

Composition and diversity of Mopaneveld herbaceous vegetation: an exclosure experiment

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Declaration

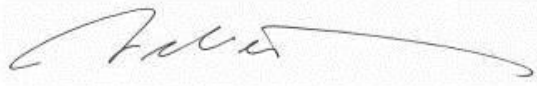
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Abstract

The herbaceous vegetation layer of the semi-arid Mopaneveld savanna possess a distinctive homogeneity and is highly dynamic in its response to disturbances such as herbivory. Understanding how this ecosystem reacts to selective herbivore exclusion, provides valuable information for conservation management. Dynamic responses of the herbaceous vegetation in the past have always been tested on either plant species or functional groups. Very little is known of the herbaceous dynamics if a direct comparison is made of simultaneously tested responses on species and functional level and whether one approach will be more sensitive to detect changes in the herbaceous community than the other. The Letaba research exclosures in the Kruger National Park (KNP), provided opportunities to investigate how long-term herbivore exclusion effects composition, richness and diversity of the herbaceous layer in a Mopaneveld savanna at both species and functional group levels. The study aimed to analyse the herbaceous response patterns while specifically focussing on (a) the quantification of changes in herbaceous plant community structure, (b) how species composition, richness and diversity respond at both species as well as functional group level and (c) assessment of community stability as given by the variability of assessed parameters and calculated measures. The three herbivore exclusion treatments of the Letaba exclosures consisted of (1) a fully fenced area, excluding all herbivores larger than a hare, (2) a partially fenced area, excluding only elephants and giraffes and (3) an open, unfenced control area. Field data collection entailed sampling herbaceous vegetation in two 1 m² circular sub-plots in the eastern and western corners of each of the 151 fixed plots (data of subplots were then pooled for a better species representation per plot). Biomass data for each plot were sampled using a Disc Pasture Meter (DPM). Literature-based soft functional traits representing adaptations to herbivory in a semi-arid system were used to classify all sampled species into functional groups. Repeated measures ANOVA was used to test for the significant effect of herbivore exclusion over time. Non-Metric Dimensional Scaling was used for the species level data and one-way ANOVA for the functional group data to test for composition changes. Cluster analysis and Principal Component Analysis were used to identify refined plant functional types. After nine years of herbivore exclusion, few significant response patterns were revealed at both species and functional levels. At the species level, no significant herbivore exclusion effect could be detected over time for either composition, richness or diversity. Herbivore exclusion led to a significant increase in grass biomass (above-ground phytomass). The exclusion of large herbivores (i.e. elephant and giraffe), promoted herbaceous community evenness. At the functional group level, perennial groups dominated. Since the exclusion of both all herbivores and just large herbivores resulted in increased dominance by perennials, it was concluded that this change was due to the effects of the large herbivores only and that large herbivores are required to maintain a more evenly distributed composition of functional groups. In terms of diversity, differences between treatments were detected at the start of the experiment, but significant time and treatment effects indicated that the

absence of only large herbivores promoted a higher and more evenly distributed functional group diversity. Despite dynamic fluctuations in the herbaceous community structure that could have occurred between 2003 and 2012, the herbaceous community did not change significantly on species or functional group level, which may suggest high resilience to the environmental disturbances present at the study site.

Key words: *herbaceous vegetation; herbivore exclusion; homogeneity, herbivory, functional group; species composition, species richness; species diversity; biomass.*

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Table of Contents

Abstract	i
Acknowledgements	iii
List of Figures	vii
List of Tables	ix
Chapter 1	1
1.1. Background	1
1.2. Motivation and Rationale	2
1.3. Aim and Objectives	3
1.4. Structure of the thesis	4
References	6
Chapter 2	13
2.1. Mopaneveld vegetation	13
2.2. Drivers of herbaceous vegetation patterns	14
2.2.1. Herbivory	15
2.2.2. Rainfall variability	16
2.2.3. Fire	17
2.3. Diversity measures: species vs functional approaches	17
2.3.1. Diversity at the species level: Defining components and importance	18
2.3.2. Diversity at the functional level: Defining components and importance	19
References	22
Chapter 3	35
3.1. History and significance of the Letaba Enclosures	35
3.2. Locality	35
3.3. Topography and Landscape	36
3.4. Climate (Rainfall & Temperature)	36

3.4.1. Rainfall	36
3.4.2. Temperature	39
3.5. Geology	39
3.6. Soils	39
3.7. Vegetation	40
3.8. Herbivory	40
References	41
Chapter 4	43
4.1. Experimental design	43
4.2. Field data collection	45
4.3. Data Analysis	46
4.3.1. Species diversity analysis (Chapter 5)	46
4.3.2. Functional analysis (Chapter 6)	46
4.3.2.1. Response patterns of single life forms and Plant Functional Types	46
4.3.2.2. Response patterns in overall life-form diversity	47
References	48
Chapter 5	51
5.1. Introduction	51
5.1.1. Herbaceous community responses to disturbance	51
5.1.2. Study objectives	53
5.2. Material and methods	54
5.2.1. Composition:	54
5.2.2. Richness, Diversity and Productivity:	54
5.3. Results	55
5.3.1. Vegetation composition changes	55
5.3.2. Changes in species richness, diversity, evenness and biomass	59
5.4. Discussion	64

5.4.1. Herbivore exclusion effect on vegetation composition	64
5.4.2. Herbivore exclusion effect on species richness, diversity, evenness and biomass	64
5.5. Summary	67
References	69
Chapter 6	77
6.1. Introduction	77
6.1.1. Advantages of Plant Functional Type approach to detect herbivory effects	77
6.1.2. Study objectives	78
6.2. Material and methods	79
6.2.1. Response patterns of single life forms and PFT's	79
6.2.2. Effect of time, treatment and combined effect on plant functional level	81
6.3. Results	82
6.3.1. Changes in composition (i.e. abundance, relative abundance, and richness) of life-form groups	82
6.3.2. Changes in diversity of life-form groups	89
6.4. Discussion	94
6.4.1. Herbivore exclusion effect on life-form composition	94
6.4.2. Herbivore exclusion effect on overall life-form diversity	95
6.5. Summary	96
References	99
Chapter 7	108
7.1. Introduction	108
7.2. Main findings	108
7.3. Future recommendations	109
Appendix 1	111
Appendix 2	112

List of Figures

- Figure 3.1:** Map indicating the position of exclosures in the KNP in relation to the main restcamps and roads, including the location of the study site (Letaba Exclosures). 37
- Figure 3.2:** The total rainfall for the climatological years (July 2002 - June 2003; July 2011 - June 2012). Data as measured at the Letaba restcamp ranger station. 38
- Figure 3.3:** The total rainfall of the four months preceding vegetation surveys for each year (December 2002 – March 2003; September – December 2011). Data was measured at the Letaba restcamp ranger station. 39
- Figure 4.1:** Diagrammatic representation of the Letaba exclosures illustrating the different treatments and transects. The Full, Partial and Control treatments are each represented by two fire and two no fire transects. The solid line represents the full exclosure, perforated line the partial exclosure and the red line the treatments and transects protected from fire activity. 45
- Figure 5.1:** NMDS ordination scatter plots to visually display the distribution of the herbaceous vegetation composition across the different vegetation zones in 2003 for the (a) full exclusion treatment in 2003, (b) partial exclusion treatment in 2003, and (c) control, and in 2012 for the (d) the full exclusion treatment, (e) partial exclusion treatment and (f) control. 56
- Figure 5.2:** NMDS ordination scatter plots to visually display the distribution of the herbaceous vegetation composition of (a) the two sampling years (2003 vs 2012), (b) the herbivory treatments (full exclosure, partial exclosure, control in 2003, (c) the herbivory treatments in 2012, (d) the full herbivore exclusion treatment over time, (e) the partial herbivory treatment over time, (f) the control herbivory treatment over time. 57
- Figure 5.3:** Repeated measures ANOVA pair-wise comparisons of (a) number of individuals, (b) number of species, (c) Margalef's species richness, (d) Shannon-Wiener diversity index, (e) Simpson diversity index, (f) Pielou's evenness and, (g) biomass across the herbivory treatments over time in a semi-arid Mopaneveld savanna. 61
- Figure 6.1:** One-Way ANOVA of the average abundance of major life forms across different herbivory treatments over time of the a) annual graminoids in the Full, b) annual graminoids in the Partial, c) annual graminoids in the Control, d) perennial graminoids in the Full, e) perennial graminoids in the Partial, f) perennial graminoids in the Control, g) annual forbs in the Full, h) annual forbs in the Partial, i) annual forbs in the Control, j) perennial forbs in the Full, k) perennial forbs in the Partial, l) perennial forbs in the Control. 86
- Figure 6.2:** One-Way ANOVA of the average relative abundance of major life forms across different herbivory treatments over time of the a) annual graminoids in the Full, b) annual graminoids in the Partial, c) annual graminoids in the Control, d) perennial graminoids in the Full,

e) perennial graminoids in the Partial, f) perennial graminoids in the Control, g) annual forbs in the Full, h) annual forbs in the Partial, i) annual forbs in the Control, j) perennial forbs in the Full, k) perennial forbs in the Partial, l) perennial forbs in the Control. 87

Figure 6.3: One-Way ANOVA of the average richness of major life forms across different herbivory treatments over time of the a) annual graminoids in the Full, b) annual graminoids in the Partial, c) annual graminoids in the Control, d) perennial graminoids in the Full, e) perennial graminoids in the Partial, f) perennial graminoids in the Control, g) annual forbs in the Full, h) annual forbs in the Partial, i) annual forbs in the Control, j) perennial forbs in the Full, k) perennial forbs in the Partial, l) perennial forbs in the Control. 88

Figure 6.4: Summary plots indicating the effects of sampling year (time), herbivory and time and herbivory combined on the major life-form groups of the herbaceous layer in terms of a) Number of Life-Forms, b) Margalef Species Richness, c) Shannon-Wiener diversity, d) Simpson Diversity and e) Pielou's evenness. Vertical bars denote 0.95 confidence intervals with standard error. 91

List of Tables

Table 3.1: The historical average monthly and annual rainfall as well as the number of days that rainfall is expected at the Letaba Restcamp in the Kruger National Park (taken from Zambatis, 2003).	38
Table 5.1: The different measures of alpha diversity used in the study.	55
Table 5.2: Responses of herbaceous species composition to herbivore treatments (full, partial, control), within and between sampling years. Statistical significance among clusters was tested through the application of a One-way ANOSIM to the catenal effect of the the herbivory treatments (full exclosure, partial exclosure, control) in 2003, the catenal effect of the the herbivory treatments in 2012, the two sampling years (2003 vs 2012), the herbivory treatments (full exclosure, partial exclosure, control) in 2003, the herbivory treatments in 2012, the full herbivore exclusion treatment over time, the partial herbivore treatment over time, the control herbivore treatment over time.	58
Table 5.3: Effects of sampling year and herbivory on plant species abundance, measures of alpha diversity and standing biomass of the herbaceous layer.	60
Table 5.4: Treatment effects on diversity components of the herbaceous Mopaneveld vegetation per sampling year and averaged over sampling years. ANOVA with Bonferroni corrected post hoc test.	62
Table 6.1: Plant functional traits used in the study to define plant functional types.	80
Table 6.2: The average abundance (mean number of individuals per life form group per plot), average relative abundance (proportional abundance) and average richness (number of species in each life form) of the major life form groups of the herbaceous Mopaneveld vegetation per treatment and sampling year.	83
Table 6.3: The One-Way ANOVA of the average abundance, average relative abundance and average richness of the major life-form groups across different herbivory treatments over time.	84
Table 6.4: Effects of sampling year and herbivory on plant life-form abundance and alpha diversity.	90
Table 6.5: Treatment effects on major life-form components of the herbaceous Mopaneveld vegetation per sampling year and averaged over sampling years. ANOVA with Bonferroni corrected post hoc test.	92

Chapter 1

Introduction

1.1. Background

Savanna ecosystems cover approximately 50-60% of the land surface in sub-Saharan Africa (Scholes & Archer, 1997; Buitenwerf *et al.*, 2011) and possess one of the richest and most unique assemblages of plant species on the African continent. Savannas are described as heterogeneous ecosystems characterized by the coexistence of trees at various densities and heights, and a continuous herbaceous layer (Scholes & Archer, 1997; Augustine, 2003; Barnes, 2012). The herbaceous layer of savanna ecosystems hosts a high species richness (Shackleton, 2000; Jacobs & Naiman, 2008; Van Coller, 2013) and exhibits vastly dynamic responses to environmental heterogeneity and disturbances (Shackleton, 2000; Stromberg, 2007; Bond & Parr, 2010; Lettow *et al.*, 2014; Siebert & Scogings, 2015). The herbaceous layer serves as important forage for a variety of herbivores (Treydte *et al.*, 2013; Siebert & Scogings, 2015). It is primarily comprised of graminoids (Jacobs & Naiman, 2008, Van Coller *et al.*, 2013), dicotyledonous and non-graminoid monocotyledonous and geophytic forb species (Siebert & Scogings, 2015), where the forbs form the largest component of herbaceous species richness (Shackleton, 2000; Jacobs and Naiman, 2008; Pavlovic *et al.*, 2011; Van Coller *et al.*, 2013). However, herbaceous layer dynamics are seldom studied and still poorly understood (Archibald *et al.*, 2005; Jacobs & Naiman, 2008; Siebert & Eckhardt, 2008; Van Coller *et al.*, 2013), especially the ecological role of forb species (Siebert & Scogings, 2015).

Heterogeneity in savanna landscapes (which influences herbaceous vegetation dynamics, Pickett *et al.*, 2003) are maintained and driven by disturbances, either anthropogenic or natural (Pickett *et al.*, 2003; Venter *et al.*, 2003; Swemmer *et al.*, 2007; Sasaki *et al.*, 2009; Hopcraft *et al.*, 2010; Baudena & Rietkerk, 2013; Gibbes *et al.*, 2014). These disturbances can determine the vegetation type that dominates in a savanna ecosystem and simultaneously influence the vegetation structure and functioning of the system (and hence heterogeneity) (Shackleton *et al.*, 1994; Augustine, 2003; Otieno *et al.*, 2011). Heterogeneity in semi-arid savannas is primarily driven by herbivory (O'Connor, 1991; O'Connor, 1995; Weber & Jeltsch, 2000; Archibald *et al.*, 2005; Augustine & McNaughton, 2006; Hempson *et al.*, 2007; Jacobs & Naiman, 2008; Otieno *et al.*, 2011; Rutherford *et al.*, 2012; Porensky *et al.*, 2013), particularly those with a long evolutionary history of herbivory and fire (Van Wilgen *et al.*, 2000; Augustine, 2003; Van Wilgen *et al.*, 2003; Govender *et al.*, 2006; Pettit & Naiman, 2007; Jacobs & Naiman, 2008; Trollope & Potgieter, 2013; Trollope *et al.*, 2014).

By reducing the standing biomass, herbivory promotes herbaceous species co-existence through enhancement of spatial heterogeneity and changing the structure of the herbaceous layer (Skarpe,

1991; Olf & Ritchie, 1998; Augustine, 2003; Jacobs & Naiman, 2008; Porensky *et al.*, 2013; Van Coller & Siebert, 2015). Herbaceous richness and diversity are also directly influenced by herbivory (Oba *et al.*, 2001; Hickman *et al.*, 2004; Jacobs & Naiman, 2008; Van Coller *et al.*, 2013), with the absence of herbivores or overgrazing usually associated with a lower herbaceous species richness and diversity than those of the herbaceous species occurring in the same areas but subjected to intermediate levels of herbivory (Augustine, 2003; Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Van Coller & Siebert, 2015).

The dynamics of a savanna ecosystem are best studied in the herbaceous layer due to its quick response to environmental disturbances (Jacobs & Naiman, 2008; Buitenwerf *et al.*, 2011; Van Coller, 2013). Response of the herbaceous vegetation to disturbances can be quantified by measuring or sampling the composition, richness and diversity of herbaceous communities change over time. This can be done at the plant species level by using species diversity indices (Gunderson, 2000; O'Keefe & Alard, 2002; Jacobs & Naiman, 2008) which serves as a good indicator of ecosystem health (Gunderson, 2000) in dynamic vegetation zones of savannas (Van Coller *et al.*, 2013). However, ecosystem functioning is not accurately measured and incorporated by normal species diversity indices alone (Kennedy *et al.*, 2003; Devineau & Fournier, 2005; Mori *et al.*, 2013). Therefore the changes in composition and diversity of the herbaceous vegetation should also be analysed at the functional group level, because it is based on plant functional trait classifications that describe the function of species and their response to environmental disturbances (Lavorel & Garnier, 2002; Schleuter *et al.*, 2010; Pillar *et al.*, 2013). By considering changes of functional group composition and diversity, an indication of the flexibility of the herbaceous layer to adapt to and survive an environmental disturbance can be revealed, supporting the "Insurance Hypothesis" of Yachi and Loreau (1999) (Ives *et al.*, 1999; Ives *et al.*, 2000; Valone & Hoffman, 2003; Valone & Barber, 2008). It remains challenging to detect trends in the herbaceous layer in response to disturbances over a short time period, making long-term data of species compositional and diversity changes essential when attempting to understand savanna ecosystems (O'Connor, 1991; Fuhlendorf *et al.*, 2001; Buitenwerf *et al.*, 2011).

1.2. Motivation and Rationale

The focus of past studies regarding the effect of herbivory disturbance on the herbaceous vegetation in savanna ecosystems has been on responses of standing biomass and changes in composition, richness or diversity at either the species or functional level (e.g. Diaz *et al.*, 2001; Grime, 2006; Jacobs & Naiman, 2008; Rusch *et al.*, 2009; Van Coller *et al.*, 2013; Young *et al.*, 2013; Koerner *et al.*, 2014; Kartzinel *et al.*, 2014; Van Coller & Siebert, 2015 etc.). In some studies, species richness and diversity indices have been the main measures of vegetation responses, leading to heavy criticism from the studies done from a functional standpoint (Kennedy *et al.*, 2003; Devineau & Fournier, 2005; Mori *et al.*, 2013). This was primarily due to the uncertainty about the

lack of functional importance of species richness and diversity indices. Therefore, very little is known of how herbaceous vegetation in semi-arid savannas responds to disturbances on a species as well as functional level and whether the one approach is more sensitive to changes in the herbaceous community than the other.

The focus of this study was therefore on the impact of herbivory (or the exclusion thereof) on the composition, richness and diversity of the herbaceous vegetation in a semi-arid Mopane savanna at both plant species and functional group level. Classic species richness and diversity measures were considered in combination with measures of change on functional group level. Species richness and diversity indices provided insight on changes in the species pool of the herbaceous community. But to further understand the herbaceous species pool adaptability to herbivory, the functional response was tested by measures of change of the composition, richness and diversity of functional groups (classified according to functional traits based on adaptability to herbivory). This provided the most reliable indication of how the herbaceous vegetation in a Mopaneveld savanna is taxonomically and functionally adapted to the presence or absence of herbivory.

It could be expected that the variation in the herbaceous vegetation at plant species and functional group level will be difficult to detect when only two data samplings are considered, namely at the start (2002/2003) and at the end of a nine year experimental period. However, directional changes in the overall herbaceous community structure might be observable after nine years of herbivore exclusion. Previous research on herbaceous floristics in semi-arid savanna ecosystems have generally focussed on only a few species, and have almost all been conducted in rangelands, with few studies from conservation areas (Tainton, 1999; Bond & Parr, 2010; Treydte *et al.*, 2013; Koerner *et al.*, 2014; Scott-Shaw & Morris, 2014; Siebert & Scogings, 2015). The research presented here includes total herbaceous floristics (i.e. all types of grasses and forbs in the semi-arid Mopaneveld savanna system of the study site) and forms part of a long-term vegetation survey project in the conservation area of Kruger National Park (KNP), which aims to improve conservation planning of South African National Parks (SANParks).

1.3. Aim and Objectives

Aim: To investigate the effect of long-term herbivore exclusion on the composition, richness and diversity of the herbaceous layer in a Mopaneveld savanna at both the species and functional group level.

Objectives: The overall objective was to analyse herbaceous vegetation response patterns over time through the quantification of changes in plant community structure.

Specific objectives were to quantify the response of

- species composition, richness and diversity to different treatments of herbivory (Chapter 5)
- plant functional composition, richness and diversity to different treatments of herbivory (Chapter 6)

After assessing the response patterns at both the species and functional level, predictions regarding the herbaceous community stability will be made (Chapter 7).

1.4. Structure of the thesis

This thesis follows the structural guidelines as described by the North West University. It contains seven chapters, with the introduction as the first (Chapter 1), the related literature that applies to this study in Chapter 2, description of the study area in Chapter 3, followed by the applied methodology (Chapter 4). This chapter provides a description of the methodology that is generic to both analyses (species responses and functional responses) and excludes descriptions of methods that are relevant to specific results chapters only. The results and discussions are assigned to two chapters (i.e. Chapter 5 and 6) and the format followed in these chapters is in accordance with the preparation of manuscripts for submission to scientific journals, hence including the methodology relevant to those objectives only. Chapter 7 provides the primary conclusions of this study and also future recommendations for similar studies focusing on the response patterns of the herbaceous layer in the semi-arid Mopaneveld. Each of the chapters will contain its own reference list. The content of each chapter are briefly outlined below:

Chapter 1: Introduction- background information on the herbaceous layer of the semi-arid Mopaneveld and its dynamics, motivation and rationale behind the study, as well as the aim and objectives of the study.

Chapter 2: Literature Review- a discussion on Mopaneveld and the dynamics of semi-arid savannas, the influence of environmental stressors on herbaceous vegetation and its unique responses, as well as the importance of analysing the herbaceous layer on functional as well species diversity measures. This discussion includes earlier work done on these specific topics together with their shortcomings as well as an analysis of sources and methods related to the study.

Chapter 3: Study Area- a comprehensive description of the study area, i.e. brief history, locality, topography, climate (rainfall and temperature), geology and vegetation.

Chapter 4: Materials and Methods- a detailed explanation of the enclosure and experimental layout, as well as the methods that were used to acquire all floristic data and how the data was analysed (on both species diversity and functional level).

Chapter 5: Results and discussion- herbivory effects on species composition and diversity.

Chapter 6: Results and discussion- herbivory effects on composition and diversity of plant functional groups.

Chapter 7: Conclusion- a final conclusion on the important findings of the study, including a description on whether the the study's aims and objectives have been accomplished, as well as recommendations for further research.

Definitions and terms applicable to this study:

- **Biomass:** Biomass in this study is defined as the mass of total above ground plant material, including both living and moribund / dead material, and not just as living material only as stated by Trollope *et al.* (1990).
- **Diversity:** For the purpose of this study, the term “diversity” includes measures of alpha diversity (diversity at a single locality or in a specific community) (Sepkoski, 1988) instead of beta (diversity between sites or communities) (Sepkoski, 1988) or gamma (diversity between geographic regions) (Sepkoski, 1988) diversity, because it can be analyzed on both species diversity and functional levels and is a better tool for detecting and quantifying disturbance effects on ecosystems (Hanke *et al.*, 2014).

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Chapter 2

Literature review

2.1. Mopaneveld vegetation

Mopaneveld is a semi-arid savanna type where the tree species *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J.Léonard, is dominant in multiple communities within this savanna type (Mapaure, 1994; Siebert *et al.*, 2003). Although it covers vast areas of southern African savannas, it is frequently interrupted by other vegetation types (Siebert *et al.*, 2003; Siebert, 2012). Mopaneveld vegetation stretches across the subtropical central and southern regions in the African savanna biome, including central regions of Angola, Malawi and Mozambique, northern regions of Botswana, Namibia and South Africa and southern, eastern and northern parts of Zambia and Zimbabwe (Mapaure, 1994; Siebert *et al.*, 2003; Mlambo *et al.*, 2005; Siebert, 2012; Makhado *et al.*, 2014). Environmental conditions that are correlated with the distribution of Mopaneveld across its range include fine-textured soil in wide, flat and frost free valley bottoms of river valleys (Siebert *et al.*, 2003; Rutherford *et al.*, 2012a; Siebert, 2012), low to moderate annual rainfall (± 400 mm), high temperatures (mean daily of $>25^{\circ}\text{C}$) and low altitudes (<800 m above sea level) (Makhado *et al.*, 2014). Temperature and dry season day length have been highlighted as factors driving the distribution of *Colophospermum mopane* (Stevens *et al.*, 2014).

