals into burned areas (Gureja & Owen-Smith, 2002; Archibald *et al.*, 2005). Two long-term consequences of this ‘magnet-effect’ are suggested, 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 (Archibald *et al.*, 2005). 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 (Archibald *et al.*, 2005).

Fires dilute the impact of grazing (Hobbs *et al.*, 1991; Archibald *et al.*, 2005). Grazers are spread more widely in the burned area and are attracted away from unburned grazed patches (Archibald *et al.*, 2005). Fire and grazing, two primary determinants of savanna dynamics have strong and opposing effects on pattern and diversity (Augustine, 2003). Fire sometimes competes with, replaces and, especially in savannas, acts together with herbivory (Van Wilgen *et al.*, 2003; Archibald *et al.*, 2005). The effects of fires are in many ways similar to those of herbivores (Bond & Keeley, 2005). Nevertheless fire differs from herbivory in that it consumes dead and living material, and plants that

are inedible for herbivores are commonly fuel for fires (Bond & Keeley, 2005). Most of the grasses in the KNP are perennial and resprouts from tuft bases after fires, while annual grasses regenerate from seed (Scholes *et al.*, 2003). If the soil is even slightly moist as a result of water carried over from the previous wet season, seepage from the upslope or recent rainfall, forage will be available in days, and herbivores will move into these patches immediately (Scholes *et al.*, 2003). This leads to the possibility of overgrazing if only a small fraction of the landscape is burned, specifically if the fire is preceded or followed by a long dry period (Scholes *et al.*, 2003).

The necessity of fire in the maintenance of savannas remains a conflicting issue (Van Wilgen *et al.*, 2003). The exclusion of fire from African savannas could potentially lead to an increase in woody biomass and the development of closed woodlands under the current climate, since tree cover is limited by fire (Van Wilgen *et al.*, 2003; Bond & Keeley, 2005; Govender *et al.*, 2006), and it is thought that this can be seen as evidence that fire is necessary for the maintenance of savannas (Van Wilgen *et al.*, 2003).

When fires are few, intensively utilized grassland patches would develop and spread, possibly leading to the invasion of grazing-tolerant lawn grasses (Archibald *et al.*, 2005). In systems where fires are frequent, these intensively utilized patches would not occur as commonly and tall, fast growing grasses that are grazing-intolerant, but highly flammable, would dominate the landscape (Scholes *et al.*, 2003; Archibald *et al.*, 2005). Fires would suppress the woody layer and cause a reduction in the height of dominant woody species on all soil types (Bond & Keeley, 2005). This suggests that both frequently and infrequently burned areas may be necessary for the conservation of biodiversity (Smit *et al.*, 2012).

2.2.4 The effect of fire on herbaceous species richness and diversity

Fire is a major factor and prominent feature in shaping savanna ecosystem species diversity (Van Langevelde *et al.*, 2003; Savadogo *et al.*, 2008). The effects of such a disturbance are highly variable and dependent on the type of plant community and its interaction with ecological factors within that specific community (Savadogo *et al.*, 2008).

Herbaceous vegetation may be either positively or negatively effected by fire, depending on fire intensity and severity, climate, topography and dominant vegetation type (Hoffman, 1999; Hargrove

et al., 2000; Garnier & Dajoz, 2001; Farina 2007a; Sheuyange *et al.*, 2005; Savadogo *et al.*, 2008; Smit *et al.*, 2012). Low intensity fires early in the dry season enhance colonization processes, inducing germination and flowering, leading to an overall increase in productivity as a result of litter removal, and the enhancement of nutrient, space and light availability (Savadogo *et al.*, 2008). Conversely, high intensity fires may alter the pH and osmotic conditions rendering it unfavourable for some species to germinate (Bond & Keeley, 2005; Savadogo *et al.*, 2008). Post-fire gaps may be prone to drought and causative of enhanced extinction processes as a result of increased exposure and evaporation, as well as reduced moisture availability at shallow depths where germination occurs (Savadogo *et al.*, 2008). Establishment and emergence of herbaceous species in savannas is considered to be inhibited by high fire intensities, causing increased seed mortality and therefore eventually decreased species richness (Savadogo *et al.*, 2008).

Fire removes waning vegetation and creates an opportunity for the establishment of species-rich plant communities that host rare species which may otherwise have been suppressed by dominant species (Masunga *et al.*, 2013). It has also been associated with increases in plant tissue nutrient quality, plant species composition, primary production and cover; however some studies have shown little or no significant effect of fire on soil, plant chemical properties or plant species richness (Jensen *et al.*, 2001; Masunga *et al.*, 2013). Van Coller *et al.* (2013) suggested that fire suppresses diversity and richness of herbaceous species in the sodic riparian zone of a semi-arid African savanna.

It is therefore difficult to predict or generalize exactly what the effect of fire will be on the species diversity and richness of the herbaceous layer, since it is influenced by so many variables and floristic monitoring over a longer time scale under similar conditions is required (Van Coller *et al.*, 2013).

2.3 Herbivory as a driver of ecosystems

Herbivores are considered as some of the key agents of disturbance, although they contribute to core focus areas of conservation as they drive ecosystem changes and shape species diversity (Savadogo *et al.*, 2008; Asner *et al.*, 2009; Burns *et al.*, 2009). Herbivory is an important ecosystem modifier, particularly in semi-arid African savannas, and influences ecosystem structure, function, dynamics, stability and resilience in many different ways (Bucher, 1987; Jacobs & Naiman, 2008; Waldram *et al.*, 2008). Grazing may change spatial heterogeneity of vegetation, and influence ecosystem processes and biodiversity (Adler *et al.*, 2001).

Large mammalian herbivores (hereafter herbivores) can be regarded as ‘ecosystem engineers’, since they can directly and indirectly regulate resource availability to other species, altering the physical state of biotic and abiotic materials, modifying, maintaining and creating habitats (Jones *et al.*, 1994; Waldram *et al.*, 2008). Too many or too few herbivores in a landscape may have marked non-trophic impacts and lead to losses in ecological functioning through changes in ecosystem structure, function and biodiversity (Waldram *et al.*, 2008; Asner *et al.*, 2009).

Ecosystem structure and function is influenced by herbivores through the alteration in standing biomass, woody and herbaceous plant diversity and soil characteristics (Jacobs & Naiman, 2008). A key interest to ecologists, and essential to well-balanced management practices, is to understand how large herbivores change terrestrial ecosystems, and more specifically, the impacts they have on species diversity, productivity and composition (Bråthen *et al.*, 2007; Shannon *et al.*, 2008).

2.3.1 *Herbivores in semi-arid savannas*

In the coevolution of African savannas and large herbivores, the latter acted, and still act, as main determinants of ecosystem structure and functioning in uplands as well as associated riparian areas (Jacobs & Naiman, 2008). Plants and herbivores of African savannas have coexisted for many years. This, together with the wide variety of organisms hosted by African savannas, makes them ideal for examining plant-animal interactions (Scholes & Walker, 1993).

Large herbivores have numerous direct and indirect effects on the savanna ecosystem, not only do they directly consume biomass, but affect ecosystems through, amongst others, trampling, urinating and trashing (Skarpe, 1991). On a world-wide scale, 12-13 % of savannas are formally protected by World Conservation Union (IUCN) standards, and much of the rich biodiversity of African savannas, including most large mammals, inhabit these protected areas (Buitenwerf *et al.*, 2011).

Local colonisation processes are enhanced by herbivores through improved dispersal of propagules, increased light availability and improved soil conditions, while they cause a reduction in the local extinction rate by consuming competitively dominant species and allowing more species that are functionally different to coexist (Savadogo *et al.*, 2008). Contrariwise, herbivores can reduce colonisation processes by consuming seeds and reproductive structures, while enhancing extinction

processes by preferentially consuming high-quality species, such as forbs, causing increases in abundances of a few species tolerable to high grazing pressure (Savadogo *et al.*, 2008).

A key mechanism in the maintenance of the functional properties of grazing systems in savannas is the migratory behavior of ungulate species (Augustine & McNaughton, 2006). Heterogeneity in the abundance and quality of food and minerals, as well as predation can lead to different types of migration (Bergström & Skarpe, 1999). Many large herbivore species of the semi-arid southern African savanna embark on long-distance movements, reacting upon the availability of food and water (Bergström & Skarpe, 1999). They choose their diets from an environment made up of plants or plant parts varying with respect to accessibility, nutrient value and anti-herbivore defense (Du Toit, 2003). Herbivores act as a primary disturbance reducing biomass and canopy cover of certain species, creating grazing patches, wallows and game paths, which leads to an increase in spatial and physical heterogeneity (Olff & Ritchie, 1998; Jacobs & Naiman, 2008).

Removal of grazing pressure causes significant reductions in herbaceous species richness, which can be attributed to the increase in grass biomass in the absence of herbivores (Jacobs & Naiman, 2008). This suggests that large herbivores are essential to sustain low levels of field biomass, allowing more functionally different species to coexist, and that increase of grass biomass appear to negatively influence forb species richness (Jacobs & Naiman, 2008). Selective and non-selective grazing or soil disturbance may potentially have an increasing or decreasing effect on plant species diversity, depending on the severity of grazing activity (Hartnett *et al.*, 1996).

The KNP is a leading natural protected area, both nationally and globally, yet, uncertainty still prevails with respect to the scales and geographic locations at which vegetation and ecosystem processes are impacted by large herbivores (Asner *et al.*, 2009). Results show that a loss of dominant herbivore species from grassland ecosystems in North America leads to a decline in species richness and diversity, and it is thought that the effects of herbivore losses in African savannas are likely to be more complex, yet recent advances show that losses of herbivores generally result in declines in plant diversity (Burns *et al.*, 2009; Van Coller *et al.*, 2013).

The responses of plant communities and species diversity in reaction to grazing by ungulates can be strongly influenced by management practices (Hickman *et al.*, 2004). Management of African savannas is being reinforced, posing a challenge to decision makers to find a balance between the

requirements of large herbivore populations and ecosystem sustainability and maintenance (Asner *et al.*, 2009).

2.3.2 Herbivory and fire

Fire and herbivory can act independently or together and when fire and grazing occur together, they generally have a collective effect on plant communities, both spatially and temporally (Savadoogo *et al.*, 2008; Masunga *et al.*, 2013). The manner in which these disturbances effect the system varies significantly, depending on the types of plant communities and their interactions with ecological factors such as soil and rainfall (Savadoogo *et al.*, 2008). It is widely known that fire and herbivory influence vegetation composition, annual aboveground net primary productivity and nutrient cycling (Archibald *et al.*, 2005). Very little is known about the interaction between these two agents of disturbance, since fire and herbivory have usually been studied independently (Archibald *et al.*, 2005; Masunga *et al.*, 2013). Perhaps this gap in the research is understandable, when one takes into account that fire and grazers interact at a scale that is much greater than the scale at which grazer and fire effects are normally studied (Archibald *et al.*, 2005). Ruthven *et al.* (2000) reported that both fire and grazing significantly increased forb cover, yet the interaction between them was non-significant.

Grazing is affected by fire through the large scale alteration in foraging patterns (Archibald *et al.*, 2005). Grazers are often attracted to recently burnt areas, feeding on post-fire short, palatable and nutritious regrowth, reducing fuel loads through consumption and trampling, lowering the fire frequency and intensity in a landscape (Archibald *et al.*, 2005; Savadoogo *et al.*, 2008). Grazers may indirectly affect their habitat through alteration of the fire regime, i.e. when grazers keep grasses short enough, they create biologically induced obstacles to stop fire spread, and potentially change the size, distribution and frequency of fires (Waldram *et al.*, 2008; van der Waal *et al.*, 2011).

Disturbance agents such as grazers are to a greater or lesser extent under human control, and the development of tools that predict vegetation change as a management function is an important goal (Holdo, 2007). For managers to achieve optimal sustainable usage of rangelands, an understanding of the dynamic interactions between herbivores, plants and the physical environment (e.g., fire) is required (Skarpe, 1991).

2.3.3 Herbivores and herbaceous vegetation

Herbivores base their choice of habitat on maximum quality or quantity of forage intake and minimum risk of predation, often having to trade-off between the two (Riginos & Grace, 2008). Available habitats for African savanna herbivores range from relatively open areas with only a few trees to dense, semi-closed woodlands (Riginos & Grace, 2008).

Elephant and giraffe have been known to alter ecosystems, causing the conversion of woodlands to scrubland or grassland states through suppressing and reducing the woody component (Young *et al.*, 2005; Levick & Rogers, 2007). Elephants alter the vegetation structure and composition of ecosystems through the removal of forage biomass, debarking of trees, breaking of branches, stems and trees, this in turn, has the potential to promote ecosystem heterogeneity (Kohi *et al.*, 2011). Elephants include both grasses and forbs in their diet, however research on how elephants effect the herbaceous layer is deficient (Young *et al.*, 2005). Finding a way to manage increasing elephant numbers in the KNP and elsewhere in South Africa, while satisfying stakeholders, interested parties and both the national and international public, remains a controversial issue (Owen-Smith *et al.*, 2006).

Grazing may alter the floristic composition of herbaceous species (Angassa, 2012). In general, it is assumed that herbivores promote plant diversity by directly consuming competitively dominant plant species and thereby lessening plant competition (Olf & Ritchie, 1998). Herbivory reduces biomass and canopy cover, which increases spatial heterogeneity and allowing for more species to co-exist (Jacobs & Naiman, 2008). It has been widely recognized that large herbivores enhance or at least maintain herbaceous species richness in rangelands with a balanced moisture supply due to the facilitation of herbivores to seed dispersal, while hoof action of ungulates create various soil microhabitats which in turn facilitate the establishment of less common plant species (Jacobs & Naiman, 2008; Riginos & Grace, 2008). Yet, other studies show that herbivores may sometimes have a weak or even negative effect on plant diversity (Olf & Ritchie, 1998). Therefore, their effect can be either positive or negative (Olf & Ritchie, 1998; Augustine & McNaughton, 2006).

The quantification of the relationships between large herbivores, species richness and biomass enhances our understanding of herbivores as ecosystem drivers and modifiers in savannas and riparian zones (Jacobs & Naiman, 2008). The hump-shaped relationship between biomass and species richness predicts that optimum herbaceous species richness will occur at intermediate levels of biomass or

grazing pressure (Figure 1) (Bhattarai *et al.*, 2004; Jacobs & Naiman, 2008). When biomass levels are high and grazing pressure is low, a few dominant species replace many species as a result of competition for light and resources (Jacobs & Naiman, 2008). On the contrary, when rangelands are heavily grazed, only a few species resistant to trampling are supported (Jacobs & Naiman, 2008).

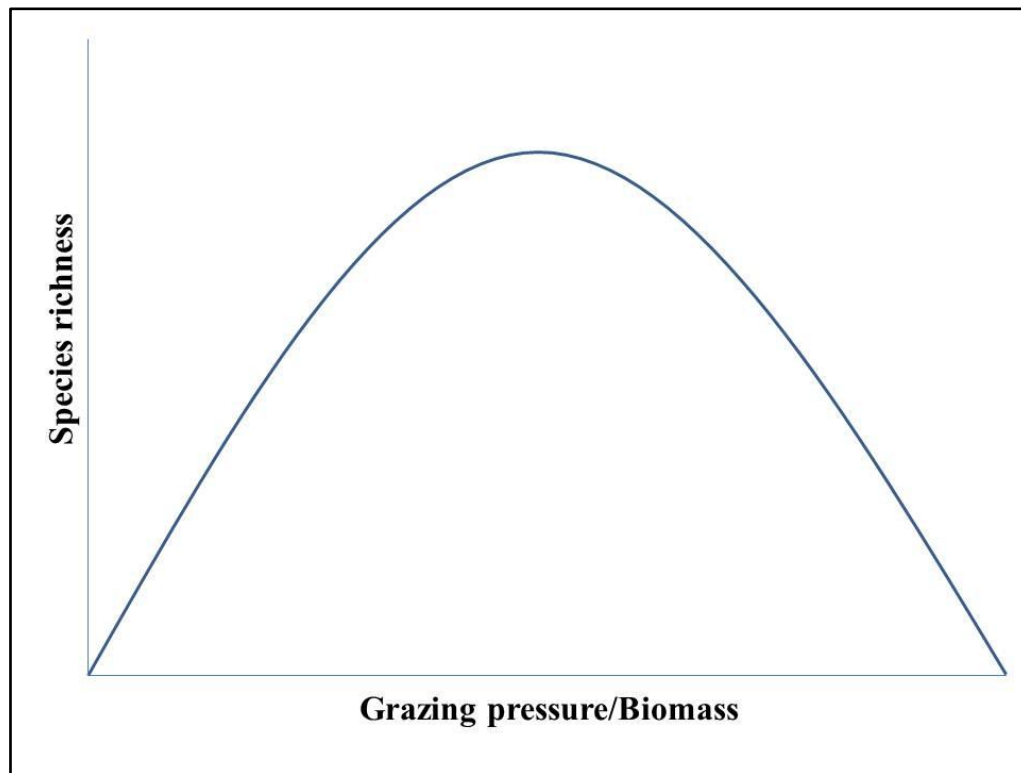


Figure 1. Hump-shaped response model between grazing pressure/biomass and species richness (Adapted from Oba *et al.*, 2001).

The generally wetter riparian zones are extensively utilized by herbivores, more specifically so in the drier seasons, when green forage is not as readily available anywhere else (Jacobs & Naiman, 2008). Jacobs and Naiman (2008) showed that increasing biomass in the riparian zone led to a loss of species, yet such a loss was not evident in the sodic zone. Van Coller *et al.* (2013) showed that, contrary to the intermediate disturbance hypothesis, the highest species richness occurred in areas with the highest disturbance and that increases in biomass as a result of the absence of herbivory suppresses the richness of the herbaceous species in the sodic zone.

The primary mandate of SANParks is to safeguard South Africa's biodiversity, landscapes and associated heritage sites in all its facets and fluxes on the land that they manage (Rogers, 2003; Van Wilgen *et al.*, 2011). Subsequently sustainable and ethical management of herbivores has become an

important factor in management efforts to restore and maintain the biodiversity, specifically in grasslands (Olf & Ritchie, 1998). An understanding of the role herbivores play in vegetation patterns of savanna ecosystems is urgently required (De Knecht *et al.*, 2008).

In a highly managed park, such as the KNP, changing of herbivore populations whilst trying to maintain ecosystem biodiversity can become controversial (Asner *et al.*, 2009). Interactions among the environment, society and different cultural values are intensifying, placing increased pressure on managers to base ecosystem management on comprehensive ecological principles (Naiman & Rogers, 1997). Research and management should integrate and develop this understanding in an organized knowledge management system (Rogers, 2003).

When herbivore numbers are too high or too low it can impact the ecological functioning of the system due to alterations in vegetation composition and structure, i.e. the removal of large herbivores may alter ecosystem functioning through an increase in biomass, leading to decreased herbaceous species richness (Jacobs & Naiman, 2008; Asner *et al.*, 2009). Herbivores are considered essential in savanna riparian zones to keep grass biomass low, allowing more herbaceous species to coexist (Jacobs & Naiman, 2008). When herbivores are excluded from savanna riparian zones, it leads to losses of game paths, feeding patches and wallows, consequently leading to increased homogeneity and decreased species richness, since heterogeneity is thought to promote the coexistence of herbaceous species (Jacobs & Naiman, 2008). In the sodic zone along the Sabie River, KNP, herbivory is considered to be the primary driver of herbaceous vegetation dynamics, suppressing biomass and maintaining higher levels of herbaceous species richness (Van Coller *et al.*, 2013).

2.4 Response models to relate biomass and species richness

Central to community ecology is the relationship between diversity and productivity, which is relevant in issues concerning effective conservation of biodiversity and the maintenance of ecosystem function (Michalet *et al.*, 2006). Plant species richness is regulated by disturbance, productivity and spatial heterogeneity (Pollock *et al.*, 1998.). The literature is abound with hypotheses and models attempting to explain patterns in species diversity (Shmida & Wilson, 1985; Chesson, 2000; Mittelbach *et al.*, 2001).

2.4.1 Intermediate disturbance hypothesis (*Hump-back response model*)

The relationship between plant species richness and biomass or productivity within groups of herbaceous plant communities which are amply heterogeneous, is commonly observed to be hump-shaped or unimodal, predicting that herbaceous species richness will be the highest at an intermediate level of biomass correspondent to moderate levels of competition or disturbance (Grime, 1973; Pollock *et al.*, 1998; DeForest *et al.*, 2001; Bhattarai *et al.*, 2004; Michalet *et al.*, 2006). The intermediate disturbance hypothesis (IDH) proposes that species show a hump or bell-shaped response along a stress gradient, limiting diversity at high levels of disturbance or stress, through low productivity at the one extreme, and by competitive exclusion at the other (Figure 2) (Grime, 1973; Milchunas *et al.*, 1988; DeForest *et al.*, 2001). The IDH is the most frequently suggested explanation for the relationship between species diversity and biomass in ecological communities (Roxburgh *et al.*, 2004).

2.4.2 Competitive exclusion

Volterra (1928) was the first to suggest the possibility for two or more species limited by the same resource to coexist indefinitely. Expanded by numerous authors, this theme has now become known as the ‘competitive exclusion principle’ (Armstrong & McGehee, 1980). This principle suggests that n species cannot coexist on fewer than n resources (MacArthur & Levins, 1964; Armstrong & McGehee, 1980) or in fewer than n niches (Rescigno & Richardson, 1965; Armstrong & McGehee, 1980) or when limited by fewer than n limiting factors (Armstrong & McGehee, 1980). Or stated more briefly by Hardin (1960), complete competitors cannot coexist.

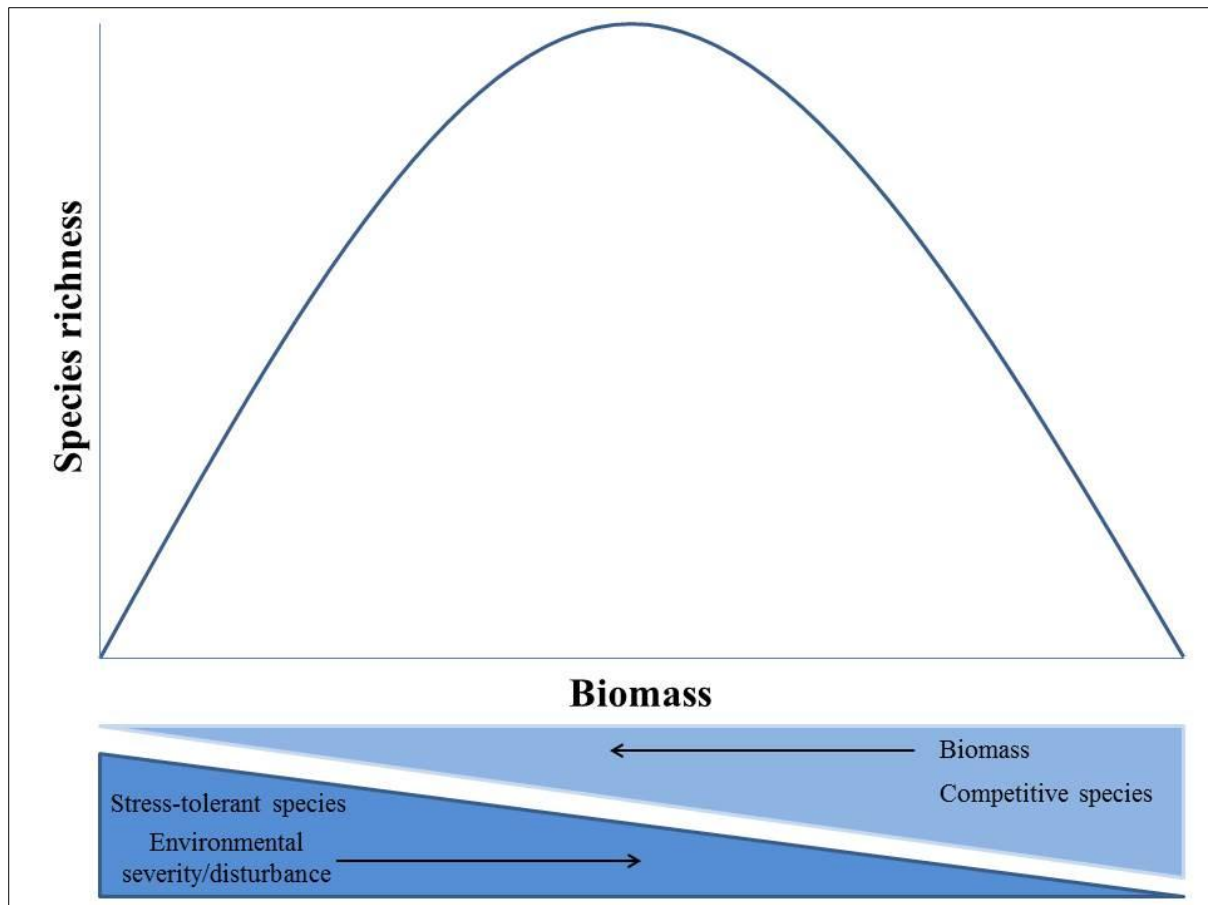


Figure 2. Illustration of the response of species richness to various levels of biomass and environmental severity or disturbance (Adapted from Michalet *et al.*, 2006).

2.4.2.1 Competitive exclusion in herbaceous vegetation

Dynamic interactions between colonisation processes from species pools at large spatial scales, and extinction as a result of competitive exclusion, which are influenced by disturbances, maintain local species richness and diversity of savanna ecosystems (Savadoogo *et al.*, 2008). Competitive exclusion assumes that one life-form will, over time, dominate resource usage as to virtually deplete it from the others (House *et al.*, 2003). Competitive exclusion among species becomes an important process in structuring plant communities when biomass levels increase and/or accumulate over time (Gough & Grace, 1998; Franklin *et al.*, 2002).

Competitive exclusion will occur when productivity is high, i.e. areas where mammalian herbivores are excluded from the system, and defoliation, disturbance and damage is of low intensity (Grime, 1973). This is consistent with the findings of Jacobs and Naiman (2008) that when mammalian

herbivores are excluded from the system, grass biomass shows a net increase and forb species are outcompeted for water, nutrients and light. Conversely, heavily grazed systems show reduced effects of competitive exclusion on diversity (Grace, 1999). Disturbances such as floods can strongly influence the competitive abilities of plants, i.e. during a flood plant species adapted to wetter conditions will have the competitive edge, but less so when water levels drop (Pollock *et al.*, 1998). Disturbances can therefore delay the rates of competitive exclusion, without destroying plant species, through changing the environmental conditions and therefore also changing the rate and direction of competitive exclusion (Pollock *et al.*, 1998).

Competitive exclusion will tend to drive the system away from an unstable equilibrium, i.e. the system will tend to become more homogeneous (House *et al.*, 2003). In essence, consumption by herbivores relax and/or counteract competitive interactions between plant species, allowing more species that are functionally different to coexist, in turn promoting system heterogeneity and species richness and diversity (Olff & Ritchie, 1998). Disturbances tend to favour less competitive species, allowing the coexistence of many species with different competitive abilities (Zobel, 1992).

In conclusion, higher numbers of species are able to coexist in intermediately stressful or disturbed environments than in fertile or highly productive environments, as a result of less competition in the environments with intermediate levels of stress and disturbance (Milchunas *et al.*, 1988; Zobel, 1992).