Mopaneveld is characterized by its homogeneity at landscape scale, which leads to its associated vegetation being much more homogenous to other common savanna types of the region (Siebert *et al.*, 2003; Mucina & Rutherford, 2006). The Mopaneveld also characteristically has a lack of a dense herbaceous plant layer (Mlambo *et al.*, 2005). Despite its homogeneity, the herbaceous layer is still described as dynamic and varies strongly in response to disturbance factors such as moisture availability (usually low average rainfall conditions) (Danckwerts & Stuart-Hill, 1988; O'Connor, 1998; Siebert *et al.*, 2003; Smith *et al.*, 2012), herbivory (Illius & O'Connor, 1999; Treydte *et al.*, 2009; Rutherford *et al.*, 2012a; O'Connor, 2015) and fire (Van Wilgen *et al.*, 2003; Van Wilgen *et al.*, 2007; Smith *et al.*, 2012; Trollope *et al.*, 2014).

The diversity of the Mopaneveld vegetation are described as having a high alpha diversity but low beta-diversity (Timberlake, 1995, Siebert *et al.*, 2003; Siebert *et al.*, 2010) and the mentioned environmental disturbances play an important part in the maintenance of species richness and diversity in these systems. The variation in species richness, diversity and functional group patterns of semi-arid Mopaneveld are related to temporal vegetation states caused by these disturbances (Siebert *et al.*, 2003; Murwira & Skidmore, 2007). The high total species richness of semi-arid savannas is largely due to the richness of the herbaceous vegetation and more specifically of herbaceous forbs (which contribute to over 70% of the total richness) (Siebert &

Scogings, 2015). The species richness in the Mopaneveld however, is also determined by the cover of the tree species *Colophospermum mopane*, which influences the richness of both the herbaceous and woody species in its presence (Du Plessis, 2001; O'Connor, 1992; Siebert *et al.*, 2010). A lower species richness is usually associated with areas densely covered by *C. mopane*, while higher richness is related to lower *C. mopane* cover (O'Connor, 1992). The Mopaneveld vegetation of the study area has an overall lower species richness when compared to wetter semi-arid savannas in the KNP (Siebert *et al.*, 2010).

2.2. Drivers of herbaceous vegetation patterns

The herbaceous layer of semi-arid Mopaneveld is referred to as being “event-driven” (Siebert *et al.*, 2010) and exhibits unique responses to the environmental disturbances it is regularly exposed to. Different conceptual frameworks that explain these dynamic responses of the herbaceous layer, includes the Intermediate Disturbance Hypothesis (IDH) (Grime, 1973; Connell 1978), the Dynamic Equilibrium Model (DEM) (Huston, 1979a; Kondoh, 2001) and the evolutionary history of grazing in a specific area (Milchunas *et al.*, 1988). The IDH states that in response to disturbances, the vegetation richness and diversity will be at its highest at intermediate levels of disturbance (Grime, 1973; Connell 1978; Jacobs & Naiman, 2008; Sasaki *et al.*, 2009; Angassa, 2012; Van Coller *et al.*, 2013; Hanke *et al.*, 2014). According to the DEM, vegetation communities can persist in states of either equilibrium or non-equilibrium depending on the specific conditions and disturbances it is regularly exposed to, and will fluctuate between these states when specific thresholds are crossed (Huston, 1979a; Skarpe, 1992; Kondoh, 2001; Briske *et al.*, 2003; Holdo *et al.*, 2013). The DEM also contributes to the IDH by stating that moderate disturbance intensities could lead to increases in species diversity in systems with a high productivity, while diversity in low productivity systems will be negatively affected (Hanke *et al.*, 2014). Considering the long evolutionary history of wild African herbivores in the KNP (Du Toit, 2003; Jacobs & Naiman, 2008; Rutherford *et al.*, 2012a), it can also be expected that the response to the removal grazing will be weaker compared to a system where large herbivores have been introduced more recently (Milchunas *et al.*, 1988; Cingolani *et al.*, 2005; Jacobs & Naiman, 2008; Rutherford *et al.*, 2012a; Hanke *et al.*, 2014).

Disturbances and the availability of resources are the primary drivers of both woody and herbaceous plant community structure and composition (Linstädter *et al.*, 2014). The vegetation response patterns in reaction to different drivers in the Mopaneveld are better understood in the woody layer (O'Connor, 1998; Smallie & O'Connor, 2000; Kennedy & Potgieter, 2003; Mlambo *et al.*, 2005; Mlambo, 2006; Mlambo & Mapaure, 2006; Hempson *et al.*, 2007; Rutherford *et al.*, 2012a) than in the herbaceous layer. Herbaceous layer dynamics are difficult to comprehend, since they are usually described through either an equilibrium and/or non-equilibrium concept depending on the scale of the study (Vetter, 2005; Peel *et al.*, 2005; Von Wehrden *et al.*, 2012). The equilibrium model concept considers the importance of biotic feedbacks in the ecosystem,

such as the density dependent regulation of herbivore populations and the impact of herbivore density on the productivity and composition of the herbaceous vegetation (Vetter, 2005; Von Wehrden *et al.*, 2012). The non-equilibrium concept focuses on the impacts / effects of the abiotic elements of the ecosystem, such as the impact of rainfall or nutrient variability on the productivity of the herbaceous vegetation (Vetter, 2005; Von Wehrden *et al.*, 2012). Further, the dynamic responses of herbaceous vegetation are also consistent with the State-and-Transition (S&T) model often proposed for savanna ecosystems (Westoby *et al.*, 1989; O'Connor 1998; Peel *et al.*, 2005; Lohmann *et al.*, 2012; Rutherford *et al.*, 2012a; O'Connor, 2015), i.e. species composition may persist or shift to an alternate state in response to a disturbance and this could happen very rapidly. The herbaceous layer's specific response to effects of drivers such as herbivory, moisture variability and fire are therefore difficult to entangle.

2.2.1. Herbivory

Herbivory is known as a key driver of ecosystem functioning in semi-arid African savannas, but its impact on herbaceous vegetation dynamics is poorly understood (Jacobs & Naiman, 2008). Regulated herbivore presence can positively affect the herbaceous spatial heterogeneity, species richness and diversity of semi-arid savanna ecosystems (Jacobs & Naiman, 2008; Angassa, 2012; Van Coller *et al.*, 2013; Hanke *et al.*, 2014) which allows for improved species co-existence (Ollf & Ritchie, 1998; Angassa, 2012). Spatial heterogeneity can be enhanced through physical alterations of the standing biomass (game paths and feeding patches (Jacobs & Naiman, 2008)), facilitation of seed dispersal (O'Connor & Pickett, 1992; Ollf & Ritchie, 1998) and hoof action (Riginos & Grace, 2008; Jacobs & Naiman, 2008; Cassidy *et al.*, 2012). Intermediate herbivory levels conserve and promote key forage species in savanna ecosystems and enhance the herbaceous species richness and diversity (Cingolani *et al.*, 2005; Jacobs & Naiman, 2008; Sasaki *et al.*, 2009; Angassa, 2012; Van Coller *et al.*, 2013; Hanke *et al.*, 2014) (as predicted by the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978)). As in other savanna types with a long evolutionary history of herbivory, the utilization of the Mopaneveld herbaceous vegetation may cause low species turnover over time, due to the tolerance that these species developed to herbivory (Rutherford *et al.*, 2012a).

The impact of too high herbivory rates in savannas (even those systems with a long history of grazing) are negative for the herbaceous vegetation, especially in over utilized areas (Ollf & Ritchie, 1998; Augustine & McNaughton, 2006; Riginos & Grace, 2008). Over utilization causes productive palatable species to be replaced by unpalatable species, leading to an overall decline in ecosystem productivity in savannas (Skarpe, 1991; Cassidy *et al.*, 2012; Jacobs & Naiman, 2008). The absence of herbivores may also negatively affect herbaceous species richness and diversity in savannas (Jacobs & Naiman, 2008; Van Coller & Siebert, 2015) where the grass production is high. Total herbivore absence will cause fast-growing grass species to overtop herbaceous forbs

and smaller grass species, directly leading to dominance by a few species and an increased homogeneity (McNaughton, 1983; Young *et al.*, 1997; Adler *et al.*, 2001; Jacobs & Naiman, 2008; Van Coller *et al.*, 2013), as well as a reduction in the overall species richness and diversity (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Van Coller & Siebert, 2015).

2.2.2. Rainfall variability

The dynamics of semi-arid savanna herbaceous vegetation is sensitive to climate and spatial variability in rainfall (Illius & O'Connor, 1999). Rainfall variability is considered as a principal driver of herbaceous vegetation composition and structure in semi-arid savannas (O'Connor, 1998), including Mopane savannas and the non-equilibrium nature of these savannas can be directly linked to annual variability in rainfall (O'Connor, 1995; Vetter, 2005; Von Wehrden *et al.*, 2012). Annual rainfall measurements serves as a good indicator of the effect of rainfall on the above-ground primary productivity of herbaceous vegetation (Swemmer *et al.*, 2007). Annual rainfall affects the growing season, composition and growth potential of any semi-arid savanna vegetation type, especially when the vegetation is dominated by short-lived perennial or annual herbaceous species (Fynn & O'Connor, 2000). Plant species richness in semi-arid Mopaneveld savannas is usually enhanced by a dense sward of annual species that establishes after a disturbance caused by rainfall variability, such as a prolonged drought (Rutherford *et al.*, 2012a; Gibbes *et al.*, 2014). Drought can lead to high mortality rates among species (O'Connor, 1998; Illius & O'Connor, 1999). When compared to other disturbances that may affect vegetation composition and structure, drought will have an overriding effect on herbaceous vegetation community changes in semi-arid systems (O'Connor, 1994; O'Connor, 1995; Illius & O'Connor, 1999; Augustine & McNaughton, 2006; Vetter, 2009).

Additional disturbances (such as herbivory) can interact with the impacts of rainfall variability (O'Connor, 1995; Fynn & O'Connor, 2000; Peel *et al.*, 2005). In a study on the effects of a sustained drought and heavy grazing in a Mopaneveld savanna it was revealed that forbs (annual and perennial) and annual grass abundances increased at the expense of perennial grasses, although certain perennial grass species reappeared when the rainfall and soil moisture increased (O'Connor, 1998). Heavily grazed savannas will more likely undergo irreversible changes caused by drought or varying rainfall patterns (O'Connor, 1995; Peel *et al.*, 2005), but the probability for herbivore induced degradation is considered to be lower in systems with reasonably variable rainfall patterns (Von Wehrden *et al.*, 2012). The impact of high rainfall variability in arid and semi-arid rangelands may also alter the effects of long-term herbivore exclusion (Young *et al.*, 1997; Fuhlendorf *et al.*, 2001; Augustine & McNaughton, 2006; Sasaki *et al.*, 2009). For instance, a study conducted in semi-arid grasslands of Mongolia revealed significant treatment effects of herbivory in heavily grazed and fully excluding plots (Sasaki *et al.*, 2009), but despite the herbivory effects, the

main driver of the observable herbaceous vegetation patterns were predetermined by the rainfall variability in the time before the experiment was conducted (Sasaki *et al.*, 2009).

2.2.3. Fire

Fire as driver of heterogeneity is one of the most researched topics in savanna ecology. Despite the below-average fuel load in Mopane savannas compared to other savanna types (Trollope *et al.*, 2014), fire is still considered as an important abiotic factor that contribute to complex vegetation patterns (Kennedy & Potgieter, 2003; Smith *et al.*, 2012; Stevens *et al.*, 2014; Makhado *et al.*, 2014; Trollope *et al.*, 2014), although herbivory and climate are regarded as more important.

2.3. Diversity measures: species vs functional approaches

To test the effect of environmental disturbances on diversity patterns in the herbaceous layer of semi-arid ecosystems, measures that best address the dynamic nature of these ecosystems should be considered. Species diversity measures aim to quantify the number and abundance of species of a given area at a specific time and space (Diaz & Cabido, 2001; Carmona *et al.*, 2012; Hanke *et al.*, 2014). Functional diversity measures the variety of functional traits or groups in a community to give an indication of how the vegetation community is functionally adapted to disturbances (Hulot *et al.*, 2000; Diaz & Cabido, 2001; Villegger *et al.*, 2008; Poos *et al.*, 2009; Schleuter *et al.*, 2010; Kotschy, 2013). The choice of diversity measures and the ecological scale at which they are applied can dramatically influence the outcome of disturbance studies (Mackey & Currie, 2001; Hanke *et al.*, 2014).

The most frequently used measures of vegetation dynamics are species diversity indices based on species richness and -abundance (Lande, 1996; Hanke *et al.*, 2014). Species diversity indices are commonly used in herbaceous vegetation studies in savanna ecosystems (O'Connor, 1991; Fuhlendorf *et al.*, 2001; Jacobs & Naiman, 2008; Buitenwerf *et al.*, 2011; Hanke *et al.*, 2014) and may even give an indication of the heterogeneity / homogeneity of these ecosystems (Dörgeleh, 1999). In some cases, species diversity measures are considered to be inappropriate when applied at different levels of biological organisation or for management and/or conservation purposes (Mori *et al.*, 2013; Hanke *et al.*, 2014) since it neglects the functional role of species in ecosystems (Kennedy *et al.*, 2003; Mayfield *et al.*, 2010). Functional diversity as a biodiversity metric is steadily increasing in use (Diaz & Cabido, 2001; Petchey & Gaston, 2002; Cadotte *et al.*, 2011) and can in some circumstances be more adventitious than species diversity indices (Petchey & Gaston, 2002; Petchey *et al.*, 2004; Schleuter *et al.*, 2010; Cadotte *et al.*, 2011; Mori *et al.*, 2013; Hanke *et al.*, 2014).

When comparing functional and species diversity, the methods for quantifying species diversity (species diversity indices) are universal and well defined, but the methods for measuring functional

diversity frequently differ and are prone to a high level of subjectivity (Petchey & Gaston, 2002; Mayfield *et al.*, 2010; Schleuter *et al.*, 2010; Cadotte *et al.*, 2011). By promoting the relationship between the responses of vegetation on species diversity as well as on functional diversity levels, wiser management decisions can be made regarding biodiversity and ecosystem function-based conservation (Mayfield *et al.*, 2010).

2.3.1. Diversity at the species level: Defining components and importance

Species diversity can be defined in the simplest manner as the richness in species in a system that can be appropriately measured as the number of species in a sample of standard size (Whittaker, 1972). Species diversity measures ordinarily consist of species richness and diversity indices that describes the overall within or between community diversity in a strictly non-parametric manner (Huston, 1979b; Lande, 1996; Dörgeleh, 1999; Rutherford & Powrie, 2013). The species richness indices are calculated as the number of species present per specified size area or community (Lande, 1996; Rutherford & Powrie, 2013), while the species diversity indices are dependent on not only species richness, but also the evenness (measure of species dominance in a community over time (Kricher, 1972)) indicating the spread of abundance of each species in a specified area or community (Lande, 1996; Rutherford & Powrie, 2013). Diversity and richness are at times used synonymously without proper distinction between the two components (Kent & Coker, 1992; Rutherford *et al.*, 2012b; Rutherford & Powrie, 2013). Species diversity components should also be applied at the correct scale (Diaz & Cabido, 2001; Mackey & Currie, 2001; Lundholm, 2009; Carmona *et al.*, 2012; Hanke *et al.*, 2014) and sampling size (Keeley & Fotheringham, 2005) in the experimental area to ensure that the richness and abundance components can effectively reflect an ecosystem's responses to disturbance.

Richness and abundance have successfully been applied in savanna ecology as a measure of ecosystem responses to disturbances such as herbivory, fire and rainfall variability (O'Connor, 1991; Fynn & O'Connor, 2000; Fuhlendorf *et al.*, 2001; De Bello *et al.*, 2006; Jacobs & Naiman, 2008; Buitenwerf *et al.*, 2011; Rutherford *et al.*, 2012b; Smith *et al.*, 2012; Rutherford & Powrie, 2013; Van Coller *et al.*, 2013; Gibbes *et al.*, 2014; Hanke *et al.*, 2014). In terms of herbivory, the richness and diversity measured can reflect the herbaceous vegetation's unique response to herbivory that may even be similar to the Intermediate Disturbance Hypothesis, the Dynamic Equilibrium Model or the influence that the evolutionary history of grazing in an area can have (Briske *et al.*, 2003; Du Toit, 2003; Jacobs & Naiman, 2008; Sasaki *et al.*, 2009; Angassa, 2012; Holdo *et al.*, 2013; Hanke *et al.*, 2014). Species richness and diversity often reflect the response of savanna vegetation to fire, also in semi-arid ecosystems such as the Mopaneveld (Smith *et al.*, 2012).

2.3.2. Diversity at the functional level: Defining components and importance

The most basic component of vegetation diversity on a functional level is plant functional traits. Plants possess certain functional traits that can be expressed throughout the whole vegetation community of an ecosystem and in different scientific fields (Violle *et al.*, 2007). Different species can be defined as an assortment of individuals processing similar phenotypic and behavioral traits that regulates their existence in a specific habitat and their interaction with other species (Cadotte *et al.*, 2011). A trait is a detectable feature of a species that has an effect on its performance or ecological fitness (Cadotte *et al.*, 2011; Kotschy, 2013). Traits provide an indication of how plants in a specific ecosystem are adapted to biotic and abiotic changes by means of different survival strategies in response to specific environmental disturbances (Lavorel *et al.*, 1997; Lavorel & Garnier, 2002; Diaz *et al.*, 2004; Devineau & Fournier, 2005; Violle *et al.*, 2007; Moretti *et al.*, 2013). The functional traits expressed in an ecosystem can have a significant influence on the ultimate functioning of that system (Cornelissen *et al.*, 2003; Mori *et al.*, 2013; Pillar *et al.*, 2013). Due to their sensitivity to disturbances, plant functional traits can also be regarded as an equally dominant component of vegetation communities as species, when vegetation responses to disturbances is measured (Mayfield *et al.*, 2010; Cadotte *et al.*, 2011; Mori *et al.*, 2013). Functional traits can be categorized into soft or hard traits, depending on the accessibility of the traits during functional measurements. The use of soft and hard functional traits is a relevant method of evaluating ecosystem dynamics in African savannas, because it reflects the functional properties of plants (Devineau & Fournier, 2005). Soft traits (e.g. seed mass / shape) are rapidly measureable and easy to obtain for a large number of species and sites, while hard traits (e.g. seed persistence) serve a more direct functional role at different scales (Cornelissen *et al.*, 2003), but are usually less accessible or too expensive to obtain (Lavorel & Garnier, 2002; Violle *et al.*, 2007) (Appendix 1). Although methods for measuring plant functional traits have been standardized (Cornelissen *et al.*, 2003; Kattge *et al.*, 2011; Pérez-Harguindeguy *et al.*, 2013), different sets of traits are used in different ecosystems to test the adaptability of the vegetation to that ecosystems environmental disturbances (Kleyer *et al.*, 2012; Schöb *et al.*, 2013; Mori *et al.*, 2013; Veski, 2013). For instance, specific functional traits in arid and semi-arid ecosystems provide adaptability to drought conditions through drought adaptation / avoidance organs or root systems to preserve or absorb maximum moisture through taproot and/or highly succulent stems (Skarpe, 1996; Diaz *et al.*, 1998; Diaz *et al.*, 1999; Voltaire, 2008; Comas *et al.*, 2013; Voltaire *et al.*, 2014). Functional traits developed to provide insurance against herbivory include defensive organs or plant strategies to combat herbivory by means of spinescence or by reducing the palatability of the herbaceous species by having a more rigid or woody texture (Grubb, 1992; Rebollo *et al.*, 2002; Agrawal & Fishbein, 2006; Wesuls *et al.*, 2013).

Different species use the same functional traits or combinations of traits to achieve similar reactions or to cause similar ecosystem responses (Lavorel & Garnier, 2002; Lavorel *et al.*, 2013;

Moretti *et al.*, 2013; Pillar *et al.*, 2013). This enables the species with similar functional traits and trait combinations to be grouped together as a collective unit that can be called a functional group or type (Diaz & Cabido, 1997; McLaren & Turkington, 2010; Kattge *et al.*, 2011; Hanke *et al.*, 2014). Overall, plant functional types are defined according to different study objectives or the different scales at which a study is conducted, because no universal classification system exist for the identification of plant functional types in plants (Cornelissen *et al.*, 2003; Schleuter *et al.*, 2010; Kotschy, 2013; Pérez-Harguindeguy *et al.*, 2013). The functional type approach is a method where a collection of functional traits adapted to specific disturbances are used to form groups and the diversity of these groups is measured as the overall functional diversity (Magurran *et al.*, 2011). It is a unique way of evaluating ecosystem complexity and vegetation response dynamics (Lavorel *et al.*, 1997; Devineau & Fournier, 2005; Franks *et al.*, 2009). By using functional types as indicator of functional diversity, predictions regarding ecosystem stability can be made on the basis of the specific ecosystem's flexibility in response to disturbances (Lavorel *et al.*, 1997; McIntyre *et al.*, 1999a; McIntyre *et al.*, 1999b; Franks *et al.*, 2009; Mori *et al.*, 2013; Hanke *et al.*, 2014). Functional diversity at functional group level indicates the vegetation community's insurance to persist, as explained by the Insurance Hypothesis (IH) (Yachi & Loreau, 1999). The IH entails that biodiversity (in this instance functional group diversity) is used to provide a buffer against environmental fluctuations through the ability of different species to respond differently to the fluctuations, which in turn can lead to a more predictable stable or resilient community with specific ecosystem properties (Yachi & Loreau, 1999; Loreau *et al.*, 2001; Pillar *et al.*, 2013; Kotschy, 2013). The higher the diversity, the stronger the insurance to maintain ecosystem processes under changing environmental conditions. However, under favourable environmental conditions, an ecosystem does not benefit from higher diversity in the preservation of ecosystem processes (Loreau *et al.*, 2001; Loreau *et al.*, 2003; Downing *et al.*, 2012).

The emphasis of previous functional diversity studies in savannas was to find an integrating platform for different scientific disciplines by means of a functional trait based approach, or the focus was on the variation between species and how these differences will impact ecosystem functioning at a specific point in time (Kotschy, 2013). The combined use of species diversity indices and plant functional types as indicators of ecosystem responses to disturbances is limited for savanna ecosystems. Topics involving plant functional types in savannas include changes in vegetation responses to climate change and other disturbances and the basic classification of plant functional types (Skarpe, 1996; Diaz *et al.*, 1998; Diaz *et al.*, 1999; Díaz *et al.*, 2001; Devineau & Fournier, 2005; Volaire *et al.*, 2008; Comas *et al.*, 2013; Hartnett *et al.*, 2013; Linstädter *et al.*, 2014; Koerner *et al.*, 2014). Some sources such as Petchey *et al.* (2004) also suggest that using different functional diversity indices rather than the measurement of functional traits, would give a better indication of the overall functioning and functional diversity of a system. Functional group diversity however remains a very decent indicator when quantifying the effects of environmental

disturbances on functional diversity of an ecosystem (Diaz *et al.*, 1998; Laliberte & Legendre, 2010; Mayfield *et al.*, 2010; Schleuter *et al.*, 2010; Cadotte *et al.*, 2011; Kleyer *et al.*, 2012; Pillar *et al.*, 2013; Veski, 2013; Wesulski *et al.*, 2013).

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Chapter 3

Study Area

3.1. History and significance of the Letaba Enclosures

The Letaba Enclosures were constructed in the Kruger National Park (KNP) directly after the 2000 floods as part of a set of enclosures (Letaba Enclosures in the north on the banks of the Letaba River and the Nkhuflu Enclosures in the south of the park, on the banks of the Sabie River) to monitor vegetation heterogeneity patterns (both spatially and temporally) and to determine the effect of herbivory exclusion and fire (Siebert & Eckhardt, 2008; Siebert *et al.* 2010). The enclosures granted the opportunity to study the successional expansion and pattern formations of new vegetation developing in these areas (O'Keefe & Alard, 2002) which provides a better understanding of savanna ecosystems as integrated, heterogeneous systems and gives an indication of the species and functional significance of the different vegetation communities (Rogers, 1997; O'Keefe & Alard, 2002; Siebert & Eckhardt, 2008; Asner *et al.*, 2009). The information gathered from these enclosures, will feed into the knowledge-base of the KNP Scientific Services, the Kruger National Park River Research Program and the River Savanna Boundaries Program (in collaboration with several universities, government departments, and research organizations) (O'Keefe & Alard, 2002). Although enclosure sites have been erected extensively in the KNP in the past (Yessoufou *et al.*, 2013), to answer questions directly related to specific management issues such as elephant management (O'Keefe & Alard, 2002; Siebert *et al.*, 2010; Smit *et al.*, 2013), these enclosures are used to answer a multitude of different research questions (from different scientific fields and perspectives) relevant to the sites. These enclosures also simultaneously addresses certain management issues in the park itself (O'Keefe & Alard, 2002).