2.5 Effective management in SANParks

KNP is a leading natural protected area of South Africa and the world, with approximately 2646 plant and 147 large mammalian animal species, protected on roughly 2 million ha (Asner *et al.*, 2009). Distinct phases can be seen within the evolution of management practices in KNP (Roux & Foxcroft, 2011), including periods of elephant culling, large-scale water augmentation and fire manipulation (Asner *et al.*, 2009). Recently, management has shifted toward strategic adaptive management approaches, aiming to maintain biodiversity and vegetation heterogeneity for the populations within the park, through regular monitoring and feedback cycles as to update re-evaluation of objectives and techniques for the conservation of biodiversity (Asner *et al.*, 2009; Kruger & MacFadyen, 2011; Swemmer & Taljaard, 2011; Van Wilgen *et al.*, 2011).

Uncertainty within dynamic social-ecological systems is dealt with by managers through using the adaptive management approach (Holling, 2001; Roux & Foxcroft, 2011; Holness & Biggs, 2011). The principle of adaptive management is based upon a practice of ‘learning-by-doing’ in a scientific way, conforming and changing direction and behaviour as new knowledge becomes available (Roux & Foxcroft, 2011). Scientists and managers need to adapt and learn from their management actions for conservation of species and ecosystems to be successful (Kruger & MacFadyen, 2011).

Adaptive management has become an established research field and practice, and provides a structure for the enhancement of understanding, through the process of setting objectives, the implementation of policy decisions and the evaluation of the implications of outcomes to make future decisions, while recognizing the heterogeneity of ecological systems (Kruger & MacFadyen, 2011; Roux & Foxcroft, 2011). When an adaptive management approach is followed, policies become hypotheses and management practices become experiments to test those hypotheses (Roux & Foxcroft, 2011).

SANParks show a history of successful biodiversity conservation which can be attributed to the sound development of management strategies and the application of focused monitoring programmes (Swemmer & Taljaard, 2011). The implementation of the adaptive management approach has enhanced the effectiveness of the management for the biodiversity component of SANParks at numerous levels (Swemmer & Taljaard, 2011).

2.5.1 Long-term monitoring in KNP

To comprehend savanna vegetation dynamics, studies should be done at various spatial and temporal scales, using, depending on availability, data covering many years (Gillson, 2004). Long-term data is essential for understanding temporal and spatial changes in savanna vegetation, and will help with the development of attainable ecological management plans (Gillson, 2004). The interpretation of long-term data is often limited due to a lack in commitment to maintain the measurements at regular intervals over long periods of time (Clarke *et al.*, 2005). The KNP, with its remarkable long-term information base, is a leading example of how future conservationists should proceed (Du Toit *et al.*, 2003). Species are being lost at a higher rate than ever before in human history, placing substantial pressure on scientists, stakeholders, management and policy makers to provide necessary management strategies and to take appropriate action to conserve and protect natural resources to advance and develop the science-based adaptive management approach of SANParks (Cumming, 2007; Foxcroft & McGeoch, 2011; Roux & Foxcroft, 2011).

Understanding ecological processes that facilitate vegetation change is promoted by long-term measurements of floristic changes (Gillson, 2004; Clarke *et al.*, 2005). The effects of disturbance regimes, i.e. intensity, frequency, season and extent are difficult to unravel in arid and semi-arid environments, due to fluctuations in climate (Clarke *et al.*, 2005). Long-term data is necessary in this instance in recognizing fluctuations, not only in climate, but also other variables such as fire, grazing and invasive species (Clarke *et al.*, 2005; Lindenmayer & Likens, 2009).

Effective monitoring is vital in the adaptive management process (Grant *et al.*, 2011). Herbivore exclosures, erected along the Sabie and Letaba rivers in the KNP in 2001/2, as part of a long-term monitoring project, where vegetation changes due to herbivory and fire can be monitored, are valuable reference sites, and play an important role in understanding vegetation dynamics (O’Keefe & Alard, 2002; Siebert & Eckhardt, 2008; Grant *et al.*, 2011). Changes in ecological processes do not occur overnight, and these exclosures will provide valuable long-term information and insight on important ecological processes, that will not be possible to be obtained in any other manner (O’Keefe & Alard, 2002). Long-term monitoring and research can lead to improved management of ecosystems and natural resources, through the provision of important ecological insights (Lindenmayer & Likens, 2009).

2.9 Summary

Structure and function of savannas are determined by dynamic interacting factors such as fire and herbivory. A science-based model should be developed to understand these interactions, and to develop management plans in accordance with the adaptive management approach of SANParks.

Fire, being a major shaping agent of savanna ecosystems, can have variable effects, i.e. positive or negative, on the species richness and diversity of the herbaceous layer, depending on the type of plant community. The effect of fire on the richness and diversity of herbaceous vegetation in the sodic zone of African savannas is not yet known. It is also difficult to generalize and predict how fires will affect herbaceous vegetation richness and diversity, because it is influenced by many other variables, and more floristic monitoring of the herbaceous vegetation in the sodic zone is required. Like fire, herbivory is a key driver of savanna ecosystem heterogeneity and the effect thereof still remains a controversial issue. Herbivores are, however considered essential in savanna riparian zones to keep grass biomass low, and consequently promoting herbaceous species richness and diversity.

Finding a balance between the needs of large herbivores and the maintenance of vegetation and ecosystem diversity is becoming increasingly challenging for decision makers, since management of African savannas is being intensified. Studies are required to investigate the combined effects of fire and herbivory on semi-arid ecosystems, especially sensitive systems such as sodic plant communities. Sodic zones are often referred to as ecologically sensitive nutrient hotspots, producing high quality forage and consequently being overgrazed by large mammalian herbivores.

Indicated in this review of selected aspects regarding semi-arid savanna ecosystems, is the importance as well as the need for long-term monitoring, with the primary focus on the effects of fire and herbivory on the herbaceous vegetation of these generally overgrazed and bush-thickened systems.

Chapter 3

Study Area

3.1 Locality

The study was conducted at the Nkuhlu large-scale, long-term exclusion experiment (known as the 'Nkuhlu exclosures') situated on the northern bank of the perennial Sabie River (24°58'S, 31°46'E), approximately 18 km downstream from Skukuza in KNP, South Africa. The exclosures are 139 ha and divided into smaller units, each which is subjected to a different treatment of fire and herbivory (Siebert & Eckhardt, 2008). A detailed description of the experimental design is given in Chapter 4.

3.2 History

Research and ecosystem conservation is rated as two of the core activities by SANParks. Fire and herbivory often act together and therefore are considered important ecosystem modifiers, especially in semi-arid southern African savannas (Archibald *et al.*, 2005). Fire and herbivory are considered as dominant mediators of vegetation change in the KNP, and interact strongly with rainfall unpredictability and prolonged droughts (Du Toit, 2003). The impact of fire and herbivory on herbaceous biomass dynamics is, however, poorly understood (Archibald *et al.*, 2005; Jacobs & Naiman, 2008).

The floods of February 2000 provided a unique research opportunity in which the long-term development and recovery of riverine ecosystems after a major disturbance could be characterized (O'Keefe & Alard, 2002).

The Nkuhlu exclosures form part of the set of exclosures which were constructed in 2002 by SANParks in collaboration with a team of international scientists. The rationale behind the construction of these long-term experimental sites was to study the effect of floods, fire and herbivory on spatial and temporal heterogeneity of herbaceous and woody vegetation patterns (O'Keefe & Alard, 2002; Siebert & Eckhardt, 2008).

3.3 Topography

The landscape of the study area is undulating, ranging in altitude between 200 m and 230 m above sea level. Typically of landscapes originating from granite and gneiss, this heterogeneous terrain includes a complete sequence of terrain morphology from footslope to crest (Scogings *et al.*, 2011). On a national scale, the Nkuhlu exclosures are located within the Granite Lowveld vegetation unit (SVI 3) of the Savanna Biome (Mucina & Rutherford, 2006). It is characterised by tall shrubland with few trees to moderately dense low woodland on deep sandy uplands. The herbaceous layer is dominated by the graminoids *Aristida congesta*, *Urochloa mosambicensis*, *Chloris virgata* and *Panicum maximum* (Siebert & Eckhardt, 2008). The riparian zone of the exclosures forms part of the Subtropical Alluvial vegetation unit (AZa 7), which is described by Mucina and Rutherford (2006) as having flat alluvial riverine terraces that supports a complex river channel morphology including marginal reed belts, as well as flooded grasslands, ephemeral herblands and riverine thickets.

3.4 Plant communities and vegetation

Plant communities of the Nkuhlu exclosures were described by Siebert & Eckhardt (2008), and revealed five main plant communities which include: 1) *Sporobolus nitens-Euclea divinorum* Dry Sodic Savanna; 2) *Enneapogon scoparius-Combretum apiculatum* Dry Mixed Savanna; 3) *Jasminum fluminense-Spirostachys africana* Riverine Forest; 4) *Echinochloa colona-Litogyne gariepina* Seasonal Pan and, 5) *Phragmites mauritanus-Vernonia glabra* River Reedbed. This dissertation will focus exclusively on the *Sporobolus nitens-Euclea divinorum* Dry Sodic Savanna. The *Sporobolus nitens-Euclea divinorum* Dry Sodic Savanna comprise of two sub-communities, namely the *Adenium multiflorum-Acacia grandicornuta* Sodic Bushveld and *Evolvulus alsinoides-Dichrostachys cineria* Sodic Patches (Figure 3) (Siebert & Eckhardt, 2008).

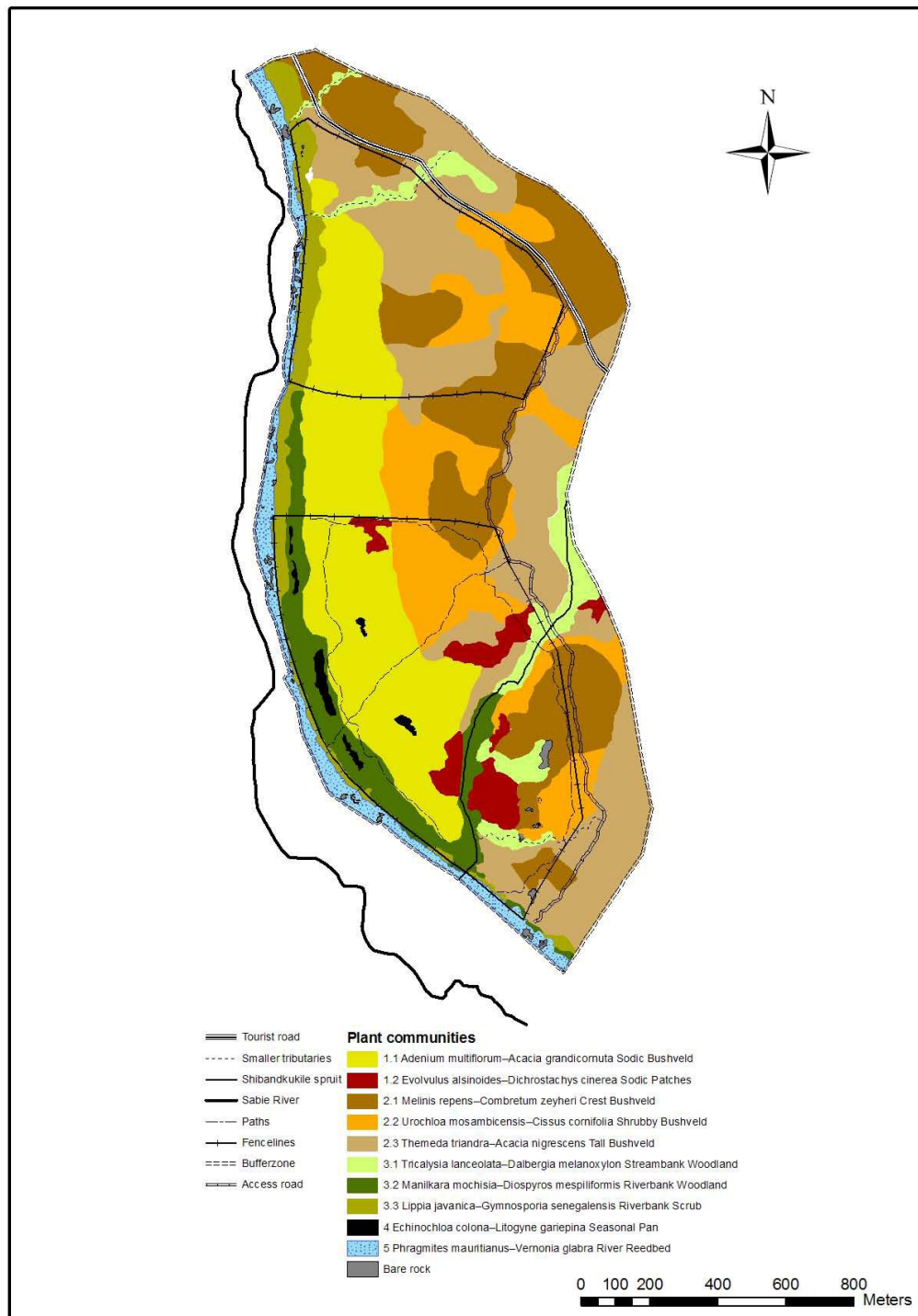


Figure 3. Vegetation map of the Nkuhlu research enclosure site (prepared by F. Siebert for SANParks).

The sodic plant community, as described by Siebert and Eckhardt (2008), covered roughly 23% of the total sampling area of the Nkuhlu enclosures. The sodic plant community supports distinct vegetation and herbivore activities that differ from those found on soil of the upland (Du Toit *et al.*, 2003). It

stretches across the different enclosure treatments (Van Coller *et al.*, 2013), and shows noticeable visual differences for herbivory and fire treatments.

The sodic plant community possesses a relative continuous herbaceous layer (Grant & Scholes, 2006) dominated by forbs such as *Abutilon austro-africanum*, *Portulaca kermesina* and *Ocimum americanum*, and graminoids, such as *Chloris virgata*, *Enteropogon monostachyus* and *Sporobolus nitens* (Siebert & Eckhardt, 2008), and a discontinuous woody component (Grant & Scholes, 2006) with abundant woody species such as *Acacia grandicornuta*, *Euclea divinorum*, *Spirostachys africana* and *Pappea capensis* (Scogings, 2011).

Vegetation of the sodic area is considered more palatable than crest vegetation (Scogings, 2011), which is why sodic patches are deemed ‘nutrient hotspots’ as they produce high quality forage for large herbivores, particularly grazers and mixed feeders (intermediate feeders) (Grant & Scholes, 2006; Scogings, 2011).

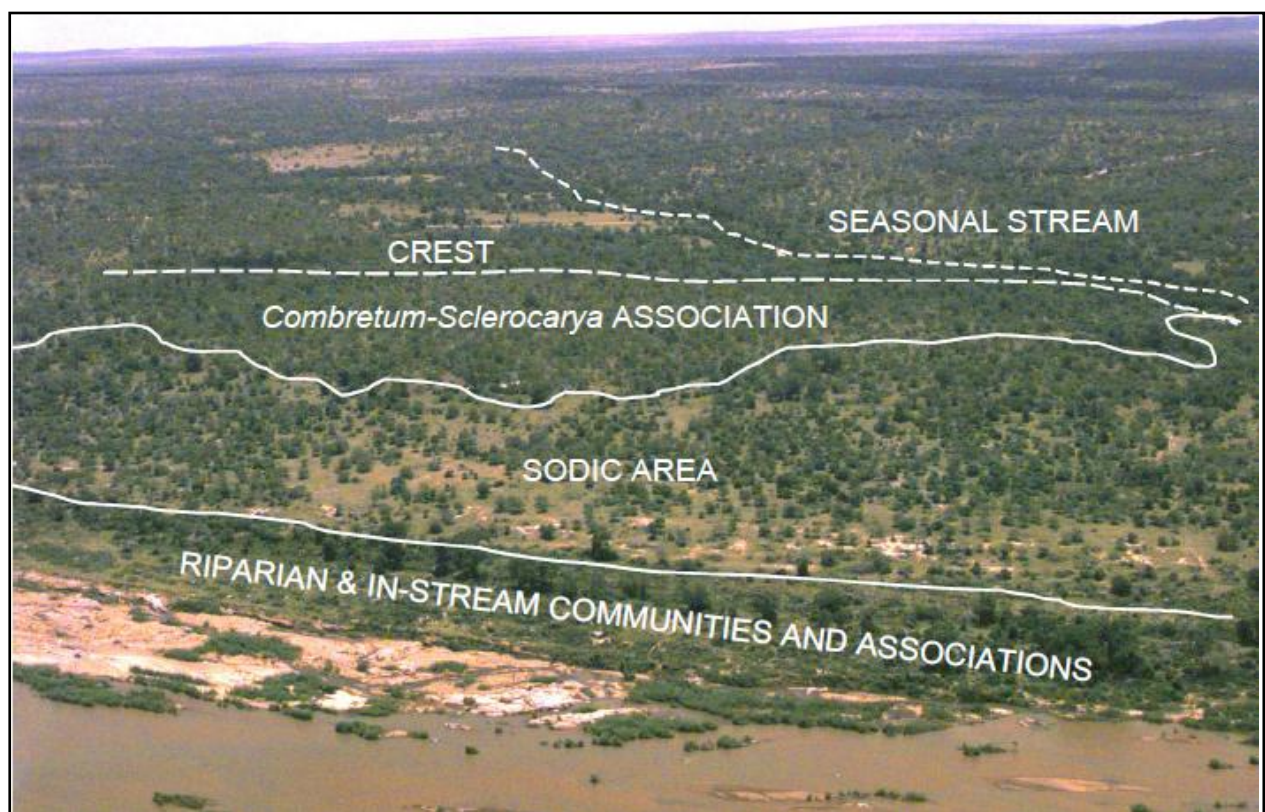


Figure 4. Aerial view of the vegetation communities in the Nkuhlu research enclosures (O’Keefe & Alard 2002).

3.5 Climate

3.5.1 Rainfall

This semi-arid, sub-tropical savanna has two distinct seasons: a hot, sporadically wet growth season from October to April and a warm, dry, non-growing season (Venter *et al.*, 2003; Scogings *et al.*, 2012). The south and central part of the KNP falls into the lowveld bushveld zone with a rainfall of 500-700 mm per year and potential evaporation of 6 mm per day in October (Venter *et al.*, 2003). The mean annual rainfall measured at Skukuza, 30 km west of Nkuhlu, is 561 mm (Siebert & Eckhardt, 2008; Scogings *et al.*, 2012). During summer months, the combined effects of moisture and heat cause thunderstorms that provide most of the rainfall (Venter *et al.*, 2003). Tropical cyclones occasionally penetrate from the warm waters of the Mozambique Channel, and produce half of the mean annual rainfall within a few days (Venter *et al.*, 2003).

3.5.2 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 °C mean minimum in winter to a mean maximum of 32.6 °C in the summer months (Siebert & Eckhardt, 2008; Scogings, 2011; Scogings *et al.*, 2012).

3.6 Geology

Granite underlies the study site, which weathered into a variety of soil types that support different plant communities and animal populations (Venter *et al.*, 2003). Archaean granite and gneiss weather into sandy soil in the uplands and clayey soil with high sodium content in the lowlands (Mucina & Rutherford, 2006).

3.7 Soil

Crests and midslopes are characterized by coarse, shallow, sandy soil overlying weathered rock, while footslopes below the seep-line are characterized by deep, duplex soil which is a distinctive pattern on catenas of granite-derived, semi-arid landscapes (Khomu & Rogers, 2005; Siebert & Eckhardt, 2008; Scogings *et al.*, 2012). The duplex soil on footslopes is referred to as the sodic zone.

The majority of the *Sporobolus nitens-Euclea divinorum* Dry Sodic Savanna community is underlain with the Montagu soil form (Mu (Figure 5)) (Siebert & Eckhardt, 2008). Montagu soil has calcium-

rich yellow-brown sandy clay loam subsoil, overlain by deep, grey-brown sandy loam topsoil (Siebert & Eckhardt, 2008).

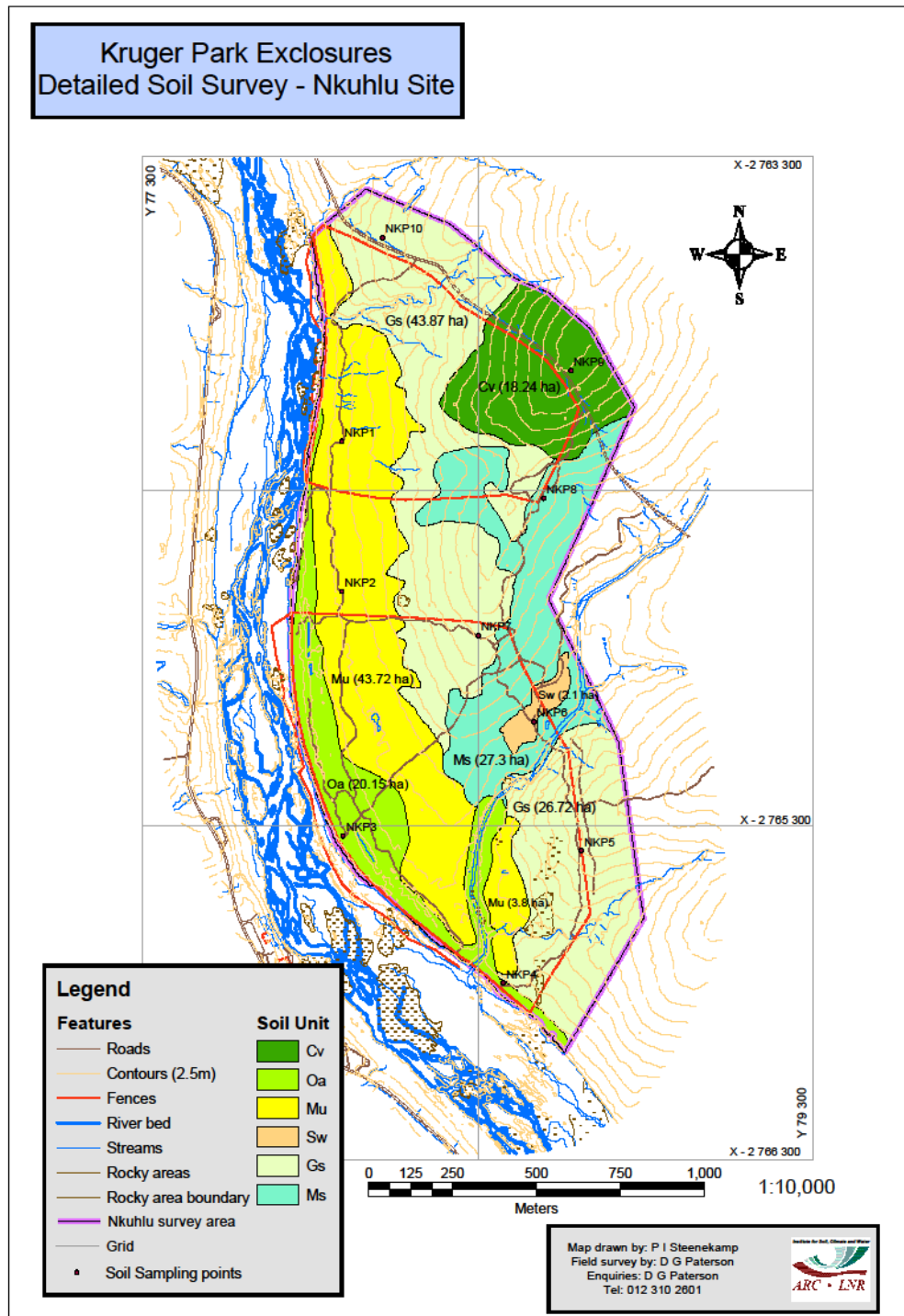


Figure 5. Soil map of the Nkuhlu research exclosures (ARC-Institute for Soil, Climate and Water, 2003).

Deep, duplex soils contain 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). 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 leading to poor plant growth and germination (Davis *et al.*, 2012).

Chapter 4

Materials and Methods

4.1 Introduction

This chapter offers general background information on the methods used during the study. Methodology of relevance to a specific research question is outlined and discussed in each Results & Discussion chapter respectively to avoid repetition and to accommodate the format of the dissertation.

4.2 Experimental design and sampling

The Nkuhlu research exclosures comprise 139 ha of semi-arid savanna in the riparian zone of the Sabie River and consist of three herbivory treatments, each divided into a fire and no-fire treatment, hence six treatment combinations (Figure 6). The herbivory treatments consist of a (1) partially fenced area (hereafter the partial exclosure) of 44 ha that was designed to specifically exclude elephant (giraffe are also excluded due to their body size), (2) an unfenced area or 'control site' (hereafter the open area) of 25 ha, and (3) a fully fenced area (hereafter the full exclosure) of 70 ha, which was designed to exclude all herbivores larger than a hare (Siebert & Eckhardt, 2008).

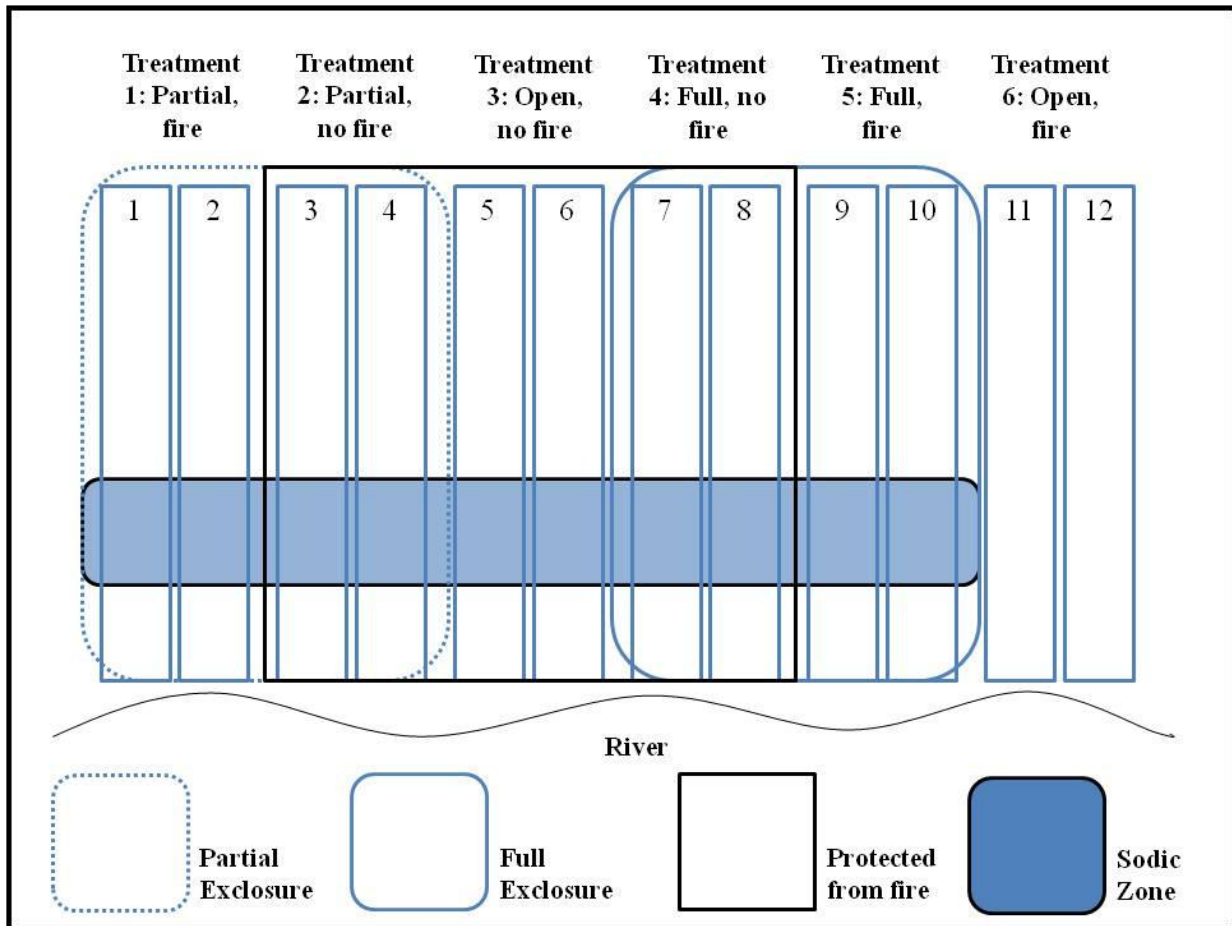


Figure 6. Experimental lay-out of 12 transects within six different fire and herbivory treatments of the Nkuhlu research exclosures. Treatment 6 was excluded from this study to include sodic sites only.