The Letaba enclosures must be recognized as an enclosure site in the KNP with some distinctive characteristics. It has a very specific local homogeneity (much more homogenous than the southern savannas of the KNP, both physiognomically and floristically (Siebert *et al.*, 2010; Yessoufou *et al.*, 2013)), it has a lower rate of vegetation changes overall, lower animal concentrations, lower mean annual rainfall (± 400 mm annually compared to 560 mm of the Nkhuflu enclosures) (Siebert *et al.*, 2010), but still a vegetation diversity that is frequently altered by periodic flood activities and herbivore disturbance (Parsons *et al.*, 2005).

3.2. Locality

The Letaba enclosures are situated in a protected wilderness area on the northern bank of the Letaba River in the KNP (Figure 3.1) in the north-eastern Limpopo province of South Africa,

roughly 5 km upstream of the Mingerhout Dam (23°45.530'S, 31°25.942'E) (O'Keefe & Allard, 2002; Siebert *et al.*, 2010).

3.3. Topography and Landscape

The Letaba exclosures fall within the Mopaneveld Bioregion in the Limpopo valley (Mucina & Rutherford, 2006), an area which is associated with flat to undulating terrain with interruptions of scattered inselbergs (koppies / outcrops) (Siebert, 2012). Mopaneveld areas of this Bioregion are associated with broad river valleys on deep, clayey to loamy clayey soil and the terrain varies from level or slightly raised to an undulating landscape categorized by the varying dominance of *Colophospermum mopane* and *Combretum* tree species (Siebert, 2012). However, the landscape in which the Letaba exclosures are located is described as a gently undulating landscape, without any prominent koppies (Siebert *et al.*, 2010). It is located in a low-lying area that is approximately 250 m above sea level (Gertenbach, 1983). It is a typical riparian landscape with a distinct catenal sequence caused by a unique geomorphology (Siebert *et al.*, 2010), gradually expanding into a steeper crest and upland area and small tributaries of streams flowing down to the river. This catenal sequence is responsible for a characteristic vegetation structure and formation along the different vegetation zones of the sequence, primarily determining the woody vegetation composition and structure and to a much lesser extent the herbaceous vegetation component.

3.4. Climate (Rainfall & Temperature)

3.4.1. Rainfall

Highly variable seasonal rainfall distribution is typically associated with Mopaneveld and the study area (Du Plessis, 2001; Siebert, 2012). Due to the size of the park, rainfall in the KNP is usually experienced as multiple separate events, but historical rainfall patterns reveal a trend of decreasing mean annual rainfall from the south to the north and from the east to the west of the KNP (Venter *et al.*, 2003). The range of annual rainfall in the KNP where Mopaneveld dominate is approximately 250 mm – 400 mm (Siebert, 2012). The Letaba exclosures area is classified as a summer rainfall region in the Mopaneveld, with a mean annual rainfall of approximately 400 mm (Siebert *et al.*, 2010). Historical (Figure 3.2) and actual (Figure 3.3) rainfall figures reported in the study area are those of SANParks, measured at the ranger station in the Letaba restcamp (± 15 km from the Letaba exclosures and in the same rainfall area) in the KNP.

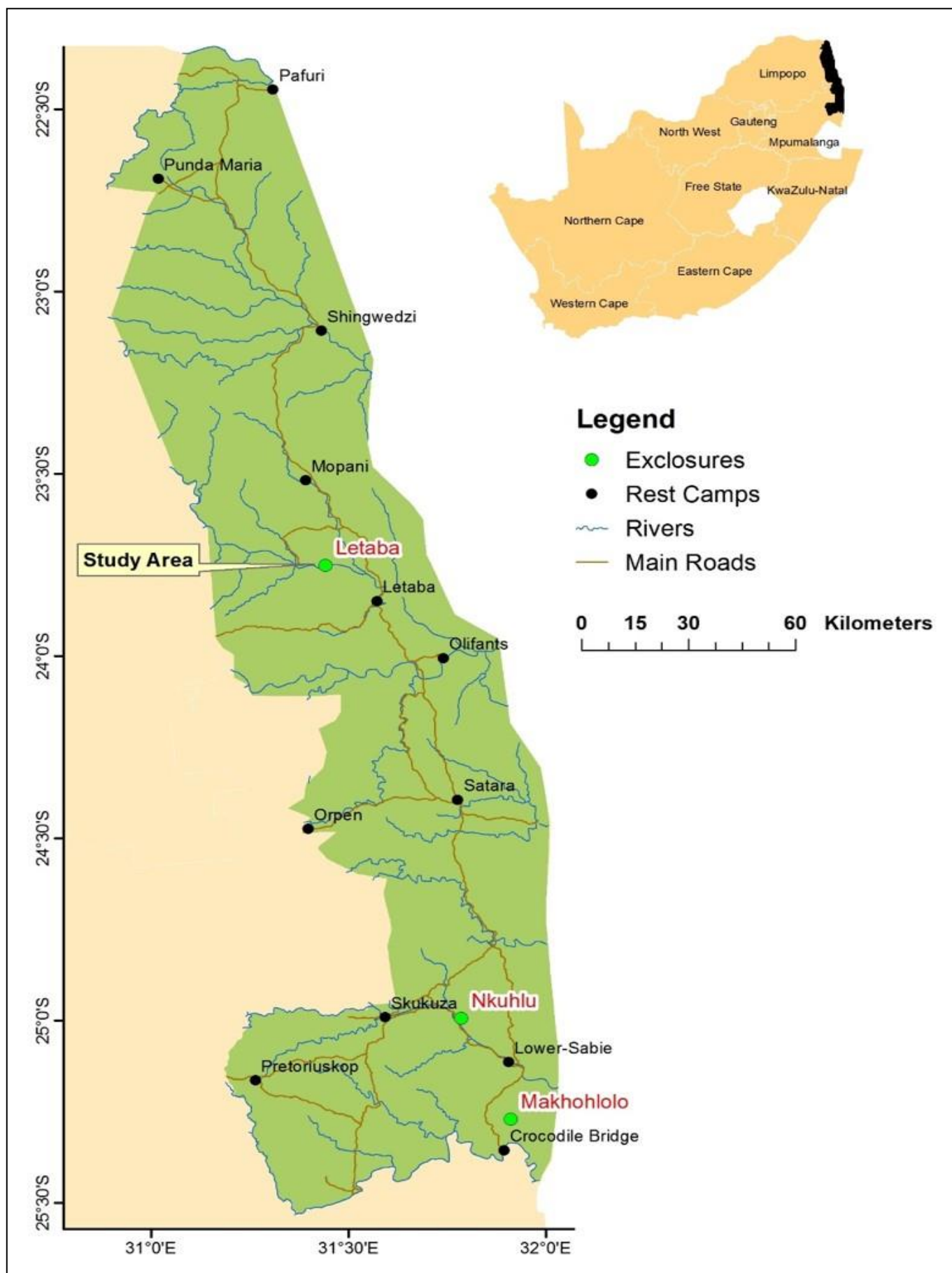


Figure 3.1: Map indicating the position of exclosures in the KNP in relation to the main restcamps and roads, including the location of the study site (Letaba Exclosures).

The data reported here include the historical average monthly and annual rainfall figures for the Letaba area (Table 3.1) as well as the actual total rainfall data for the climatological years (Figure 3.2). Monthly rainfall was the rainfall variable of most relevance to the study, especially the total rainfall of the last four months prior to the sampling periods (December 2002 – March 2003; September 2011 – December 2011) (Figure 3.3), indicating the moisture conditions just before the vegetation sampling took place.

Table 3.1: The historical average monthly and annual rainfall as well as the number of days that rainfall is expected at the Letaba Restcamp in the Kruger National Park (taken from Zambatis, 2003).

<i>Month</i>	<i>Rainfall average (mm)</i>	<i>Average number of days with rain</i>
<i>January</i>	85	7
<i>February</i>	77	7
<i>March</i>	42	6
<i>April</i>	27	3
<i>May</i>	10	2
<i>June</i>	4	1
<i>July</i>	7	1
<i>August</i>	6	1
<i>September</i>	15	2
<i>October</i>	31	4
<i>November</i>	67	6
<i>December</i>	87	7
<i>Average Annual Total</i>	458	47

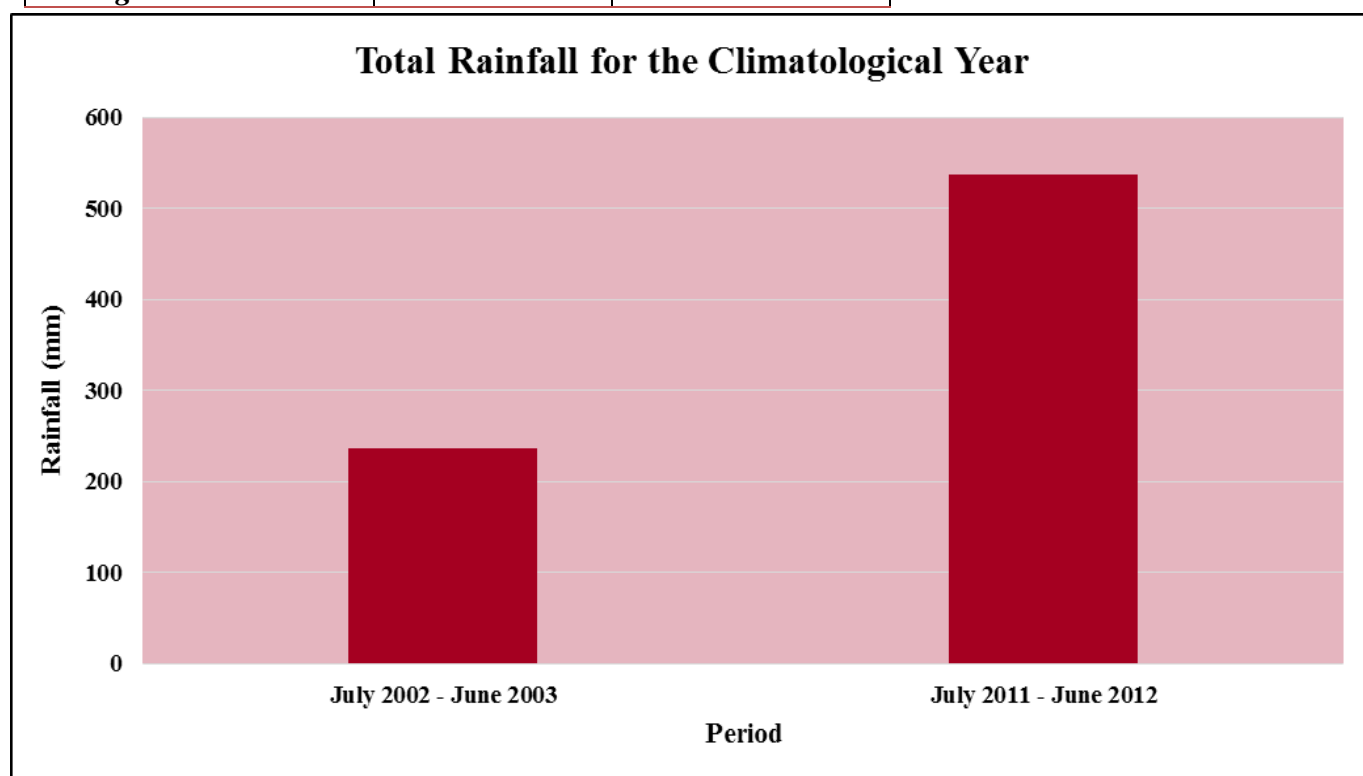


Figure 3.2: The total rainfall for the climatological years (July 2002 - June 2003; July 2011 - June 2012). Data as measured at the Letaba restcamp ranger station.

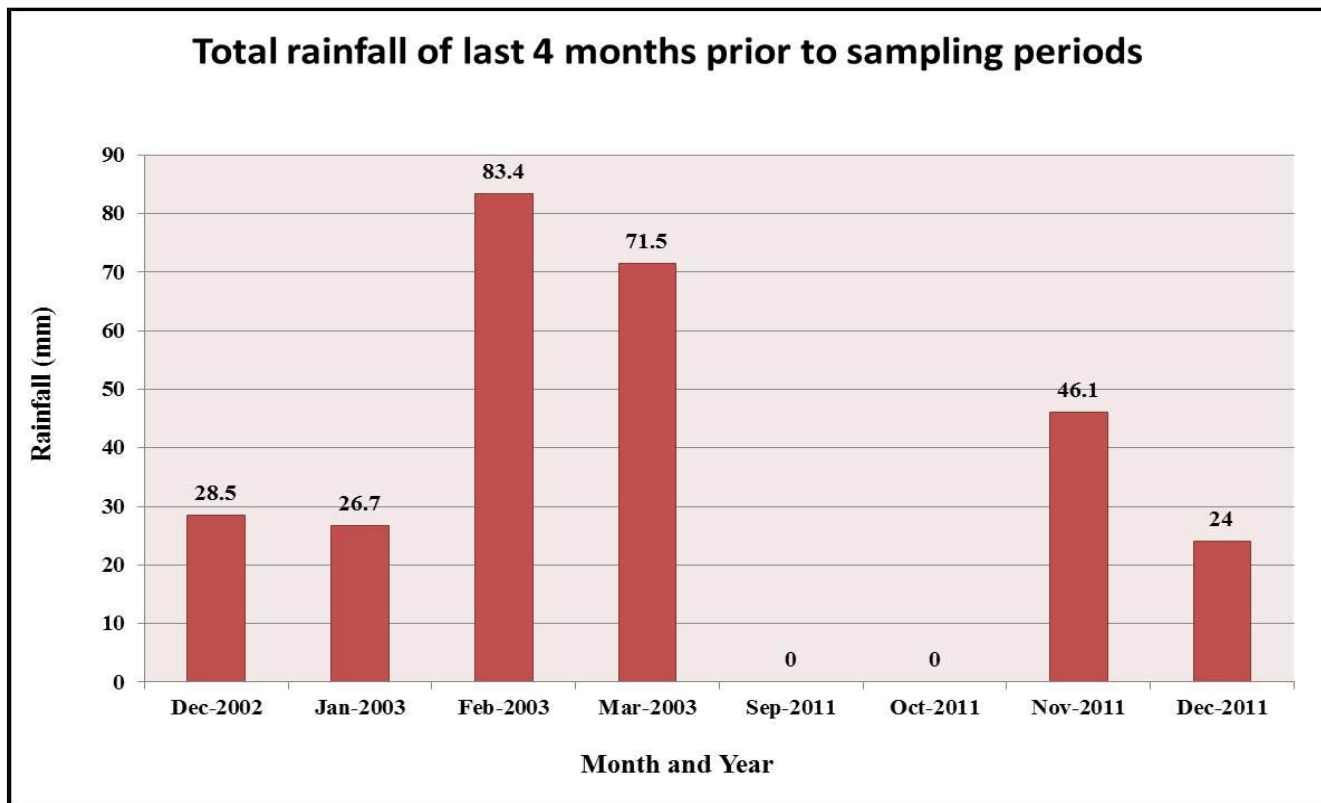


Figure 3.3: The total rainfall of the four months preceding vegetation surveys for each year (December 2002 – March 2003; September – December 2011). Data was measured at the Letaba restcamp ranger station.

3.4.2. Temperature

Temperatures fluctuate between extremely hot in summer, to mild in winter. Temperatures rarely drop below freezing point (Venter & Gertenbach, 1986; Venter *et al.*, 2003). Temperatures range from mean minimums of 7.8 °C in winter, to mean maximums of about 34.1 °C in summer. The mean daily temperature is approximately 23.3 °C, but maximum summer temperatures may reach as high as 44°C (Venter & Gertenbach, 1986; Venter *et al.*, 2003; Siebert *et al.*, 2010).

3.5. Geology

The most representative and main type of underlying geological formations in the Letaba exclosures area can be described as Granite and Makhutswi gneiss containing Swaziland rock formations (Siebert *et al.*, 2010; Venter *et al.*, 2003) like amphibolite and migmatite (Siebert *et al.*, 2010), and schist (Gertenbach, 1983). The Makhutswi Gneisses are considered as some of the oldest rock formations known in the KNP and its geological formation can be described as having a tonalitic composition with an intense migmatization, displaying schlieren and amphibolitic material that could represent mafic dykes (Schutte, 1986).

3.6. Soils

The study area covers a relatively uncomplicated soil distribution (Siebert *et al.*, 2010; Paterson & Steenkamp, 2003). The soils of the Letaba River Rugged Veld are freely drained, but can also be

shallow and stony, especially in the east (Mucina & Rutherford, 2006). The banks of the Letaba River are dominated by alluvial soils of the Oakleaf soil form (Siebert *et al.*, 2010), consisting of a complex association of black and brown calcareous alluvial clay and loam in various stages of profile development (Venter *et al.*, 2003). The footslopes possess a strip of deeper red-yellow apedal Hutton soils (Siebert *et al.*, 2010; Mucina & Rutherford, 2006) consisting of moderately deep to deep black expansive calcareous clay (Venter *et al.*, 2003). The midslopes and crests of the study area are mostly represented by Mispah and Glenrosa soil forms (Siebert *et al.*, 2010).

3.7. Vegetation

The vegetation of the Letaba exclosures can be described as being part of the 'Letaba River Rugged Veld' (Gertenbach, 1983; Mucina & Rutherford, 2006; Siebert *et al.*, 2010) and can be further categorised on a broader scale as being part of the *Cissus cornifolia* – *Colophospermum mopane* vegetation type and as part of the *Combretum apiculatum* – *Colophospermum mopane* major plant community (Siebert *et al.*, 2003). The riparian zone of the study site forms part of the Subtropical Alluvial Vegetation (Mucina & Rutherford, 2006). The dominant woody species in the riparian zone are *Croton megalobotrys*, *Nuxia oppositifolia*, *Gymnosporia senegalensis*, *Philenoptera violacea*, *Diospyros mespiliformis*, *Combretum microphyllum* and *Trichilia emetica*. The upland area is dominated by *Colophospermum mopane* with some variation of other species that co-exists with it in the woody layer such as *Combretum apiculatum*, *Terminalia prunioides*, *Dichrostachys cinerea*, *Maerua parvifolia*, *Cissus cornifolia*, *Commiphora mollis*, *C. africana*, *Grewia bicolor*, *Combretum imberbe*, *Acacia nigrescens*, *Acacia exuvialis* and *Rhigozum zambeziacum* (Siebert *et al.*, 2010). The most representative herbaceous species are grasses such as *Panicum coloratum*, *Schmidtia pappophoroides*, *Melinis repens*, *Bothriochloa radicans* and forbs such as *Crabbea velutina*, *Ocimum americanum*, *Phyllanthus maderaspatensis*, *Pavonia burchellii*, *Hibiscus micranthus* and *Jasminum stenolobum* (Siebert *et al.*, 2010).

3.8. Herbivory

The species of herbivore present at the Letaba exclosures include African elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), Cape buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*), hippo (*Hippopotamus amphibius*), zebra (*Equus quagga*), kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), scrub hare (*Lepus saxatilis*) and impala (*Aepyceros melampus*) (Skinner & Chimimba, 2005). Although no estimate of herbivore density or any form of grazing intensity were measured for this study, it is known that the density of specifically elephants in the Letaba exclosures area is estimated to be as high as 1.5 - 2.6 per km² (Grant *et al.*, 2008). The level of herbivory at the site are also considered to be lower when compared to that of the Mopaneveld in general, due to overall lower animal concentrations (Parsons *et al.*, 2005).

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Chapter 4

Material and Methods

This chapter provides the general experimental and sampling design for both species diversity and functional group analyses as well as an overview of the methods that are applicable to both species and functional analyses. Methods that are unique for either species- or functional responses are presented in the respective chapters under a 'Methods' heading (Chapter 5 for methods applicable to species level responses, and Chapter 6 for methods applicable to functional level responses).

4.1. Experimental design

The study was conducted in the Kruger National Park (KNP) in South Africa. The conservation area of the KNP provided the perfect opportunity for herbivory exclusion experiments, because it still has uninterrupted functioning of vegetation heterogeneity and ecological responses to environmental disturbances at both spatial and temporal scales (Van Coller *et al.*, 2013). The data were collected in the Letaba exclosures situated on the banks of the Letaba River in the northern part of KNP. The exclosures have been constructed for the purpose of examining the role of herbivory and fire in modifying spatial and temporal vegetation patterns in order to guide conservation management (O'Keefe & Alard, 2002; Siebert *et al.*, 2010).

The experimental area extends over 129 ha of semi-arid savanna riparian zone (Siebert *et al.*, 2010) and is subdivided into three herbivory treatments: (1) a fully fenced area excluding all herbivores from the size of a hare and upwards (full exclosure hereafter); (2) a partially fenced area where large herbivores such as giraffe and elephants are excluded (partial exclosure hereafter); and (3) a control area that is unfenced (O'Keefe & Alard, 2002). A fire and no fire area were allocated to each of the three herbivory treatments, giving rise to six experimental treatments in total (O'Keefe & Alard, 2002). The last fire that entered the study area (including the full exclosure) was in 2007, which was considered not recent enough to have had an effect on the diversity and composition of the herbaceous layer in the study area. The full and partial exclosures are about 400 m apart and separated by the unfenced control treatment (O'Keefe & Allard, 2002) (Fig. 4.1). The different treatments vary in size, i.e. 42 ha, 51 ha and 36 ha for the full exclosure, partial exclosure and unfenced area, respectively (Siebert *et al.*, 2010). The treatments expand over different habitat types from the channel of the river up to the crest and stretch gradually along the catena of the Letaba River (O'Keefe & Alard, 2002).

Within each of the three treatments, two permanent transects were laid out perpendicular to the river over the whole catenal sequence, stretching from the macro channel bank up to the crest of the riparian landscape. The transects were as equally spaced as possible, about 100 m away from fences, and 30 m from firebreaks and construction areas (O'Keefe & Alard, 2002). Permanent markers were placed at the ends of each transect to relocate the exact position of that transect in the future. These markers were placed along the transects and correspond with the positions of the permanent vegetation plots into which each of the transects are divided (O'Keefe & Alard, 2002). The permanent vegetation sampling plots (10m x 20m) was established downstream from the transects, with the long side of the plot parallel to the river channel (O'Keefe & Alard, 2002). The four corners of each plot have been marked with 0.5 m long steel pens, hammered into the ground and leaving only 10 cm exposed above the ground to avoid injuring animals. The four individual exposed pens are each marked with a different number of grooves, enabling the location of a specific corner of a plot at all times. Overall, the different herbivory treatments consisted of 2 permanent transects per treatment (12 transects in total), with a total of 151 plots in the transects.

For the purpose of this study, all the vegetation plots located in the riparian zone of the catenal sequence were excluded from the analysis because:

- The riparian plots were specifically designed to allow and sustain natural damage to the enclosures caused by reoccurring flooding of the river's banks (O'Keefe & Alard, 2002; Siebert *et al.*, 2010). At the time of the two field data collections, the permanent transect and plot corner markers of the riparian plots were washed away by flooding events and could not be relocated.
- The riparian plots have a high diversity in the narrow riparian zone and are very variable due to frequent flooding disturbances. The riparian zone are described as the catenal zone with the highest rate of vegetation succession after a flooding event (O'Keefe & Alard, 2002). Two sampling periods at only two specific points in time (as in this study), will not be able to successfully reflect the constantly changing diversity of this highly variable zone.