Floristic sampling, which conformed to the guidelines stipulated in the Field Operations Manual for Herbivore and Fire Exclosures (O’Keefe & Alard, 2002), was conducted during the 2010 rainy season (i.e. October to March, Van Wyk & Fairall, 1969) when plant cover was at its maximum and most plant species were present (Keller, 2002). All treatments were sampled, although only data from the sodic zone were analysed for this study. Since the sodic zone did not extend into the control site with fire, two transects could not be considered for floristic analyses (Figure 6). Each treatment of fire and/or herbivory consisted of two permanent transects (Figure 6). Transects stretched from the river to the crest of the catena and ran perpendicular to the Sabie River. Permanent transects were marked with metal droppers. Fixed plots were situated 5 m downstream from each transect dropper. The position of transects and plots were plotted on the vegetation map of the Nkuhlu exclosures (Siebert & Eckhardt, 2008) to identify plots that are representative of the sodic zone. Fixed transects have varying numbers of 10 m x 20 m plots (with longest side running parallel to the river channel) within each treatment. Data from 82 fixed plots were sampled within the sodic zone (Figure 7) and could be analysed to address the research questions of this study.

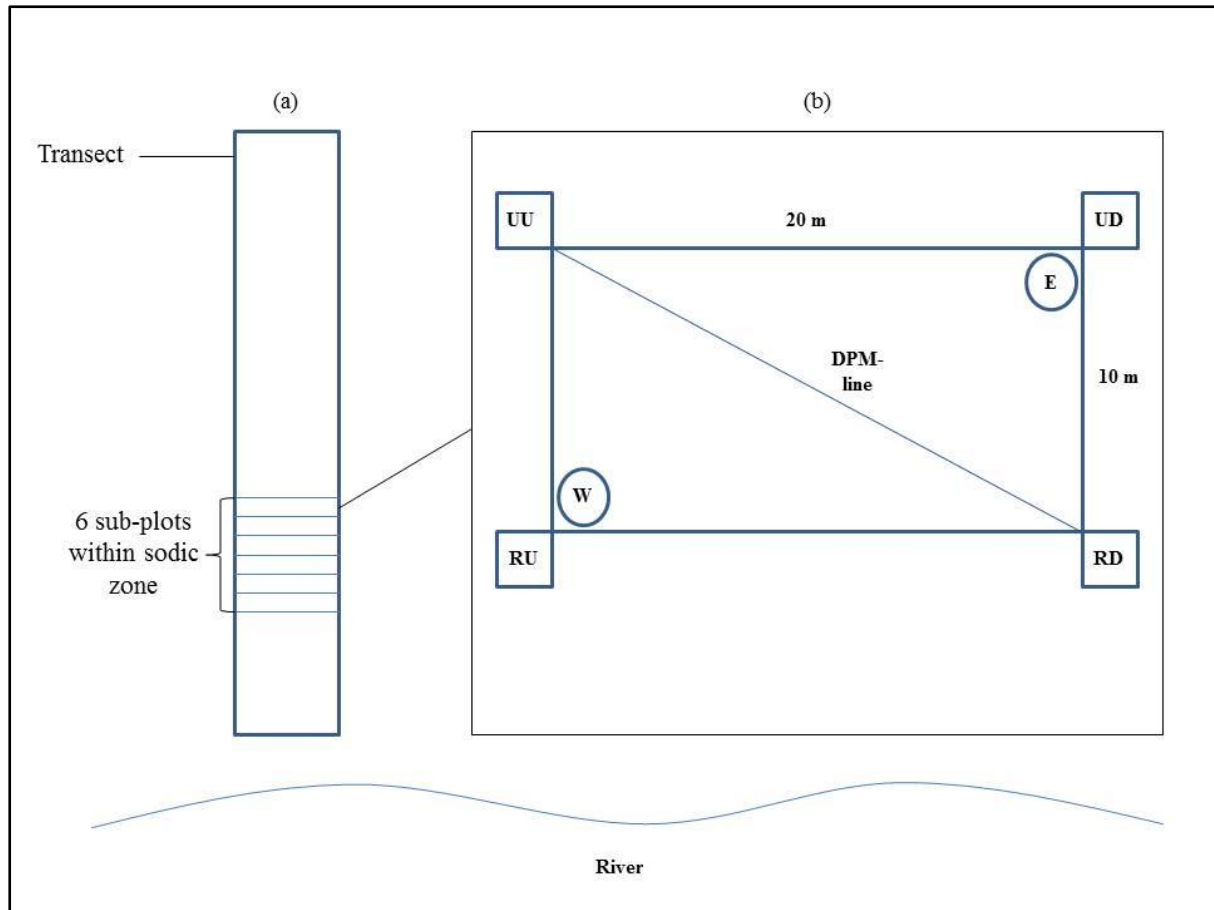


Figure 7. Experimental layout of (a) sodic plots within a typical transect at the Nkuhlu research enclosures experimental site, and (b) the position of 1 m² sub-plots for herbaceous species sampling and the diagonal sampling line for DPM readings within a fixed plot. Corners of each plot are permanently 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.

Two 1 m² circular sub-plots placed in the eastern (upland downstream) and western (river upstream) corners of each fixed plot respectively were used to sample herbaceous vegetation (Figure 7) (O’Keefe & Alard, 2002). Herbaceous individuals (forbs and grasses) rooted within the circle were counted and identified up to species level, conforming to Germishuizen and Meyer (2003). Estimation of biomass was done by taking 10 readings with a Lowveld Savanna-calibrated disc pasture meter (DPM) along the diagonal of the plot, (Figure 7) (Van Coller *et al.*, 2013). DPM-readings were then converted to kg/ha in accordance with the latest biomass conversions for the Lowveld Savanna (Zambatis *et al.*, 2006).

4.3 Data preparation

Data were captured and consolidated in a database in an Excel (Windows 2010) spreadsheet. The complete data matrix consisted of quantitative floristic (i.e. species and individual counts) and biomass data for each transect, across all treatments and plant communities for the years 2001 and 2010 (Siebert & Eckhardt, 2008). Plots that were sampled in the sodic zone were extracted from the master database. Data were then formatted to be imported into *PRIMER* 6 (2012) and *STATISTICA* (2012).

Herbarium specimens of unknown species collected during floristic sampling were sent to the National Herbarium, South African National Biodiversity Institute (SANBI) in Pretoria for identification.

4.4 Data analysis

Statistical methods are described in more detail in each chapter respectively, although an outline of the statistical approach is presented below:

Chapter 5: One-way Analysis of Variance (ANOVA) in combination with *post-hoc* pair-wise comparisons of treatments (Tukey unequal N HSD (Honestly Significant Difference) test) were applied to the 2010 dataset to determine whether (1) herbaceous plant species richness, diversity and biomass varied significantly across different fire and herbivory treatments and (2) whether increasing biomass, an artifact of herbivory and fire exclusion suppress diversity and richness of herbaceous vegetation in the sodic zone of the Nkuhlu research exclosures.

Chapter 6: (1) Repeated measures analysis of variance (ANOVA) in combination with the Bonferroni *post-hoc* significance test was performed on the data to determine if herbaceous species diversity, richness and biomass varied across fire and herbivory treatments over nine years (from 2001 to 2010); (2) Non-metric Multi-Dimensional Scaling (NMDS) analyses were done along with the application of the Bray-Curtis Dissimilarity Index to determine whether species composition shifted over time; (3) Similarity Percentage (SIMPER) method was applied to the data set to determine which species contributed most to dissimilarities in the herbaceous species composition over time along with Analysis of SIMilarities (ANOSIM) to test for significant differences in herbaceous species

composition over time (nine years); and (4) t-tests for independent samples by groups were applied to determine how abundances of dominant species within various fire and herbivory treatments changed over time.

Chapter 7: LOWESS (Locally Weighted Scatterplot Smoothing) regression provided a visual representation of the relationship between biomass and the different dependent variables, in combination with quadratic regression analyses to determine whether the quadratic relationship between herbaceous species richness/diversity and field biomass was significant.

Diversity indices and variables that were used in this study include total species (S), i.e. the mean number of species per circular sub-plot (1 m²); total individuals (N), i.e. mean total individuals per plot; Margalef's species richness (d), where $d = (S-1) / \text{Log } N$, and both Margalef's species richness and Pielou's evenness is highly sensitive to sample size (Warwick & Clarke, 1995); Pielou's evenness, also known as equitability, which is higher when the abundances of species in the sample is as equal as possible in the population (Kricher, 1972), various formulas may be used to calculate evenness, the formula used in this study was $J' = H' / \text{Log } (S)$, where H' is the species diversity index calculated with the Shannon-Wiener formula, and $\text{Log } (S)$ is the log of total species; Shannon-Wiener diversity index, which is sensitive to both species richness and the number of individuals (abundance) per species (Keller, 2002), where $H' = -\sum (p_i \ln p_i)$, and p_i is the relative abundance of the i^{th} species. This index provides a rough measure of diversity, which is much less biased by sample size than species richness; Simpson's index of diversity (1-Lambda), with the formula $1 - \sum (N_i(N_i-1)/N(N-1))$, where N is the mean total individuals per plot and N_i represents the number of individuals in the i^{th} species (Peet, 1974), and biomass converted to kg/ha according to Zambatis *et al.* (2006).

Even though different diversity analyses such as repeated measures ANOVA could be done in PAST (Paleontological Statistics software) (Hammer *et al.*, 2001), to determine a trend between them, this was not done for the purpose of this study, but will be incorporated for future publications.

Chapter 5

Sodic herbaceous species diversity turnover

5.1 Introduction

Sodic patches are often associated with footslopes of undulating granitic landscapes (Venter, 1990) and are commonly referred to as ‘nutrient hotspots’ as they produce high quality forage (Grant & Scholes, 2006). Deep, duplex soil containing dispersed clay with a low infiltration capacity and high concentrations of nitrogen, phosphorus and sodium characterise sodic patches (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). 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). Soil is classified as sodic when the SAR is above 13; at levels below 13, sodium can cause deterioration of soil structure and problems with water infiltration (Davis *et al.*, 2012).

Sodic patches form an integral part of savanna ecosystems because of the ecosystem services and functioning they provide, such as, (1) the accumulation of nutrients, (2) the provision of open spaces for predator vigilance and (3) the formation of wet season wallowing points (Khomo & Rogers, 2005). Furthermore, these key resource areas sustain animal body condition for dry season survival and support reproduction through nutritional benefits (Grant & Scholes, 2006). Despite their ecological significance, sodic patches are often considered as desolate land because of their disturbed appearance and low aesthetic value (Khomo & Rogers, 2005) caused by overgrazing, which, in turn, impacts on herbaceous species diversity, richness and biomass (Jacobs & Naiman, 2008).

Fire and herbivory are regarded as important ecosystem modifiers, especially in semi-arid southern African savannas, often acting together (Archibald *et al.*, 2005). Fire and herbivory are considered as dominant mediators of vegetation change in KNP and interact strongly with rainfall unpredictability and prolonged droughts (Du Toit, 2003). The impact of fire and herbivory on herbaceous biomass dynamics is, however, poorly understood (Archibald *et al.*, 2005; Jacobs & Naiman, 2008). The establishment of the Nkuhlu research exclosures in the KNP in 2001 provided an opportunity to study the spatial and temporal heterogeneity patterns within and around riparian zones, as well as how these

patterns are affected by herbivory and fire. By excluding these drivers from the system it is believed that their effects could be determined over time (O'Keefe & Alard, 2002).

Jacobs and Naiman (2008) were the first to report on the relationship between herbivory and species richness at the Nkuhlu research exclosures. After 2 years of herbivory exclusion, a marked increase in standing biomass was recorded, along with lower species richness in the absence of herbivores. These patterns were, however, less significant along the sodic zone (Jacobs & Naiman 2008). This chapter is therefore aimed at reporting on herbaceous plant species richness, diversity and biomass specifically along the sodic zone of the Nkuhlu research exclosures after an additional 5-year cycle of herbivory and fire exclusion.

The objectives of this study were to test (1) whether significant variation in herbaceous plant species diversity, richness and biomass could be detected across different combined treatments of herbivory and fire and (2) whether increasing biomass, an artifact of herbivory and fire exclusion, suppresses diversity and richness of herbaceous plant species in the sodic zone of the Nkuhlu research exclosures.

5.2 Methods

Vegetation of sodic soil is considered to be more palatable than crest vegetation as it is preferred by large herbivores, particularly grazers and mixed feeders (intermediate feeders) (Scogings, 2011). Large mammalian herbivores residing in the study area include browsers (giraffe (*Giraffa camelopardalis*), black rhino (*Diceros bicornis*), greater kudu (*Tragelaphus strepsiceros*) and the scrub hare (*Lepus saxatilis*)); grazers (Cape buffalo (*Syncerus caffer*), hippo (*Hippopotamus amphibius*), blue wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*)) and mixed or intermediate feeders (impala (*Aepyceros melampus*), African elephant (*Loxodonta africana*) and steenbok (*Raphicerus campestris*)) (Scogings *et al.*, 2012). The density of elephants in the study area fluctuates, but has been estimated and considered high at 0.5-2/ km² (Scogings *et al.*, 2012).

Fire treatment of the Nkuhlu research exclosures was dependant on whether the larger KNP burn blocks (fire management units) in which the exclosures lie, were burned irrespective of the source and the actual extent of the fire. Fires occurred in October 2002 and August 2007.

Herbaceous vegetation was sampled in two 1 m² circular sub-plots at the eastern (upland downstream) and western (river upstream) corners of each fixed plot respectively (Figure 8). Only herbaceous

individuals rooted within the circle were recorded. Each living individual (forbs and grasses) was counted and all species names conform to Germishuizen and Meyer (2003). The biomass of each plot was estimated with a Lowveld Savanna-calibrated Disc Pasture Meter (DPM) by taking ten readings along the diagonal of the plot, (Figure 8). These readings were converted to kg/ha according to the latest conversion of DPM-readings to biomass for the Lowveld Savanna (Zambatis *et al.*, 2006).

Two equations for DPM height groups (≤ 26 cm and > 26 cm) were proposed by Zambatis *et al.* 2006:

$$\text{kg ha}^{-1} = [31.7176 (0.3218^{1/x}) x^{0.2834}]^2 r = 0.9796; r^2 = 0.951; P < 0.0005 \quad [\text{Eqn 1}]$$

$$\text{kg,ha}^{-1} = [17.3543 (0.9893^x) x^{0.5413}]^2 r = 0.948; r^2 = 0.882; P < 0.0005 \quad [\text{Eqn 2}]$$

where x is the mean DPM height in cm of a site.

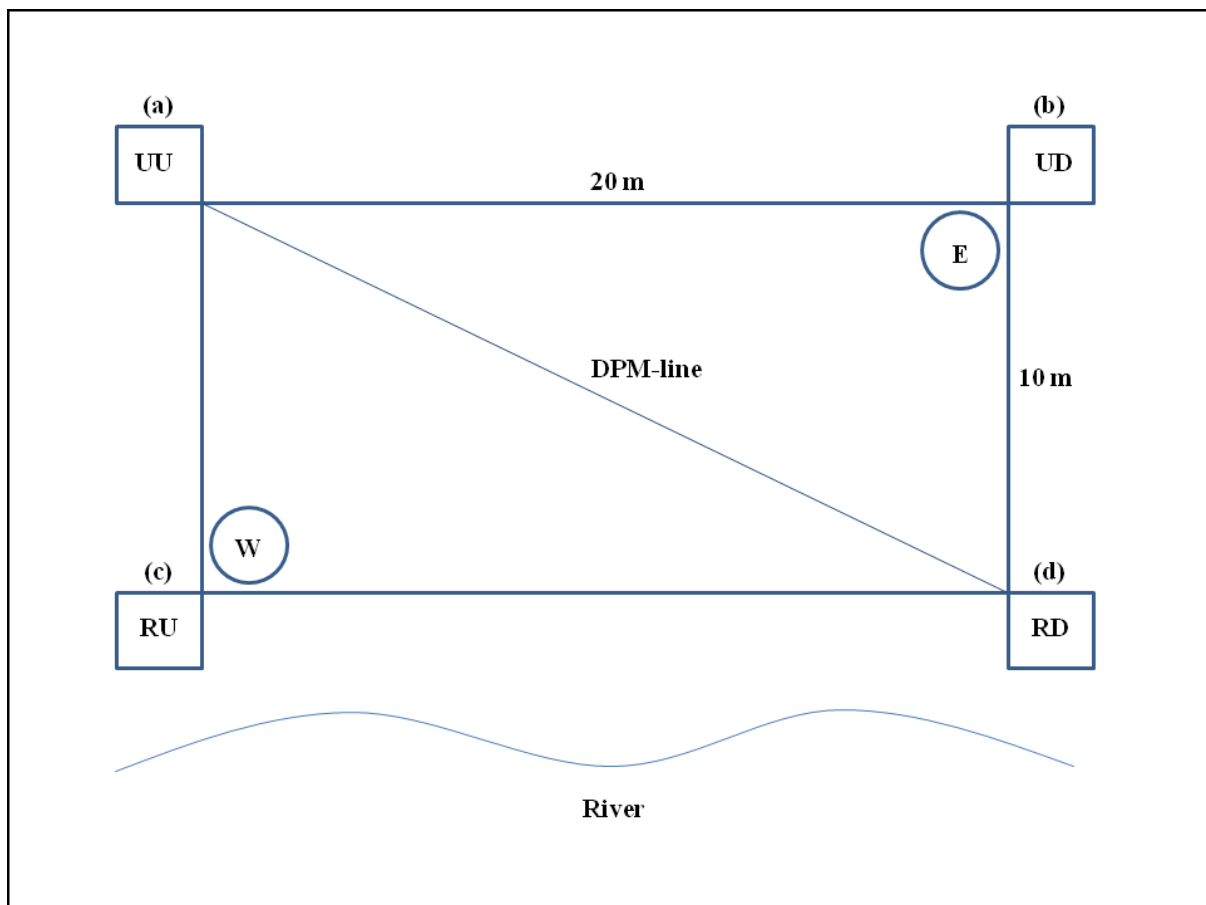


Figure 8. Positioning of the 1 m² sub-plots for herbaceous species sampling and the sampling line for DPM readings within a typical fixed plot along a transect at the Nkuhlu research exclosures. The corners of each plot are permanently marked with metal droppers which represent a different position

parallel to the Sabie River. Corners: UU, upland-upstream; UD, upland-downstream; RU, river-upstream; RD, river-downstream.

Species richness is the number of species present in a defined area (Begon *et al.*, 2006). In this study, richness was considered as the number of species per circular sub-plot (1 m²). Species diversity was calculated for the plots with the Shannon-Wiener Index of Diversity (H'), which is sensitive to both species richness and the number of individuals (abundance) per species (Keller, 2002). The greater the number of species and the higher the evenness (proportion of each species), then the higher the H'-value, which suggests that the diversity in the plot is high (Keller, 2002; Begon *et al.*, 2006). The function of Shannon-Wiener diversity index (H') used in this study is:

$$H' = -\sum (p_i \ln p_i) \dots \quad [\text{Eqn 3}]$$

where p_i is the relative abundance of the i^{th} species. This index provides a rough measure of diversity, which is much less biased by sample size than species richness.

To test for significant variation in species diversity, richness and biomass of the herbaceous layer among the five different treatments of fire and herbivory, One-way Analysis of Variance (ANOVA) was applied to the data set in Statistica version 10 (Statsoft 2010). Where statistically significant results were obtained, *post-hoc* pair-wise comparisons of the treatments (Tukey unequal N HSD (Honestly Significant Difference) test) were conducted.

5.3 Results

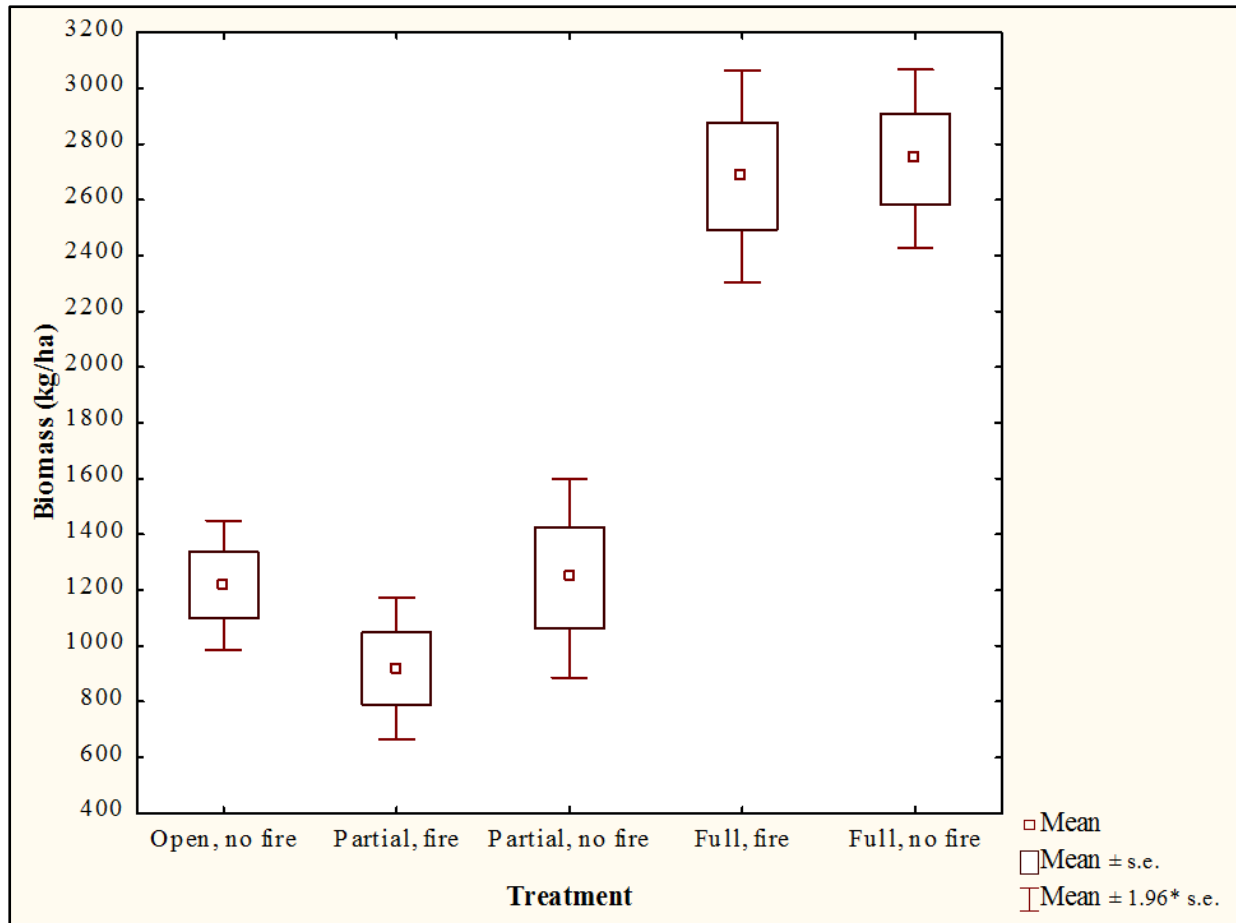
Analysis of variance (Table 1) for all variables revealed significant effects of herbivory, with or without fire, for both biomass ($p < 0.0001$) and species richness ($p = 0.0002$) across the different treatments, while the effects of herbivory, with or without fire, on species diversity was non-significant ($p = 0.4$).

Table 1. One-way ANOVA of the mean values for herbaceous biomass and species richness and diversity across treatments along the sodic zone of the Nkuhlu research exclosures, KNP.

Response	Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Biomass	Treatment	4	51135137.00	12783784.00	26.161340	< 0.0001
	s.e.	76	37137528.00	488651.70	26.161340	< 0.0001
Species richness	Treatment	4	2883.00	234.10	6.170180	0.0002
	s.e.	76	2883.00	37.94	6.170180	0.0002
Shannon-Wiener diversity index	Treatment	4	0.76	0.20	1.011267	0.4
	s.e.	76	14.00	0.19	1.011267	0.4

s.e., standard error; *df*, degrees of freedom; SS, sum of squared differences; MS, mean square; *F*, whether variability within and between treatments is significantly different; *p*, *p*-values below a certain threshold indicates the significant differences between groups.