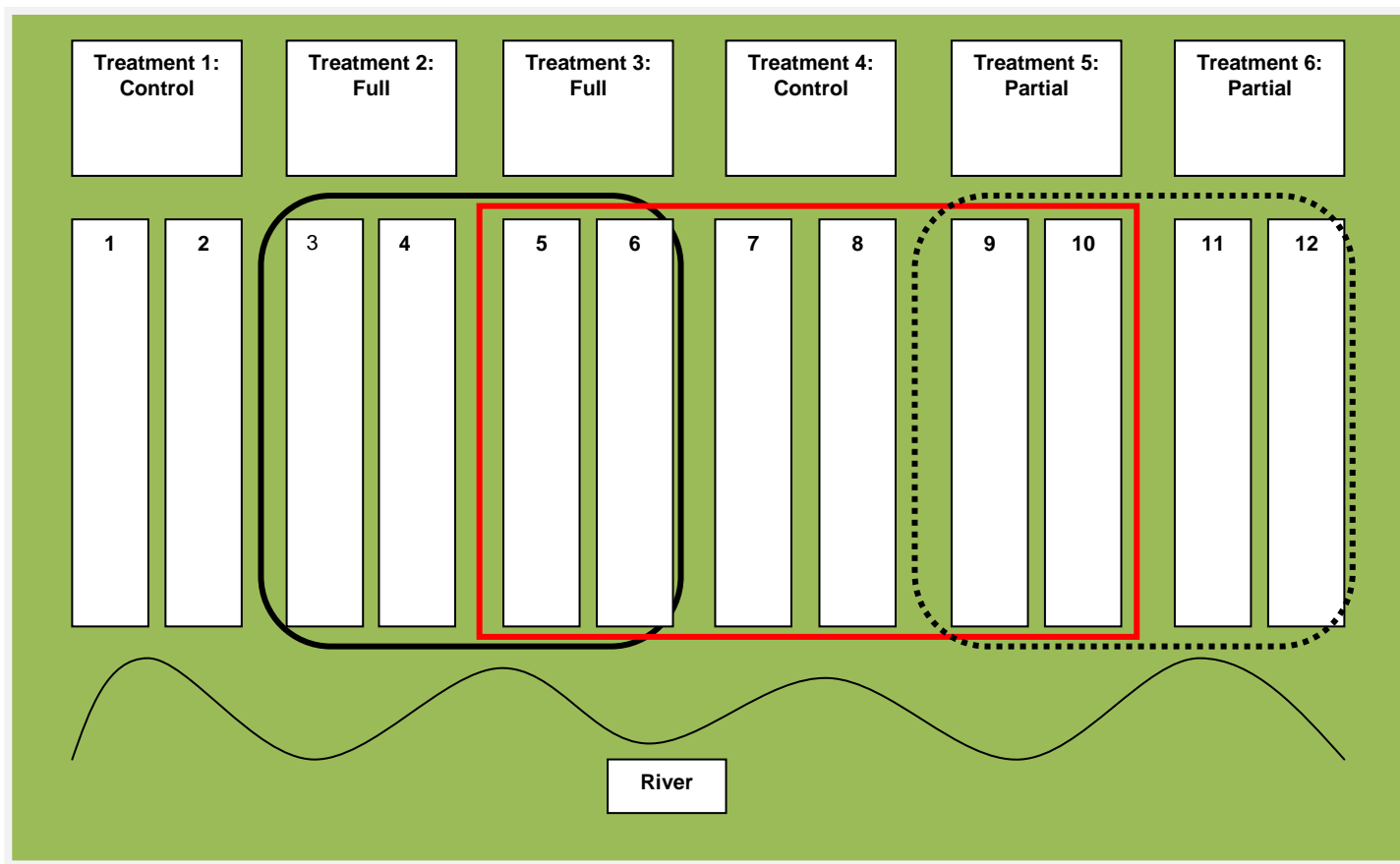


Figure 4.1: Diagrammatic representation of the Letaba exclosures illustrating the different treatments and transects. The Full, Partial and Control treatments are each represented by two fire and two no fire transects. The solid line represents the full exclosure, perforated line the partial exclosure and the red line the treatments and transects protected from fire activity.

4.2. Field data collection

Herbaceous plant species and biomass data were collected by two independent research groups in 2003 (SANParks) and 2012 (myself and the research team from North West University) respectively. Species data were recorded within two 1-m² circular sub-plots nested within the 200-m² plots (10 m x 20 m) along transects. Sub-plots were placed in the eastern and western corner of each plot and all herbaceous individuals rooted inside the sub-plots were identified and counted up to species level (O'Keefe & Alard, 2002). The data of the two subplots were pooled to gain a more representative sample of the species inventory per plot. The above-ground herbaceous biomass was determined by taking ten equally spaced measurements with a disc pasture meter (DPM) (Bransby *et al.*, 1977) specifically calibrated for Lowveld Savanna conditions, along one diagonal of each plot (1510 DPM measurements in total). The DPM-measurements were converted into dry matter production in kg ha⁻¹ based on the revised DPM-calibration for the KNP by Zambatis *et al.* (2006).

4.3. Data Analysis

4.3.1. Species diversity analysis (Chapter 5)

- Nonmetric Multi-Dimensional Scaling (NMDS) analysis in *PRIMER* 6 (2012) was used to test for similarities of herbaceous species composition over time, between and within different herbivory treatments based on a Bray-Curtis distance matrix. One-way Analysis of SIMilarity (ANOSIM) was conducted in *PAST* (Hammer *et al.*, 2001) to identify significant differences.
- Repeated measures analysis of variance (Repeated Measures ANOVA) in *STATISTICA* (StatSoft, 2012) was applied to fourth-root transformed datasets of 2003 and 2012 to test for the effect of sampling year, treatment and the combined effect (year*treatment) on: (1) abundance (N), (2) species richness (S) (number of species per plot), (3) Margalef's species richness (d), (4) Shannon-Wiener diversity index (H'), (5) Simpson's diversity index ($1-\text{Lambda}$), (6) Pielou's evenness (J') and (7) biomass production across herbivory treatments. Bonferroni post-hoc significance tests were also applied.

4.3.2. Functional analysis (Chapter 6)

The sampled vegetation data were analysed on functional level by considering firstly the compositional (abundance and species richness) patterns of single life-forms and the plant functional types within these life forms, and secondly the response patterns in overall life-form diversity.

4.3.2.1. Response patterns of single life forms and Plant Functional Types

Major life-form groups

- Four major life-form groups were identified (1) Annual Graminoids, (2) Perennial Graminoids, (3) Annual Forbs and (4) Perennial Forbs. Abundance, relative abundance and richness of each life-form were calculated for each herbivore treatment. One-way analysis of variance (ANOVA) in *STATISTICA* (StatSoft, 2012) was applied to test for significant differences.

PFT's inside major life-form groups

- To identify plant functional types inside major life-form groups, specific plant functional traits were selected to define the PFT's. The selection of traits occurred on a very broad basis at species level, concentrating on soft functional traits (usually easily obtainable from literature or easily measurable in the field, e.g. plant height class) rather than hard functional traits (usually difficult to obtain and primarily only obtainable from hard field measurements, e.g. plant seed persistence). Plant functional traits were selected to indicate the species response to different herbivory exclusion treatments in a semi-arid system (Appendix 1) and was recorded in both binary and categorical format. The species soft trait information was primarily obtained from

literature sources and websites (including floras of several countries), as well as additional herbarium specimens. The main literature sources were: Germishuizen (1997); Van Wyk & Malan (1998); Van Wyk (2000); Germishuizen & Meyer, 2003; Van Oudtshoorn (2006); Smith & Crouch (2009); Crouch *et al.* (2011); Kirby (2013). The main flora sources were: Flora of southern Africa (Huntley *et al.*, 2007), Flora of Zimbabwe (Hyde *et al.*, 2015a), Flora of Mozambique (Hyde *et al.*, 2015b), Flora of Zambesiaca (KEW, 2015). The main website sources were: Kyffhäuser (2014); Biodiversity Explorer (2015); South African National Biodiversity Institute (SANBI) (2015) and the Global Plants database (JSTOR, 2015).

- Within each major life-form group, plant functional types were identified by means of cluster analysis in *PRIMER* 6 (2012), using the Gower similarity coefficient (Gower, 1981).
- Principal Components Analysis (PCA) was conducted in *PAST* (Hammer *et al.*, 2001) to visualize and check the previously derived cluster groupings in ordination space and to quantify the different traits' contribution to the variation among species in the different functional groups (Leyer & Wesche, 2008).
- The abundance, relative abundance and richness of each life-form in the different treatments were calculated and One-way analysis of variance (ANOVA) in *STATISTICA* (StatSoft, 2012) was applied to test for significant differences between treatments and over time.

4.3.2.2. Response patterns in overall life-form diversity

- Repeated measures analysis of variance (ANOVA) in *STATISTICA* (StatSoft, 2012) was applied to the fourth-root transformed datasets (Sasaki *et al.*, 2009) of 2003 and 2012 to test for the effect of sampling year, treatment and the combined effect (year*treatment) on the: (1) species richness (S), (2) Margalef's species richness (d), (3) Shannon-Wiener diversity index (H'), (4) Simpson's diversity index ($1-\text{Lambda}$) and (5) Pielou's evenness (J') of the major life-forms across herbivory treatments. Bonferroni post-hoc significance tests were also applied.

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Chapter 5

Herbivory effects on species composition and diversity

5.1. Introduction

5.1.1. *Herbaceous community responses to disturbance*

Disturbances such as herbivory take place over various spatio-temporal scales causing numerous effects at different levels of vegetation organization (O'Connor, 1995). Therefore a need exists for long-term datasets to quantify the effects of herbivory on savanna vegetation over long time scales. Even when long-term studies are undertaken, it still remains a challenge to identify the origins of specific vegetation patterns (O'Connor, 1994; Fuhlendorf *et al.*, 2001). Because semi-arid savannas typically function in different states (both equilibrium and non-equilibrium) and at different spatio-temporal scales (Fuhlendorf *et al.*, 2001), understanding responses at the local scale by using long-term datasets is important to better define and interpret response patterns at larger spatial scales. The impact of specific disturbances on savanna vegetation structure, composition and diversity is also better quantified after long-term exclusion of the disturbance agent (Buitenwerf *et al.*, 2011; Savadogo *et al.*, 2008; O'Connor, 1994). By using local-scale assessments of floristic composition changes over time, a better understanding emerges of what ecological processes and disturbances are responsible for these vegetation changes (Clarke *et al.*, 2005).

Competitive interactions of the woody and grass component are distinctive when explaining vegetation response patterns of savanna ecosystems (Scholes & Walker, 1993). These interactions are well studied in semi-arid savanna ecosystems, although less attention is given to the ecology of the herbaceous layer, which forms an important part in the overall richness, diversity and dynamics of the savanna system (McIntyre *et al.*, 1999; Shackleton, 2000; Rutherford *et al.*, 2012; Siebert & Scogings, 2015) and accounts for more than 80 % of the herbaceous taxa in semi-arid savanna types, such as in the Kruger National Park (KNP) (Trollope *et al.*, 2014).

The direct impact of herbivory (or the exclusion thereof) on compositional changes in the herbaceous vegetation of savannas is difficult to detect over a short period of time (< 10 years), but in the long-term, the presence or absence of herbivores may significantly alter the vegetation composition (Skarpe, 1991; Fynn & O'Connor, 2000; Adler *et al.*, 2001). Some studies suggest that the exclusion of herbivores for extended periods may increase the cover of palatable perennial herbaceous species and decrease the cover of unpalatable annual species (Pettit & Froend, 2001; Valone *et al.*, 2002; Guo, 2004; Firincioglu *et al.*, 2007). In semi-arid African savannas, herbaceous species richness peaks at intermediate levels of grazing, hence at intermediate levels of biomass

and declines with increasing biomass when the system is released from herbivory for longer than five years (Angassa, 2012; Jacobs & Naiman, 2008; Van Coller *et al.*, 2013).

In semi-arid savannas it remains challenging to disentangle the effects of all environmental factors that could possibly contribute to observed changes in the herbaceous layer. For instance, herbivory, fire events, rainfall variability, topography and soil type affect herbaceous species composition and structure, on their own or in close interactions (O'Connor, 1998; Illius & O'Connor, 1999; Jacobs & Naiman, 2008; Smith *et al.*, 2012; Van Coller *et al.*, 2013; Hanke *et al.*, 2014; Linstädter *et al.*, 2014; Stevens *et al.*, 2014). This combined effect is often enlarged when both disturbances cause similar vegetation changes (Danckwerts & Stuart-Hill, 1988; O'Connor, 1995; O'Connor, 1998; Fynn & O'Connor, 2000; Swemmer *et al.*, 2007; Sasaki *et al.*, 2009; Gibbes *et al.*, 2014). Low rainfall in a semi-arid savanna causes increased mortality among perennial herbaceous species (O'Connor, 1994; O'Connor, 1998; Vetter, 2009), especially under heavy grazing intensities, leading to a further loss in palatable perennials (O'Connor, 1995; O'Connor, 1998; Fuhlendorf *et al.*, 2001; Swemmer *et al.*, 2007). However, studies on drought effects revealed that systems dominated by perennial herbaceous species are more resistant than those dominated by annual species, since these systems suffer less in terms of productivity after a drought (Ruppert *et al.*, 2015). Inter-annual rainfall is highly variable in semi-arid savanna ecosystems (Buitenwerf *et al.*, 2011), stressing the importance of annual repeats of data sampling within a long-term monitoring experiment to detect trends in vegetation composition changes caused by rainfall variability (Fuhlendorf *et al.*, 2001; Gillson, 2004; Buitenwerf *et al.*, 2011; Swemmer *et al.*, 2007; Gibbes *et al.*, 2014).

The combined effect of herbivory and rainfall variability over time is prominent in semi-arid Mopane savannas (O'Connor, 1998; Rutherford *et al.*, 2012; Siebert, 2012), particularly in the northern KNP, where rainfall is unpredictable and extended drought events occur regularly. To best understand herbaceous layer dynamics in these semi-arid ecosystems, vegetation should be monitored annually accompanied by detailed rainfall measures. Unfortunately the data suitable for analyses in this study were limited to two sampling occasions, which were both sampled during below-average preceding rainfall months (Chapter 3). However, since sampling was done at the start of the experiment and 10 years thereafter, the effect of long-term herbivore exclusion on herbaceous community structure (i.e. species composition, richness, diversity and productivity) could be tested for, regardless of rainfall variability, which was assumed to be similar across all treatments of herbivory.

5.1.2. Study objectives

The research presented in this chapter aims to test the effect of nine years of herbivore exclusion (selected exclusion and exclusion of all mammalian herbivores) on the composition, species richness, species diversity and biomass of the herbaceous vegetation in a semi-arid Mopaneveld savanna. It compares vegetation data from two years (2003 and 2012), which were repeatedly recorded in a herbivory-exclusion experimental setup. Only the response of the herbaceous vegetation component (i.e. graminoids and forbs) was considered in the study.

The research question:

How does the herbaceous community structure (i.e. species composition, diversity, richness and biomass) of a semi-arid Mopaneveld savanna respond to different treatments of herbivore exclusion over time?

It was hypothesized that:

1. Herbaceous species assemblages are unique to specific catenal positions, despite herbivore treatment effects and time.
2. After nine years of total herbivore exclusion (i.e. full exclosure), herbaceous species composition is significantly different, species richness and –diversity is lower and standing biomass is significantly higher compared to areas excluded from elephant and giraffe (i.e. partial exclosure) and from areas exposed to all herbivores (i.e. control).
3. Within each herbivore treatment, time (i.e. nine years) will not affect herbaceous species composition, although species richness and –diversity are negatively affected, and productivity positively affected by the duration of herbivore exclusion.

5.2. Material and methods

Data analysis

5.2.1. Composition:

To test for differences in the herbaceous composition, a Bray-Curtis dissimilarity matrix was produced by Nonmetric MultiDimensional Scaling (NMDS) in PRIMER 6 (2012), providing a visual representation of (1) species assemblage differences across the catenal sequence (Crest Savanna; Lowland Savanna (Mixed Bushveld and Mopane Bushveld (Siebert *et al.*, 2010)) within each herbivory treatment, and (2) between the different herbivory treatments and (3) between sampling years. When plots sampled at different catenal positions (so-called vegetation zones) separated in ordinal space, it was assumed that they host a different combination of herbaceous species and should be compared separately in statistical analyses. All plots were assigned to one of three catenal positions based on a visual representation achieved by combining the exact GPS-coordinates of each plot with the known coordinates of the vegetation zone map of the Letaba exclosures. Before analysis, normality of the data was tested, and where not normally distributed, the species data were fourth-root transformed to down-weight the influence of dominant species.

In combination with the NMDS, the visual differences in plot distribution in two-dimensional ordination space were tested through the application of a One-way Analysis of Similarity (ANOSIM; Clarke, 1993) based on the Bray-Curtis dissimilarity index in Past (Hammer *et al.* 2001). ANOSIM gives a R-statistic between 0 and 1 indicating the level of dissimilarity (where a value of 1 indicates total dissimilarity and 0 indicates that the compared groups are indistinguishable, Clarke, 1993).

5.2.2. Richness, Diversity and Productivity:

Five measures of alpha diversity were calculated from the pooled species data of the sub-plots (Table 5.1). The reason for choosing both Species richness and Margalef's richness was because Species richness only takes abundance into account, while Margalef's richness are sensitive to both richness and abundance. Similarly, both Shannon-Wiener and Simpson's diversity indexes were used because Shannon-Wiener are sensitive to diversity and abundance, while Simpson's index are sensitive to diversity and evenness.

Table 5.1: The different measures of alpha diversity used in the study.

<i>Measure</i>	<i>Data Type</i>	<i>Formula</i>
<i>Species richness (S)</i>	Incidence	number of species
<i>Margalef's species richness (d)</i>	Incidence	$d = (S-1) / \log N$
<i>Shannon-Wiener diversity index (H')</i>	Abundance	$H' = -\sum (p_i \ln p_i)$
<i>Simpson's diversity index (1-Lambda)</i>	Abundance	$1 - \sum (N_i^2 / N^2)$
<i>Pielou's evenness (J')</i>	Abundance	$J' = H' / \log (S)$

Note: S represents the number of species per plot (2 x 1 m² circular sub-plots); N is the mean richness per plot; p_i represents proportional cover of entity "i" (i.e., cover of entity "i" / total cover per plot); N_i is the richness in the ith plot (Peet, 1974).

The effect of herbivory treatment, time as well as the interaction effect (time*treatment) on alpha diversity and biomass were analysed through the application of repeated measures ANOVA (Type III decomposition) in *STATISTICA* (StatSoft, 2012). This statistical model was chosen since it is commonly applied to orthogonal data, with high variation which is typical of the data used in this study. Sampling year was used as the within-subject factor and herbivory treatment as the between-subject factor. Where statistically significant results were obtained, the Bonferroni *post-hoc* significance test (Lindgren & Sullivan, 2001) was used for pairwise comparisons. Before analysis, normality of the data was tested, and where not normally distributed, the species data were fourth-root transformed to down-weight the influence of dominating species. For biomass, a Log 10 (x+1) transformation was applied to account for variability in the data set regarding unequal variances.

5.3. Results

5.3.1. Vegetation composition changes

NMDS and ANOSIM results of catenal position effects on species composition revealed no significant effect ($R < 0.2$ for all herbivore treatments) (Figure 5.1, Table 5.2). Results obtained from each herbivore treatment were therefore representative of the treatment without an underlying catenal effect, which allowed for the data to be pooled per herbivore treatment for all further analyses.

When herbivore treatments were pooled for each sampling year respectively to test for overall composition changes over time (i.e. 2003 vs 2012), plots sampled in 2003 separated slightly from the same plots sampled in 2012 in two-dimensional space (Figure 5.2 (a)). These differences could however not be confirmed by ANOSIM ($R = 0.24$, Table 5.2). This illustrates that the herbaceous species composition at the experimental site remained almost similar over time, irrespective of herbivore treatment. Although plots sampled in the Partial enclosure treatment separated slightly

from the other herbivore treatments in both sampling years (Figure 5.2 (b) & (c)) a very similar species composition could be detected through the application of ANOSIM to test for differences between treatments (2003: $R < 0.25$; 2012: $R < 0.2$, Table 5.2). Within-treatment species assemblages revealed no distinct changes over time for all three herbivore treatments (Figure 5.2 (d), (e) and (f); Table 5.2). Species composition in the Partial exclusion treatment revealed some temporal changes when viewed in ordination space (Figure 2 (e)), although these changes were minor ($R = 0.31$, Table 5.2).

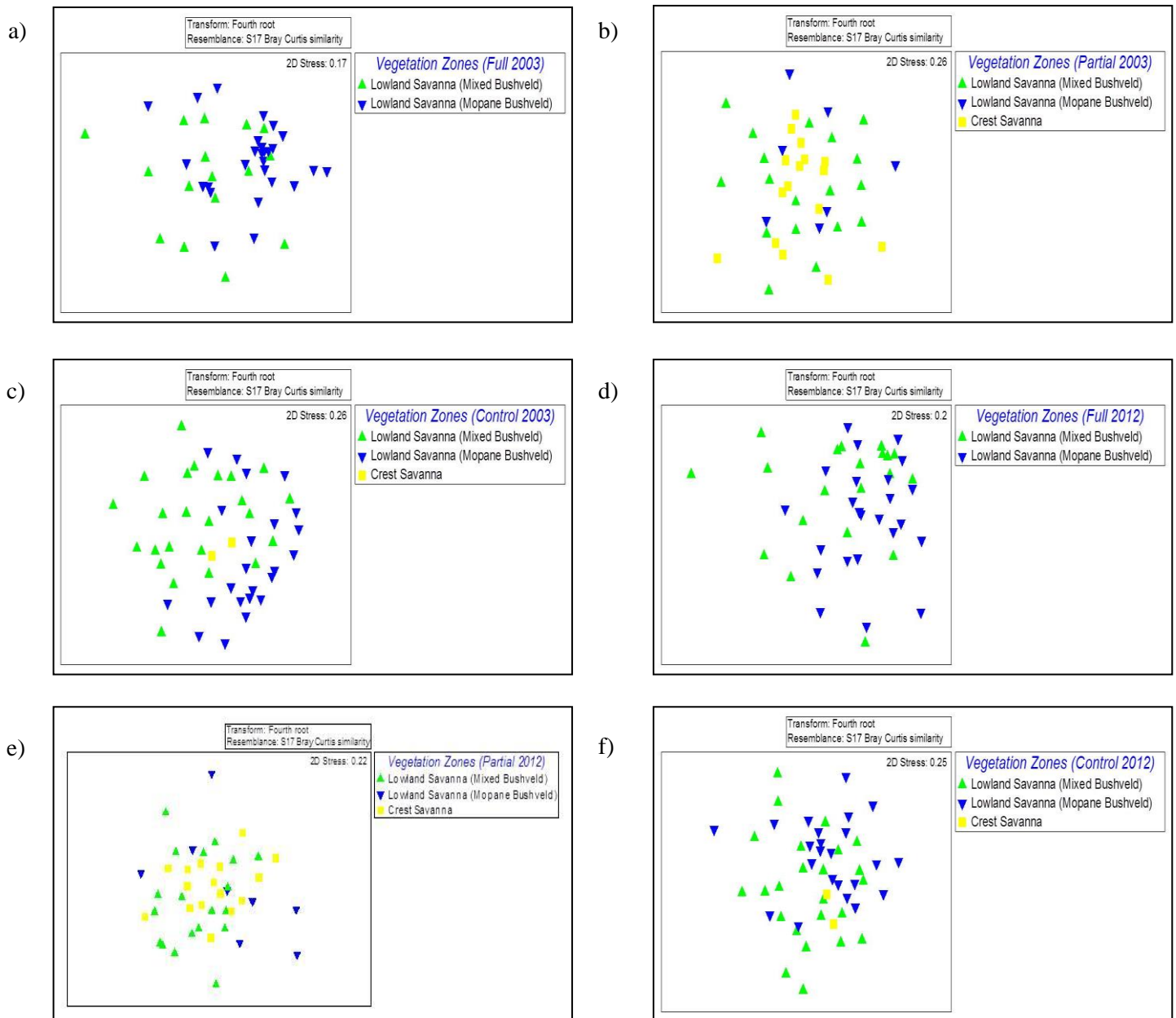


Figure 5.1: NMDS ordination scatter plots to visually display the distribution of the herbaceous vegetation composition across the different vegetation zones in 2003 for the (a) full exclusion treatment in 2003, (b) partial exclusion treatment in 2003, and (c) control, and in 2012 for the (d) the full exclusion treatment, (e) partial exclusion treatment and (f) control.