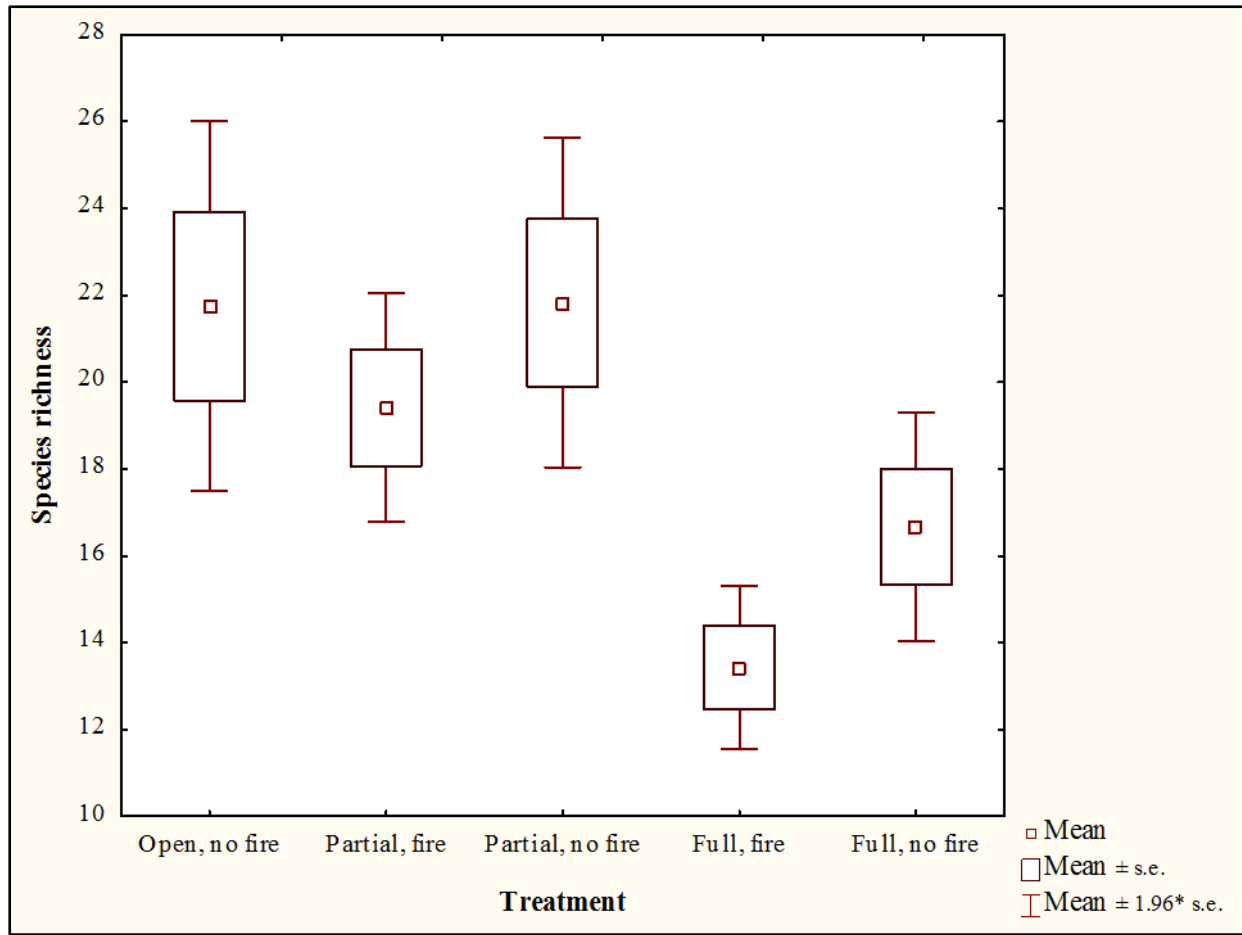
Mean biomass (kg/ha) varied significantly across treatments ($p = 0.0001$) (Table 1; Figure 9). As would be expected, mean biomass was highest in the fully fenced plots as a result of herbivore exclusion. In pair-wise comparisons of biomass means, significant differences were revealed between the control (i.e. open, no fire) site with unrestricted herbivory and the fully fenced area, both with (Tukey: $p < 0.05$) and without fire (Tukey: $p < 0.05$) treatment. Furthermore, both of the partial herbivore treatments showed significant differences compared to both fully fenced herbivore exclusion treatments. Although the effect of fire seems secondary to herbivory, mean biomass was consistently lower in the fire treatments (Figure 9).



± 1.96*, standard deviations of the mean; s.e., standard error.

Figure 9. Mean biomass ($p < 0.0001$) across fire and herbivory treatments in the sodic zone of the KNP.

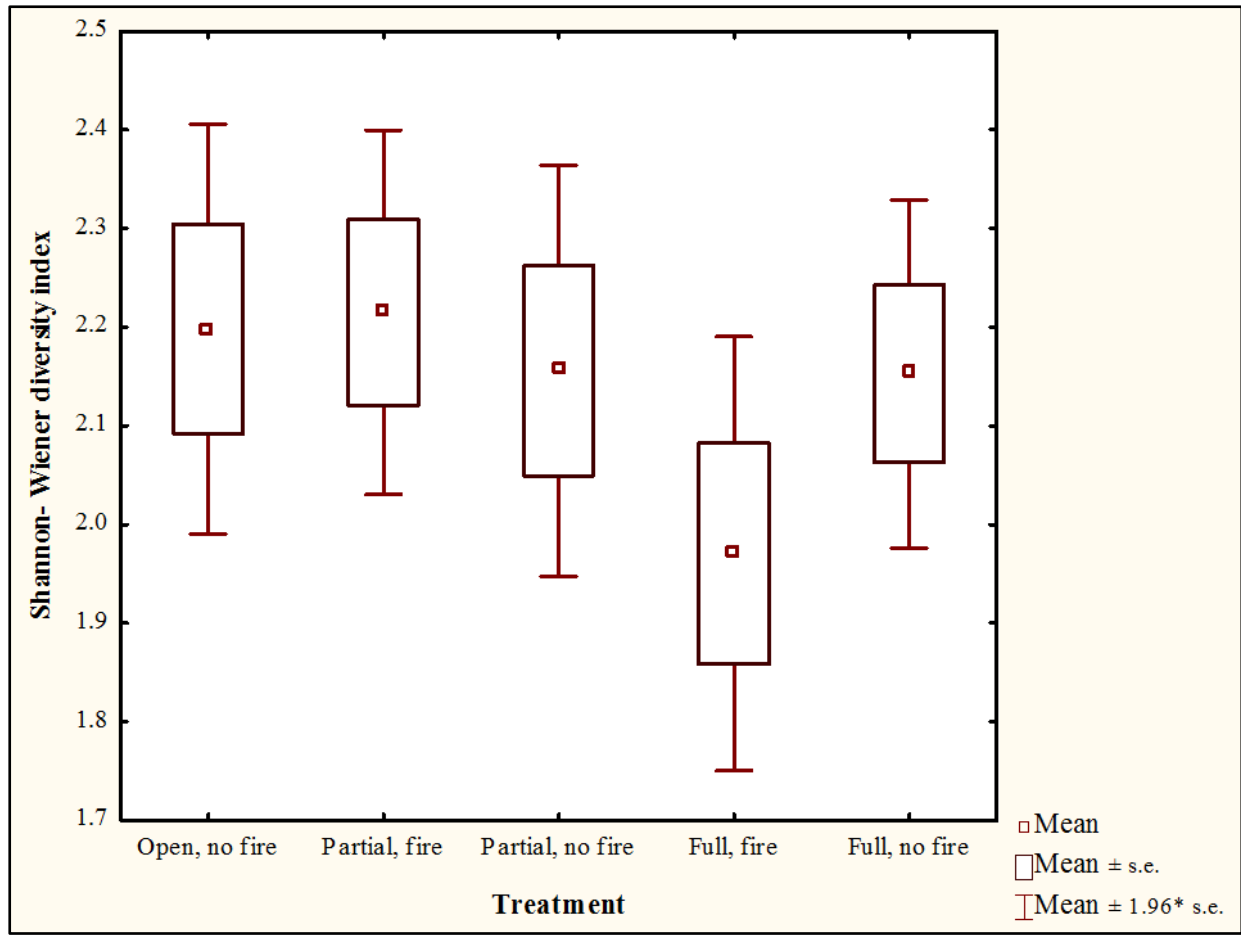
A total of 187 herbaceous plant species were recorded in the sodic zone of the Nkuhlu research enclosures. Species richness varied significantly across the combinations of herbivory and fire ($p = 0.0002$) (Table 1). Highest species richness was associated with areas exposed to herbivory (Figure 10), although species richness in the control site (i.e. open, no fire) and the partially fenced treatment without fire was significantly higher compared to the fully fenced treatment with fire. Species richness in the partially fenced site with fire was, however, not significantly higher than the full enclosure treatments (Tukey: $p > 0.05$).



± 1.96*, standard deviations of the mean; s.e., standard error.

Figure 10. Mean species richness ($p = 0.0002$) across fire and herbivory treatments in the sodic zone of the KNP.

Shannon-Wiener diversity index values showed no significant variation across the five combinations of herbivory and fire ($p = 0.4$) (Table 1).



$\pm 1.96^*$, standard deviations of the mean; s.e., standard error.

Figure 11. Mean Shannon-Wiener diversity index values ($p = 0.4$) across fire and herbivory treatments in the sodic zone of the KNP.

5.4 Discussion

The effect of herbivore exclusion on total herbaceous biomass has been shown to be lower in the sodic zone than elsewhere in the riparian zone (Jacobs & Naiman, 2008). This phenomenon could be attributed to the drier conditions prevailing in the sodic zone throughout the year, as well as the shallow surface soils and relative impenetrability, making herbaceous species establishment and growth even more challenging. As would be expected, the exclusion of herbivores from the sodic zone lead to herbaceous biomass increases. The biomass range of 2500 kg/ha – 2900 kg/ha (Figure 9) in the full enclosure is unusually high for sodic sites in semi-arid savanna ecosystems, because sodic soil is usually sparsely vegetated and therefore associated with land degradation and gully formation that can become self-reinforcing as a result of its susceptibility to sheet erosion (Khomu & Rogers, 2005). The exclusion of herbivores, however, brings forth a gradual improvement in soil surface

conditions, which re-establishes the predominance of topsoil water and allows for an increase in the biomass of grasses (Walker *et al.*, 1981).

Furthermore, herbivory reduces biomass and canopy cover of certain plants and promotes spatial heterogeneity (Jacobs & Naiman, 2008). Sodic zones are favoured as forage patches by large herbivores, which gain essential nutrients from the herbaceous species growing there. The total exclusion of these herbivores from savanna riparian zones leads to a loss of game paths, feeding patches and wallows, causing a reduction in plant community heterogeneity (Jacobs & Naiman, 2008). According to Bakker *et al.* (2003), this heterogeneity, caused by different patches with long and short biomass, is thought to enhance the coexistence of a greater number of herbaceous species, hence boosting species richness. Although Jacobs and Naiman (2008) found no consistent effects of increasing biomass on species richness in the drier sodic zone after 4 years of herbivory exclusion (i.e. 2004/2005), results from this 2012 study indicated that the significantly higher biomass in the absence of herbivory seemed to suppress species richness after nine years of herbivory exclusion. Highest species richness was associated with areas exposed to herbivory (Figure 10), thus areas where plant community heterogeneity was highest.

No significant variation in species diversity could be confirmed. As the Shannon-Wiener index of species diversity acknowledges the abundance of individual species, it could be expected that variation in species diversity is less perceptible than species richness. The sodic zone, in particular, is often dominated by few forb species that are well adapted to harsh conditions. Jacobs and Naiman (2008) reported that the succulent forb, *Trianthema salsoides*, contributed to a substantial proportion of the forb biomass in 2003–2004. Although *T. salsoides* was still prevalent in the 2010 data set, it was replaced as the dominant forb species by *Achyranthes aspera*. Dominance by a single species reduces the evenness of the sodic zone ecosystem, hence suppressing diversity. Lowest species richness was recorded in areas where herbivores were excluded. This is in accordance with the findings of Oba *et al.* (2001), that long-term exclusion of herbivores may not necessarily have an increasing effect on species diversity and richness. The dynamic character of the vegetation in the sodic zone ecosystem therefore results in less predictable temporal changes in herbaceous species diversity.

5.5 Conclusion

It may be argued that the data that are presented in this research represents only a moment in time within a very complex and dynamic ecosystem. Yet, it provides valuable baseline information to build upon to broaden our knowledge on the reaction of herbaceous vegetation upon disturbances such as fire and herbivory. As there is a lack of understanding pertaining to this issue, this chapter contributes

to the knowledge pool that can be used to better our understanding of savanna ecosystem dynamics, and more specifically, sodic zones.

Considering that sodic zones are nutrient hotspots and form a key part in savanna ecosystems with respect to ecosystem services and functioning, more knowledge of the ecological functioning of these areas is necessary to fully understand all of their features. The dynamic nature of vegetation in the sodic zone leads to less predictable temporal changes in the herbaceous layer, an aspect that will be discussed in the next chapter.

This chapter stands in contradiction with the ‘intermediate disturbance hypothesis’, which suggests that highest diversity is maintained at intermediate levels of disturbance (Begon *et al.*, 2006). However, highest species richness was associated with highest disturbance (i.e. open treatment). Increasing biomass as a result of the absence of herbivory suppresses the richness of herbaceous species in the sodic zone, although species richness is even lower in its combined effect of fire treatment. Whilst species diversity patterns showed no significant differences across the treatments, lowest diversity was also measured in the absence of herbivory, but with fire treatment. It is therefore inferred that, although sodic patches are often associated with overgrazed, trampled vegetation, herbivores play an important role in the maintenance of species richness and diversity in these nutrient hotspots. Although statistically not significant, fire seems to suppress diversity and richness of the herbaceous layer in the sodic riparian zone. Floristic monitoring over a larger time scale under similar conditions is still required to support these premature findings.

As the conservation of total biodiversity is the mandate of SANParks, these findings have direct implications for the management of sodic zones in the KNP. The exclusion of herbivores may alter ecosystem functioning, especially at smaller scales, by increasing biomass at the cost of herbaceous species richness. Herbivores play an essential role in the reduction of herbaceous plant competition, in that herbivores decrease grass biomass which, in turn, promotes herbaceous species richness as fast-growing grasses can no longer overtop and shade out forbs. Herbivores are therefore considered imperative in the maintenance of species richness and diversity and ecosystem functioning in African savanna ecosystems, especially in sodic zones.

Chapter 6

Temporal shifts in plant species composition and diversity

6.1 Introduction

Diversity patterns of vegetation are directly linked to temporal and spatial variability of natural communities (Small & McCarthy, 2002). Measures of floristic changes in vegetation composition over time within these communities may provide insight to the ecological processes that generate vegetation change (Clarke *et al.*, 2005).

It is widely recognized that fire and herbivory stand central to savanna ecosystem structure and function, yet very few studies acknowledge the combined effect of these drivers on ecosystem dynamics (Anderson & Briske, 1995; Belsky, 1995; Archibald, 2005; Jacobs & Naiman, 2008; Masunga *et al.*, 2013). Both fire and herbivory have been shown to change species composition of ecosystems (Archibald *et al.*, 2005; Bond & Keeley, 2005; Masunga *et al.*, 2013). The removal of vegetation by fires provides opportunity for communities to accommodate rare species that would alternatively have been outcompeted by other dominant species. Likewise, grazing removes grass biomass above the ground, creating open patches where colonization by new species can take place (Van de Vijver *et al.*, 1999; Masunga *et al.*, 2013).

In African grasslands, changes in grazing regimes cause rapid changes in species composition and community physiognomy (Milchunas *et al.*, 1988). As grazing pressure increases, herbaceous community structure and composition shifts (Archer, 1989; Angassa, 2012). The growth of grazing-tolerant species is stimulated by grazing (Adler *et al.*, 2001; Augustine & McNaughton, 2006; Angassa, 2012), leading to increased species diversity and productivity (Masunga *et al.*, 2013). Although grazing may only slightly effect species composition in one year, over time their effect can become more severe, and cause a significant impact on the vegetation composition and heterogeneity of ecosystems (Fynn & O'Connor, 2000; Adler *et al.*, 2001; Burns *et al.*, 2009). If all herbivores were to be removed from the system, the vegetation composition will stay in this 'new' state for at least 20 years (Walker *et al.*, 1981).

In a study to test for significant effects of fire and herbivory on herbaceous species richness and diversity, Van Coller *et al.* (2013) concluded that fire had a non-significant effect within the sodic

zone of the Nkuhlu research exclosures. This chapter will attempt to provide better insight on the combined effects of fire, herbivory and time on herbaceous species richness and diversity at these long-term herbivory exclosures.

Specific objectives of this chapter were to (1) determine whether herbaceous richness and diversity changed over nine years across various fire and herbivory treatments, (2) assess whether species composition changed over time and, (3) identify and determine if dominant herbaceous (forbs and grasses) species changed in abundance over time and across different combinations of fire and herbivory treatments.

6.2 Methods

The 2010 floristic dataset of the Nkuhlu exclosures was compared to baseline data collected in 2001 to investigate long-term changes in herbaceous vegetation composition and diversity. Significance levels for all analyses (i.e. repeated measures Analysis of Variance (ANOVA), Bonferroni significance tests and t-tests for independent samples by groups) were set at the standard significance level of $p < 0.05$, enabling confident conclusions made from statistical results (Lindgren & Sullivan, 2001).

Repeated measures ANOVA was applied to the data set in *STATISTICA* version 11 (2012) to test whether species diversity, richness and biomass of the herbaceous layer varied significantly among the five combinations of fire and herbivory treatments over time (nine years). Where statistically significant results were obtained, differences among treatment means over time were determined through pair-wise comparisons of variable means of treatments - using the Bonferroni *post-hoc* significance test (Lindgren & Sullivan, 2001).

PRIMER 6 version 1.1.15 (2012) was used to conduct a Non-metric Multi-Dimensional Scaling analysis (NMDS), along with the application of the Bray Curtis Dissimilarity Index, providing a visual two-dimensional representation of the similarities or dissimilarities of herbaceous species composition between treatments over nine years, as well as the partially and fully fenced plots for 2010 and 2001 individually (Burns *et al.*, 2009). The Similarity Percentage (SIMPER) method (Clarke, 1993) was applied to the data set in the PAST computer software package (Hammer *et al.*, 2001) to determine which species contributed most to dissimilarities in the herbaceous species

composition over time. Analysis of SIMilarities (ANOSIM), a non-parametric test for significant differences, was performed to test for significant differences in herbaceous species composition over time (nine years) in PAST (Hammer *et al.*, 2001). T-tests for independent samples by groups were applied in *STATISTICA* version 11 (2012) to determine if abundance of dominant species within the different fire and herbivory treatments shifted over time.

6.3 Results

6.3.1 Indices

Repeated measures ANOVA (Table 2) revealed significant effects of herbivory, with or without fire, and time (nine years) on total species ($p = 0.0000$), total individuals ($p = 0.0000$), Margalef's species richness ($p = 0.0000$), Shannon-Wiener diversity index ($p = 0.0261$) and biomass ($p = 0.0039$), while the effects of herbivory were non-significant for Pielou's evenness ($p = 0.2187$) and Simpson's index of diversity ($p = 0.3292$).

Pair-wise comparisons of variable means indicated substantial increases across different fire and herbivory treatments over nine years (Figure 12). Total species ($p = 0.0000$) revealed significant increases from 2001 to 2010 in the site with restricted herbivory, both with ($p = 0.0000$) and without fire ($p = 0.0000$), the control site (i.e. open, no fire) ($p = 0.0000$) and the fully fenced herbivore exclusion treatment with no fire ($p = 0.0030$) (Table 3) (Figure 12(a)). The difference in the fully fenced area with fire treatment was non-significant ($p > 0.05$) over nine years (Figure 12(a)).

Table 2. Repeated measures ANOVA for total species, total individuals, richness/diversity indices and biomass of the herbaceous vegetation across treatments and over time along the sodic zone of the Nkuhlu research exclosures, KNP. (Significant changes indicated with *).

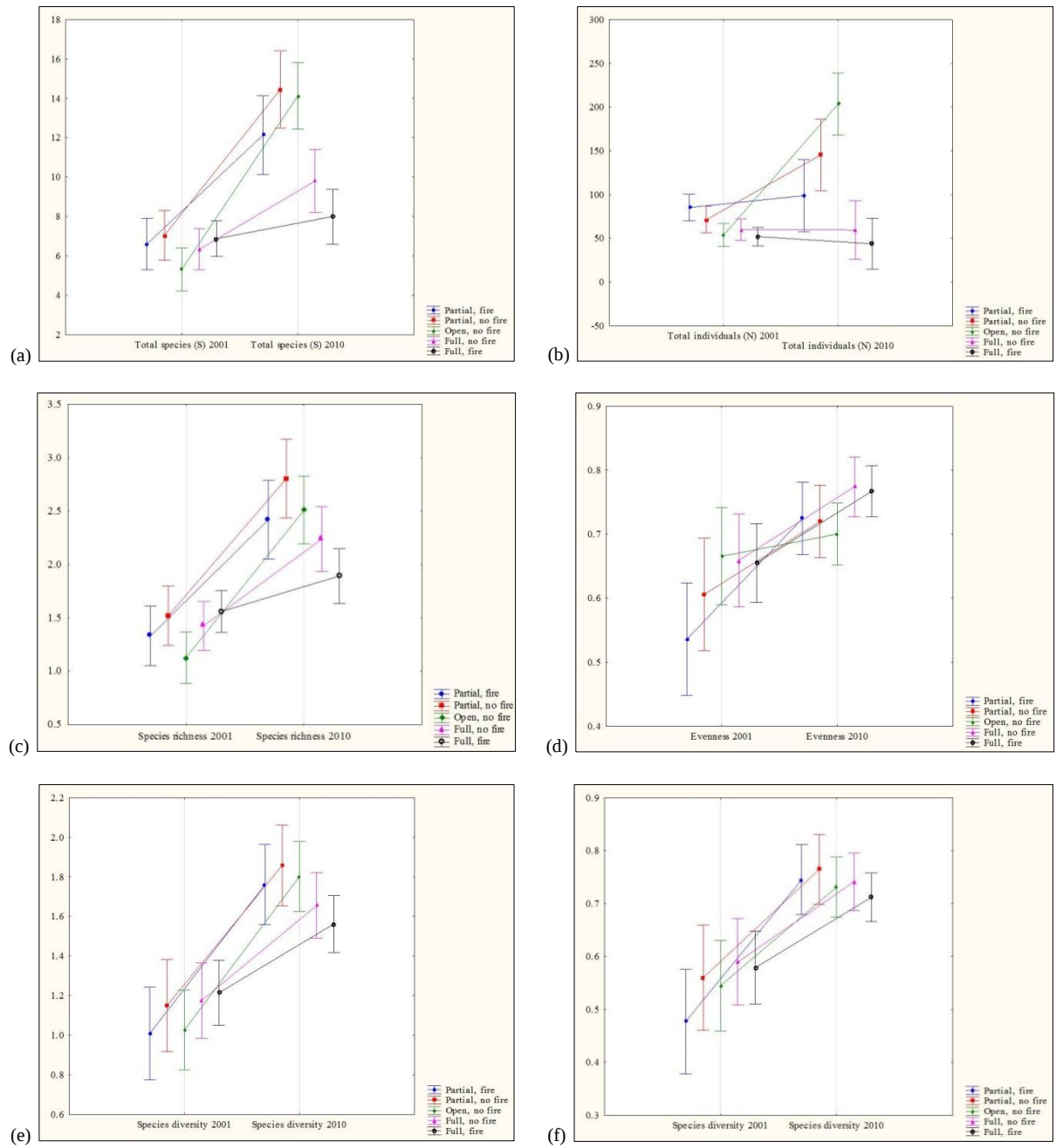
Response	Source	Df	SS	MS	F	p
Total species	Time*Treatment	4	700.80	175.20	13.508	0.0000*
	s.e.	158	3250.93	20.58	.	.
Total individuals	Time*Treatment	4	299406	74851	13.7688	0.0000*
	s.e.	159	159726	6344	.	.

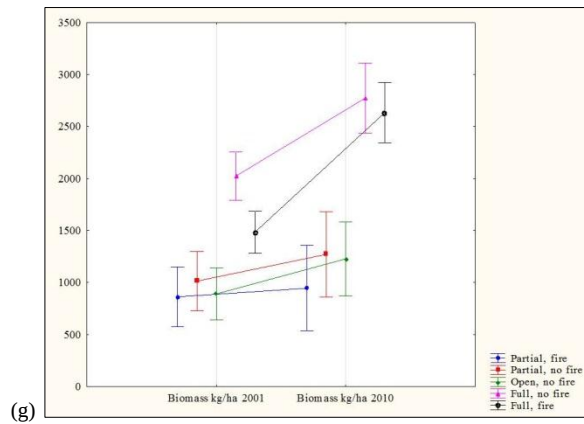
Response	Source	Df	SS	MS	F	p
Margalef's species richness	Time*Treatment	4	13.381	3.345	7.219	0.0000*
	s.e.	153	121.686	0.795	.	.
Pielou's evenness	Time*Treatment	4	0.1596	0.0399	1.455	0.2187
	s.e.	153	5.6686	0.0370	.	.
Shannon-Wiener diversity index	Time*Treatment	4	2.6286	0.6571	2.839	0.0261*
	s.e.	159	56.7991	0.3572	.	.
Simpson's index of diversity	Time*Treatment	4	0.1622	0.0405	1.163	0.3292
	s.e.	153	7.4636	0.0488	.	.
Biomass	Time*Treatment	4	6647132	1661783	4.2106	0.0039*
	s.e.	77	27973418	363291	.	.

s.e., standard error; *df*, degrees of freedom; SS, sum of squared differences; MS, mean square; *F*, whether variability within and between treatments is significantly different, i.e. the higher the *F*-value, the more significant the difference; *p*, *p*-values below a certain threshold indicates the significant differences between groups, *p*-value is significant at $p < 0.05$.

Total individuals increased significantly from 2001 to 2010 in the partially fenced area with no fire treatment ($p = 0.0289$) and the control site ($p = 0.0000$) (Table 3), whilst the partially fenced area with fire treatment and the fully fenced area, both with and without fire treatment revealed no significant ($p > 0.05$) changes over time (Figure 12(b)). Margalef's species richness was significantly higher across all treatments of fire and herbivory after nine years, except for the fully fenced area with fire treatment, where no significant ($p > 0.05$) changes were revealed across treatments and over time (Figure 12 (c)). Pielou's evenness for all fire and herbivory treatments varied non-significantly over time, except for the partially fenced area with fire treatment ($p = 0.0000$) (Table 3), where Pielou's evenness was significantly higher in 2010 than in 2001 (Figure 12 (d)).

Shannon-Wiener diversity index varied significantly from 2001 to 2010 among the five combinations of fire and herbivory (Figure 12 (e)), showing significant increases across all treatments (Table 3). Simpson's index of diversity was higher in the area with restricted herbivory and fire ($p = 0.0000$) (Table 3) in 2010, while no significant changes were revealed for any of the other combinations of fire and herbivory treatments from 2001 to 2010 (Figure 12 (f)).





Vertical bars denote 0.95 confidence intervals with standard error.

Figure 12. Pair-wise comparisons of (a) total species ($p = 0.0000$), (b) total individuals ($p = 0.0000$), (c) Margalef's species richness ($p = 0.0000$), (d) Pielou's evenness ($p = 0.2186$), (e) Shannon-Wiener diversity index ($p = 0.0261$), (f) Simpson's index of diversity ($p = 0.3292$) and (g) biomass ($p = 0.0039$) across fire and herbivory treatments over time in the sodic zone of the Nkuhlu research exclosures, KNP.

In pair-wise comparisons of biomass means, significant differences were revealed only in the fully fenced herbivore exclusion treatments, both with ($p = 0.0000$) and without fire ($p = 0.0264$) treatment (Table 3; Figure 12(g)). As expected, the mean biomass showed significant increases from 2001 to 2010 as a result of herbivory exclusion (Figure 12 (g)). No significant changes with respect to biomass were revealed across treatments exposed to herbivory over nine years, i.e. partially fenced areas (both with and without fire treatment) and the control site (Table 3).

Table 3. Summary of significant Bonferroni *post hoc* test p -values for variables across different fire and herbivory treatments, over nine years in the sodic zone of the Nkuhlu research exclosures.

Variable	Treatment	p
Total species	Partial, fire	0.0000
	Partial, no fire	0.0000
	Open, no fire	0.0000
	Full, no fire	0.0030
Total individuals	Partial, no fire	0.0298

Variable	Treatment	<i>p</i>
Margalef's species richness	Open, no fire	0.0000
	Partial, fire	0.0000
	Partial, no fire	0.0000
	Open, no fire	0.0000
Pielou's evenness	Full, no fire	0.0000
	Partial, fire	0.0000
Shannon-Wiener diversity index	Partial, fire	0.0000
	Partial, no fire	0.0000
	Open, no fire	0.0000
	Full, no fire	0.0017
Simpson's index of diversity	Full, fire	0.0230
	Partial, fire	0.0000
	Full, no fire	0.0264
Biomass	Full, fire	0.0000

6.3.2 Composition

Significant variation observed for the diversity indices might be attributed to changes in the species composition (Hooper & Vitousek, 1997; Burns *et al.*, 2009). To establish where these compositional changes occurred, NMDS, along with the Bray Curtis Dissimilarity Index, were applied.

Limited temporal shifts were observed for plant species assemblages in treatments not exposed to herbivory, i.e. the fully fenced plots, both with and without fire treatment (Figure 13 (a) & (b)). The overlapping of plots in two dimensional space (Figure 13 (a) & (b)) suggests limited changes in species composition over time in the herbivory exclusion treatment. In contrast, plots within the partially fenced treatment (both with and without fire treatment) as well as plots in the control site (i.e. the open area with no fire treatment), indicated clustering according to the sampling year, which illustrate temporal shifts in herbaceous plant species assemblages (Figure 13 (c) (d) & (e)). These changes in composition were further confirmed through the application of Bray-Curtis similarity in ANOSIM (at $p < 0.05$) (Clarke, 1993).



Figure 13. NMDS ordinations of herbaceous sodic vegetation in (a) fully fenced plots with no fire treatment, (b) fully fenced plots with fire treatment, (c) partially fenced plots with fire treatment, (d) partially fenced plots with no fire treatment and (e) control plots, i.e. open with no fire treatment in the Nkuhlu research exclosures, KNP.

Within the partially fenced plots with fire treatment the grass species *Sporobolus nitens* and *Aristida congesta*, along with the forb species *Blepharis integrifolia*, contributed to more than 5 % of dissimilarity between the two sampling years according to SIMPER analysis (Clarke, 1993). SIMPER

analysis of partially fenced plots with no fire treatment, revealed *Sporobolus nitens*, *Tragus berteronianus* and *Panicum maximum* as the species contributing most to temporal change. In the control site *Sporobolus nitens*, *Panicum maximum* and *Alternanthera pungens* contributed to more than 5 % of dissimilarity between sampling years.

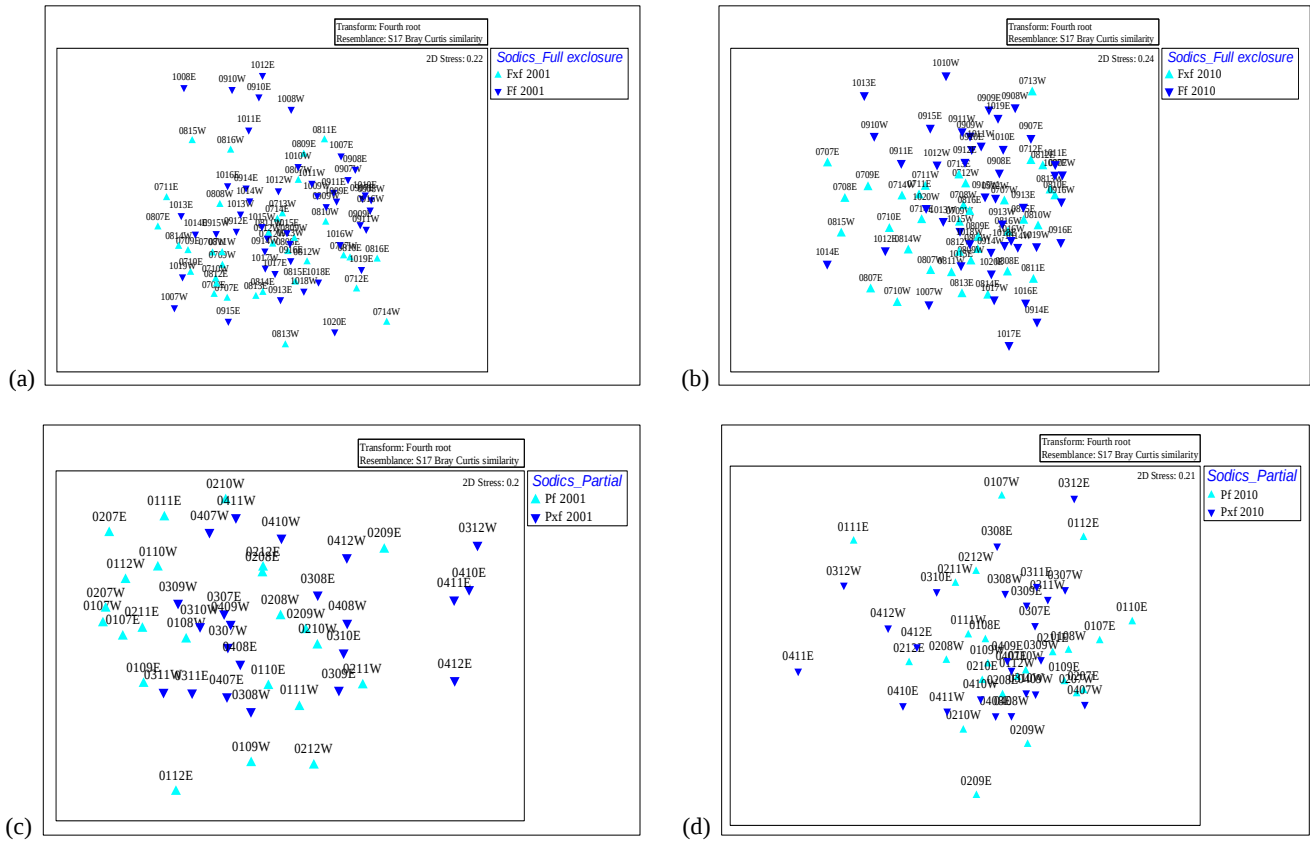


Figure 14. NMDS ordinations of the effect of fire on herbaceous sodic vegetation composition in different sampling years in (a) fully fenced plots in baseline sampling year, i.e. 2001, (b) fully fenced plots in 2010, (c) partially fenced plots (2001) and (d) partially fenced plots (2010).

Lack of clustering, but rather overlapping of plots in two dimensional space (Figure 14) suggests that fire did not affect herbaceous species composition in the sodic zone in the baseline sampling year (2001) (Figure 14 (a) & (c)), or in 2010 (Figure 14 (b) & (d)).

6.3.3 Changes in dominant species abundances between 2001 and 2010

Prominent herbaceous species within the sodic zone of the Nkuhlu exclosures as identified by Siebert & Eckhardt (2008) included forb species such as *Alternanthera pungens*, *Blepharis integrifolia*, *Hypertelis bowkeriana* and *Justicia protracta* and grasses, i.e. *Cynodon dactylon*, *Panicum maximum*, *Sporobolus nitens* and *Urochloa mosambicensis*. T-test results (Table 4) revealed that only the dominant forbs *Alternanthera pungens* and *Justicia protracta* and dominant grass species *Panicum maximum* and *Sporobolus nitens* showed significant differences over time across various fire and herbivory treatments.

Table 4. Dominant species abundances i.e. total individuals per treatment, over time and across various treatments of fire and herbivory in the Nkuhlu research exclosures, KNP (Significant changes indicated with *).

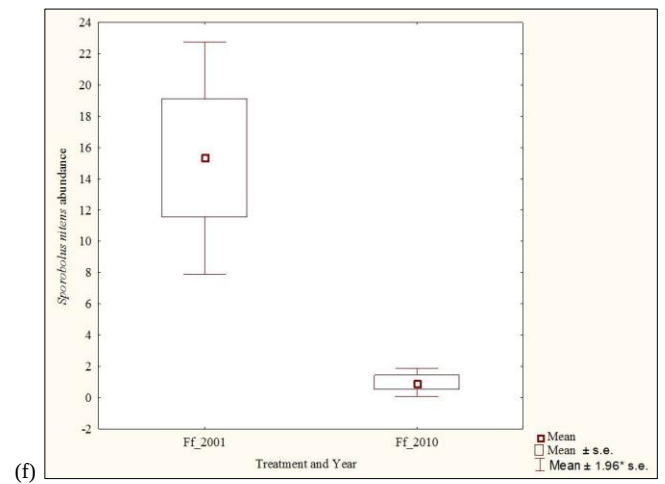
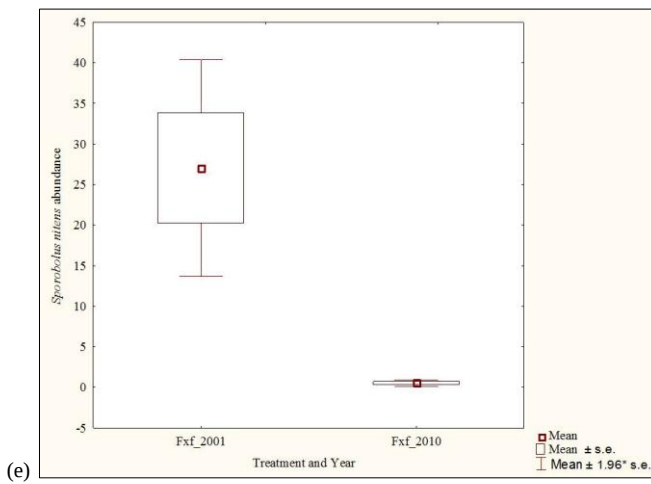
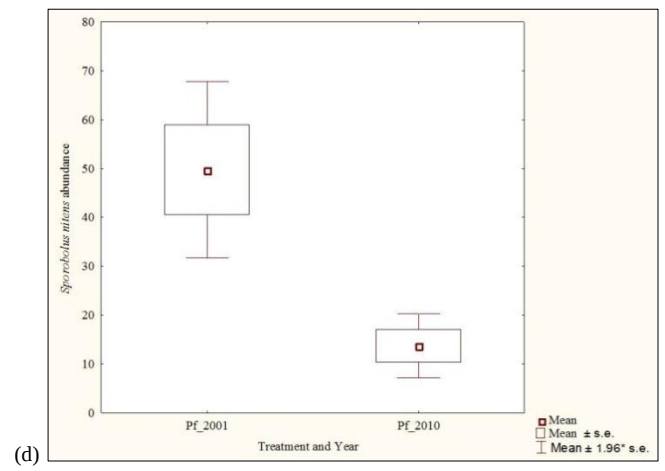
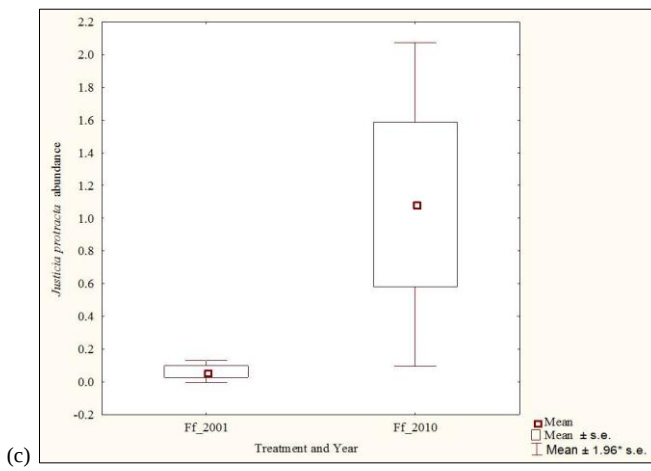
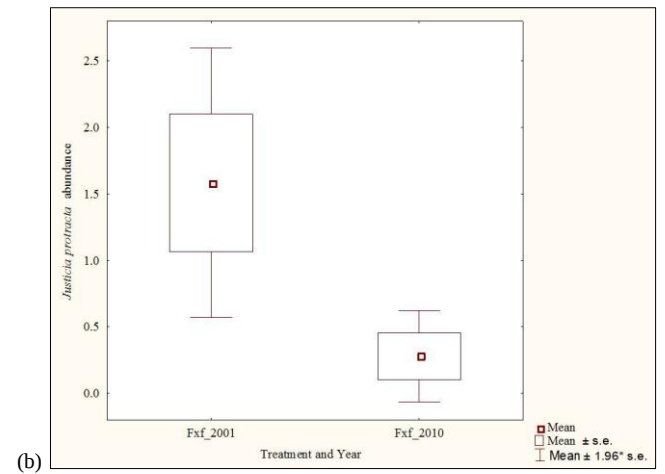
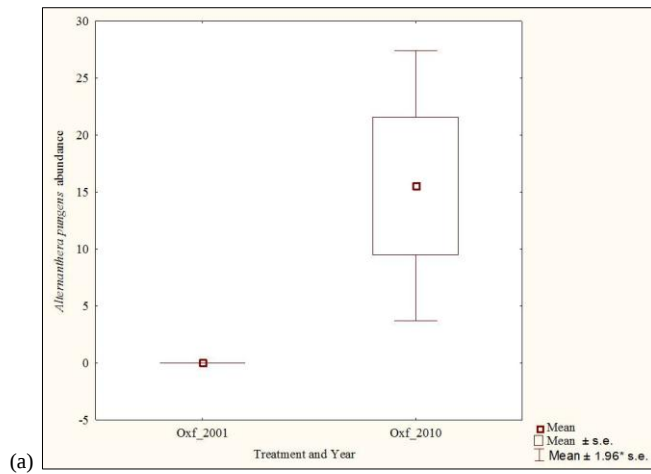
2001 Abundance		2010 Abundance		<i>p</i>
Partial, fire				
<i>Sporobolus nitens</i>	1193	<i>Sporobolus nitens</i>	329	0.0006*
<i>Panicum maximum</i>	102	<i>Panicum maximum</i>	39	0.1847
<i>Blepharis integrifolia</i>	78	<i>Blepharis integrifolia</i>	280	0.0816
<i>Justicia protracta</i>	35	<i>Justicia protracta</i>	28	0.8114
<i>Urochloa mosambicensis</i>	12	<i>Urochloa mosambicensis</i>	84	0.1478
<i>Alternanthera pungens</i>	0	<i>Alternanthera pungens</i>	20	0.1112
<i>Hypertelis bowkeriana</i>	0	<i>Hypertelis bowkeriana</i>	6	0.2415
<i>Cynodon dactylon</i>	0	<i>Cynodon dactylon</i>	0	0
Partial, no fire				
<i>Sporobolus nitens</i>	837	<i>Sporobolus nitens</i>	454	0.0584
<i>Panicum maximum</i>	150	<i>Panicum maximum</i>	63	0.0918
<i>Blepharis integrifolia</i>	60	<i>Blepharis integrifolia</i>	146	0.3638
<i>Justicia protracta</i>	22	<i>Justicia protracta</i>	29	0.6979
<i>Urochloa mosambicensis</i>	25	<i>Urochloa mosambicensis</i>	2	0.1667
<i>Alternanthera pungens</i>	0	<i>Alternanthera pungens</i>	223	0.0811
<i>Hypertelis bowkeriana</i>	0	<i>Hypertelis bowkeriana</i>	196	0.3199
<i>Cynodon dactylon</i>	0	<i>Cynodon dactylon</i>	0	0
Open, no fire				
<i>Sporobolus nitens</i>	641	<i>Sporobolus nitens</i>	907	0.3259
<i>Panicum maximum</i>	244	<i>Panicum maximum</i>	65	0.0080*
<i>Blepharis integrifolia</i>	140	<i>Blepharis integrifolia</i>	235	0.2445
<i>Justicia protracta</i>	50	<i>Justicia protracta</i>	54	0.9046
<i>Urochloa mosambicensis</i>	38	<i>Urochloa mosambicensis</i>	107	0.1614
<i>Alternanthera pungens</i>	0	<i>Alternanthera pungens</i>	497	0.0127*
<i>Hypertelis bowkeriana</i>	0	<i>Hypertelis bowkeriana</i>	9	0.1136

2001 Abundance		2010 Abundance		<i>p</i>
<i>Cynodon dactylon</i>	0	<i>Cynodon dactylon</i>	0	0
Full, no fire				
<i>Sporobolus nitens</i>	974	<i>Sporobolus nitens</i>	19	0.0002*
<i>Panicum maximum</i>	170	<i>Panicum maximum</i>	234	0.3212
<i>Blepharis integrifolia</i>	35	<i>Blepharis integrifolia</i>	19	0.4986
<i>Justicia protracta</i>	57	<i>Justicia protracta</i>	10	0.0195*
<i>Urochloa mosambicensis</i>	75	<i>Urochloa mosambicensis</i>	208	0.1089
<i>Alternanthera pungens</i>	0	<i>Alternanthera pungens</i>	0	0
<i>Hypertelis bowkeriana</i>	0	<i>Hypertelis bowkeriana</i>	0	0
<i>Cynodon dactylon</i>	0	<i>Cynodon dactylon</i>	0	0.3207
Full, fire				
<i>Sporobolus nitens</i>	736	<i>Sporobolus nitens</i>	47	0.0003*
<i>Panicum maximum</i>	484	<i>Panicum maximum</i>	281	0.0379*
<i>Blepharis integrifolia</i>	12	<i>Blepharis integrifolia</i>	0	0.1502
<i>Justicia protracta</i>	3	<i>Justicia protracta</i>	52	0.0463*
<i>Urochloa mosambicensis</i>	100	<i>Urochloa mosambicensis</i>	56	0.2869
<i>Alternanthera pungens</i>	9	<i>Alternanthera pungens</i>	0	0.1262
<i>Hypertelis bowkeriana</i>	0	<i>Hypertelis bowkeriana</i>	51	0.3004
<i>Cynodon dactylon</i>	208	<i>Cynodon dactylon</i>	227	0.9326

p-value significant at $p < 0.05$

Mean abundance of *Alternanthera pungens* increased significantly from 2001 to 2010 in the area with unrestricted herbivory and no fire treatment ($p = 0.0127$) (Figure 14 (a)) (Table 4). *Justicia protracta* abundance was significantly higher in 2001, and declined during nine years of herbivory exclusion with no fire treatment ($p = 0.0195$) (Figure 14 (b)) (Table 4). The mean abundance of *J. protracta* increased significantly from 2001 to 2010 in the absence of herbivory, but in the presence of fire ($p = 0.0463$) (Figure 14 (c)) (Table 4).

Abundance of *Sporobolus nitens* in the area with restricted herbivory and fire treatment was significantly higher in 2001, opposed to 2010 ($p = 0.0006$) (Figure 15 (d)) (Table 4). Significant decreases in abundance of *S. nitens* were revealed in the fully fenced herbivore exclusion treatments, both with ($p = 0.0003$) (Figure 15 (f)) and without ($p = 0.0002$) (Figure 15 (e)) fire treatment (Table 4). *Panicum maximum* abundance was significantly higher in the baseline vegetation survey in 2001, in both the control site, i.e. open area with no fire treatment ($p = 0.0080$) (Figure 15 (g)) (Table 4) and the fully fenced area with fire treatment ($p = 0.0379$) (Figure 15 (h)) (Table 4).



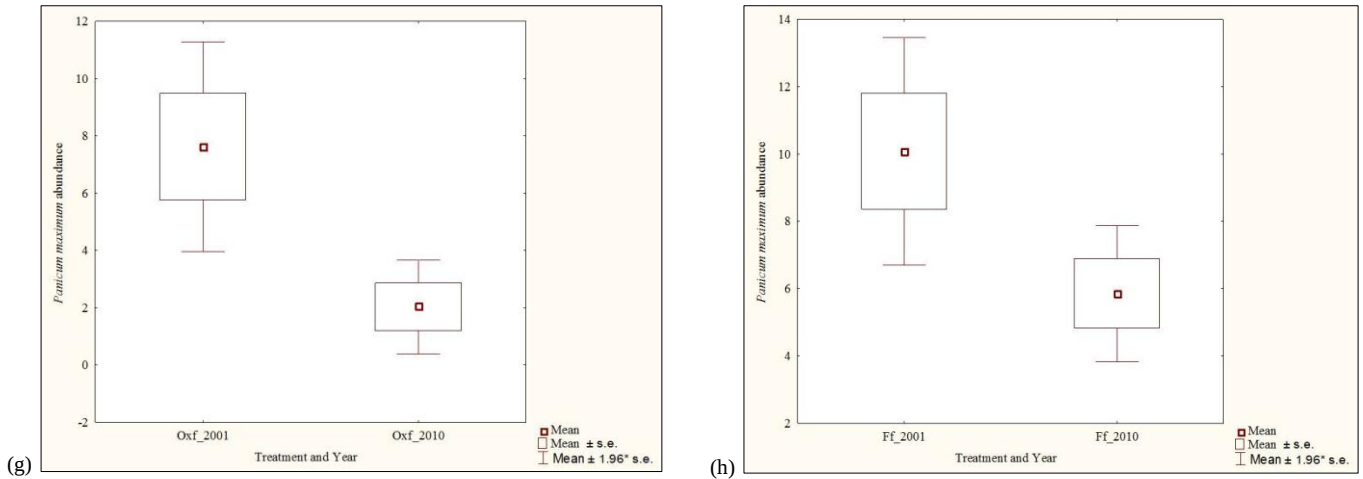


Figure 15. Mean abundances of (a) *Alternanthera pungens* in the control site, i.e. open area with no fire treatment, (b) *Justicia protracta* in the fully fenced herbivore exclusion treatment, with no fire, (c) *J. protracta* in the fully fenced treatment, with fire, (d) *Sporobolus nitens* in the area with restricted herbivory and fire treatment, (e) *S. nitens* in the fully fenced herbivory exclusion treatment with no fire, (f) *S. nitens* in the fully fenced plots with fire treatment, (g) *Panicum maximum* in the control site and (h) *P. maximum* in the fully fenced herbivore exclusion treatment with fire over nine years at the Nkuhlu research exclosures study site.

6.4 Discussion

Herbaceous species richness and diversity increased over time and across different fire and herbivory treatments along the sodic zone of the Nkuhlu exclosures, KNP. Mean monthly rainfall in months preceding floristic vegetation sampling in 2001 was 89 mm (Kruger National Park weather and rainfall data (pre 1960-2008)). These low averages could possibly explain low species richness and diversity recorded in the baseline herbaceous vegetation survey. Higher average rainfall prior to the 2010/1 sampling, i.e. 199 mm might be a plausible explanation for increased species richness and diversity across treatments over time (Damschen *et al.*, 2006). These unlikely increases in herbaceous species richness and diversity of the fully fenced areas could further be attributed to sampling divergence or bias, since sampling of the different years were undertaken by different research institutions.

Density of herbaceous species (depicted from the number of individuals per plot) is enhanced by herbivory, with or without elephants. In an ecosystem where herbivores and fire are important

disturbance agents, annual species have a competitive advantage over perennials, which are less adapted to stressed environments (Skarpe, 1991; Schippers *et al.*, 2001). The significant increases in total individuals over time in the areas exposed to herbivory, i.e. when the system is closer to its natural state, may therefore be attributed to high levels of disturbance caused by herbivores, which favour rapid colonization and growth of annual herbaceous species (Skarpe, 1991; Aronson *et al.*, 1993; Bergstöm & Skarpe, 1999; Sawadogo *et al.*, 2005; Van Oudtshoorn, 2006).

Significant increases in herbaceous species richness of the open and partially fenced plots, i.e. areas where herbivores are present, correspond with the findings of Jacobs & Naiman (2008) and Van Coller *et al.* (2013), who suggested that herbaceous species richness will decline in the absence of herbivory, because of increased biomass. Environmental conditions within the fully fenced areas therefore showed less potential to support more species, as opposed to areas exposed to herbivory under the same climatic conditions. This is also in accordance with Van Coller *et al.* (2013) who concluded that herbivores are the primary drivers of herbaceous vegetation dynamics in the sodic zone of the KNP, and essential for the maintenance of high herbaceous species richness.

Conditions within the fully fenced areas with fire treatment were not suitable for a significant increase in Margalef's species richness, suggesting that richness of herbaceous species is suppressed by high biomass levels and hot fires (in accord with Van Coller *et al.*, 2013). However, increases in Margalef's species richness in the areas exposed to herbivory, reinforces the need for herbivores to drive and maintain system heterogeneity, allowing for more functionally different species to coexist (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013). These increases can further be supported by the intermediate disturbance hypothesis, suggesting that highest species richness will occur at intermediate levels of biomass corresponding to moderate levels of competition or disturbance (Grime, 1973; Pollock *et al.*, 1998; DeForest *et al.*, 2001; Bhattarai *et al.*, 2004; Michalet *et al.*, 2006).

Pielou's evenness and Simpson's index of diversity are indicators of the heterogeneity of a system, and high evenness suggests that all species in the system is equally represented, and that no one species dominates (Peet, 1974). Contrary to the findings of Burns *et al.* (2009), Pielou's evenness and Simpson's index of diversity, and essentially heterogeneity, increased significantly only in the partially fenced plots with fire treatment, suggesting that the absence of elephants, but the presence of fire and all other herbivores is the ideal environment for optimal herbaceous species richness in the sodic zone of the KNP.

Herbaceous species diversity increased significantly in areas exposed to herbivory (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013), whilst the fully fenced treatment showed the least improvement in species diversity. It can therefore be inferred that high biomass levels, as a result of herbivory exclusion in the fully fenced treatments of the sodic zone suppress diversity of the herbaceous layer. This corresponds with Jacobs and Naiman (2008) who suggested that many of the smaller forbs and grasses are outcompeted for resources, i.e. niches, water and sunlight by tall statured herbaceous species. Herbivores can therefore be considered primary disturbance agents in the sodic zone of the Nkuhlu exclosures, KNP, through directly, i.e. the removal of biomass and indirectly, i.e. trampling, altering the system and consequently allow more species to coexist, promoting species richness and diversity and overall system heterogeneity (Skarpe, 1991; Jacobs & Naiman, 2008).

As would be expected, biomass levels of areas where herbivores were excluded from the system for nine years increased significantly, reinforcing the need for herbivores in these systems to regulate biomass levels, and maintain herbaceous species richness and diversity (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013).

Herbaceous species composition changed over nine years, more prominently so in areas exposed to herbivory (Figure 13). Patterns of species composition response to herbivory and fire, correspond with Archer (1989) and Angassa (2012), who suggested that increased grazing pressure will alter community structure and cause shifts in herbaceous species composition. This phenomenon was observed in the study site, where the areas exposed to herbivory showed clear shifts in species composition over nine years (Figure 13 (c-e)), while no shifts in herbaceous species composition were revealed for areas where herbivory was excluded (Figure 13 (a & b)). Herbivory causes disturbance, i.e. killing, displacing or damaging individuals, which directly or indirectly creates opportunity for new individuals to become established, therefore changing species composition and habitat diversity (Sousa, 1984; Milchunas *et al.*, 1988; Adler *et al.*, 2001; Bråthen *et al.*, 2007).

Areas with unrestricted grazing showed significant decreases in abundance of the highly palatable, decreaser sub-climax, or climax grass species *Panicum maximum* over time (Figure 15 (g)) (Table 4). Similarly, *P. maximum* numbers declined in areas where herbivores were totally excluded from the system in the presence of fire (Figure 15 (h)) (Table 4), suggesting that, contrary to Belsky *et al.* (1989), *P. maximum* seedlings have a low survival rate in shady conditions in the presence of fire (in accord with Zacharias *et al.*, 1988). These decreases correspond with Trollope *et al.* (1989) and Van Oudtshoorn (2006) stating that *P. maximum* is known to decrease in numbers when the veld is

overgrazed (i.e. the open area) or under-grazed, i.e. the fully fenced area where no herbivory took place for nine years.

Sporobolus nitens which has low grazing value, an increaser II species (Trollope *et al.*, 1989; Van Oudtshoorn, 2006), declined in abundance in areas with minimal (i.e. partial enclosure) and no (i.e. total herbivory exclusion in full enclosure) disturbance. In accordance with Van Oudtshoorn (2006) and Trollope *et al.* (1989), *S. nitens* was abundant in overgrazed veld (Table 4), and less so in areas with no or minimal disturbance. The decline in *S. nitens*, a short perennial grass species, in the fully fenced area suggests that it was relatively shade-intolerant (Belsky, 1992), possibly being outcompeted for resources by taller herbaceous species.