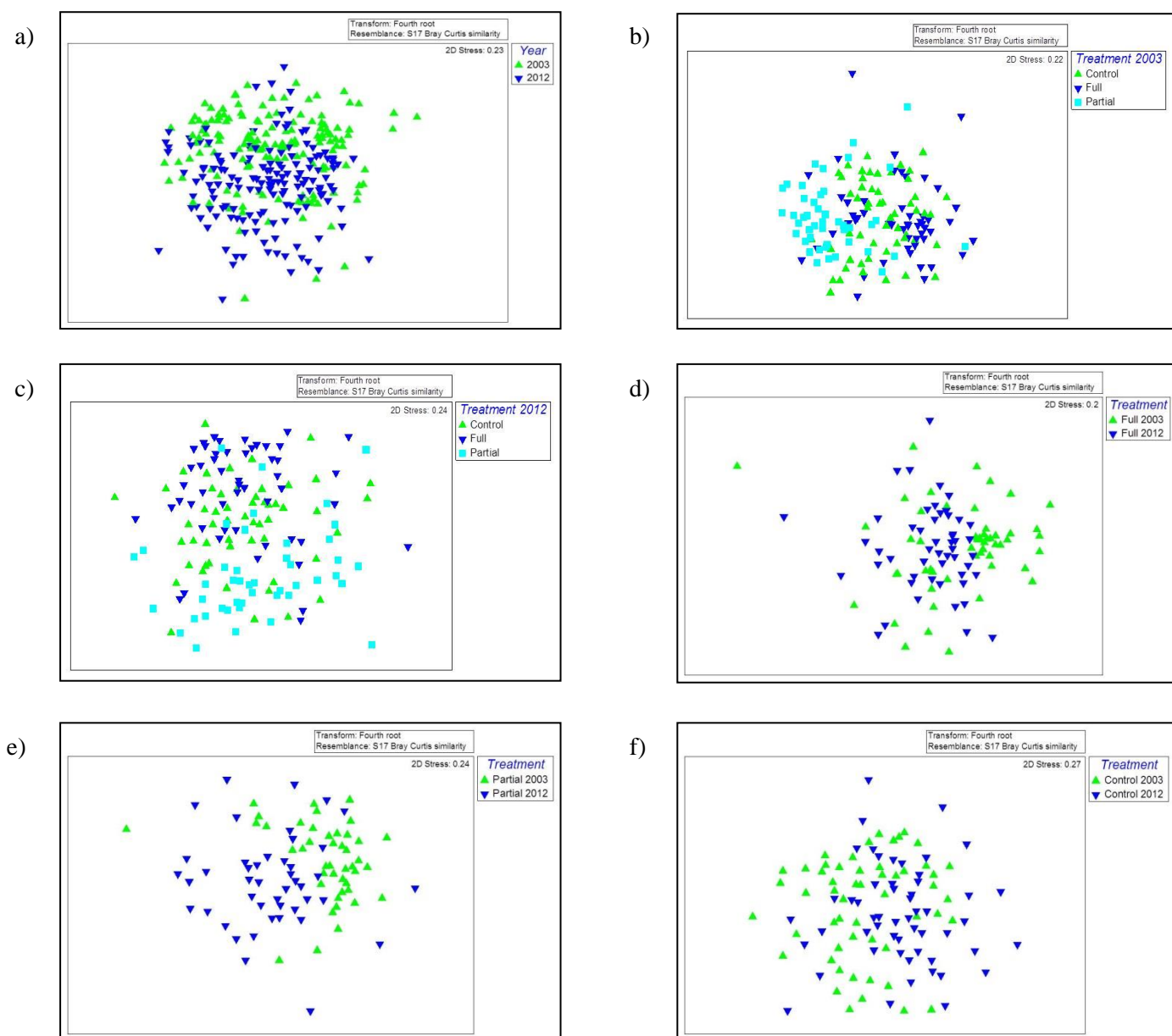


Figure 5.2: NMDS ordination scatter plots to visually display the distribution of the herbaceous vegetation composition of (a) the two sampling years (2003 vs 2012), (b) the herbivory treatments (full exclusion, partial exclusion, control) in 2003, (c) the herbivory treatments in 2012, (d) the full herbivore exclusion treatment over time, (e) the partial herbivory treatment over time, (f) the control herbivory treatment over time.

Table 5.2: Responses of herbaceous species composition to herbivore treatments (full, partial, control), within and between sampling years. Statistical significance among clusters was tested through the application of a One-way ANOSIM to the catenal effect of the the herbivory treatments (Full enclosure, Partial enclosure, Control) in 2003, the catenal effect of the the herbivory treatments in 2012, the two sampling years (2003 vs 2012), the herbivory treatments (full enclosure, partial enclosure, control) in 2003, the herbivory treatments in 2012, the full herbivore exclusion treatment over time, the partial herbivore treatment over time, the control herbivore treatment over time.

<i>Sample</i>	<i>p-value</i>	<i>Mean Rank Within</i>	<i>Mean Rank Between</i>	<i>R-value</i>
Catenal Effect				
<i>Full 2003</i>	< 0.01	386.6	480.3	0.1982
<i>Partial 2003</i>	< 0.05	377.4	457.5	0.1775
<i>Control 2003</i>	< 0.05	533.9	600.6	0.1134
<i>Full 2012</i>	0.30	459.1	474.6	0.0329
<i>Partial 2012</i>	< 0.001	321.1	461.7	0.3114
<i>Control 2012</i>	< 0.05	537.9	599.7	0.105
Time Effect				
<i>2003 vs 2012</i>	< 0.001	185.1	239.3	0.2353
<i>2003</i>	< 0.001	4764	5999	0.2181
<i>2012</i>	< 0.001	4997	5912	0.1616
Treatment Effect				
<i>Full enclosure</i>	< 0.001	2601	2962	0.1298
<i>Partial enclosure</i>	< 0.001	1593	2207	0.3065
<i>Control treatment</i>	< 0.001	2725	3051	0.1128

5.3.2. Changes in species richness, diversity, evenness and biomass

There was only a significant interaction effect (year*treatment effect) for Pielou's evenness and for biomass (Table 5.3). The lack of significant interaction effect for all other variables show that the observable changes could have been present at the onset of the experiment. Treatment effect was significant for all variables (Table 5.3). No significant time effect was revealed for the diversity indices or biomass (Table 5.3), except for density measured as the number of individuals per plot.

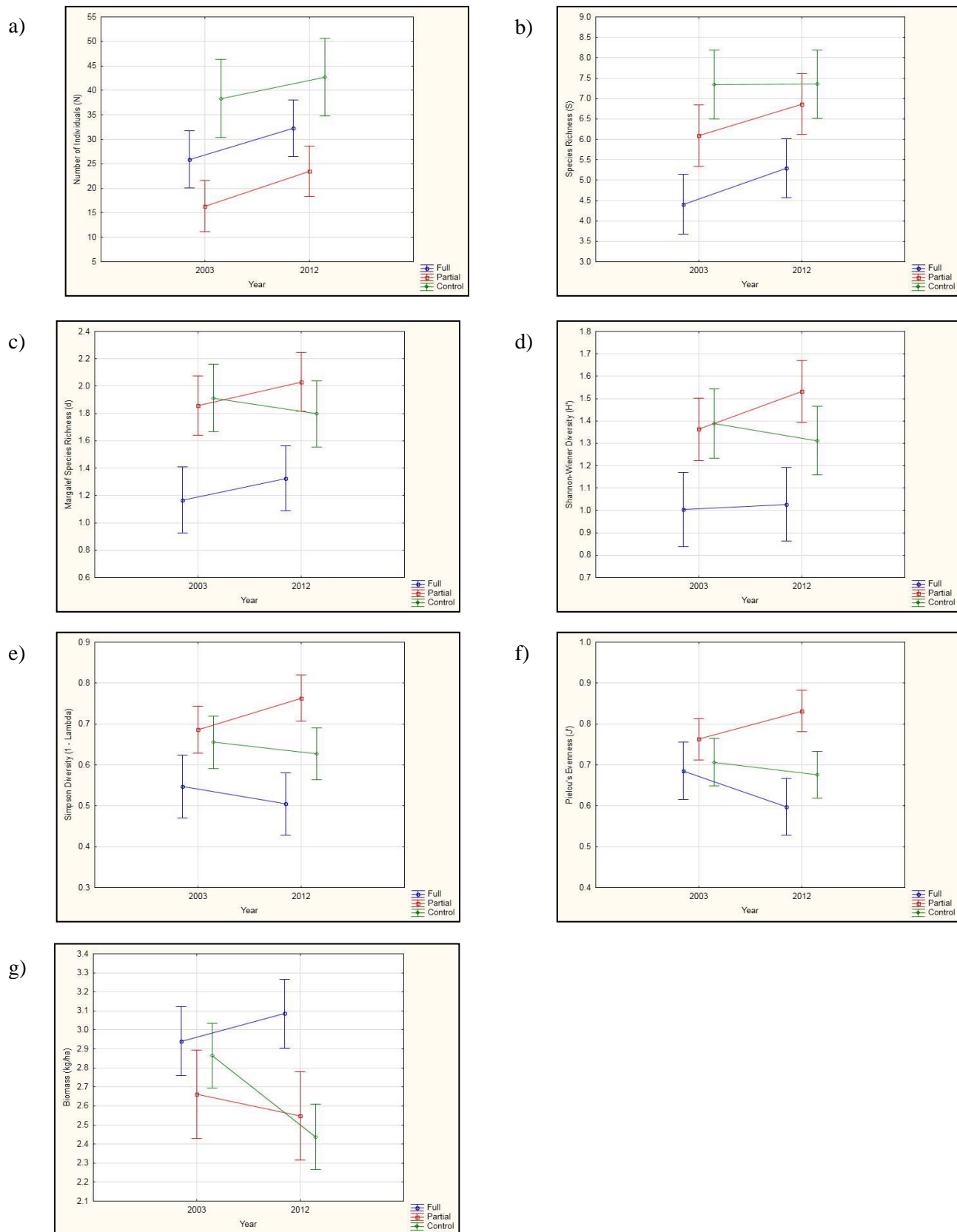
The significant interaction effect for Pielou's evenness could be ascribed to the increase in the Partial exclosure and a simultaneous decrease in the Full and Control treatments (Figure 5.3 (f)). Post-hoc within-year comparisons (Table 5.4) revealed that evenness was significantly higher in the Partial exclosure in 2012 (Table 5.4), which suggests that the species present in the Partial treatment were nearly equally abundant. The significant interaction effect (time*treatment) for biomass is possibly related to increases over time in the Full exclosure, whilst biomass in the Partial and Control treatments (Figure 5.3 (g)) decreased. Post-hoc within-year comparisons (Table 5.4) revealed significantly higher biomass in the Full- and Partial exclosures in 2012 compared to the Control treatment.

The significant treatment effect revealed throughout all the indices and biomass, is an indication that the response of each treatment varied independently and that this variation could have been present at the onset of the experiment. The post-hoc within year comparisons (Table 5.4) show that when significant effects between two treatments were present in 2012, those same effects already existed in 2003 (i.e. density in Partial exclosure vs Control treatment, species richness in the Full exclosure vs Control treatment, Margalef's richness and Shannon-Wiener diversity in the Full exclosure vs Partial exclosure etc). The post-hoc within-year comparisons did however also reveal that for the within-effect of treatment, some significant differences between treatments that were present in 2003 lost significance in 2012 (i.e. species richness in Full exclosure vs Partial exclosure, Margalef's richness and Shannon-Wiener diversity in Full exclosure vs Control treatment). Furthermore, some significant differences between treatments were present in 2012, but not in 2003 (i.e. Pielou's evenness and Simpson diversity in Full exclosure vs Partial exclosure, biomass in the Full exclosure vs Partial exclosure and Full exclosure vs Control treatment).

Table 5.3: Effects of sampling year and herbivory on plant species abundance, measures of alpha diversity and standing biomass of the herbaceous layer (repeated measures ANOVA; significant effects indicated by *).

<i>Response</i>	<i>Symbol</i>	<i>Source</i>	<i>Df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<i>Number of Individuals</i>	N	Time	1	2334.6	2334.6	4.7995	0.03*
		Treatment	2	18976.7	9488.3	20.8615	< 0.001*
		Time*Treatment	2	92.4	46.2	0.1016	0.90
		s.e.	174	79139.7	454.8		
<i>Species Richness</i>	S	Time	1	20.69	20.69	3.155	0.08
		Treatment	2	286.50	143.25	20.866	< 0.001*
		Time*Treatment	2	9.93	4.96	0.723	0.49
		s.e.	174	1194.54	6.87		
<i>Margalefs Species Richness</i>	d	Time	1	0.3426	0.3426	0.628	0.43
		Treatment	2	25.6328	12.8164	19.670	< 0.001*
		Time*Treatment	2	1.1883	0.5942	0.912	0.40
		s.e.	174	113.3706	0.6516		
<i>Shannon-Wiener Diversity Index</i>	H'	Time	1	0.0997	0.0997	0.433	0.51
		Treatment	2	9.1339	4.5669	16.150	< 0.001*
		Time*Treatment	2	0.6730	0.3365	1.190	0.31
		s.e.	174	49.2033	0.2828		
<i>Simpson's Diversity Index</i>	1-Lambda	Time	1	0.0003	0.0003	0.007	0.93
		Treatment	2	1.7705	0.8853	16.865	< 0.001*
		Time*Treatment	2	0.1929	0.0965	1.838	0.16
		s.e.	174	9.1333	0.0525		
<i>Pielou's Evenness</i>	J'	Time	1	0.0187	0.0187	0.521	0.47
		Treatment	2	1.1249	0.5624	13.060	< 0.001*
		Time*Treatment	2	0.2815	0.1408	3.268	0.04*
		s.e.	174	7.4936	0.0431		
<i>Biomass</i>	kg.ha ⁻¹	Time	1	1.171	1.171	2.569	0.11
		Treatment	2	8.979	4.489	10.369	< 0.001*
		Time*Treatment	2	3.668	1.834	4.236	< 0.05*
		s.e.	176	76.197	0.433		

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 $p < 0.05$.



Vertical bars denote 0.95 confidence intervals with standard error.

Figure 5.3: Repeated measures ANOVA pair-wise comparisons (indicating the means and standard errors) of (a) number of individuals, (b) number of species, (c) Margalef's species richness, (d) Shannon-Wiener diversity index, (e) Simpson diversity index, (f) Pielou's evenness and, (g) biomass across the herbivory treatments over time in a semi-arid Mopaneveld savanna.

Table 5.4: Treatment effects on diversity components of the herbaceous Mopaneveld vegetation per sampling year and averaged over sampling years. ANOVA with Bonferroni corrected post hoc test (p -value is significant at $p < 0.05$, significant value indicated with *).

<i>Response</i>	<i>Treatments</i>	<i>p</i>
<i>Number of Individuals</i>	Full over time	1.0
	Partial over time	1.0
	Control over time	1.0
	Full vs Partial (2003)	0.56
	Full vs Control (2003)	0.10
	Partial vs Control (2003)	< 0.001*
	Full vs Partial (2012)	0.77
	Full vs Control (2012)	0.33
	Partial vs Control (2012)	< 0.001*
<i>Species Richness</i>	Full over time	1.0
	Partial over time	1.0
	Control over time	1.0
	Full vs Partial (2003)	0.04*
	Full vs Control (2003)	< 0.001*
	Partial vs Control (2003)	0.40
	Full vs Partial (2012)	0.07
	Full vs Control (2012)	< 0.01*
	Partial vs Control (2012)	1.0
<i>Margalef's Species Richness</i>	Full over time	1.0
	Partial over time	1.0
	Control over time	1.0
	Full vs Partial (2003)	< 0.01*
	Full vs Control (2003)	< 0.001*
	Partial vs Control (2003)	1.0
	Full vs Partial (2012)	< 0.001*
	Full vs Control (2012)	0.09
	Partial vs Control (2012)	1.0
<i>Shannon-Wiener Diversity Index</i>	Full over time	1.0
	Partial over time	1.0
	Control over time	1.0
	Full vs Partial (2003)	0.03*
	Full vs Control (2003)	0.01*
	Partial vs Control (2003)	1.0
	Full vs Partial (2012)	< 0.001*

<i>Response</i>	<i>Treatments</i>	<i>p</i>
	Full vs Control (2012)	0.18
	Partial vs Control (2012)	0.78
<i>Simpson's Diversity Index</i>	Full over time	1.0
	Partial over time	1.0
	Control over time	1.0
	Full vs Partial (2003)	0.08
	Full vs Control (2003)	0.42
	Partial vs Control (2003)	1.0
	Full vs Partial (2012)	< 0.001*
	Full vs Control (2012)	0.17
	Partial vs Control (2012)	0.08
<i>Pielou's Evenness</i>	Full over time	0.60
	Partial over time	1.0
	Control over time	1.0
	Full vs Partial (2003)	1.0
	Full vs Control (2003)	1.0
	Partial vs Control (2003)	1.0
	Full vs Partial (2012)	< 0.001*
	Full vs Control (2012)	1.0
	Partial vs Control (2012)	0.01*
<i>Biomass</i>	Full over time	1.0
	Partial over time	1.0
	Control over time	< 0.05*
	Full vs Partial (2003)	0.70
	Full vs Control (2003)	1.0
	Partial vs Control (2003)	1.0
	Full vs Partial (2012)	< 0.01*
	Full vs Control (2012)	< 0.001*
	Partial vs Control (2012)	1.0

5.4. Discussion

5.4.1. Herbivore exclusion effect on vegetation composition

A very similar herbaceous vegetation composition existed across the catenal sequence of the individual treatments both in 2003 and 2012. In the semi-arid Mopaneveld, catenal position plays an important role in the delineation of the woody vegetation community assemblage (Witkowski & O'Connor, 1996; Venter *et al.*, 2003; Smit *et al.*, 2013; Scholtz *et al.*, 2014; Stevens *et al.*, 2014), but there seems to be a low turnover in herbaceous species assemblages across the same catenal sequence (Venter *et al.*, 2003; Siebert *et al.*, 2010). The different vegetation zones present at different positions along the catenal sequence of the study area (Siebert *et al.*, 2010) were therefore not an influential factor for the delineation of the herbaceous vegetation composition. After nine years of exclusion, the species composition did not change significantly within any of the herbivore treatments and a very similar species composition also existed between the treatments when the individual years were analysed separately. Of all the treatments, the Partial enclosure was the only one that did appear to have a slightly different species composition in 2012 than in 2003, indicating a possible shift towards a different vegetation state. The vegetation composition of a semi-arid savanna is often described as being episodic (a specific herbaceous composition often persists, but it can shift to an alternate state in a short period of time as a result of environmental disturbances, including climatic events such as rainfall) (Westoby *et al.*, 1989; O'Connor 1998; Peel *et al.*, 2005; Lohmann *et al.*, 2012; Rutherford *et al.*, 2012; O'Connor, 2015). Whether this possible new state is only temporary in response to differences in disturbance intensities of herbivory (or other disturbances such as a possible lower preceding rainfall) is still unknown. The next repeated sampling of the herbaceous layer in 2017 is expected to reveal stronger herbivore exclusion effects on species composition. The similar vegetation composition could refer to the described higher vegetation homogeneity of this study area (Siebert *et al.*, 2010), when compared to moister semi-arid savannas with the same experimental design (Jacobs & Naiman, 2008; Siebert & Eckhart, 2008; Van Coller *et al.*, 2013), but no sound conclusions could be made regarding this.

5.4.2. Herbivore exclusion effect on species richness, diversity, evenness and biomass

No significant interaction effect (herbivory over time) could be detected after 9 years on species diversity and richness of the herbaceous vegetation, except for evenness and the biomass (which is not a measure of diversity but rather productivity). Because evenness can be seen as a measure of species dominance in a community over time (Kricher, 1972; Heip *et al.*, 1998), the significant difference in evenness in 2012 between the Partial treatment and the two extremes of the herbivory gradient (i.e. absence of herbivory in the Full treatment and continuous herbivore disturbance in the Control treatment), indicated that the Full and Control treatments began to

favour certain species. The herbivory treatment excluding only elephants and giraffes (Partial treatment) showed a significantly higher evenness than the other treatments in 2012, indicating much less dominance of herbaceous species. The lack of species dominance in the Partial enclosure in 2012, versus species possibly dominating the vegetation layer in the Full enclosure and Control treatment at the same time, were also strongly supported by the same significant differences between the Partial and the other two treatments in the results of Simpson diversity as well as a slightly different (more heterogeneous) species composition in the Partial treatment when all treatments were compared. Evenness remains a very strong measure to detect changes in especially homogeneous ecosystems as well as a good measure of ecosystem stability (Crowder *et al.*, 2010), as was proven in this study. Loss in evenness over time may infer long-term losses of ecosystem function, but as this was not the case in the study and the study only deals with two assessments separated by nine years, conclusions regarding stability in the herbaceous community cannot be made, even though it seems there had not been much change over time in ecosystem function in the complete absence of herbivores or continuous presence of herbivores.

Over nine years, the complete absence of herbivores (Full enclosure) seemed to favour only the production of standing biomass and not diversity and evenness. Biomass decreased over time in the absence of only elephants and giraffe, biomass significantly decreased over time in the continuous presence of herbivory and both the Partial and Control treatments differed significantly from the Full treatment in terms of biomass. Total herbivore exclusion in semi-arid Mopaneveld proved to be in line with what is usually observed in terms of biomass in other moister savanna areas where similar exclusion experiments were undertaken (at the Nkhulu enclosures, Jacobs & Naiman, 2008; Van Coller *et al.*, 2013). The semi-arid Mopaneveld, as in other studies of semi-arid herbaceous systems (Milchunas *et al.*, 1988; Adler *et al.*, 2004; Sasaki *et al.*, 2009), did also confirm the need for the presence of herbivores in semi-arid ecosystems to regulate biomass levels. If this is not done, undesirable vegetation changes and the dominance of some species can occur (Milchunas *et al.*, 1988; Adler *et al.*, 2004; Sasaki *et al.*, 2009), but this could not be detected in this study.

When considering the significant treatment effect present for all the measures of community structure, some significant differences between treatments at the onset of the experiment were no longer significant in 2012. These significant differences however became weaker over time, inferring that long-term changes took place in the herbaceous community, causing the differences to be weaker in 2012. It is suggested that herbaceous vegetation changes over time was caused by an underlying herbivore effect that might only surface later, but the specific experimental design of the study limits the ability to precisely identify the disturbances responsible for the changes that caused the loss of the initial significant differences. This limitation was primarily because of the experimental time period that was too short to make any sound conclusions regarding the exact vegetation changes that took place. It is expected that if the non-significant differences between

the treatments in 2012 (where the values of species richness, Margalef's richness and Shannon-Wiener diversity are now closer together than in 2003 where they differed significantly) are considered as a new starting point in experimental time, or even if more time (e.g. another 10 years) are allocated to the current experimental timeframe, more distinctive vegetation patterns will be visible and the changes in the herbaceous vegetation and the disturbances responsible will be quantified with less difficulty.

Significant differences between treatments in the 2012 data set only (i.e. no significant treatment effect in 2003) suggest that herbaceous vegetation changes did take place over time, and that nine years of herbivory exclusion already led to some observable patterns and changes of herbaceous vegetation. For instance, the total exclusion of herbivores and the exclusion of only elephants and giraffe showed significant differences in terms of evenness, Simpson diversity and biomass. More specifically where all herbivores were excluded, biomass was significantly higher than in the presence of all herbivores or select absence of herbivores. Other studies in savanna ecosystems that used herbivore exclosures to test their long-term effect on the herbaceous vegetation assemblage (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Young *et al.*, 2013; Koerner *et al.*, 2014; Kartzinel *et al.*, 2014; Van Coller & Siebert, 2015), all suggest or have been done over longer periods of time (10+ years). This was to ensure that slower herbaceous vegetation responses in reaction to herbivore disturbances can be detected (Fuhlendorf *et al.*, 2001; Turner *et al.*, 2003; Clarke *et al.*, 2005; Buitenwerf *et al.*, 2011). After the nine years of this study, more distinct changes in terms of herbaceous density, richness and diversity was expected (as in the longer studies where a higher diversity and richness at intermediate levels of herbivory was evident, or a lower richness and diversity was observed in areas with a high biomass production in the absence of all herbivores (Jacobs & Naiman 2008; Sasaki *et al.*, 2009; Angassa, 2012; Van Coller *et al.*, 2013; Hanke *et al.*, 2014)). Very little significant density, richness and diversity effects were observed however and a longer experimental time period could have been beneficial to possibly detect if this more homogeneous semi-arid system will also start to show more distinct patterns. The need for continued presence of herbivores to maintain higher levels of species richness and diversity in savanna ecosystems (Lucas *et al.*, 2004; Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Treydte *et al.*, 2013), could not be confirmed by the richness and diversity patterns of this study.