Abundances of the perennial herb *Alternanthera pungens* increased over time in areas with unrestricted herbivory, coinciding with Lock (1972) suggesting that *A. pungens* is usually abundant on bare soil in disturbed areas. It is uncertain how *Justicia protracta* reacts upon fire, but it is known that the thin herbaceous stems of *Justicia dalaensis* resprouts after fire (Champluvier, 2002). Similarly, results indicated that *J. protracta* seems to be dependent upon fire, since abundances increased significantly in the presence of fire (Figure 14 (c)) and declined in the absence of it (Figure 14 (b)).

As would be expected, biomass levels increased significantly from 2001 to 2010 in the fully fenced herbivory exclusion treatment, both with and without fire treatment (Figure 12 (g)), due to the complete exclusion of all large herbivores over nine years (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013). Accumulation of biomass in the fully fenced area with fire treatment may be attributed to fires occurring twice, October 2002 and August 2007, since the first survey. Biomass accumulation due to the complete exclusion of herbivores alters the functioning of savanna ecosystems at the expense of herbaceous species richness and diversity (Jacobs & Naiman, 2008; Angassa, 2012; Van Coller *et al.*, 2013). Total exclusion of herbivores from the system leads to a decline in game paths, feeding patches and wallows, thus causing a decline in plant community heterogeneity, leading to a more homogeneous system (Figure 13 (a) & (b)) (Jacobs & Naiman, 2008).

6.5 Conclusion

Herbaceous species richness, diversity and biomass of the sodic zone in the Nkuhlu exclosures increased over time (nine years) and across various fire and herbivory treatments. High levels of disturbance in the open area, and to some extent the partially fenced area (i.e. areas exposed to meso-herbivores that directly impact the herbaceous layer) of the sodic zone leads to increased total number of herbaceous individuals (i.e. density), species richness and diversity. These results imply that herbivory is essential to keep biomass levels low to promote and maintain sodic herbaceous density (i.e. number of individuals per plot), species richness and diversity in the Nkuhlu exclosures. However, herbaceous species richness, diversity and evenness increased significantly in partially fenced plots with fire treatment, suggesting that the absence of elephants, but in the presence of fire and all other herbivores is ideal for high herbaceous species richness, diversity and evenness in the sodic zone of the Nkuhlu exclosures, KNP.

Herbaceous species composition showed less distinct changes in the herbivory exclusion treatment, both in the presence and absence of fire. However, areas exposed to herbivores, both with and without fire, showed substantial changes in herbaceous species composition after nine years. Herbivores are therefore suggested to act as the primary drivers of compositional changes in the herbaceous layer of the sodic zone along the Sabie River, while fire seems to have a very limited effect on herbaceous species composition (Figure 14).

Dominant forb species *Alternanthera pungens* and *Justicia protracta* and dominant grass species *Panicum maximum* and *Sporobolus nitens* in the sodic zone of the Nkuhlu exclosures revealed significant variation over nine years, across different fire and herbivory treatments. *Alternanthera pungens* was abundant in areas with unrestricted grazing and no fire treatment, inferring that this forb species is grazing tolerant in the sodic zone. Further research on this species in the sodic zone is required to determine how abundances will react upon the presence of fire. *Justicia protracta* in the sodic zone along the Sabie River is dependent on fire to resprout, however more research over a longer time period and a larger spatial scale is required to confirm these preliminary findings. Abundances of the highly palatable grass species *P. maximum* decrease when all large herbivore species are present, inferring that *P. maximum* can be considered a preferred grass species for foraging by large herbivores in the sodic zone of the Nkuhlu exclosures, KNP. *Panicum maximum* numbers decline in the absence of herbivores and the presence of fire. *P. maximum* in the sodic zone is not tolerant to overgrazing, undergrazing, shady conditions or the presence of fire. The low grazing value grass species *S. nitens* is abundant in the control site of the Nkuhlu exclosures, indicating that this

area, open to all large herbivores is overgrazed. *Sporobolus nitens* abundances decline in moderately to low disturbance areas, inferring that this grass species is shade-intolerant. The Similarity Percentage (SIMPER) method showed *S. nitens* to contribute the most to differences in species composition over time in areas exposed to herbivory, i.e. open area with no fire and partially fenced plot in fire presence and absence. These species could act as indicators of fire and herbivory in the sodic zone of the Nkuhlu exclosures, KNP, i.e. *Alternanthera pungens* is an indicator of overgrazing; the presence of *Justicia protracta* will most likely indicate fire presence; absence of *Panicum maximum* indicates over- or undergrazing and fire presence, and *Sporobolus nitens* is indicative of overgrazed veld.

Herbivory and fire are considered main drivers of spatial and temporal dynamics of the herbaceous layer in the sodic zone of the Nkuhlu exclosures, KNP. However, temporal changes observed in herbaceous species richness, diversity and density across different fire and herbivory treatments could also be attributed to fluctuating rainfall patterns between sampling years. Rainfall is therefore an important aspect that should receive ample consideration in future long-term herbaceous vegetation studies.

Conservation implications: Results obtained through studying the temporal effect of fire and herbivory on the herbaceous layer of the sodic zone in the Nkuhlu exclosures, KNP, can be used as a baseline to do further long-term monitoring within these exclosures. Through this study, more research questions should be raised to inform management of these ecologically important areas.

Major recommendations for the sodic zone of the Nkuhlu exclosures, KNP include: (1) herbivory is essential to keep biomass levels low and maintain sodic herbaceous density (i.e. numbers of individuals per plot), species richness and diversity, (2) the absence of elephants, but presence of fire and all other herbivores is ideal for high herbaceous species richness, diversity and evenness, (3) herbivores act as primary drivers of compositional changes in the herbaceous layer, (4) fire has a limited effect on herbaceous species composition, (5) Dominant forb species *Alternanthera pungens* is grazing tolerant, yet further research is required to determine how abundances will react upon the presence of fire, (6) *Justicia protracta* is dependent on fire to resprout, however more research over a longer time period and larger spatial scale is needed to confirm these preliminary findings, (7) the highly palatable *Panicum maximum* is a preferred grass species for foraging by large herbivores and is not tolerant to overgrazing, undergrazing, shady conditions or the presence of fire, (8) the low grazing value grass species *Sporobolus nitens* is abundant in overgrazed sodic areas and is shade-intolerant, (9) these species could be used as indicators of fire and herbivory, and (10) rainfall is an important aspect that should receive ample consideration in future long-term herbaceous vegetation studies.

Chapter 7

Relationship between field biomass and herbaceous species richness and diversity

7.1 Introduction

One of the central components of community ecology is the relationship between field biomass and species richness and diversity (Guo & Berry, 1998; Mittelbach *et al.*, 2001; Bhattarai *et al.*, 2004; Michalet *et al.*, 2006). Likewise, one of the most deliberated topics surrounding plant communities is the ‘hump-shaped’ or unimodal relationship that exists between biomass and species richness, suggesting that highest species richness will occur at low to intermediate levels of habitat biomass (Grime, 1979; Gough *et al.*, 1994; Guo & Berry, 1998; DeForest *et al.*, 2001; Oba *et al.*, 2001; Bhattarai *et al.*, 2004; Michalet *et al.*, 2006).

At low levels of productivity, i.e. high levels of environmental stress or disturbance, diversity decreases, since only a few species are able to survive and tolerate these extreme conditions (Grime, 1973, Milchunas *et al.*, 1988; DeForest *et al.*, 2001). The decrease in diversity at high levels of productivity can be attributed to competitive exclusion (Oba *et al.*, 2001), where tall, fast-growing species, such as grasses, out-compete other species for resources, therefore leading to increased spatial homogeneity (Abrams, 1995; Jacobs & Naiman, 2008).

In areas where environmental conditions homogenize, i.e. when herbivores are removed from the system, the relationship between biomass and species richness will be either positive or negative (Guo & Berry, 1998). The relationship will be positive when biomass is low directly following an episode of disturbance, when competitive interactions are counteracted and the coexistence of more functionally different species is promoted (Guo & Berry, 1998; Olff & Ritchie, 1998). The relationship becomes negative after a certain biomass threshold is reached, due to the occurrence of competitive exclusion (Grime, 1973; Milchunas *et al.*, 1988; DeForest *et al.*, 2001). However, when a larger habitat with a wider range of environmental conditions is considered, the relationship becomes more hump-shaped (Guo & Berry, 1998). Despite this relationship, there are many exceptions and some recent studies show that the relationship between biomass and richness is sometimes found to be weak, or not even detectable at all (Guo & Berry, 1998; Waide *et al.*, 1999; Grace, 2001). This may be attributed to the fact that not only the basic underlying conditions that produce unimodal patterns are still uncertain, but also that herbaceous plant community’s variation in richness can be explained by many other factors than biomass (Guo & Berry, 1998; Grace, 2001). The relationship between

biomass and species richness is scale dependent, and the exact scale to best study this relationship has not yet been refined (Waide *et al.*, 1999). Therefore the relationship between biomass and diversity and richness in ecosystems has been described as unimodal, negative, positive or undetectable (Grace, 2001; Osem *et al.*, 2002).

In a study done by Jacobs and Naiman (2008), three years after the Nkuhlu research exclosures were established, the relationship between herbaceous vegetation productivity and richness of the sodic zone did not reveal to be hump-shaped, because mean biomass did not increase beyond a threshold of 500 g.m², which seems to be the biomass threshold to yield highest species richness, indicating that not enough time had passed to detect a hump-shaped relationship. Understanding the relationship between ecosystem biomass and species richness and diversity can not only promote successful management, conservation and maintenance of ecosystem function and diversity (Michalet *et al.*, 2006), but also help ecologists understand the mechanisms that drive this relationship and inherently the sources of biodiversity (Mittelbach *et al.*, 2001).

The main objective of this chapter was to determine and interpret the relationship between field biomass and herbaceous species richness and diversity over time (nine years) and across various fire and herbivory treatments in the sodic zone of the Nkuhlu exclosures, KNP.

7.2 Methods

The *Sporobolus nitens-Euclea divinorum* Dry Sodic plant community stretches across various fire and herbivory treatments which, for the purpose of this study, will be considered as smaller, homogeneous ‘habitats’ within the sodic plant community. The environmental conditions, i.e. disturbances such as fire and herbivory, soil type, species composition and biomass levels, within these smaller habitats are considered homogeneous (Guo & Berry, 1998). Please refer to section 4.2 (Experimental design and sampling) on how biomass data was sampled.

LOWESS (Locally Weighted Scatterplot Smoothing) regression (Trexler & Travis, 1993) was applied to the data to provide a visual representation of the relationship between biomass and the different dependent variables. LOWESS regression allowed for variation of the degree of smoothing as well as the drawing resolution of the curved line, to provide a clear picture of the relationship between biomass and the dependent variables (Pélissier & Goreaud, 2001; STATISTICA version 11, 2012).

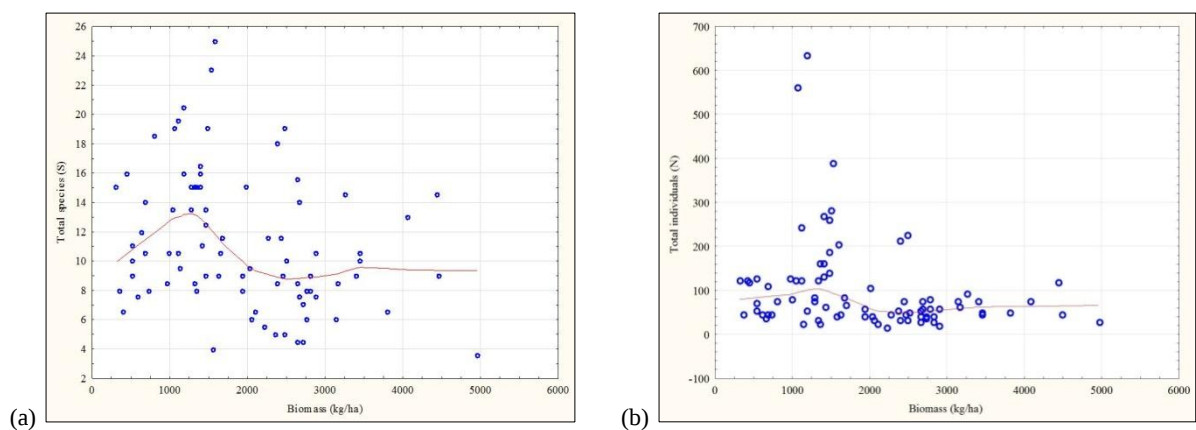
Where the relationship between biomass and the dependent variables was nonlinear, but rather curvilinear, the independent variable, i.e. biomass, was square root transformed and quadratic regression analyses were applied. The square root transformation on biomass ensured that biomass and the dependent variables, i.e. total species, total individuals, Margalef's species richness, Pielou's evenness, Shannon-Wiener diversity index and Simpson's index of diversity had equal variance, improved linearity and resolved variance heterogeneity (Johnson *et al.*, 2000; Naeem *et al.*, 2000; Axmanova *et al.*, 2012).

After preliminary results were obtained, plots with biomass exceeding 3500 kg/ha were omitted from the data set due to the small number of plots in this biomass range (i.e. statistically too few repetitions). LOWESS and quadratic regression was again applied to the data.

7.3 Results

7.3.1 LOWESS and quadratic regression analyses with biomass

The relationship between biomass and dependent variables revealed to be nonlinear, and quadratic regression analyses were applied to determine whether there existed a significant quadratic relationship between biomass (biomass and biomass²) and the dependent variables.



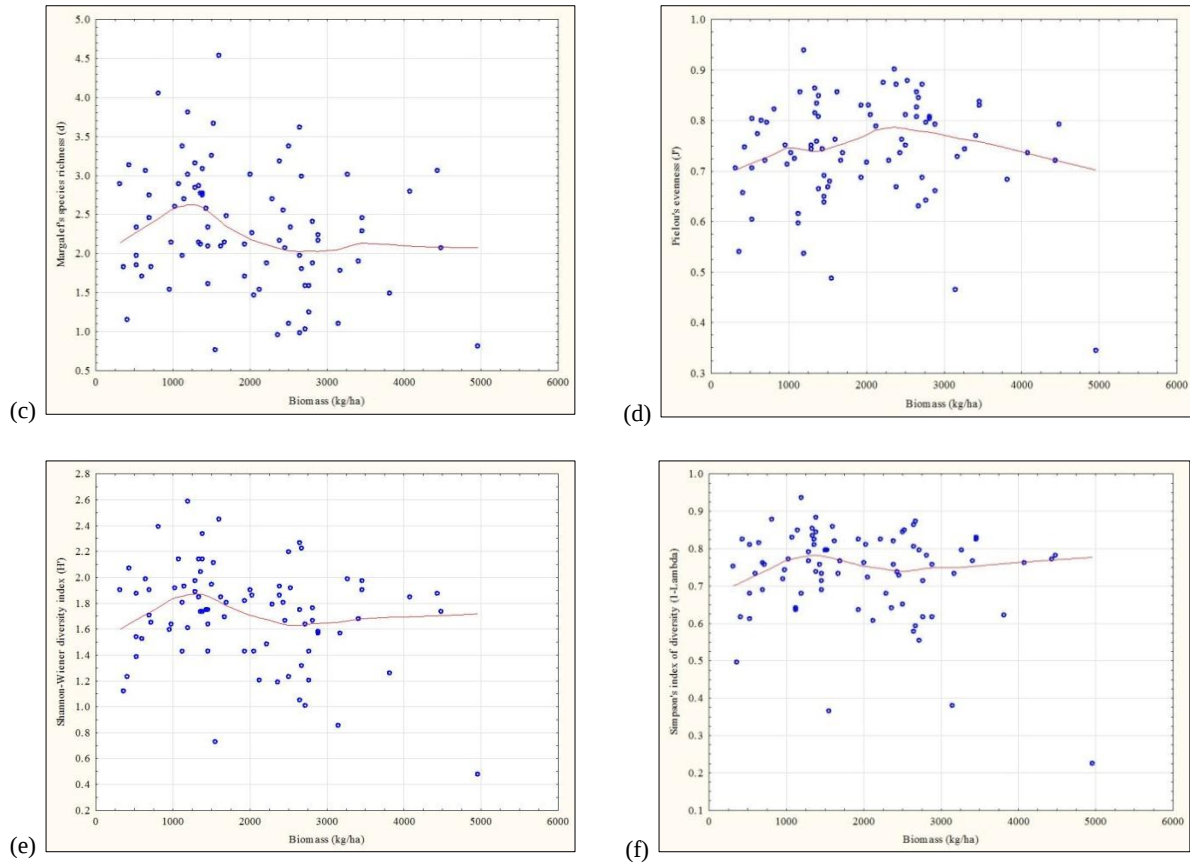


Figure 16. LOWESS (Locally Weighted Scatterplot Smoothing) regression between herbaceous biomass (kg/ha) and mean values per 200 m² plot for (a) total species, (b) total individuals, (c) Margalef's species richness, (d) Pielou's evenness, (e) Shannon-Wiener diversity index, and (f) Simpson's index of diversity in the sodic zone of the Nkuhlu research exclosures, KNP.

Table 5. Regression summary of biomass (biomass and biomass²) for different variables in the sodic zone of the Nkuhlu exclosures, KNP. Significant relationships ($p < 0.05$) are indicated with *

Dependent variable	R ²	Adjusted R ²	F	P
Total species	0.0853	0.0621	3.6837	0.0295*
Total individuals	0.0647	0.0410	2.7326	0.0712
Margalef's species richness	0.0585	0.0347	2.4537	0.0925
Pielou's evenness	0.1325	0.1106	6.0352	0.0036*
Shannon-Wiener diversity index	0.0807	0.0574	3.4662	0.0361*
Simpson's index of diversity	0.1041	0.0814	4.5895	0.0130*

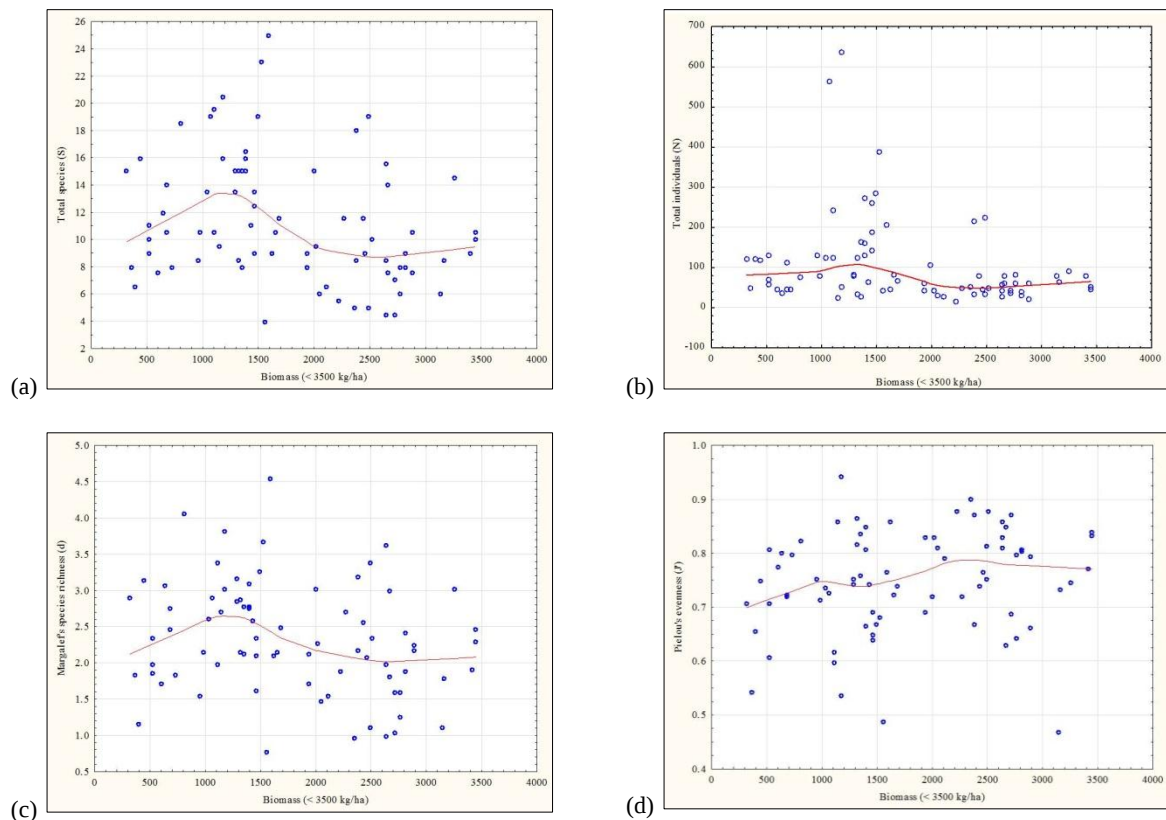
R², also known as *coefficient of determination* is used to assess model fit, i.e. if the correlation between the dependent and independent variables is small, R² will be closer to 0, conversely when the correlation is large, the R² coefficient will be closer to 1 (STATISTICA

version 11, 2012); Adjusted R^2 , compensates for the addition of variables to the model, and will always be smaller than unadjusted R^2 (STATISTICA version 11, 2012); F, the F-value shows the degree of a variable's contribution to the overall correlation achieved, i.e. the higher the F-value, the bigger the correlation between the dependent and the independent variables (Vuilleumier, 1970; Wheeler & Giller, 1982); p , p -value is significant at $p < 0.05$.

Quadratic regression analysis of data revealed a statistical significant quadratic relationship between biomass and total species ($p = 0.0295$), Pielou's evenness ($p = 0.0036$), Shannon-Wiener diversity index ($p = 0.0361$) and Simpson's index of diversity ($p = 0.0130$) (Table 5). The quadratic relationship between biomass and both total individuals ($p = 0.0712$) and Margalef's species richness ($p = 0.0925$) (Table 5) was non-significant.

7.3.2 LOWESS and quadratic regression analyses with biomass < 3500 kg/ha

After omitting five plots with a biomass level in the range of 3500-5000 kg/ha (statistically non-representative), the relationship between biomass and dependent variables still proved nonlinear. Quadratic regression analyses were applied to determine whether there existed a significant quadratic relationship between biomass (biomass and biomass²) and dependent variables.



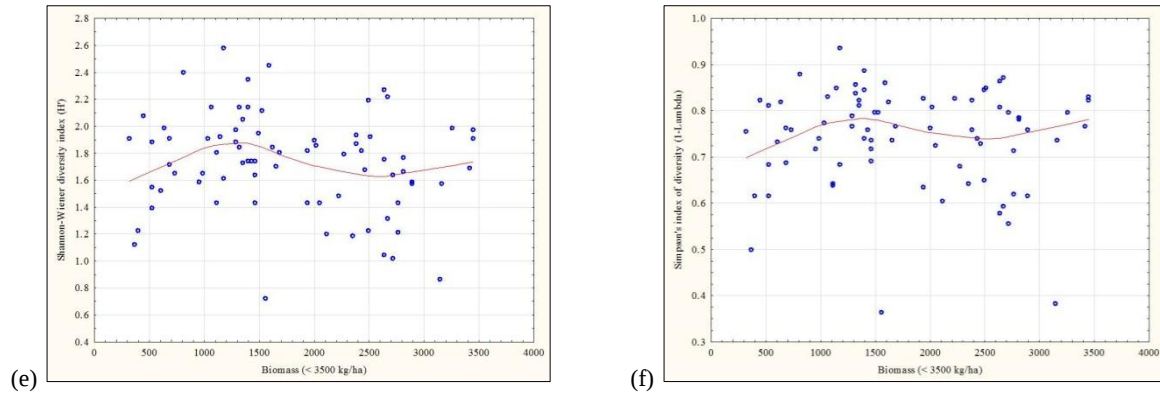


Figure 17. LOWESS (Locally Weighted Scatterplot Smoothing) regression between herbaceous biomass (< 3500 kg/ha) and (a) mean total species, (b) total individuals, (c) Margalef's species richness, (d) Pielou's evenness, (e) Shannon-Wiener diversity index and (f) Simpson's index of diversity in the sodic zone of the Nkuhlu research exclosures, KNP.

Table 6. Regression summary of biomass (biomass and biomass²) < 3500 kg/ha for different variables in the sodic zone of the Nkuhlu exclosures, KNP. Significant relationships ($p < 0.05$) are indicated with *

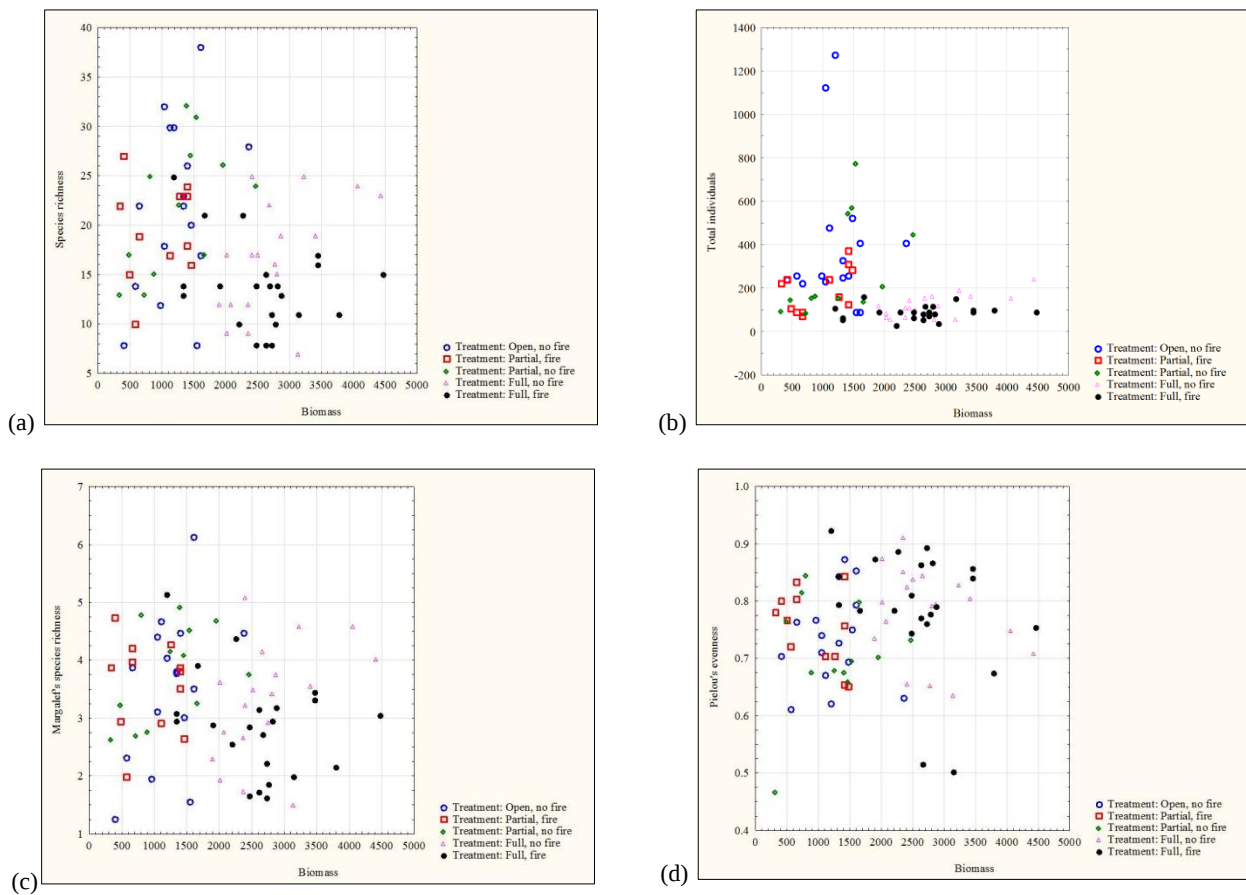
Dependent variable	R ²	Adjusted R ²	F	p
Total species	0.1034	0.0792	4.2677	0.0176*
Total individuals	0.0896	0.0650	3.6417	0.0310*
Margalef's species richness	0.0668	0.0416	2.6489	0.0774
Pielou's evenness	0.0517	0.0261	2.0198	0.1399
Shannon-Wiener diversity index	0.0358	0.0097	1.3728	0.2598
Simpson's index of diversity	0.0170	-0.0095	0.6399	0.5302

*See footnote following Table 5

Quadratic regression analysis of data revealed that total species ($p = 0.0176$), i.e. species richness, and total individuals ($p = 0.0310$) (Table 6) had a significant quadratic relation to biomass. The quadratic relation between Margalef's species richness ($p = 0.0774$), Pielou's evenness ($p = 0.1399$), Shannon-Wiener diversity index ($p = 0.2598$) and Simpson's index of diversity ($p = 0.5302$) (Table 6) all revealed to be non-significant.