A possible reason for weak significant patterns over time could be that the herbaceous layer in semi-arid savannas responds differently over time to environmental disturbances such as herbivory, than in other (moister) savannas. These different responses are regularly described by several conceptual frameworks for semi-arid systems (e.g. The Intermediate Disturbance Hypothesis (Grime, 1973; Connell 1978; Jacobs & Naiman, 2008; Sasaki *et al.*, 2009; Angassa, 2012; Van Coller *et al.*, 2013; Hanke *et al.*, 2014), the Dynamic Equilibrium Model (Huston, 1979;

Kondoh, 2001; Briske *et al.*, 2003; Holdo *et al.*, 2013) or the evolutionary history of grazing in a specific area (Milchunas *et al.*, 1988; Du Toit, 2003; Jacobs & Naiman, 2008; Rutherford *et al.*, 2012) that could influence a response pattern). Except for the known long evolutionary history of grazing in the study site, none of these unique responses could be observed in the timeframe of this study. Therefore, another possible reason could be that inter-annual and inter-seasonal effects of disturbances (e.g. rainfall experienced prior to the sampling periods) that interact with herbivory, have a stronger impact in semi-arid savannas on herbaceous vegetation responses (O'Connor, 1994; Fuhlendorf *et al.*, 2001; Buitenwerf *et al.*, 2011) than other savanna systems. The sporadic variations in rainfall primarily causes short term changes in the directional patterns of vegetation originally established by herbivory (Fuhlendorf *et al.*, 2001; Peel *et al.*, 2005; Buitenwerf *et al.*, 2011), making it difficult to distinguish the exact vegetation response patterns related to a single disturbance only. Although rainfall variability has an important influence on herbaceous vegetation dynamics in semi-arid savanna ecosystems (Danckwerts & Stuart-Hill, 1988; O'Connor, 1991; O'Connor, 1994; O'Connor, 1998; Vetter, 2009; Swemmer *et al.*, 2007; Buitenwerf *et al.*, 2011), and could even modify the effects of long-term exclosure experiments on vegetation (Sasaki *et al.*, 2009), more significant rainfall data is required to correlate rainfall patterns with the patterns of species composition, richness, diversity and productivity observed in this study.

Despite the lack of clear patterns for some of the indices, a significant combined and treatment effect was highlighted by using diversity and richness indices as a measure to detect changes in the herbaceous vegetation patterns. Although species richness and diversity indices are often regarded as insufficient if it is not applied in conjunction with a measure of functional importance as well (Kennedy *et al.*, 2003; Mayfield *et al.*, 2010; Mori *et al.*, 2013; Hanke *et al.*, 2014), it still has value as an individual measure and abides as decent indicator of herbaceous vegetation community patterns that develop in response to different disturbances and simulated experimental conditions (Lande, 1996; Van Coller & Siebert, 2015).

5.5. Summary

Delineation of the herbaceous composition was not predetermined by catenal sequence and a very similar composition between all the herbivore treatments and over time was exhibited, which is a possible indication of the homogeneous vegetation assemblage the study area. Over a longer experimental period, possible shifts in the herbaceous composition could be expected (as shown by the slightly different composition in the absence of large herbivores). Hypothesis 1 are therefore not accepted. The significant effect of herbivore treatment over time for evenness and biomass indicated that in the total absence of herbivores, biomass will be significantly higher than in areas where only large herbivores are excluded or in the continued presence of herbivory. The high biomass production caused the possible dominance of some species. Herbivores are needed to regulate biomass, and the absence of large herbivores, promotes a more evenly distributed

herbaceous community over time. Despite evenness strength as measure to detect changes in homogeneous ecosystems, predictions regarding the possible (long-term) implications of herbivore exclusion treatments on the stability of the herbaceous community could not be made, since no dominance shifts in species could be observed when within-treatment variability over time was considered. A significant treatment effect was also observed (some significant differences between treatments were already present at the onset of the experiment, but disappeared over time, while others displayed no significant differences between treatments at the onset, but over time changed to differ significantly at the end of the experiment). These results highlighted a limitation in the experimental design of the study, specifically the heterogeneous vegetation units across the different herbivore treatments in which the experiment was laid out. Furthermore the experimental period was too short to make sound conclusions on what vegetation changes took place and what disturbances (other than a lagging herbivore effect) caused them. Rainfall variability may possibly be related to the observed or delayed patterns, but more descriptive rainfall data linked to more frequent sampling is required to confirm this. An even longer monitoring period than nine years is required to detect more distinct patterns in the herbaceous vegetation assemblage in response to herbivory. The herbaceous community assemblage of this semi-arid Mopaneveld savanna therefore responded only partially to different treatments of herbivore exclusion over a nine year period, because only some patterns (evenness and biomass) were visible after nine years in response to full or partial exclusion, but most patterns (composition, richness and diversity) were not. Hypothesis 2 could therefore only be partially accepted. This was because the composition of the herbaceous community did not change in accordance to the different herbivory exclusion treatments and exhibited a very similar composition across all treatments and although a significantly higher productivity could be detected in the absence of all herbivores, no further distinct changes in herbaceous richness or diversity in accordance to the different herbivore exclusion treatments could be observed. Hypothesis 3 was not confirmed as no significant differences within the respective herbivore treatments could be detected, although standing biomass decreased significantly in the presence of all herbivores.

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Chapter 6

Herbivory effects on composition and diversity of plant functional groups

6.1. Introduction

6.1.1. Advantages of Plant Functional Type approach to detect herbivory effects

The use of Plant Functional Types (PFT's) to quantify the effect of environmental disturbances on vegetation allows species to be grouped according to their response to disturbance (including climatic effects) and / or their effect on certain ecosystem properties and processes (Lavorel & Garnier 2002; Villéger *et al.*, 2008; Laliberte *et al.*, 2010). Although the relationship between environmental disturbances and PFT's is still emergent (Lavorel & Garnier 2002; Albert *et al.* 2009), the use of PFT's in semi-arid ecosystems remains advantageous (Díaz *et al.* 1997; Díaz *et al.* 2009; Laliberte *et al.* 2010) and can provide a framework to examine the functional response of these systems (Anderson & Hoffman, 2011). The use of functional measures such as the PFT approach can be more beneficial than species diversity indices to determine the relationship between environmental disturbance and the resulting vegetation response (Kennedy *et al.*, 2003; Devineau & Fournier, 2005; Poos *et al.*, 2009; Mori *et al.*, 2013; Lewis *et al.*, 2014; Hanke *et al.*, 2014) and also provides a means to identify and quantify disturbance effects in that ecosystem (Hanke *et al.*, 2014). Species diversity measures alone may not always be effective in representing shifts in the composition or structure of vegetation in an ecosystem caused by disturbances such as herbivory or other variable factors such as climate (Kennedy *et al.*, 2003; McGill *et al.*, 2006; Cadotte *et al.*, 2011; Hanke *et al.*, 2014). However, it can add value to the improved comprehension of an ecosystems response to disturbance when it is considered in combination with a functional (trait-based diversity measures) approach (Poos *et al.*, 2009; Mayfield *et al.*, 2010; Hanke *et al.*, 2014).

A combination of different species contributes to the functional response of the herbaceous vegetation community to disturbances (Cadotte *et al.*, 2011; Porensky *et al.*, 2013; Wesuls *et al.*, 2013). The herbaceous community owns a specific set of functional trait attributes adapted and diversified in such a manner that it can be used to classify the community into different functional groups that each reflect a specific plant survival strategy in response to the disturbances they are exposed to (Gaucherand & Lavorel, 2007; Moreno García *et al.*, 2014). These specific combinations of functional traits are also determined by the vegetation heterogeneity of an ecosystem in terms of configuration and composition, which serves as filter for what traits and functional groups will prevail in the herbaceous community (Duflot *et al.*, 2014). All species in the vegetation community and their trait attributes contribute to functional response of an ecosystem (Skarpe, 1996; Albert *et al.*, 2011; Jain *et al.*, 2014), even rare species. Rare species can influence

the overall functional response of the community, but their contribution is limited by their abundance, which is in turn determined by the environmental disturbances present in their environment (Skarpe, 1996; Albert *et al.*, 2011; Jain *et al.*, 2014).

Which trait attributes actually contribute to the identification of functional groups can only be determined when the specific disturbances and their temporal variability are known (Pérez-Camacho *et al.*, 2012). Herbivory is known as the primary disturbance of the semi-arid Mopaneveld savanna, which has a long evolutionary history of herbivory (Du Toit *et al.*, 2003; Jacobs & Naiman, 2008; Rutherford *et al.*, 2012). The Mopaneveld is also subjected to other variable disturbances (e.g. rainfall variability) that determine what species will be best adapted to the drier environment (Skarpe 1996; Volaire, 2008; Sasaki *et al.*, 2009; Pérez-Camacho *et al.*, 2012; Comas *et al.*, 2013; Hartnett *et al.*, 2013; Kotschy, 2013; Volaire *et al.*, 2014; O'Connor, 2015)), which will ultimately be the species subjected to herbivory and contributing to the identification of PFT's.

In savanna ecosystems, herbivores can be responsible for drastic changes in the herbaceous plant community in terms of composition and diversity, directly influencing which plant communities with specific functional traits in response to herbivory (Augustine & McNaughton, 1998; Moreno García *et al.*, 2014) will exist there. Plant trait attributes that develop over time include those which compensate for herbivore or herbivore related disruptions such as defoliation, trampling, variability in nutrient accumulation and growth rate (Díaz *et al.*, 2007; Moreno García *et al.*, 2014). These adaptations enable the classification of plant functional types, where species of a certain plant functional type share similar response traits in response to grazing disturbance (Gubsch *et al.*, 2011; Wesuls *et al.*, 2013; Linstädter *et al.*, 2014). The functional type classification needs to be specifically tailored to include a region's unique herbivory history, but more importantly its present herbivore disturbance patterns (Díaz *et al.*, 2007). PFT classifications can therefore be used as worthy indicators of the herbaceous vegetation response to herbivore exclusion treatments. This chapter considers broader functional types (i.e. major life form groups) and related advantages (as in Lavorel *et al.*, 1999; Landsberg *et al.*, 1999; McIntyre & Lavorel, 2001; Linstädter *et al.*, 2014)), but also attempted to analyse response patterns of plant functional types inside the major life form groups in response to herbivory.

6.1.2. Study objectives

The research presented in this chapter aims to test the effect of nine years of herbivory exclusion (selected exclusion and exclusion of all mammalian herbivores) on the herbaceous vegetation layer (graminoids and forbs) of the semi-arid Mopaneveld by focussing on the response patterns of broad plant functional groups and plant functional types inside the larger groups. Community attributes (i.e. abundances, relative abundances and richness) and diversity within different functional groups identified from vegetation data from two years (2003 and 2012) will be compared.

The research question:

How does the herbaceous composition in terms of community attributes (i.e. abundance, relative abundance and richness) and diversity of major life-form groups and classified plant functional types of a semi-arid Mopaneveld savanna respond to different treatments of herbivory exclusion?

It was hypothesized that:

1. The composition of the herbaceous major life-form groups and refined plant functional types (abundance, relative abundance and richness) will change in accordance to the different herbivore exclusion treatments with the perennial graminoids and perennial forbs having a significantly higher abundance and relative abundance, but significantly lower richness than the annual graminoids and annual forbs in the Full exclusion treatment (i.e. no herbivores) when compared to the Partial exclusion treatment (i.e. no elephant or giraffe) and the Control site (i.e. all herbivores included).
2. The diversity patterns of the herbaceous major life form groups and refined plant functional types will change in accordance to different herbivore exclusion treatments and show a significantly higher number of life-forms but significantly lower richness and diversity for all life-form groups in the Full exclusion treatment when compared to the Partial exclusion treatment and Control site.

6.2. Material and methods

The hierarchical approach followed was to:

- Firstly, consider the abundance, relative abundance and richness patterns of single life forms and the plant functional types within these life forms in response to herbivore exclusion treatments.
- Secondly, test the effect of time, treatment and the combined effect (time*treatment) on the response patterns of overall life-form diversity.

6.2.1. Response patterns of single life forms and PFT's

Major life-form groups

A primary sorting of graminoid and forb species, followed by a secondary categorization into either annuals (therophytic species) or perennials (hemicryptophytic and chamaephytic species) based on the Raunkiaer life-form classification (Raunkiaer, 1907), classified the herbaceous species of

the two sampling years into four representative major life-form groups: (1) Annual Graminoids, (2) Perennial Graminoids, (3) Annual Forbs and (4) Perennial Forbs. Differences in the abundance (N), relative abundance (n) and richness (S) of major life-form groups between treatments were analyzed by one-way ANOVA using STATISTICA (StatSoft, 2012). Relative abundances of a group was calculated as the number of species for a life-form group relative to all species per sampling unit (n). Treatment effects were analyzed for each sampling year and averaged over time. Before analysis, normality of the data was tested, and where non-normality was detected the data were fourth-root transformed to create normal distributions.

PFT's inside major life-form groups

Functional trait selection

To identify plant functional types inside the four major life-form groups, specific plant functional traits were selected from the literature that relate to adaptations of herbaceous vegetation in a semi-arid Mopaneveld savanna (to soil moisture variability and herbivory) and subsequently assigned the total species list. Trait data was binary and categorical (Table 6.1) (Appendix Table 1.1).

Table 6.1: Plant functional traits used in the study to define plant functional types.

<i>Trait</i>	<i>Attributes</i>	<i>Data Type</i>
<i>Life form</i>	Chamaephyte, Hemicryptophyte, Therophyte	Categorical
<i>Growth form</i>	Prostrate forb, Erect forb, Climber, Graminoid	Categorical
<i>Spinescence</i>	Spines present or absent	Binary
<i>Shade tolerance</i>	Canopy species, Indifferent species, Matrix species	Categorical
<i>Root system</i>	Taproot, Adventitious, Succulent roots, Stolons	Categorical
<i>Clonality</i>	Non-clonal, Aboveground clonality, Belowground clonality	Categorical
<i>Succulence</i>	Succulent adaptations present or absent	Binary
<i>Nitrogen fixing ability</i>	Ability Present or Absent	Binary
<i>Flowering Period</i>	Summer, Autumn, Winter, Spring	Binary
<i>Dispersal mode</i>	Zoochory, Anemochory, Autochory	Binary
<i>Height class</i>	Height class 1: <10cm ; Height class 2: 10 - 30 cm ; Height class 3: >30cm	Categorical

Identifying plant functional types

Within each major life form group, plant functional types were identified by means of cluster analysis (using binary and categorical data in a *species x plant functional trait* input matrix) in *PRIMER* 6 (2012) using the Modified Gower dissimilarity resemblance (Gower, 1967). An indirect gradient analysis in the form of a Principal Components Analysis (PCA) in *PAST* (Hammer *et al.*, 2001) was done (using binary and categorical data in a *species x plant functional trait* input matrix) to check whether plant functional groupings derived from cluster analysis were similar to those of the PCA and to use the loadings of the respective traits on the principal components (all axes (principal components) explaining >10% variation were included) to identify traits which serve the most to distinguish the different plant functional groups (cluster of species in ordination space) (Leyer & Wesche, 2008). The cluster analysis and PCA were done only after rare species (species occurring in less than 10% of all the plots in the experimental area (Diaz & Cabido, 1997; Peco *et al.*, 2005)) and rare traits (traits that has been identified by the PCA as having a trait loading lower than 0.3 or larger than -0.3 (Leyer & Wesche, 2008)) were omitted from the covariance data matrix.

During this analysis step, several difficulties arose:

- Overall, at the outset of the experiment, it proved very difficult to successfully assign identified and meaningful soft plant functional traits (identified from a variety of literature sources instead of field measurements) to the combined species list of the two sampling years. For example, traits such as shade tolerance, root system, nitrogen-fixing ability, flowering period and dispersal mode was difficult to assign based solely on literature sources. Of the initially identified 11 traits, only the life-form trait could be used for further analysis.
- After omitting rare species and traits of minor relevance, resulting plant functional types were represented by too few species (e.g. only one species to Group 1, 2, 8 and 11), particularly within the major life-form groups Annual Graminoids, Annual Forbs and Perennial Forbs (compare Appendix 2). This hampered a sound and interpretable analysis of response patterns on PFT level.

Due to these limitations, in the following only some aspects of the results of the PCA trait loadings of the most influential plant functional traits and the cluster analysis are reported on and discussed. For detailed results and information regarding this analysis step refer to Appendix 2.

6.2.2. Effect of time, treatment and combined effect on plant functional level

To test for the effects of sampling year (time), herbivore exclusion treatment and the combined effect (time*treatment) on the overall life-form richness and diversity a Repeated Measures ANOVA (Type III decomposition) in *STATISTICA* (StatSoft, 2012) was applied. The type III

decomposition was chosen since it is commonly applied to orthogonal data as those of the study (StatSoft, 2012). The indices used included species richness, Margalef's species richness, Shannon-Wiener diversity index, Simpson's diversity index and Pielou's evenness (all indices were based on the presence and relative abundance of the 4 major life-forms per plot). Herbivory treatment was used as the between-subject factor and sampling year as the within-subject factor. Where statistically significant results were obtained, the Bonferroni *post-hoc* significance test (Lindgren & Sullivan, 2001) was used for pairwise comparisons. Before analysis, normality of the data was tested, and where not normally distributed, the data were fourth-root transformed to down-weight the influence of dominating life-forms.

6.3. Results

6.3.1. *Changes in composition (i.e. abundance, relative abundance, and richness) of life-form groups*

The average abundance, average relative abundance and average richness of the major life-form groups indicated an overall dominance of perennial life forms (graminoids and forbs), which were represented by much higher values than the annual life forms, in both 2003 and 2012 (Table 6.2). The Perennial Graminoids was the single major life-form group that had the highest abundance, relative abundance and richness in all treatments when considering the values of both sampling years. Only in the Partial treatment in 2012, the richness of Perennial Forbs was higher than Perennial Graminoids. On the contrary, the Annual Graminoids was the single major life form that had the overall lowest average abundance, average relative abundance and average richness in all treatments when considering both sampling years. The Annual Graminoids showed no significant differences between any of the community attributes in the Full treatment, but a significantly higher abundance in the Partial treatment and significantly higher abundance and richness in the Control treatment in 2012 than in 2003 (Table 6.3, Figure 6.1-6.3). The Perennial Graminoids exhibited a significantly higher abundance, but significantly lower richness in the Full and Partial treatments in 2012 than in 2003. However, no significant differences between abundance, relative abundance or richness were observed in the Control treatment. The Annual Forbs displayed a significantly higher abundance in all three treatments in 2012 than in 2003, but a significantly higher proportional abundance in only the Partial treatment. The Control treatment exhibited a significantly lower richness in 2012 than in 2003. The Perennial Forbs in the Full treatment had a significantly higher proportional abundance and richness in 2012 than in 2003. A significantly higher abundance and proportional abundance in the Partial treatment in 2012 than in 2003 was also revealed, while the Control treatment showed a significantly lower abundance in 2012 than in 2003.

Table 6.2: The average abundance (mean number of individuals per life form group per plot), average relative abundance (proportional abundance) and average richness (number of species in each life form) of the major life form groups of the herbaceous Mopaneveld vegetation per treatment and sampling year.

<i>Treatment</i>	<i>Year</i>	<i>Life form</i>	<i>Abundance ± Standard Deviation</i>	<i>Relative Abundance ± Standard Deviation</i>	<i>Richness ± Standard Deviation</i>
<i>Full</i>	2003	Annual Graminoids	0.57±8.55	0.03±0.34	0.19±0.89
		Perennial Graminoids	21.19±8.55	0.84±0.34	2.60±0.89
		Annual Forbs	0.94±8.55	0.05±0.34	0.81±0.89
		Perennial Forbs	3.26±8.55	0.08±0.34	0.96±0.89
	2012	Annual Graminoids	0.57±10.72	0.02±0.29	0.23±0.76
		Perennial Graminoids	26.87±10.72	0.73±0.29	2.15±0.76
		Annual Forbs	2.42±10.72	0.08±0.29	1.11±0.76
		Perennial Forbs	3.75±10.72	0.14±0.29	1.96±0.76
<i>Partial</i>	2003	Annual Graminoids	0.56±4.91	0.04±0.28	0.31±0.90
		Perennial Graminoids	12.6±4.91	0.74±0.28	2.84±0.90
		Annual Forbs	1.64±4.91	0.11±0.28	1.42±0.90
		Perennial Forbs	1.71±4.91	0.11±0.28	1.47±0.90
	2012	Annual Graminoids	1.04±4.77	0.04±0.16	0.36±0.89
		Perennial Graminoids	13.76±4.77	0.46±0.16	2.11±0.89
		Annual Forbs	3.62±4.77	0.18±0.16	1.64±0.89
		Perennial Forbs	5.13±4.77	0.31±0.16	2.78±0.89
<i>Control</i>	2003	Annual Graminoids	0.91±10.46	0.05±0.30	0.28±1.27
		Perennial Graminoids	26.69±10.46	0.76±0.30	3.81±1.27
		Annual Forbs	1.74±10.46	0.07±0.30	1.52±1.27
		Perennial Forbs	6.43±10.46	0.13±0.30	1.70±1.27
	2012	Annual Graminoids	2.39±13.02	0.06±0.28	0.59±1.14
		Perennial Graminoids	33.17±13.02	0.73±0.28	3.57±1.14
		Annual Forbs	2.48±13.02	0.07±0.28	1.22±1.14
		Perennial Forbs	4.61±13.02	0.14±0.28	2.33±1.14

Table 6.3: The One-Way ANOVA of the average abundance, average relative abundance and average richness of the major life-form groups across different herbivory treatments over time.

<i>Life-Form Group</i>	<i>Response</i>	<i>Treatment</i>	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Annual Graminoids	<i>Average Abundance</i>	<i>Full</i>	1	0.000069	0.000069	0.13930	0.71
		<i>s.e.</i>	104	0.051414	0.000494		
		<i>Partial</i>	1	0.003889	0.003889	4.43842	< 0.05*
		<i>s.e.</i>	88	0.077104	0.000876		
		<i>Control</i>	1	0.025362	0.025362	11.31111	< 0.01*
		<i>s.e.</i>	106	0.237671	0.002242		
	<i>Average Relative Abundance</i>	<i>Full</i>	1	0.000002	0.000002	0.997670	0.32
		<i>s.e.</i>	104	0.000172	0.000002		
		<i>Partial</i>	1	0.000000	0.000000	0.053733	0.82
		<i>s.e.</i>	88	0.000196	0.000002		
		<i>Control</i>	1	0.000001	0.000001	0.220603	0.64
		<i>s.e.</i>	106	0.000404	0.000004		
	<i>Average Richness</i>	<i>Full</i>	1	0.000008	0.000008	0.26075	0.61
		<i>s.e.</i>	104	0.003365	0.000032		
		<i>Partial</i>	1	0.000004	0.000004	0.07386	0.79
		<i>s.e.</i>	88	0.004184	0.000048		
		<i>Control</i>	1	0.000512	0.000512	17.03065	< 0.001*
		<i>s.e.</i>	106	0.003190	0.000030		
Perennial Graminoids	<i>Average Abundance</i>	<i>Full</i>	1	0.282963	0.282963	8.648048	< 0.01*
		<i>s.e.</i>	104	3.402863	0.032720		
		<i>Partial</i>	1	0.606578	0.606578	7.756840	< 0.001*
		<i>s.e.</i>	88	6.881523	0.078199		
		<i>Control</i>	1	0.125092	0.125092	1.709683	0.19
		<i>s.e.</i>	106	7.755664	0.073167		
	<i>Average Relative Abundance</i>	<i>Full</i>	1	0.000057	0.000057	7.578551	< 0.01*
		<i>s.e.</i>	104	0.000783	0.000008		
		<i>Partial</i>	1	0.000044	0.000044	6.679230	< 0.05*
		<i>s.e.</i>	88	0.000586	0.000007		
		<i>Control</i>	1	0.000001	0.000001	0.083899	0.77
		<i>s.e.</i>	106	0.000737	0.000007		
	<i>Average Richness</i>	<i>Full</i>	1	0.001934	0.001934	5.46171	< 0.05*
		<i>s.e.</i>	104	0.036836	0.000354		
		<i>Partial</i>	1	0.005975	0.005975	10.40295	< 0.01*
		<i>s.e.</i>	88	0.050546	0.000574		
		<i>Control</i>	1	0.000537	0.000537	0.77745	0.38
		<i>s.e.</i>	106	0.073166	0.000690		
Annual Forbs	<i>Average Abundance</i>	<i>Full</i>	1	0.023252	0.023252	19.02788	< 0.001*
		<i>s.e.</i>	104	0.127090	0.001222		
		<i>Partial</i>	1	0.050896	0.050896	30.39879	< 0.001*
		<i>s.e.</i>	88	0.147337	0.001674		
		<i>Control</i>	1	0.006044	0.006044	7.42774	< 0.01*
		<i>s.e.</i>	106	0.086258	0.000814		
	<i>Average Relative Abundance</i>	<i>Full</i>	1	0.000007	0.000007	3.14315	0.08
		<i>s.e.</i>	104	0.000218	0.000002		
		<i>Partial</i>	1	0.000043	0.000043	11.81173	< 0.001*
		<i>s.e.</i>	88	0.000317	0.000004		

		<i>Control</i>	1	0.000000	0.000000	0.38750	0.53
		<i>s.e.</i>	106	0.000092	0.000001		
	<i>Average Richness</i>	<i>Full</i>	1	0.000043	0.000043	0.354133	0.55
		<i>s.e.</i>	104	0.012676	0.000122		
		<i>Partial</i>	1	0.000962	0.000962	3.935127	0.06
		<i>s.e.</i>	88	0.021524	0.000245		
		<i>Control</i>	1	0.000828	0.000828	4.572967	< 0.05*
		<i>s.e.</i>	106	0.019193	0.000181		
<i>Perennial Forbs</i>	<i>Average Abundance</i>	<i>Full</i>	1	0.005797	0.005797	0.12876	0.72
		<i>s.e.</i>	104	4.682614	0.045025		
		<i>Partial</i>	1	0.025272	0.025272	20.54812	< 0.001*
		<i>s.e.</i>	88	0.108232	0.001230		
		<i>Control</i>	1	0.224987	0.224987	4.65878	< 0.05*
		<i>s.e.</i>	106	5.119061	0.048293		
	<i>Average Relative Abundance</i>	<i>Full</i>	1	0.000035	0.000035	7.16350	< 0.01*
		<i>s.e.</i>	104	0.000514	0.000005		
		<i>Partial</i>	1	0.000117	0.000117	31.54811	< 0.001*
		<i>s.e.</i>	88	0.000326	0.000004		
		<i>Control</i>	1	0.000000	0.000000	0.00123	1.0
		<i>s.e.</i>	106	0.000556	0.000005		
	<i>Average Richness</i>	<i>Full</i>	1	0.002231	0.002231	6.359126	< 0.05*
		<i>s.e.</i>	104	0.036486	0.000351		
		<i>Partial</i>	1	0.000761	0.000761	2.793951	0.10
		<i>s.e.</i>	88	0.023973	0.000272		
		<i>Control</i>	1	0.000011	0.000011	0.038229	0.85
		<i>s.e.</i>	106	0.030194	0.000285		

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 $p < 0.05$.

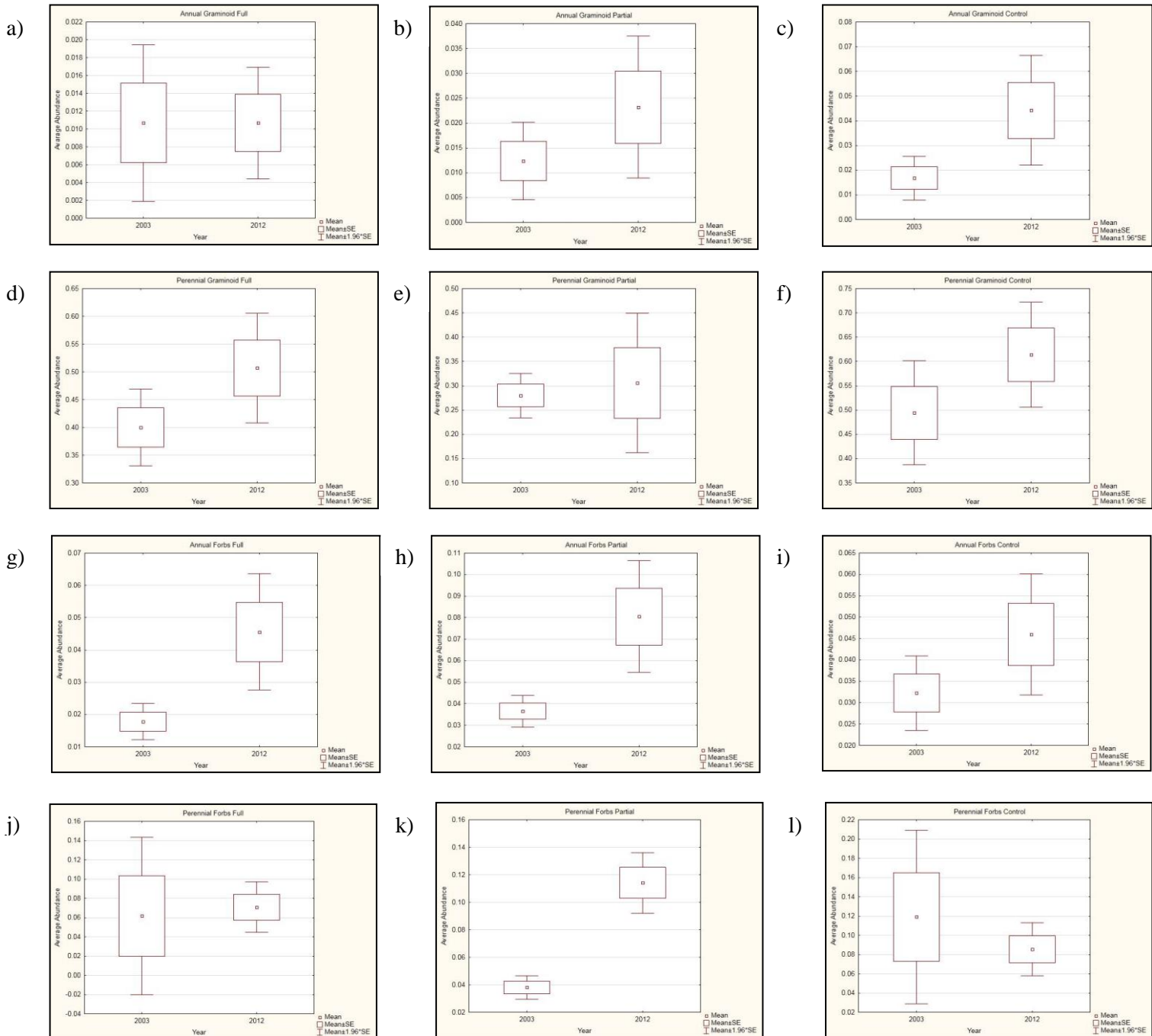


Figure 6.1: One-Way ANOVA of the average abundance (N) of major life forms across different herbivory treatments over time of the a) annual graminoids in the Full, b) annual graminoids in the Partial, c) annual graminoids in the Control, d) perennial graminoids in the Full, e) perennial graminoids in the Partial, f) perennial graminoids in the Control, g) annual forbs in the Full, h) annual forbs in the Partial, i) annual forbs in the Control, j) perennial forbs in the Full, k) perennial forbs in the Partial, l) perennial forbs in the Control.

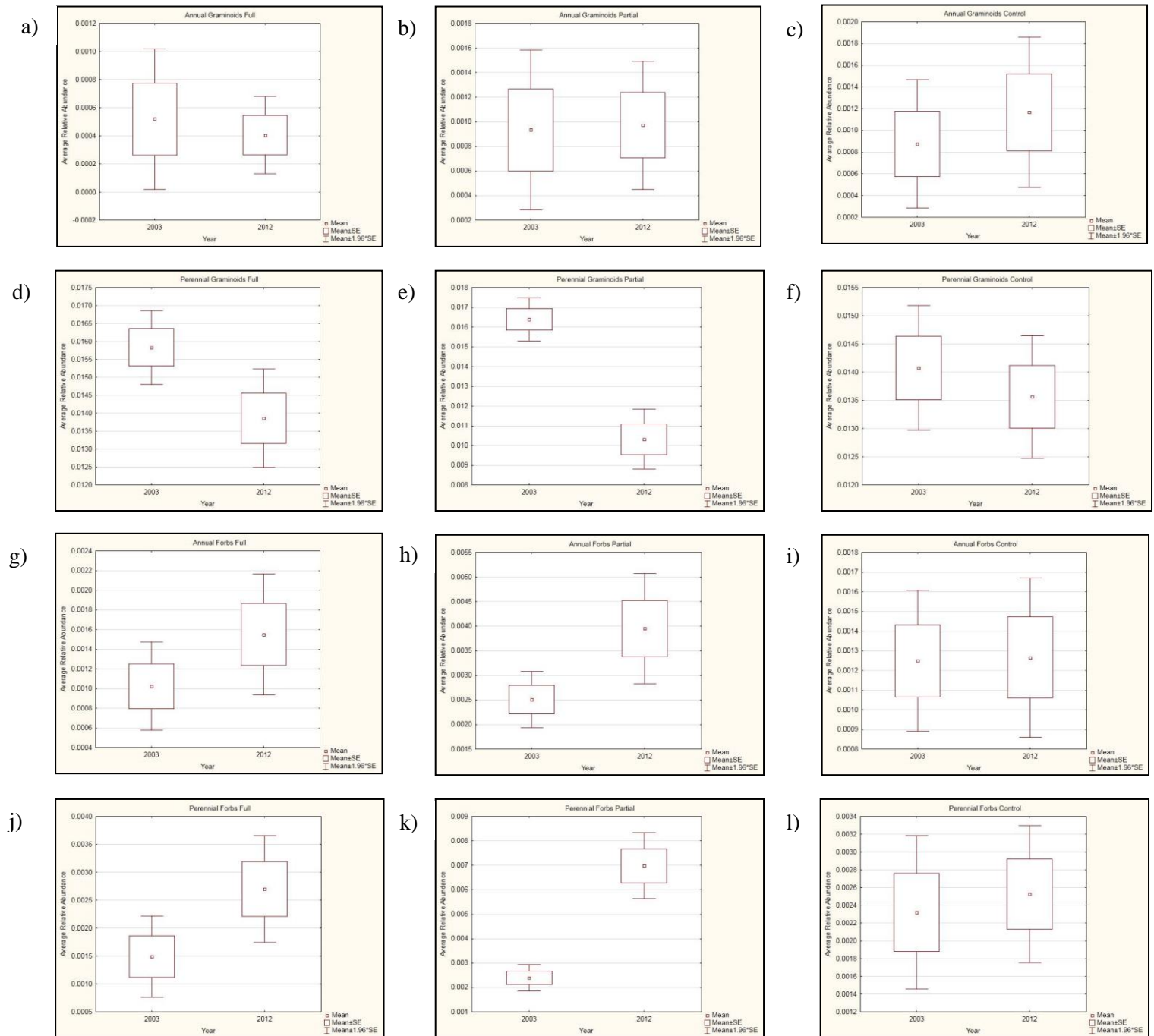


Figure 6.2: One-Way ANOVA of the average relative abundance (n) of major life forms across different herbivory treatments over time of the a) annual graminoids in the Full, b) annual graminoids in the Partial, c) annual graminoids in the Control, d) perennial graminoids in the Full, e) perennial graminoids in the Partial, f) perennial graminoids in the Control, g) annual forbs in the Full, h) annual forbs in the Partial, i) annual forbs in the Control, j) perennial forbs in the Full, k) perennial forbs in the Partial, l) perennial forbs in the Control.

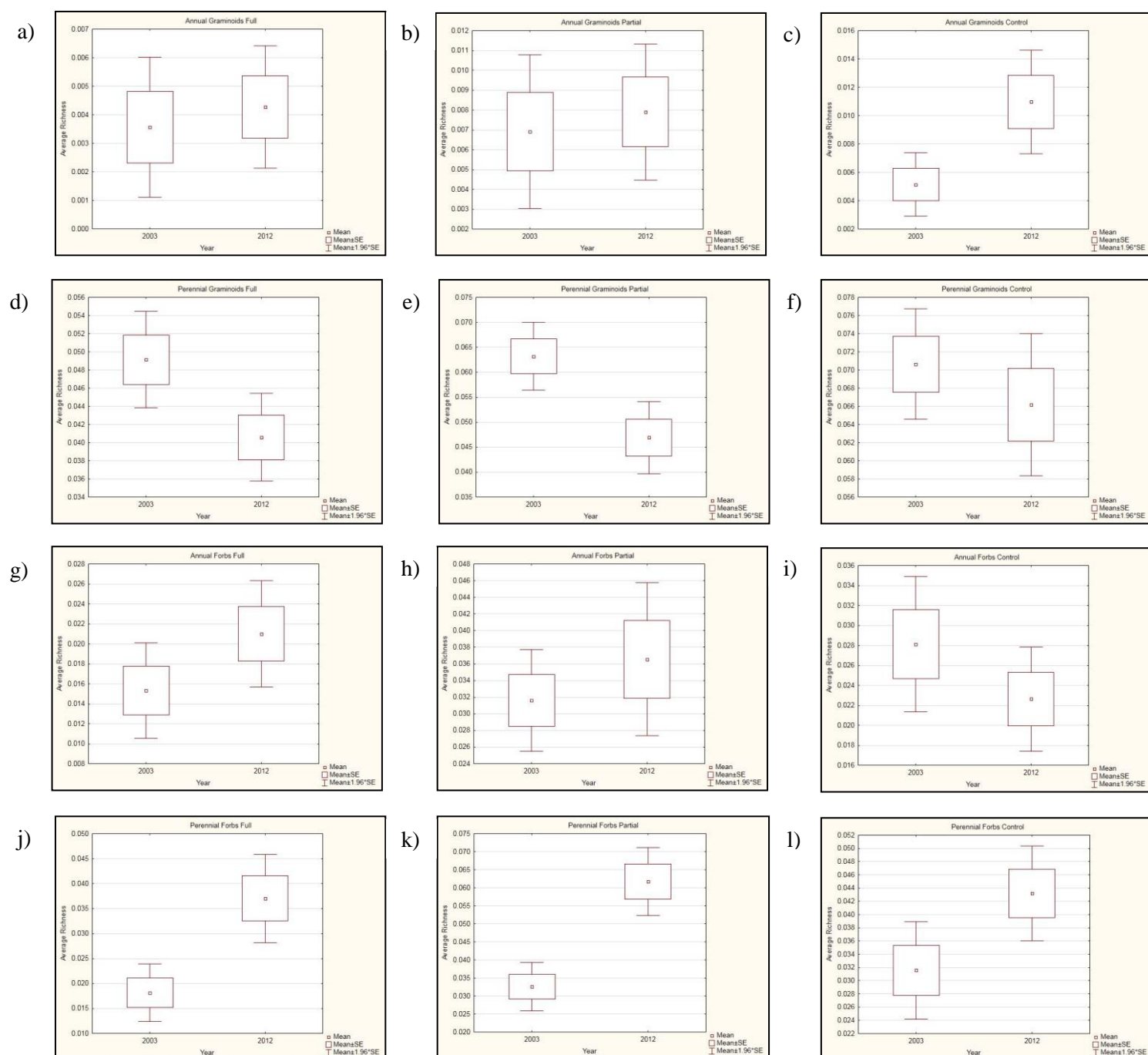


Figure 6.3: One-Way ANOVA of the average richness (S) of major life forms across different herbivory treatments over time of the a) annual graminoids in the Full, b) annual graminoids in the Partial, c) annual graminoids in the Control, d) perennial graminoids in the Full, e) perennial graminoids in the Partial, f) perennial graminoids in the Control, g) annual forbs in the Full, h) annual forbs in the Partial, i) annual forbs in the Control, j) perennial forbs in the Full, k) perennial forbs in the Partial, l) perennial forbs in the Control.

6.3.2. Changes in diversity of life-form groups

The results of the repeated measures ANOVA (Table 6.4) revealed no significant combined effect (time*treatment) for any of the diversity indices, inferring that the observable diversity patterns could have been present at the onset of the experiment. All the diversity indices revealed a significant treatment effect (Table 6.4). The time effect was also significant for all variables, except for Margalef species richness (Table 6.4).

The significant treatment effect present for all the indices indicates that the responses of individual treatments varied independently and that the variation observed in 2012, could have been present at the onset of the experiment in 2003. The post-hoc comparisons (Table 6.5) confirm that when significant effects between two treatments were present in 2012, the same significant differences already existed in 2003 (i.e. Margalef species richness, Shannon-Wiener diversity, Simpson diversity and Pielou's evenness in Full vs Partial). The post-hoc comparisons of the treatment effect did, however, also reveal that some significant differences between treatments were present in 2003, but not anymore in 2012 (i.e. number of life-forms in Full enclosure vs Partial enclosure and Full enclosure vs Control treatment), whereas some significant differences between treatments were present in 2012, but not in 2003 (i.e. Margalef species richness, Shannon-Wiener diversity, Simpson diversity and Pielou's evenness in Partial enclosure vs Control treatment).

The significant time effect present for all indices except Margalef species richness, indicates that independently of treatment, significant changes (presumably in relative abundance) of the major life-forms took place over time. Post-hoc comparisons (Table 6.5) however identified significant increases over time for two diversity indices, both Shannon-Wiener and Simpson diversity in the Partial treatment (Figure 6.4 (c), (d)).

Table 6.4: Effects of sampling year and herbivory on plant life-form abundance and alpha diversity (repeated measures ANOVA; significant effects indicated by *).

<i>Response</i>	<i>Symbol</i>	<i>Source</i>	<i>Df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<i>Number of Life forms</i>	S	Time	1	4.281	4.281	6.604	< 0.05*
		Treatment	2	20.689	10.344	13.833	< 0.001*
		Time*Treatment	2	1.030	0.515	0.688	0.50
		s.e.	176	131.615	0.748		
<i>Margalefs Richness</i>	d	Time	1	0.22650	0.22650	3.036	0.08
		Treatment	2	3.64671	1.82335	21.290	< 0.001*
		Time*Treatment	2	0.11117	0.05558	0.649	0.52
		s.e.	174	14.90190	0.08564		
<i>Shannon-Wiener Diversity Index</i>	H'	Time	1	1.69986	1.69986	19.385	< 0.001*
		Treatment	2	5.93346	2.96673	26.728	< 0.001*
		Time*Treatment	2	0.16753	0.08377	0.755	0.47
		s.e.	176	19.53550	0.11100		
<i>Simpson's Diversity Index</i>	1-Lambda	Time	1	0.78216	0.78216	20.8241	< 0.001*
		Treatment	2	2.50190	1.25095	28.7076	< 0.001*
		Time*Treatment	2	0.07015	0.03508	0.8050	0.45
		s.e.	174	7.58216	0.04358		
<i>Pielou's Evenness</i>	J'	Time	1	0.49126	0.49126	11.331	< 0.01*
		Treatment	2	1.43840	0.71920	13.861	< 0.001*
		Time*Treatment	2	0.04165	0.02083	0.401	0.67
		s.e.	132	6.84918	0.05189		

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 $p < 0.05$.

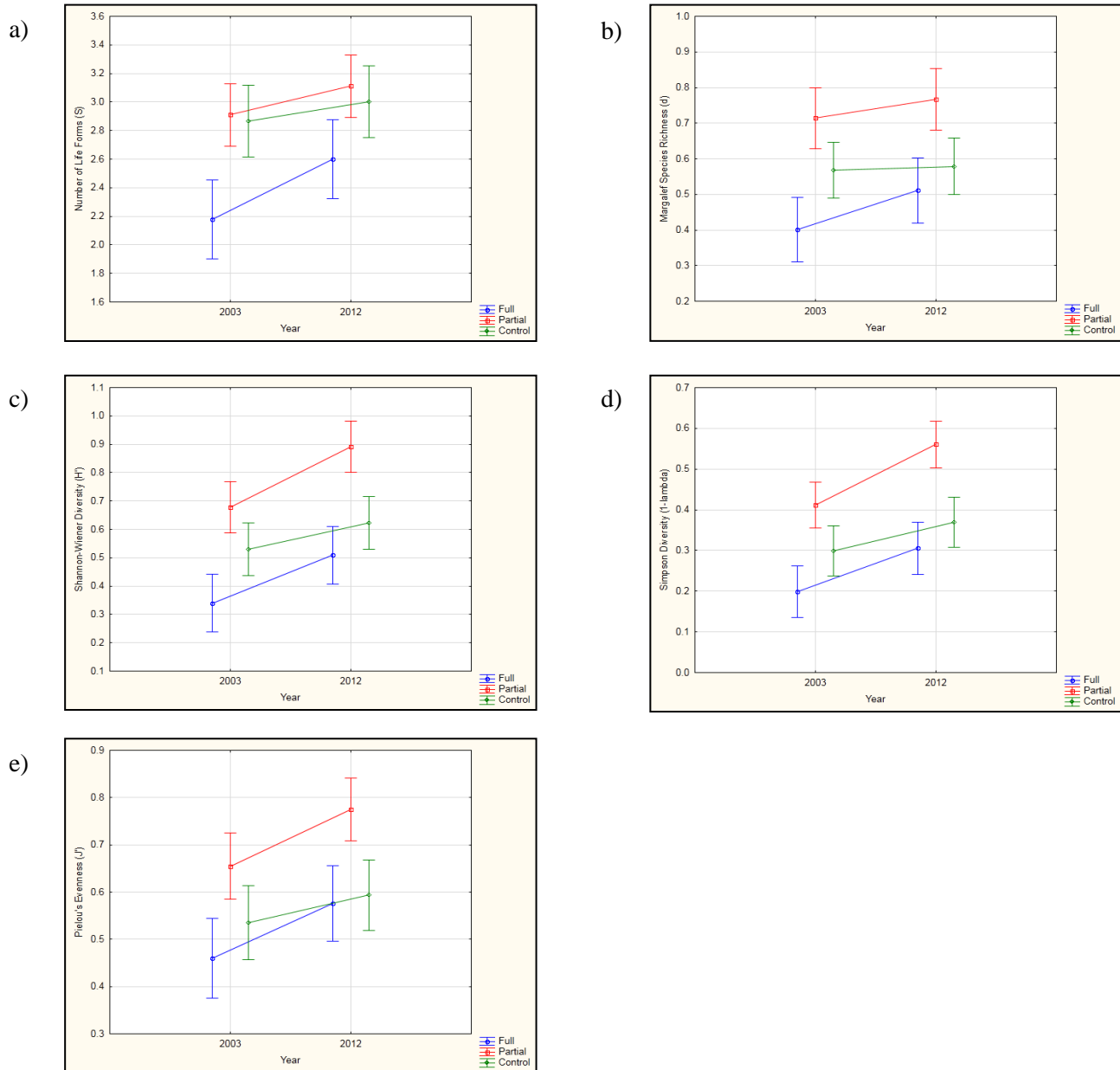


Figure 6.4: Summary plots indicating the effects of sampling year (time), herbivory and time and herbivory combined on the major life-form groups of the herbaceous layer in terms of a) Number of Life-Forms, b) Margalef Species Richness, c) Shannon-Wiener diversity, d) Simpson Diversity and e) Pielou's evenness. Vertical bars denote 0.95 confidence intervals with standard error.

Table 6.5: Treatment effects on major life-form components of the herbaceous Mopaneveld vegetation per sampling year and averaged over sampling years. ANOVA with Bonferroni corrected post hoc test (* indicate significant p-values).

<i>Response</i>	<i>Treatments</i>	<i>p</i>
<i>Number of Life forms</i>	Full over time	0.28
	Partial over time	1.0
	Control over time	1.0
	Full vs Partial (2003)	< 0.01*
	Full vs Control (2003)	< 0.01*
	Partial vs Control (2003)	1.0
	Full vs Partial (2012)	0.08
	Full vs Control (2012)	0.44
	Partial vs Control (2012)	1.0
<i>Margalef's Species Richness</i>	Full over time	1.0
	Partial over time	1.0
	Control over time	1.0
	Full vs Partial (2003)	< 0.001*
	Full vs Control (2003)	0.11
	Partial vs Control (2003)	0.29
	Full vs Partial (2012)	< 0.001*
	Full vs Control (2012)	1.0
	Partial vs Control (2012)	< 0.05*
<i>Shannon-Wiener Diversity Index</i>	Full over time	0.19
	Partial over time	< 0.05*
	Control over time	1.0

	Full vs Partial (2003)	< 0.001*
	Full vs Control (2003)	0.11
	Partial vs Control (2003)	0.51
	Full vs Partial (2012)	< 0.001*
	Full vs Control (2012)	1.0
	Partial vs Control (2012)	< 0.01*
<i>Simpson's Diversity Index</i>	Full over time	0.23
	Partial over time	< 0.01*
	Control over time	1.0
	Full vs Partial (2003)	< 0.001*
	Full vs Control (2003)	0.36
	Partial vs Control (2003)	0.18
	Full vs Partial (2012)	< 0.001*
	Full vs Control (2012)	1.0
	Partial vs Control (2012)	< 0.001*
<i>Pielou's Evenness</i>	Full over time	0.47
	Partial over time	0.40
	Control over time	1.0
	Full vs Partial (2003)	< 0.05*
	Full vs Control (2003)	1.0
	Partial vs Control (2003)	0.56
	Full vs Partial (2012)	< 0.01*
	Full vs Control (2012)	1.0
	Partial vs Control (2012)	< 0.05*

6.4. Discussion

6.4.1. *Herbivore exclusion effect on life-form composition*

The observable major life-form community attribute patterns indicated a dominant presence of perennial life forms, possibly indicating the presence of a continued disturbance in the semi-arid Mopaneveld savanna. Perennial species (especially perennial graminoids) have been known to dominate overall in continuously disturbed semi-arid savannas (Walker *et al.*, 1981; O'Connor, 1991; O'Connor, 1998; Fuhlendorf *et al.*, 2001; Clarke *et al.*, 2005; Yurkonis *et al.*, 2012; Porensky *et al.*, 2013; Ruppert *et al.*, 2015). The recruitment and establishment of primarily perennials in these ecosystems is usually not only driven exclusively by herbivory disturbances, but also by a variety of other disturbances that open up the space in the vegetation layer for quick establishing perennials (Zimmermann *et al.*, 2008; Yurkonis *et al.*, 2012). The annual major life-form groups (Annual Graminoids and Annual Forbs) had on average very low abundances, proportional abundances and richness values in the different herbivory treatments over time, but persisted to show visible response patterns over the nine year experimental period. A possible reason for this is that in semi-arid and arid ecosystems, annual life-forms and species are able to survive as seeds in the soil seed bank and require favorable environmental conditions before emerging in the above-ground vegetation layer (Grime, 1977; O'Connor, 1998; Aboling *et al.*, 2008; Dreber & Esler, 2011; Dreber *et al.*, 2011). These results suggest that very little favourable environmental conditions existed over the nine year experimental period (also suggestive of the continued presence of a significant disturbance), keeping the species contributing to the composition of annual life-forms reduced over time to only a few. The observable patterns were however only at plot level and further analysis of the species richness at a larger scale may have revealed different patterns not to ones witnessed.