Biomass levels of treatments below 2500 kg/ha (Table 7) (Figure 18), i.e. the partial exclusion (with and without fire treatment) and the control site, show a nonlinear, hump-shaped relationship with species richness (Figure 17 (a) & (c)). Similarly a nonlinear, hump-shaped relationship could also be seen between biomass and species diversity, i.e. Shannon-Wiener diversity index (Figure 17 (e)) and Simpson's index of diversity (Figure 17 (f)).

Richness and diversity of the herbaceous layer did not increase exponentially, but reached a point of stability, in treatments where biomass levels exceeded 2500 kg/ha, i.e. the full exclusion (with and without fire treatment) (Table 7; Figure 17).



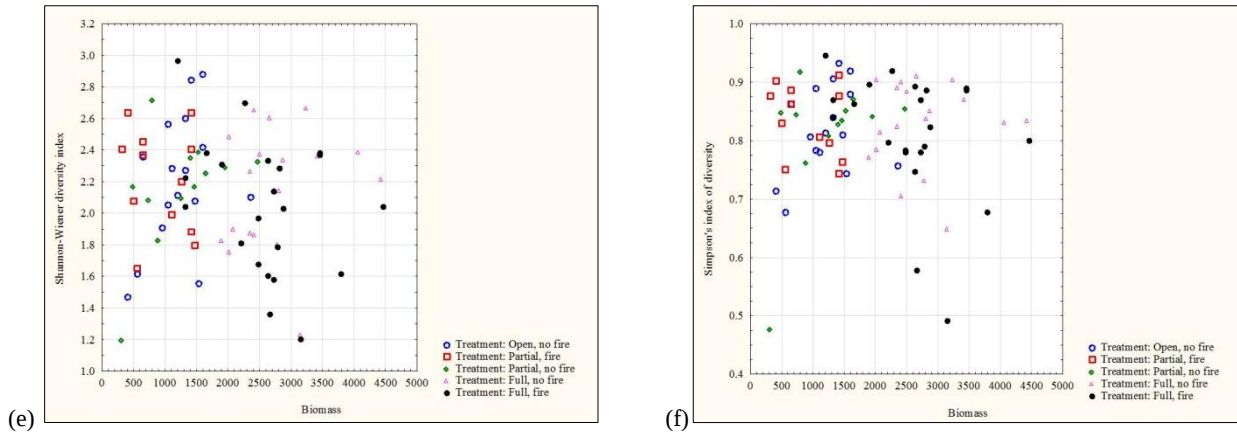


Figure 18. Scatterplots of (a) species richness, (b) total individuals, (c) Margalef's species richness, (d) Pielou's evenness, (e) Shannon-Wiener diversity index and (f) Simpson's index of diversity against biomass categorized by treatment.

Table 7. Biomass (kg/ha) ranges associated with various treatments of fire and herbivory in the Nkuhlu research exclosures, KNP.

Treatment	Biomass (kg/ha)
Partial, fire	300 - 1460
Partial, no fire	360 - 2490
Open, no fire	400 - 2380
Full, no fire	1900 - 4400
Full, fire	1400 - 5000

7.4 Discussion

LOWESS regression analyses revealed a nonlinear, hump-shaped relationship between herbaceous field biomass and species richness and diversity (Figure 17), at least for sampling plots with a biomass level below 2500 kg/ha (Table 7). Plots with a biomass level exceeding 2500 kg/ha revealed neither a hump-shaped relationship between richness, diversity and biomass, nor did it increase exponentially, but rather stabilized. The hump-shaped relationship between species richness and biomass across three of the five herbivory and fire treatments of the Nkuhlu research exclosures, i.e. the control site and the partially fenced site (with and without fire treatment) (Figure 17 (a) & (c)), correspond with findings of Guo & Berry (1998) and Guo (2003), who suggested that the hump-shaped relationship between species richness and biomass will become prominent when a larger area with a greater range

of environmental conditions is considered, i.e. herbivore presence, the presence or absence of the large herbivores namely elephant and giraffe, and the presence or absence of fire. Herbivores act as a primary disturbance reducing biomass and canopy cover of certain species, creating grazing patches, wallows and game paths, which leads to an increase in spatial and physical heterogeneity (Olff & Ritchie, 1998; Jacobs & Naiman, 2008).

Conversely, in the absence of herbivores the environment becomes more homogeneous due to a decline in disturbances, thus causing a decline in plant community heterogeneity (Jacobs & Naiman, 2008). In accordance with the findings of Guo & Berry (1998), no hump-shaped relationship could be seen between species richness/diversity and biomass in the environmentally homogeneous fully fenced herbivore exclusion treatments (with and without fire), with biomass levels exceeding 2500 kg / ha (Figure 17). In the absence of herbivores, biomass levels increase significantly (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013), causing certain herbaceous species to become dominant. This is in accordance with Abrams (1995) and Jacobs and Naiman (2008), stating that at high levels of biomass, dominant species tend to outcompete other species for resources, leading to the area being dominated by only a few species, therefore causing an increase in spatial homogeneity and a decrease in species evenness.

Quadratic regression analyses revealed that both species richness ($p = 0.0176$) (Table 6) (Figure 17 (a)) and total individuals ($p = 0.0310$) (Table 6) (Figure 17 (b)) had a statistically significant quadratic relationship with biomass. The maximum number of species and number of individuals is found at intermediate levels of biomass, which for the sodic zone is considered 1000-1500 kg/ha. Above this threshold (i.e. fully fenced areas (Table 7)) there is a quadratic response due to larger plant size and higher biomass as a result of herbivore exclusion (Jacobs & Naiman, 2008), inferring that fewer species and number of individuals can coexist and that number of individuals and species is inversely related to the square of biomass (Oksanen, 1996).

7.5 Conclusion

This chapter offers a better understanding of the dynamic relationships between herbaceous species biomass, richness and diversity in the sodic zone of the Nkuhlu research exclosures. This relationship has been central to community ecology for many years, and results from this chapter can be used to contribute to the already existing knowledge pool, as well as new knowledge gathered on the specific reactions of herbaceous diversity and richness in particular plant communities of the KNP. In doing

so, the science based management of both ecosystem fauna and flora diversity and richness may be promoted.

Results obtained confirmed that a hump-shaped relationship exists between herbaceous species richness and biomass, at least in areas where herbivores were present and with biomass levels between 500 kg/ha and 2500 kg/ha in the sodic zone. Contrariwise, in the absence of herbivores, when biomass levels exceed 2500 kg/ha, the relationship between herbaceous biomass and species richness is neither hump-shaped nor linear, but rather stable, due to a few dominant species that, after nine years, flourished in the absence of herbivory, and therefore high biomass levels.

Herbivores are necessary to drive ecosystem heterogeneity, while keeping biomass levels low. In the areas where herbivores were present, i.e. heterogeneous areas, species richness was the highest at intermediate levels of biomass. In the more homogeneous areas, i.e. areas where herbivores were excluded, no hump-shaped relationship could be seen. A significant quadratic relationship exists between herbaceous biomass and species richness in the sodic zone of the Nkuhlu exclosures in areas where biomass did not exceed 2500 kg/ha. This relationship is hump-shaped, inferring that highest species richness is found at intermediate levels of biomass which is considered between 1000 kg/ha and 1500 kg/ha for the sodic zone. However, after nine years, no significant quadratic relationship could be detected between herbaceous species diversity and herbaceous field biomass. Even though herbaceous biomass and species evenness showed no significant relationship, high evenness was associated with intermediate biomass levels, inferring that herbaceous species evenness increases as biomass levels increase and stabilizes at high biomass.

Conservation implications: Results obtained through this chapter will promote the understanding of the dynamic relationship that exists between the herbaceous layer, i.e. forb and grass, field biomass and species richness and diversity, particularly in the sodic zone of the Nkuhlu research exclosures, KNP. Broader understanding of such relationships should support improved management, conservation and maintenance of these dynamic nutrient hotspots. Major recommendations include: (1) a longer time period is needed to research the relationship between herbaceous species diversity and herbaceous field biomass, since after nine years, no significant quadratic relationship could be detected between these variables.

Chapter 8

Conclusion

8.1 Introduction

Savannas are complex and dynamic ecosystems, and a stable, typical savanna does not exist (Skarpe, 1991). Herbivory and fire are important ecosystem modifiers and agents of disturbance, particularly in African savannas where they often act together, and have played an active part in determining the structure, dynamics and functioning of ecosystems throughout evolutionary history (Archibald *et al.*, 2005; Jacobs & Naiman, 2008; Levick & Rogers, 2008). Both fire and herbivory have been shown to influence vegetation composition and structure, annual above ground net primary productivity and nutrient cycling of semi-arid African savannas (Archibald *et al.*, 2005; O'Connor, 1994). Yet, very little is known about the interaction between these two agents of disturbance, since fire and herbivory have usually been studied independently (Archibald *et al.*, 2005; Masunga *et al.*, 2013). The Nkuhlu enclosures in the Kruger National Park (KNP) provided the unique opportunity to study these two agents and their collective effects on the species richness/diversity and biomass of the herbaceous layer in the sodic zone, which is considered a 'nutrient hotspot' (O'Keefe & Alard, 2002; Grant & Scholes, 2006).

In its completeness, this study served the important aim of increasing the knowledge on a part of herbaceous vegetation which is often neglected, i.e. the forbs. This chapter will provide a synthesis of the major findings.

8.2 Main findings

This study provides a novel representation of the combined spatial and temporal effects of fire and herbivory on the richness and diversity of the herbaceous layer, i.e. forbs and grasses, of the sodic zone in the Nkuhlu research enclosures, KNP, since this has never been done for the ecologically sensitive sodic zone along the Sabie River, South Africa. Furthermore, previous studies do not consider the combined effect of fire and herbivory, but rather look at their effects independently. Herbivory, i.e. whether elephants are included (open treatment) or excluded (partial treatment) is suggested to be the primary driver of herbaceous vegetation dynamics in the sodic zone along the

Sabie River. Increasing biomass as a result of the absence of herbivory suppresses the richness of herbaceous species, although species richness is even lower in its combined effect with fire treatment.

The effects of fire on herbaceous species richness and diversity were not statistically significant, although it clearly suppressed both herbaceous species richness and standing biomass, reflecting the view that fire is a secondary driver within the herbivory treatments. Since no significant variation was detected with respect to the effects of fire and herbivory on herbaceous species diversity, these effects were tested after a nine year time period, comparing baseline data collected in 2001 with floristic data collected in 2010. After nine years, fire and herbivory significantly affected herbaceous species diversity in the sodic zone of the Nkuhlu research exclosures.

The expected increase in biomass levels after nine years of herbivory exclusion from the system was verified. These increases lead to suppression of herbaceous species richness and diversity, and the promotion of system homogeneity. The species composition in the absence of herbivory, but both in the presence and absence of fire, remained more or less unchanged over nine years, while the species composition in the areas exposed to herbivory, both with and without fire, changed substantially over nine years. Therefore, herbivory over time drives compositional changes and heterogeneity of the herbaceous vegetation in the sodic zone of the Nkuhlu research exclosures. Some prominent species abundances of the sodic zone changed over time and across various fire and herbivory treatments, while others showed no significant changes in abundance over nine years and across different combinations of fire and herbivory treatments. A possible limitation was that more long-term monitoring of the prominent herbaceous species in the sodic zone along the Sabie River is needed to form a complete picture of the species-specific effects of fire and herbivory.

Continuously grazed areas showed a hump-shaped relationship between biomass and species richness, suggesting that, for areas with a biomass level not exceeding 2500 kg/ha, the species richness is highest at intermediate levels of biomass. Conversely, the hump-shaped relationship did not reveal to be true for areas where herbivores were excluded and biomass levels exceeded 2500 kg/ha, here, the relationship between biomass and richness rather revealed to be stable. Therefore, the hump-shaped relationship does not exist in the absence of herbivory, where the system is more homogeneous, but rather in the presence of herbivores, where the system is much more heterogeneous. After nine years, no significant relationship could be detected between herbaceous species diversity and herbaceous field biomass. Even though herbaceous biomass and species evenness showed no significant relationship, high evenness was associated with high biomass levels, inferring that herbaceous species

evenness increases as biomass levels increase, reaching a point where it stabilizes and then starts to decrease.

To conclude, herbivores are deemed both primary and necessary drivers of herbaceous vegetation dynamics and heterogeneity in sodic zones, KNP, while fire is suggested to be a secondary driver. The combined effect of fire presence and herbivore absence seems to suppress richness of forbs and grasses in the sodic zone. Removal of large herbivores will lead to increased biomass levels, at the cost of herbaceous species richness and complete system heterogeneity. There seems to exist, at least for the sodic zone of the Nkuhlu research exclosures, a biomass threshold of 2500 kg/ha, over which the hump-shaped relationship between biomass and species richness will not be observed. Further long-term monitoring is needed to detect changes and patterns in herbaceous species diversity, as well as species-specific reactions upon various fire and herbivory treatments.

8.3 The way forward

Since this project forms part of a long-term monitoring project within the KNP, the continued monitoring of the herbaceous vegetation of the Nkuhlu exclosures, particularly the sodic plant community will greatly benefit future studies. While this study can be used as baseline, further research on this vegetation community will help promote our understanding of how best to manage and conserve these ecologically important vegetation communities.

Some additional areas for investigation that should be kept in mind for future studies include: (a) sampling high biomass areas (> 3500 kg/ha) to clarify the hump-shaped model, (b) herbaceous vegetation across varying plant communities of the Nkuhlu research exclosures should be sampled and analysed, to determine if the herbaceous layer of these plant communities show similar trends in reaction upon various fire and herbivory treatments, (c) functional trait comparisons should be done to comment on ecosystem functioning, (d) herbaceous species should be divided into annuals and perennials, and the percentage abundance of each should be determined for each treatment, (e) another variable that should be taken into account is rainfall of years preceding sampling.

8.4 Major recommendations for the sodic zone of the Nkuhlu exclosures, KNP

- ❖ Highest herbaceous species richness was associated with highest disturbance in 2010 (i.e. open treatment); therefore the presence of all herbivores promotes herbaceous species richness.
- ❖ Biomass levels increase in the absence of herbivory, leading to decreases in species richness; indicating that herbivores are necessary to keep biomass levels low to promote and maintain herbaceous species density (i.e. number of individuals per plot), species richness and diversity.
- ❖ Herbaceous species diversity showed no significant differences across treatments, although lowest diversity was measured in the absence of herbivory and the presence of fire.
- ❖ Although sodic patches are often deemed overgrazed and trampled, herbivores are essential for the maintenance of herbaceous species richness and diversity, and should be considered as a major driver of these systems in management practices.
- ❖ While statistically not significant, fire seems to suppress diversity and richness of the herbaceous layer.
- ❖ It is therefore recommended that floristic monitoring over a longer time period under similar conditions is required to support these preliminary findings, and to determine whether the two variables, i.e. herbaceous species diversity and fire show significant variation across treatments.
- ❖ Over time, the absence of elephants, but the presence of fire and all other herbivores provides ideal conditions for high species richness, diversity and evenness. Further long-term monitoring should be done to confirm whether or not these patterns tend to stay the same after more time had passed.
- ❖ Herbivores act as primary drivers of compositional changes in the herbaceous layer; inferring that herbivores are needed to maintain system heterogeneity.
- ❖ Over time fire shows only limited effect on herbaceous species composition; hence, the effect of fire on herbaceous species composition should further be researched over a longer time period to reinforce these findings.
- ❖ Dominant forb species *Alternanthera pungens* is grazing tolerant, yet more research is required to determine how abundances will react upon the presence of fire; management can use this species as an indicator of overgrazing.
- ❖ The forb species *Justicia protracta* is dependent on fire to resprout, however more research over a longer time period and larger spatial scale is needed to confirm these preliminary findings; this species can be used by managers to be indicative of fire presence in the sodic zone.

- ❖ The highly palatable *Panicum maximum* is a preferred grass species for foraging by large herbivores in the sodic zone, and is not tolerant to overgrazing, undergrazing, shady conditions or the presence of fire; *P. maximum* in the sodic zone can be used as an indicator species of over- or undergrazing and fire presence.
- ❖ The low grazing value grass species *Sporobolus nitens* is abundant in overgrazed sodic areas and is shade-intolerant; managers can therefore use this species to indicate overgrazed veld.
- ❖ Rainfall is an important aspect, and it is recommended that it should receive ample consideration in future long-term herbaceous vegetation studies.
- ❖ A significant quadratic relationship exists between herbaceous biomass and species richness in areas exposed to herbivory and where biomass levels are between 500 kg/ha and 2500 kg/ha, this relationship is hump-shaped and therefore the highest species richness is found at intermediate levels of biomass in the sodic zone, i.e. between 1000 kg/ha and 1500 kg/ha; herbivores are necessary to drive ecosystem heterogeneity, while keeping biomass levels low.
- ❖ When biomass levels exceed 2500 kg/ha, the relationship between herbaceous biomass and species richness is neither hump-shaped nor linear, but rather stable; management practices should include herbivores in these ecologically sensitive plant communities to maintain low biomass levels and high system heterogeneity.
- ❖ After nine years, no significant quadratic relationship could be detected between herbaceous species diversity and herbaceous field biomass; management should consider further long-term monitoring to determine what the relationship between these two variables is.
- ❖ High evenness is associated with intermediate biomass levels and herbaceous species evenness increases as biomass levels increase and stabilizes at high biomass; further research should be done to confirm these findings.

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Appendix A: Nkuhlu exclosures sodic species list

Complete herbaceous species list recorded in the sodic zone of the Nkuhlu exclosures, Kruger National Park.

Dicotyledons	
Family	Species
ACANTHACEAE	<i>Barleria elegans</i> L.
	<i>Barleria prionitoides</i>
	<i>Blepharis innocua</i> Juss.
	<i>Blepharis integrifolia</i> Juss.
	<i>Crabbea velutina</i> Harv.
	<i>Crossandra mucronata</i> Salisb.
	<i>Isoglossa grantii</i> Oerst.
	<i>Justicia flava</i> L.
	<i>Justicia petiolaris</i> L.
	<i>Justicia protracta</i> L.
	<i>Justicia</i> sp. 1
	<i>Rhinacanthus xerophilus</i> Nees
	<i>Ruellia cordata</i> L.
	<i>Ruellia patula</i> L.
AIZOACEAE	<i>Aizoon canariense</i> L.
	<i>Trianthema salsoloides</i> L.
	<i>Trianthema triquetra</i> L.
AMARANTHACEAE	<i>Achyranthes aspera</i> L.*
	<i>Aerva leucura</i> Forssk.
	<i>Alternanthera pungens</i> Forssk.*
	<i>Alternanthera sessilis</i> Forss.*
	<i>Amaranthus praetermissus</i> L.
	<i>Amaranthus thunbergii</i> L.
	<i>Celosia trigyna</i> L.
	<i>Gomphrena celosioides</i> L.*
	<i>Kyphocarpa angustifolia</i> (Fenzl) Lopr.
	<i>Pupalia lappacea</i> Juss.

ASTERACEAE	<i>Acanthospermum hispidum</i> Schrank.* <i>Bidens bipinnata</i> L.* <i>Dicoma tomentosa</i> Cass. <i>Vernonia glabra</i> Schreb.
BORAGINACEAE	<i>Heliotropium ciliatum</i> L.
CAPPARACEAE	<i>Cleome gynandra</i> L. <i>Cleome macrophylla</i> L. <i>Cleome monophylla</i> L.
CONVOLVULACEAE	<i>Convolvulus farinosus</i> L. <i>Evolvulus alsinoides</i> L. <i>Ipomoea bathycolpos</i> L. <i>Seddera suffruticosa</i> Hochst.
CRASSULACEAE	<i>Kalanchoe brachyloba</i> Adans. <i>Kalanchoe rotundifolia</i> Adans.
CUCURBITACEAE	<i>Coccinia rehmannii</i> Wight & Arn. <i>Cucumis africanus</i> L. <i>Cucumis zeyheri</i> L. <i>Gerrardanthus macrorhizus</i> Harv. Ex <i>Kedrostis foetidissima</i> Medik. <i>Momordica balsamina</i> L.
EUPHORBIACEAE	<i>Acalypha indica</i> L. <i>Acalypha segetalis</i> L. <i>Tragia dioca</i> L. <i>Tragia rupestris</i> L.

FABACEAE	<i>Alysicarpus rugosus</i> Desv. <i>Crotalaria sphaerocarpa</i> L. <i>Indigofera daleoides</i> L. <i>Indigofera filipes</i> L. <i>Indigofera nebrowiana</i> L. <i>Indigofera tinctoria</i> L. <i>Lotononis eriantha</i> (DC.) Eckl. & Zeyh. <i>Ormocarpum trichocarpum</i> P.Beauv. <i>Sesbania bispinosa</i> Scop.* <i>Senna bicapsularis</i> Mill.* <i>Tephrosia polystachya</i> Pers. <i>Tephrosia purpurea</i> Pers.
GISEKIACEAE	<i>Gisekia africana</i> L.
LAMIACEAE	<i>Acrotome hispida</i> Benth. Ex Endl. <i>Ocimum americanum</i> L. <i>Ocimum gratissimum</i> L. <i>Orthosiphon suffrutescens</i> Benth. <i>Plectranthus hadiensis</i> L'Hér.
MALVACEAE	<i>Abutilon austro-africanum</i> Mill. <i>Abutilon guineense</i> Mill. <i>Abutilon mauritianum</i> Mill. <i>Abutilon sonneratianum</i> Mill. <i>Hibiscus calyphyllus</i> L. <i>Hibiscus pusillus</i> L. <i>Hibiscus sabiensis</i> L. <i>Hibiscus schinzii</i> L. <i>Hibiscus trionum</i> L. <i>Malvastrum coromandelianum</i> A.Gray <i>Pavonia burchellii</i> Cav. <i>Pavonia senegalensis</i> Cav. <i>Sida alba</i> L.
MOLLUGINACEAE	<i>Corbichonia decumbens</i> Scop. <i>Hypertelis bowkeriana</i> E.Mey. exFenzl <i>Mollugo nudicaulis</i> L.

NYCTAGINACEAE	<i>Boerhavia diffusa</i> L.*
OLEACEAE	<i>Jasminum fluminense</i> L.
OXALIDACEAE	<i>Oxalis depressa</i> L.
PEDALIACEAE	<i>Ceratotheca triloba</i> Endl. <i>Pterodiscus ngamicus</i> Hook.
PHYLLANTACEAE	<i>Phyllanthus asperulatus</i> L. <i>Phyllanthus incurvus</i> L. <i>Phyllanthus pentandrus</i> L.
PHYTOLACCACEAE	<i>Lophiocarpus polystachyus</i> Turcz.
PORTULACACEAE	<i>Portulaca hereoensis</i> L. <i>Portulaca oleracea</i> L.* <i>Portulaca quadrifida</i> L. <i>Portulaca trianthemoides</i> L. <i>Talinum arnotii</i> Adans. <i>Talinum portulacifolium</i> Adans*
RUBIACEAE	<i>Agathisanthemum bojeri</i> Klotzsch
SCROPHULARIACEAE	<i>Aptosimum lineare</i> Burch. Ex Benth.
SOLANACEAE	<i>Solanum delagoense</i> L.
STERCULIACEAE	<i>Hermannia boraginiflora</i> L. <i>Hermannia odorata</i> L. <i>Melhania forbesii</i> Forrsk. <i>Melhania prostrata</i> Forrsk. <i>Waltheria indica</i> L.
TILIACEAE	<i>Corchorus asplenifolius</i> L. <i>Corchorus confusus</i> L.
VERBENACEAE	<i>Lantana rugosa</i> L.
ZYGOPHYLLACEAE	<i>Tribulus terrestris</i> L.
Monocotyledons	

COMMELINACEAE	<i>Commelina africana</i> L. <i>Commelina benghalensis</i> L. <i>Commelina eckloniana</i> L. <i>Commelina erecta</i> L.
CYPERACEAE	<i>Bulbostylis burchellii</i> Kunth <i>Bulbostylis hispidula</i> Kunth <i>Cyperus albobstriatus</i> L. <i>Cyperus capensis</i> L. <i>Cyperus dives</i> L. <i>Cyperus indecorus</i> L. <i>Cyperus obtusiflorus</i> L. <i>Cyperus rupestris</i> L. <i>Dioscorea cotinifolia</i> L. <i>Kyllinga alba</i> Rottb.
HYACINTHACEAE	<i>Ledebouria</i> sp. 1

POACEAE

Aristida bipartita L.
Aristida congesta subsp. *congesta* L.
Bothriochloa bladhii Kuntze
Brachiaria deflexa (Trin.) Griseb.
Cenchrus ciliaris L.
Chloris gayana Sw.
Chloris roxburghiana Sw.
Chloris virgata Sw.
Cynodon dactylon Rich.
Dactyloctenium aegyptium Willd.
Dactyloctenium australe Willd.
Digitaria eriantha Haller
Echinochloa colona P.Beauv.
Enneapogon scoparius Desv. ex P.Beauv.
Enteropogon macrostachyus Nees
Enteropogon monostachyus Nees
Eragrostis curvula Wolf
Eragrostis cylindriflora Wolf
Eragrostis gummiflua Wolf
Eragrostis heteromera Wolf
Eragrostis rigidior Wolf
Eragrostis superba Wolf
Eragrostis trichophora Wolf
Melinis repens P.Beauv.
Microchloa caffra R.Br.
Oropetium capense Trin.
Panicum coloratum L.
Panicum deustum L.
Panicum maximum L.
Perotis patens Aiton
Phragmites mauritianus Adans.
Pogonarthria squarrosa Stapf
Schmidtia pappophoroides Steud. Ex J.A.Schmidt
Sporobolus fimbriatus R.Br.
Sporobolus nitens R.Br.
Tragus berteronianus Haller

Urochloa mosambicensis P.Beauv.*Urochloa panicoides* P.Beauv.

Pteridophyta

PTERIDACEAE

Cheilanthes viridis Sw.

Appendix B: Published article (Chapter 5)



Herbaceous species diversity patterns across various treatments of herbivory and fire along the sodic zone of the Nkuhlu exclosures, Kruger National Park

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Understanding relationships between large herbivores and plant species diversity in dynamic riparian zones is critical to biodiversity conservation. The Nkuhlu exclosures in the Kruger National Park (KNP) provided opportunity to investigate spatial heterogeneity patterns within riparian zones, as well as how these patterns are affected by fire and herbivory. A monitoring project was initiated to answer questions about the dynamics of the herbaceous layer and was aimed at determining, (1) whether there exists meaningful variance in herbaceous plant species richness and diversity across different treatments in the ecologically sensitive sodic zone and (2) whether an increase in herbaceous biomass, an artefact of herbivory and fire exclusion, suppresses herbaceous plant species diversity and richness. Herbaceous vegetation was sampled in two 1 m² circular sub-plots in the eastern and western corners of 81 fixed plots. The biomass of each plot was estimated with a disc pasture meter (DPM) diagonally with the plot. DPM-readings were converted to kg/ha, according to the latest conversions for the Lowveld Savanna. Species richness and biomass showed significant variance across treatments, whereas no significant variation in herbaceous species diversity was perceived. Combined treatment of fire absence and herbivore presence contributed to higher forb species richness in the sodic zone. Biomass is significantly higher in fully fenced areas where herbivores are excluded, as opposed to the open and partially fenced areas. Although no significant variation was recorded for diversity across treatments, lowest diversity was recorded in the absence of all herbivores, especially in combination with fire treatment. Therefore herbivores are essential in sustaining herbaceous plant species richness in the sodic zone, whilst no significant results were found with regard to their effect on species diversity. Although statistically non-significant, fire seems to suppress species richness.

Conservation implications: This study could be used as framework to advance and develop science-based management strategies for, at least, the sodic zones of the KNP. Research in these exclosures will create better understanding of these landscapes, benefit ecosystem conservation planning of national parks and also provide valuable long-term information on key ecological processes.

Introduction

Sodic patches are often associated with footslopes of undulating granitic landscapes (Venter 1990) and are commonly referred to as 'nutrient hotspots' as they produce high quality forage (Grant & Scholes 2006). Deep, duplex soil containing dispersed clay with a low infiltration capacity and high concentrations of nitrogen, phosphorus and sodium characterise sodic patches (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). 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, Mallory-Smith & Ball 2007). The level of sodium in soil is often reported as the sodium adsorption ratio (SAR). Soil is classified as sodic when the SAR is above 13; at levels below 13, sodium can cause deterioration of soil structure and problems with water infiltration (Davis, Waskom & Bauder 2012).

Sodic patches form an integral part of savanna ecosystems because of the ecosystem services and functioning they provide, such as, (1) the accumulation of nutrients, (2) the provision of open spaces for predator vigilance and (3) the formation of wet season wallowing points (Khomo & Rogers 2005). Furthermore, these key resource areas sustain animal body condition for dry season survival and support reproduction through nutritional benefits (Grant & Scholes 2006). Despite their ecological significance, sodic patches are often considered as desolate land because of their disturbed appearance and low aesthetic value (Khomo & Rogers 2005) caused by overgrazing,



which, in turn, impacts on herbaceous species diversity, richness and biomass (Jacobs & Naiman 2008).

Fire and herbivory are regarded as important ecosystem modifiers, especially in semi-arid southern African savannas, often acting together (Archibald *et al.* 2005). Fire and herbivory are considered as dominant mediators of vegetation change in the Kruger National Park (KNP) and interact strongly with rainfall unpredictability and prolonged droughts (Du Toit, Rogers & Biggs 2003). The impact of fire and herbivory on herbaceous biomass dynamics is, however, poorly understood (Archibald *et al.* 2005; Jacobs & Naiman 2008). The establishment of the Nkuhlu exclosures in the KNP in 2001 provided an opportunity to study the spatial and temporal heterogeneity patterns within and around riparian zones, as well as how these patterns are affected by herbivory and fire. By excluding these drivers from the system it is believed that their effects could be determined over time (O'Keefe & Alard 2002).

Jacobs and Naiman (2008) were the first to report on the relationship between herbivory and species richness at the Nkuhlu exclosures. After 2 years of herbivory exclusion, a marked increase in standing biomass was recorded, along with lower species richness in the absence of herbivores. These patterns were, however, less significant along the sodic zone (Jacobs & Naiman 2008). This article is therefore aimed at reporting on herbaceous plant species richness, diversity and biomass specifically along the sodic zone of the Nkuhlu exclosures after an additional 5-year cycle of herbivory and fire exclusion.

The objectives of this study were to test, (1) whether significant variation in herbaceous plant species diversity, richness and biomass could be detected across different combined treatments of herbivory and fire and (2) whether increasing biomass, an artefact of herbivory and fire exclusion, suppresses diversity and richness of herbaceous plant species in the sodic zone of the Nkuhlu exclosures.

Study area

The Nkuhlu large-scale long-term exclusion experiment (24°58'S, 31°46'E) is situated on the northern bank of the Sabie River, approximately 18 km downstream from Skukuza (Siebert & Eckhardt 2008). This semi-arid, subtropical savanna has two distinct seasons: a hot, sporadically wet growth season from October to April and a warm, dry, non-growing season (Scogings *et al.* 2012). The mean annual rainfall is 561 mm, whilst temperatures range from a mean minimum of 5.6 °C in winter to a mean maximum of 32.6 °C in the summer months. Crests and midslopes are characterised by coarse, shallow, sandy soil overlaying weathered rock, whilst footslopes below the seep-line are characterised by deep, duplex soil (Scogings *et al.* 2012; Siebert & Eckhardt 2008). The duplex soil on footslopes is referred to as the sodic zone in this article.

On a national scale, the Nkuhlu exclosures are located within the Granite Lowveld vegetation unit (SVI 3) (Mucina & Rutherford 2006). It is characterised by tall shrubland with

few trees to moderately dense low woodland on deep sandy uplands. The dense herbaceous layer is dominated by the graminoids *Aristida congesta*, *Digitaria eriantha* and *Panicum maximum*. The riparian zone of the exclosures forms part of the Subtropical Alluvial vegetation unit (AZa 7), which is described by Mucina and Rutherford (2006) as having flat alluvial riverine terraces that supports a complex channel of flowing rivers and river-fed pans, marginal reed belts, as well as flooded grasslands, ephemeral herblands and riverine thickets.

The sodic zone plant community was described by Siebert and Eckhardt (2008) as *Sporobolus nitens*–*Euclea divinorum* Dry Sodic Savanna, covering roughly 23% of the total sampling area of the Nkuhlu exclosures. The sodic plant community supports contrasting vegetation and herbivore activities that differ from those found on upland savanna soil (Du Toit *et al.* 2003). It stretches across the exclosure fence lines and shows noticeable visual differences amongst herbivory and fire treatments. The diagnostic and dominant herbaceous species of the sodic community include forbs, such as *Abutilon austro-africanum*, *Portulaca kermesina* and *Ocimum americanum*, and graminoids, such as *Chloris virgata*, *Enteropogon monostachyus* and *S. nitens* (Siebert & Eckhardt 2008).

Methods

Experimental design and sampling

The Nkuhlu exclosures comprise 139 ha of semi-arid savanna in the riparian zone of the Sabie River and consist of three herbivory treatments, each divided into a fire and no-fire treatment, hence six treatment combinations overall (Figure 1). The herbivory treatments consist of, (1) a partially fenced area of 44 ha that was designed to specifically exclude elephants (giraffes are also excluded because their body size), (2) an open, unfenced area of 25 ha (referred to as the 'control site') and (3) a fully fenced area of 70 ha, which was designed to exclude all herbivores larger than a hare (Siebert & Eckhardt 2008).

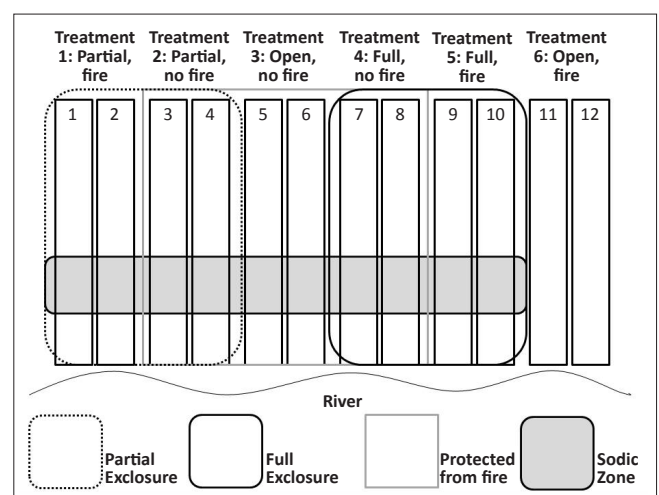


FIGURE 1: Experimental layout of 12 transects within six different fire and herbivory treatments of the Nkuhlu exclosures, Kruger National Park. Treatment 6 was excluded from this study to include sodic sites only.



Vegetation of sodic soil is considered to be more palatable by large herbivores, particularly grazers and mixed feeders (intermediate feeders) than crest vegetation (Scogings 2011). Mammalian herbivores residing in the study area include: browsers – such as giraffe (*Giraffa camelopardalis*), black rhino (*Diceros bicornis*), greater kudu (*Tragelaphus strepsiceros*) and the scrub hare (*Lepus saxatilis*), grazers – such as Cape buffalo (*Syncerus caffer*), hippo (*Hippopotamus amphibius*), blue wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*), and mixed or intermediate feeders – such as impala (*Aepyceros melampus*), African elephant (*Loxodonta africana*) and steenbok (*Raphicerus campestris*) (Scogings *et al.* 2012). The density of elephants in the study area fluctuates, but has been estimated and considered high at 0.5 km²– 2.0 km² (Scogings *et al.* 2012).

Fire treatment of the Nkuhlu exclosures was dependant on whether the larger KNP burn blocks (fire management units) in which the exclosures lie were burned irrespective of the source and the actual extent of the fire. Fires occurred in October 2002 and August 2007.

Floristic sampling, which conformed to the guidelines stipulated in the field operations manual for herbivore and fire exclosures (O'Keefe & Alard 2002), was conducted during the 2010 rainy season (i.e. October–March) (Van Wyk & Fairall 1969) when plant cover was at its maximum and most plant species were present (Keller 2002). All treatments were sampled, although only data from the sodic zone were analysed for this study. As the sodic zone did not extend into the control site with fire, two transects could not be considered for floristic analyses. Each treatment of fire and/or herbivory consisted of two permanent transects (Figure 1). Transects stretch from the river to the crest of the catena and run perpendicular to the river. Permanent transects were marked with metal droppers. Fixed plots were situated 5 m downstream from each transect dropper. The position of transects and plots were plotted on the vegetation map of the Nkuhlu exclosures (Siebert & Eckhardt 2008) to identify plots that are representative of the sodic zone. The data of 81 fixed plots of 10 m × 20 m (long side parallel to the river channel) within the sodic zone (Figure 2) were analysed.

Herbaceous vegetation was sampled in two 1 m² circular sub-plots at the eastern (upland downstream) and western (river upstream) corners of each fixed plot respectively (Figure 2). Only herbaceous individuals rooted within the circle were recorded. Each living individual (forbs and grasses) was counted and all species names conform to Germishuizen and Meyer (2003). The biomass of each plot was estimated, by taking 10 readings along the diagonal of the plot, with a Lowveld Savanna-calibrated disc pasture meter (DPM) (Figure 2). These readings were converted to kg/ha according to the latest conversion of DPM-readings to biomass for the Lowveld Savanna (Zambatis *et al.* 2006).

Two equations for DPM height groups (≤ 26 cm and > 26 cm) were proposed by Zambatis *et al.* 2006:

$$\text{kg.ha}^{-1} = [31.7176 (0.3218^{1/x}) x^{0.2834}]^2 \quad r = 0.9796; \quad r^2 = 0.951; \quad p < 0.0005 \quad [\text{Eqn 1}]$$

$$\text{kg.ha}^{-1} = [17.3543 (0.9893^x) x^{0.5413}]^2 \quad r = 0.948; \quad r^2 = 0.882; \quad p < 0.0005 \quad [\text{Eqn 2}]$$

where x is the mean DPM height (in cm) of a site.

Species richness is the number of species present in a defined area (Begon, Townsend & Harper 2006). In this study, richness was considered as the number of species per circular sub-plot (1 m²). Species diversity was calculated for the plots with the Shannon-Wiener index of diversity (H'), which is sensitive to both species richness and the number of individuals (abundance) per species (Keller 2002). The greater the number of species and the higher the evenness (proportion of each species), the higher the H' -value, which suggests that the diversity in the plot is high (Begon *et al.* 2006; Keller 2002). The function H' used in this study is:

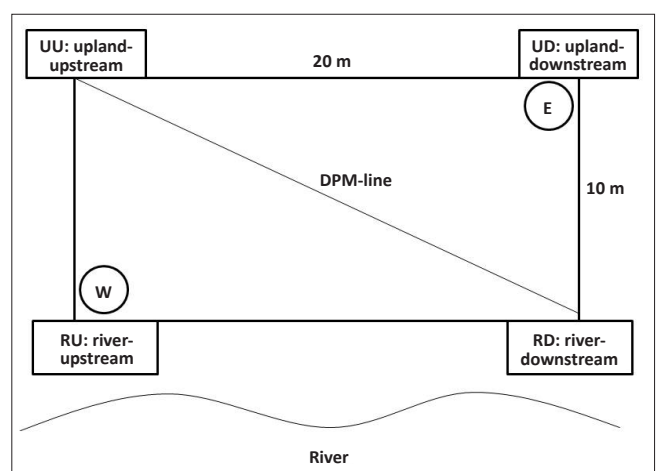
$$H' = -\sum (p_i \ln p_i) \dots \quad [\text{Eqn 3}]$$

where p_i is the relative abundance of the i th species. This index provides a rough measure of diversity, which is much less biased by sample size than species richness.

To test for significant variation in species diversity, richness and biomass of the herbaceous layer amongst the five different treatments of fire and herbivory, one-way analysis of variance (ANOVA) was applied to the data set in *Statistica* version 10 (2010). Where statistically significant results were obtained, *post-hoc* pair-wise comparisons of the treatments – using the Tukey unequal N HSD (honestly significant difference) test – were conducted.

Results

Analysis of variance (Table 1) for all variables revealed significant effects of herbivory, with or without fire, on both



W, western corner; E, eastern corner; DPM, disc pasture meter.

FIGURE 2: Positioning of the 1 m² sub-plots for herbaceous species sampling and the sampling line for disc pasture meter readings within a typical fixed plot along a transect at the Nkuhlu exclosures, Kruger National Park. The corners of each plot are permanently marked with metal droppers which represent a different position parallel to the Sabie River.

TABLE 1: One-way analysis of variance of the mean values for herbaceous biomass and species richness and diversity across treatments along the sodic zone of the Nkuhlu exclosures, Kruger National Park.

Response	Source	df	SS	MS	F	p
Biomass	Treatment	4	51135137.00	12783784.00	26.161340	< 0.0001
	s.e.	76	37137528.00	488651.70	26.161340	< 0.0001
Species richness	Treatment	4	2883.00	234.10	6.170180	0.0002
	s.e.	76	2883.00	37.94	6.170180	0.0002
Shannon-Wiener diversity index	Treatment	4	0.76	0.20	1.011267	0.4
	s.e.	76	14.00	0.19	1.011267	0.4

s.e., standard error; df, degrees of freedom; SS, sum of squared differences; MS, mean square; F, whether variability within and between treatments is significantly different; p, p-values below a certain threshold indicates the significant differences between groups.

biomass ($p < 0.0001$) and species richness ($p = 0.0002$) across the different treatments, whilst the effects of herbivory, with or without fire, on species diversity was non-significant ($p = 0.4$).

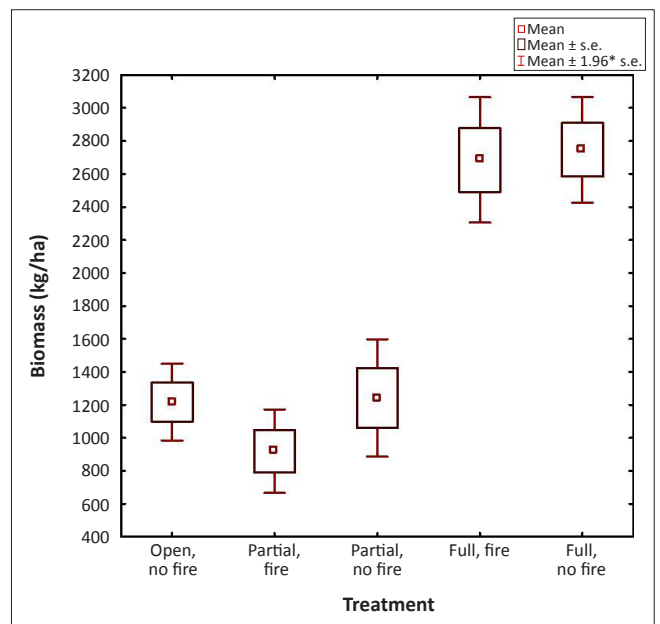
Mean biomass (kg/ha) varied significantly across treatments ($p = 0.0001$) (Table 1; Figure 3). As would be expected, mean biomass was highest in the fully fenced plots as a result of herbivore exclusion. In pair-wise comparisons of biomass means, significant differences were revealed between the control (i.e. open, no fire) site with unrestricted herbivory and the fully fenced area, both with (Tukey: $p < 0.05$) and without fire (Tukey: $p < 0.05$) treatment. Furthermore, both of the partial herbivore treatments showed significant differences compared to both fully fenced herbivore exclusion treatments. Although the effect of fire seems secondary to herbivory, mean biomass was consistently lower in the fire treatments (Figure 3).

A total of 187 herbaceous plant species were recorded in the sodic zone of the Nkuhlu exclosures. Species richness varied significantly across the combinations of herbivory and fire ($p = 0.0002$) (Table 1). Highest species richness was associated with areas exposed to herbivory (Figure 4), although species richness in the control site (i.e. open, no fire) and the partially fenced treatment without fire was significantly higher compared to the fully fenced treatment with fire. Species richness in the partially fenced site with fire was, however, not significantly higher than the full enclosure treatments (Tukey: $p > 0.05$).

Shannon-Wiener diversity index values showed no significant variation across the five combinations of herbivory and fire ($p = 0.4$) (Table 1).

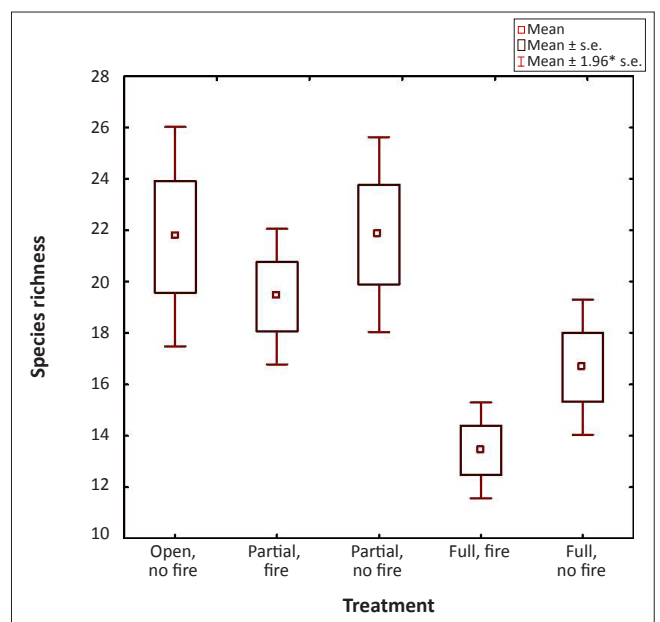
Discussion

The effect of herbivore exclusion on total herbaceous biomass has been shown to be lower in the sodic zone than elsewhere in the riparian zone (Jacobs & Naiman 2008). This phenomenon could be attributed to the drier conditions prevailing in the sodic zone throughout the year, as well as the shallow surface soils and relative impenetrability, making herbaceous species establishment and growth even more challenging. As would be expected, the exclusion of herbivores from the sodic zone lead to herbaceous biomass increases. The biomass range of 2500 kg/ha – 2900 kg/ha (Figure 3) in the full enclosure is unusually high for sodic sites in semi-arid savanna ecosystems, because sodic soil is usually sparsely vegetated



± 1.96*, standard deviations of the mean; s.e., standard error.

FIGURE 3: Mean biomass ($p < 0.0001$) across fire and herbivory treatments in the sodic zone of the Kruger National Park.



± 1.96*, standard deviations of the mean; s.e., standard error.

FIGURE 4: Mean species richness ($p = 0.0002$) across fire and herbivory treatments in the sodic zone of the Kruger National Park.

and therefore associated with land degradation and gully formation that can become self-reinforcing as a result of its

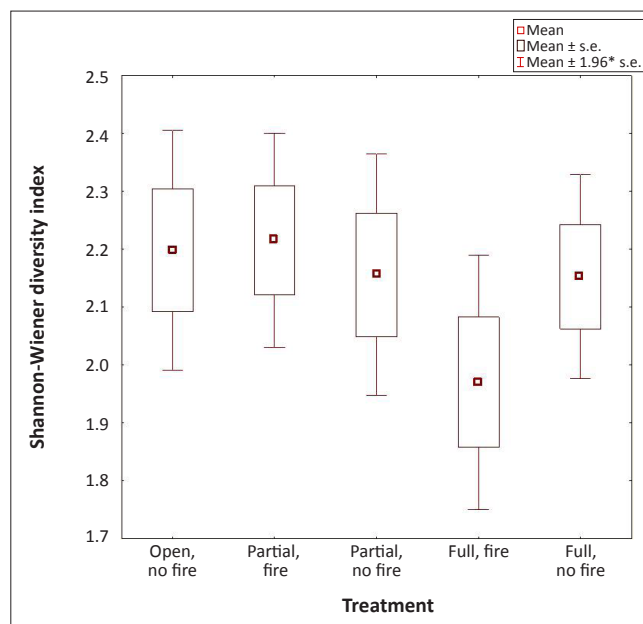
susceptibility to sheet erosion (Khomu & Rogers 2005). The exclusion of herbivores, however, brings forth a gradual improvement in soil surface conditions, which re-establishes the predominance of topsoil water and allows for an increase in the biomass of grasses (Walker *et al.* 1981).

Furthermore, herbivory reduces biomass and canopy cover of certain plants and promotes spatial heterogeneity (Jacobs & Naiman 2008). Sodic zones are favoured as forage patches by large herbivores, which gain essential nutrients from the herbaceous species growing there. The total exclusion of these herbivores from savanna riparian zones leads to a loss of game paths, feeding patches and wallows, causing a reduction in plant community heterogeneity (Jacobs & Naiman 2008). According to Bakker, Blair and Knapp (2003), this heterogeneity, caused by different patches with long and short biomass, is thought to enhance the coexistence of a greater number of herbaceous species, hence boosting species richness. Although Jacobs and Naiman (2008) found no consistent effects of increasing biomass on species richness in the drier sodic zone after 4 years of herbivory exclusion (i.e. 2004/2005), our results indicated that the significantly higher biomass in the absence of herbivory seemed to suppress species richness after 10 years of herbivory exclusion. Highest species richness was associated with areas exposed to herbivory (Figure 4), thus areas where plant community heterogeneity was highest.

No significant variation in species diversity could be confirmed. As the Shannon-Wiener index of species diversity acknowledges the abundance of individual species, it could be expected that variation in species diversity is less perceptible than species richness. The sodic zone, in particular, is often dominated by few forb species that are well adapted to harsh conditions. Jacobs and Naiman (2008) reported that the succulent forb, *Trianthema salsoides*, contributed to a substantial proportion of the forb biomass in 2003–2004. Although *T. salsoides* was still prevalent in the 2010 data set, it was replaced as a dominant forb species by *Achyranthes aspera*. Dominance by a single species reduces the evenness of the sodic zone ecosystem, hence suppressing diversity. Lowest species richness was recorded in areas where herbivores were excluded. This is in accordance with Oba, Vetaas and Stenseth (2001) who suggested that long-term exclusion of herbivores may not necessarily have an increasing effect on species diversity and richness. The dynamic character of the vegetation in the sodic zone ecosystem therefore results in less predictable temporal changes in herbaceous species diversity.

Conclusion

In contradiction with the 'intermediate disturbance hypothesis', which suggests that highest diversity is maintained at intermediate levels of disturbance (Begon *et al.* 2006), highest species richness was associated with highest disturbance (i.e. open treatment). Increasing biomass as a result of the absence of herbivory suppresses the richness of herbaceous species in the sodic zone, although species



± 1.96*, standard deviations of the mean; s.e., standard error.

FIGURE 5: Mean Shannon-Wiener diversity index values ($p = 0.4$) across fire and herbivory treatments in the sodic zone of the Kruger National Park.

richness is even lower in its combined effect of fire treatment. However, whilst species diversity patterns showed no significant differences across the treatments, lowest diversity was also measured in the absence of herbivory, but with fire treatment. It is therefore inferred that, although sodic patches are often associated with overgrazed, trampled vegetation, herbivores play an important role in the maintenance of species richness and diversity in these nutrient hotspots. Although statistically not significant, fire seems to suppress diversity and richness of the herbaceous layer in the sodic riparian zone. Floristic monitoring over a larger time scale under similar conditions is however required to support these premature results.

The combined assemblage of herbivores with (open treatment), or without (partial treatment) elephants, has the largest reduction in herbaceous standing biomass within the sodic zone of the Nkuhlu exclosures. Herbivory is suggested to be the primary driver of herbaceous vegetation dynamics in the sodic zone along the Sabie River, whether elephants are being included (open treatment) or excluded (partial treatment). Whilst suppressing standing biomass, herbivory maintains higher levels of herbaceous species richness. Fire, however, is suggested to be a secondary driver within the herbivory treatments, because it seems to suppress both herbaceous species richness and standing biomass. Despite clear patterns, no significant variation or differences with regard to herbaceous species diversity could be detected across treatments, which necessitates further long-term monitoring of herbaceous vegetation at nutrient hotspots along the Sabie River.

As the conservation of total biodiversity is the mandate of South African National Parks (SANParks), these findings have direct implications for the management of sodic zones



in the KNP. The exclusion of herbivores may alter ecosystem functioning, especially at smaller scales, by increasing biomass at the cost of herbaceous species richness. Herbivores play an essential role in the reduction of herbaceous plant competition, in that herbivores decrease grass biomass which, in turn, promotes herbaceous species richness because fast-growing grasses can no longer overtop and shade out forbs. Herbivores are therefore considered imperative in the maintenance of species richness and diversity and ecosystem functioning in African savanna ecosystems, especially in sodic zones.

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Competing interests

The authors declare that they have no financial or personal relationships which may have inappropriately influenced them in writing this article.

Authors' contributions

H.v.C. (North-West University) was a post-graduate student who collected, analysed and reported the data, whilst F.S. (North-West University) was the project leader and supervisor to H.v.C. and was responsible for project design, data collection, analyses and reporting of data. S.J.S. (North-West University) made contributions in data sampling and reporting, whilst also fulfilling the role of co-supervisor. H.v.C., F.S. and S.J.S. wrote the manuscript.

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