Rainfall variability before or even during the experimental period could be the possible continued disturbance responsible for the dominance in perennials and lack of annuals. Similar composition patterns are usually more likely to occur when rainfall patterns vary and distinct drought periods are experienced in semi-arid savannas (especially resulting in a lack of annual species- and life-forms during drought periods) (O'Connor, 1998; Clarke *et al.*, 2005; Pérez-Camacho *et al.*, 2012; Ruppert *et al.*, 2015). The rainfall experienced before sampling periods (Figure 3.2 and 3.3) are insufficient to determine the exact contribution of rainfall variability and drought in the study area. However, nine years of herbivore exclusion treatments revealed that herbivory or the selected absence thereof, led to observable compositional response patterns in some major life-forms. In semi-arid savannas, a long history of herbivory (as in this study) can sometimes have an even greater influence on vegetation response patterns than rainfall variability (Hillerislambers *et al.*, 2001; Ruppert *et al.*, 2015).

Since Perennial Graminoids were the most abundant life-form group in all the different treatments in both sampling years, it can be assumed to be the best indication of how the herbaceous

composition responds to the effect of herbivore exclusion on a broader functional level. The complete exclusion of herbivores over time favoured the abundance of the life-form group, but a significantly lower richness were experienced possibly because of the accumulation of biomass and dominance of only a few species, as is usually the case in savanna ecosystems in the complete absence of herbivores (Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Mureithi *et al.*, 2014). The absence of only elephants and giraffes proved to cause a similar life-form response in the herbaceous community, indicating that the presence of smaller mammalian herbivores were not effective enough to regulate biomass levels and that large herbivores (e.g. elephant and giraffe) are needed to reduce biomass and promote a higher proportional abundance and richness of species that make up the life-form group. The rest of the compositional response patterns (some even showing significant differences over time), were not truly reflective of the effect of herbivore exclusion. This was possibly because a vegetation composition containing more annual herbaceous species would have a higher probability of displaying a clearer pattern formation in response to herbivory than a vegetation composition containing more perennial herbaceous species (Hillerislambers *et al.*, 2001). In this study, very few annual species occurred on average in the two sampling years, and the herbaceous layer (and major life-form groups) contained mostly perennial species, making the formation of clear patterns difficult. The results also highlight the need for a longer experimental period than only nine years to be able to define clearer major life-form compositional response patterns.

6.4.2. Herbivore exclusion effect on overall life-form diversity

The significant treatment effect observed for the number of life forms exhibited a pattern where significant differences were visible only at the onset of the experiment when the Partial and Control treatments were compared to the Full treatment. The number of major life-forms were already significantly different, even before herbivores exclusion started, suggesting that a combination of disturbances known to influence the semi-arid Mopaneveld herbaceous layer (history of herbivory, moisture and nutrient variability and fire (Danckwerts & Stuart Hill, 1988; O'Connor 1995; Illius & O'Connor, 1999; O'Connor, 1998; Hillerislambers *et al.*, 2001; Augustine & McNaughton, 2006; Smith *et al.*, 2012; Fynn & Connor 2013; Gibbes *et al.*, 2014)) possibly established these patterns, over time significant changes took place and at the end of the experiment, each treatment had a number of life-forms that were not significantly distinguishable from the others. A too short experimental period prevents the conclusion that selective herbivore presence or absence alone was responsible for these changes. It is likely that if 2012 is considered as a new starting point in experimental time, or if more time (e.g. another 10 years) are allocated to the current experimental timeframe, the effect of herbivore exclusion on the number of life-forms can be detected.

The significant treatment effect for all the other diversity indices was reflected by significant differences in 2003 that were still significantly different between the same treatments in 2012 (Full enclosure vs Partial enclosure), but also by non-significant differences between treatments at the start of the experiment, that changed over the nine year exclusion period to differ significantly in 2012 between the Partial and Control treatments (Margalef species richness, Shannon-Wiener diversity, Simpson diversity and Pielou's evenness). It can be assumed that the absence of elephants and giraffes caused a higher major life-form richness, diversity and more even distribution than where all herbivores were present in the semi-arid Mopaneveld. This is in accordance to what is known for semi-arid systems, where selective herbivore pressure increased the competitiveness of all species belonging to the different major life-form groups and prevents some life forms to dominate under specific conditions (Lavorel *et al.*, 1997; Jacobs & Naiman 2008; Sasaki *et al.*, 2009; Angassa, 2012). The significantly lower life-form evenness in the presence of all herbivores suggests that a certain life form (possibly the Perennial Graminoids) started to dominate in this treatment and large herbivores such as elephants and giraffes needs to be excluded to possibly decrease the dominance of some major life-form groups and increase the competitiveness of less important major life-form groups (Lavorel *et al.*, 1999; Landsberg *et al.*, 1999; McIntyre & Lavorel, 2001; Linstädter *et al.*, 2014).

The significant time effect confirms that changes took place over time that altered number and diversity of life forms (either significant differences become non-significant or vice versa). The exact nature of the changes and the disturbances responsible for them, cannot be identified with certainty, which is usually the case in arid and semi-arid ecosystems, where it remains difficult to determine which environmental disturbances are specifically responsible for the formation of vegetation response patterns, even on a functional level (Hillerislambers *et al.*, 2001; McIntyre *et al.*, 1999; Wesuls *et al.*, 2013). However, the time effect did show that the absence of elephants and giraffe was directly responsible for a significant increase in the major life-form diversity (indicated for both Shannon-Wiener and Simpson diversity). The results at the study site showed that regulated herbivory pressure is required to enhance overall herbaceous species and life-form diversity over time, as is also the case in other parts of the semi-arid Mopaneveld (Cingolani *et al.*, 2005; Jacobs & Naiman, 2008; Van Coller *et al.*, 2013; Wesuls *et al.*, 2013; Hanke *et al.*, 2014; Mureithi *et al.*, 2014).

6.5. Summary

With the community attributes used to test the influence of herbivore exclusion treatments on composition of functional groups over a nine year exclusion period, an overall dominance of perennial functional groups over annual functional groups was revealed over all the treatments. The Perennial Graminoids were the most responsive major life-form with regard to composition on

a broader functional level and revealed that the complete exclusion of herbivores over time favoured a significantly high abundance of Perennial Graminoids, but a significantly lower richness, possibly due to accumulation of biomass and dominance of only a few species in the life-form. The compositional responses to the absence of only large herbivores showed that large herbivores (e.g. elephant and giraffe) are needed to promote a higher proportional abundance of species that make up the composition of a life-form group.

When considering the effect of herbivore exclusion treatments on the diversity of functional groups, it was revealed that some of the observable patterns already existed before the experiment was conducted and had been established there not specifically by herbivory, but also by several other disturbances not tested in this study. A possible limitation in the experimental design (i.e. too short experimental period) was highlighted by the significant treatment effect observed (some significant differences between treatments were already present at the onset of the experiment, but disappeared over time, while others displayed no significant differences between treatments at the onset, but over time changed to differ significantly at the end of the experiment). A longer experimental period might have revealed better herbaceous response patterns to herbivory exclusion or even the same response patterns to confirm that the changes observed in this study, are the nature of changes that will occur despite any length of time. However, it was revealed that the absence of only large herbivores (i.e. elephants and giraffes) caused a higher major life-form diversity, richness and more even distribution than where all herbivores were present. The significantly lower life-form evenness in the presence of all herbivores suggests that some life-forms (possibly the Perennial Graminoids) started to dominate in this treatment and large herbivores need to be excluded to possibly decrease the dominance of some major life form groups and increase the competitiveness of less important major life form groups. A significant time effect showed that the absence of large herbivores, was directly responsible for significant increases over time in the major life-form diversity.

Nine years of herbivory exclusion in a semi-arid Mopaneveld revealed that on a broad functional group level, only the effects of the Partial herbivore exclusion treatment were clearly visible for both the composition and diversity, i.e. that large herbivores are needed for a more equal composition of functional groups, but in contrast, that large herbivores need to be excluded to promote a higher functional group diversity. No conclusions could be made however on a more refined functional group level (classified functional types inside the major life-form groups). Hypothesis 1 was therefore only partially accepted, because the composition of the herbaceous major life-form groups did change in accordance to the different herbivore exclusion treatments, but only the perennial graminoids (not also the perennial forbs) indicated a clear enough significantly higher abundance, but not a significantly lower richness than the annual graminoids and annual forbs. This pattern was also not only revealed in the Full exclusion treatment, but also in the Partial exclusion treatment. Hypothesis 2 was also only partially accepted, because the diversity patterns

of the herbaceous major life-form groups did change in accordance to the different herbivore exclusion treatments, but the Full exclusion treatment did not show a significantly higher abundance than the Partial and Control treatments, and only showed a significantly lower richness and diversity compared to the Partial exclusion treatment and this lower richness and diversity were already present at the onset of the experiment.

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Chapter 7

Conclusion

7.1. Introduction

This study provided valuable insights on the effect of long-term herbivore exclusion on the herbaceous community structure of a Mopaneveld savanna in a protected area. The main findings of this study are provided here, followed by recommendations that can possibly improve the scientific value of the study if it is repeated in the future.

7.2. Main findings

Different herbivory exclusion treatments and catenal position did not affect the composition of the herbaceous layer, neither did duration of herbivore treatments have any affect on herbaceous species composition. The expected higher biomass was revealed in the absence of all herbivores. Although biomass levels were not as high as for other savannas, the significant difference when compared to the treatments where herbivores were present, suggests that herbivores are needed to regulate biomass levels at this study site. The exclusion of large herbivores only (i.e. elephant and giraffe) led to increased evenness. Large herbivores such as elephants and giraffe not only alter the herbaceous layer through herbivory, but also through additional effects such as trampling (that are not the case if only smaller herbivores are present). The exclusion of these large herbivores therefore excludes additional disturbance effects that cause species loss in the herbaceous layer, and promotes a higher evenness. No distinct effect of herbivory exclusion could be detected on the herbaceous richness and diversity patterns on species level, and the observable patterns were already established at the onset of the experiment.

A broad functional analysis based on life-form classifications revealed a herbaceous composition dominated by perennial groups, despite the influence of any herbivore exclusion treatment. Compositional response patterns suggested continued unfavorable environmental conditions over the duration of the experimental period (possibly as result of other disturbances in combination with herbivory). The complete exclusion of herbivores favoured the dominance of perennial grasses (higher abundance, but a lower richness), and large herbivores are required in this system to maintain a more evenly distributed composition of the most dominant life-form groups. A significant treatment effect suggested that most of the observable diversity response patterns on functional group level were already established at the beginning of the experiment, but unlike the composition, the absence of large herbivores was required to promote a higher and more evenly distributed functional group diversity (also confirmed by a significant time effect).

It was expected that in a system with a long evolutionary history of herbivory and where herbivores are considered as one of the main drivers of the highly variable vegetation responses, variation in herbaceous composition and diversity in response to herbivory exclusion would be very difficult to detect. Although results indeed revealed few significant changes, nine years of herbivore exclusion was sufficient to pick up some significant responses in a system where the dynamic herbaceous layer regularly changes in short periods of time. Diversity patterns on both species and functional group level highlighted that the exclusion of only large herbivores are required for a higher diversity and evenness in this system over time. The Plant Functional Type (PFT) approach were not more sensitive in detecting effects of herbivory exclusion on the herbaceous vegetation than traditional species diversity measures, and both are required for the best possible understanding of the herbaceous vegetation response patterns in the semi-arid Mopaneveld.

7.3. Future recommendations

- A better understanding of the herbaceous vegetation response to disturbance will be achieved if the influences of other disturbances known to affect the Mopaneveld are tested in combination with herbivory exclusion and sufficient field data of these disturbances are sampled and analysed. For example, the variability in rainfall over time may have a delayed effect on the herbaceous vegetation patterns observed in response to herbivory, due to the variability in standing biomass that can be analyzed at specific points in time.
- Because semi-arid ecosystems exist at different states (both equilibrium and non-equilibrium) and spatio-temporal scales, landscape-scale approaches should be followed when obtaining long-term datasets to better define the impact of specific disturbances on the components of savanna ecosystems such as structure, composition and diversity.
- Methods described and used in this study, followed those prescribed by the exclosures field manual for the Letaba and Nkhulu herbivory exclosures in the KNP. These proposed methods were written for a very small and localized area inside the greater savanna biome and were specifically developed for these areas with a long evolutionary history of herbivory. This not only makes it difficult to compare the obtained results to other studies done at larger scales in the savanna biome, but the observed response patterns to grazing can also be weaker when compared to a system where large herbivores have been introduced more recently. In the future, the prescribed methods must be further adapted and elaborated to incorporate larger scale experiments that are more representative of all areas in the savanna biome as a whole.
- Although evenness was proven to be a more responsive measure of change in homogenous systems and can give an indication of stability in a herbaceous community over time, in the future it would be necessary to look at dominance shifts in species and specifically identify the species responsible for the vegetation shifts. This is also required on functional group level, since it was attempted in this study, but no conclusions could be made regarding what species

and traits were specifically responsible for the observable changes over time. The PFT method may also prove to be more sensitive in detecting herbivore exclusion effects on the herbaceous vegetation than traditional species diversity measures if functional analysis can be done on a more in depth level.

- More time is needed to confidently comment on the long-term effect of herbivore exclusion. The experimental period was too short to observe significant compositional and diversity patterns, and only some patterns were visible on both species and functional group level. Over a longer experimental period, possible shifts in the herbaceous composition and more distinct diversity patterns could be expected.
- It proves difficult to detect herbaceous community fluctuations from data sampled only at specific points in time over a long-term experimental period. Herbaceous vegetation data needs to be sampled annually to make better conclusions regarding the overall herbaceous dynamics in semi-arid systems, but such datasets are usually limited due to high labour and financial costs.
- In terms of statistical models used to test changes in the herbaceous vegetation in response to disturbance, it remains challenging to find a statistical model that perfectly suits a specific ecological data set. Although there are many different possibilities to analyse ecological data, the statistics applied to this data set were considered suitable, although further options will be explored when the data are analysed for possible publication.

Appendix 1

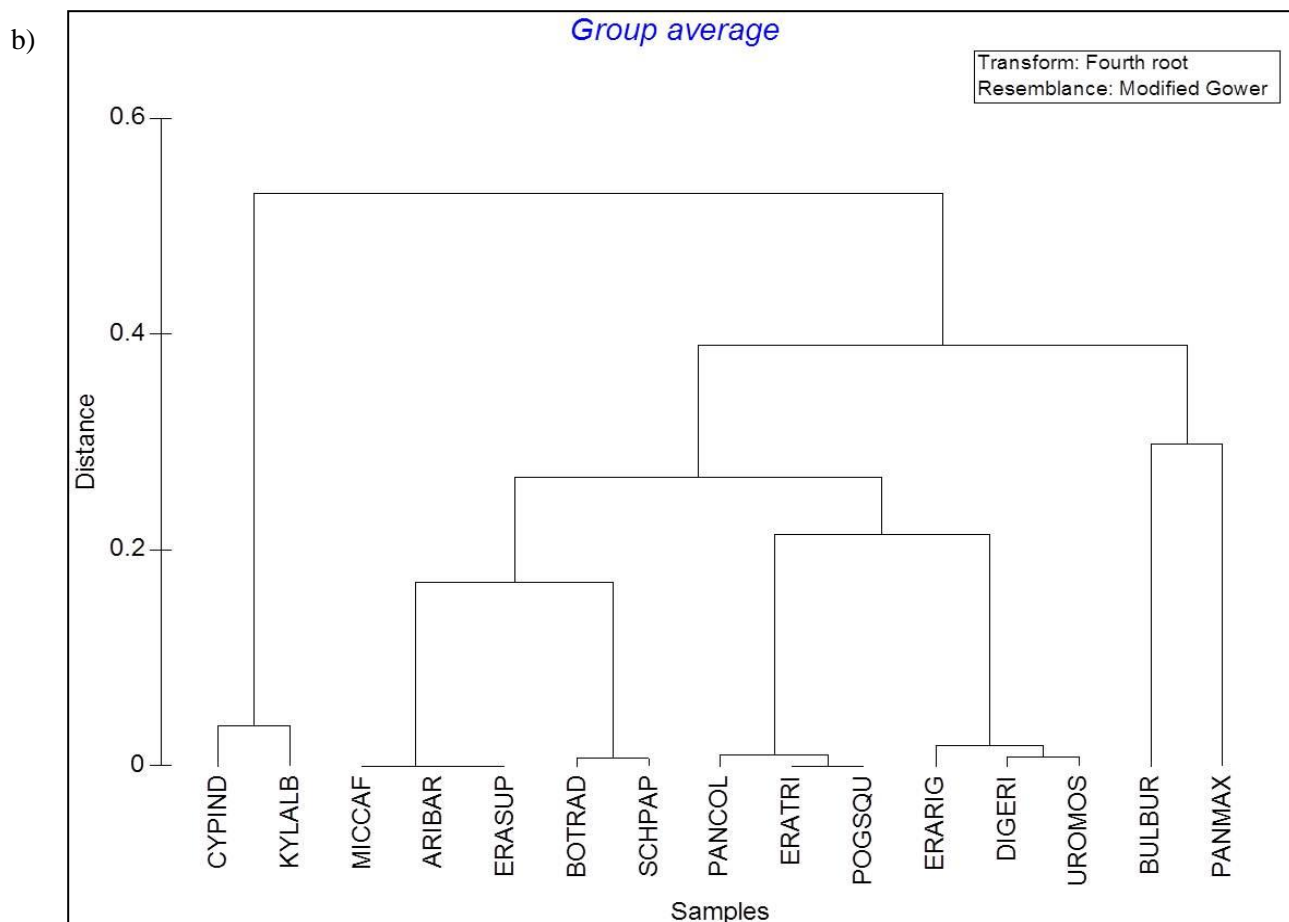
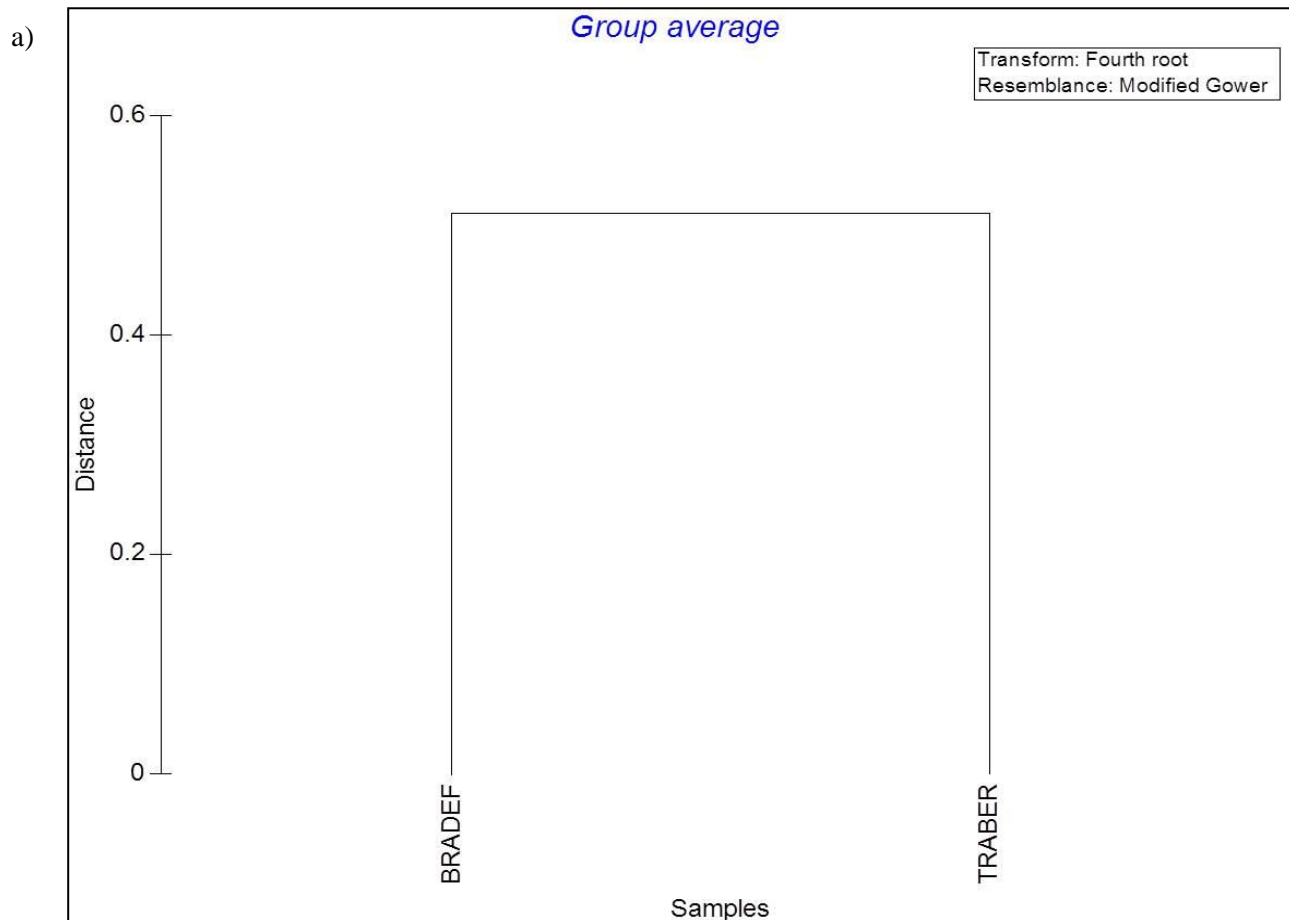
Appendix Table 1.1: The soft plant functional traits (with their trait adaptations) selected to indicate the herbaceous vegetation response to different herbivory exclusion treatments in a semi-arid savanna system highly affected by moisture availability.

<i>Trait</i>	<i>Trait Adaptation</i>
<i>Life form</i>	Indicates adaptation in area with a long evolutionary history of herbivory and climatic disturbances.
<i>Growth form</i>	Indicates how height and position of the foliage is positioned as an adaptation to herbivory and climate.
<i>Spinescence</i>	Defence mechanism against herbivory; can reduce drought stress and enable persistence during herbivory and climatic disturbances.
<i>Shade tolerance</i>	Gives indication of where species will be located, either in the sun or shade or both simultaneously.
<i>Root system</i>	Indicates which species are the best adapted to and will be able to survive moisture stress and will ultimately be the dominant species in the study area exposed to herbivory.
<i>Clonality</i>	Indicates which species are the best adapted to and will be able to survive moisture stress and will ultimately be the dominant species in the study area exposed to herbivory.
<i>Succulence</i>	Indicates which species are the best adapted to and will be able to survive moisture stress and will ultimately be the dominant species in the study area exposed to herbivory.
<i>Nitrogen fixing ability</i>	Indicates which species are the best adapted to and will be able to survive moisture stress and will therefore be the species exposed to herbivory.
<i>Flowering Period</i>	Plant strategy related to competition with other species for the best possible opportunity of germination or seed dispersal, giving an indication of which species will be present at different times of the year to be exposed to herbivory.
<i>Dispersal mode</i>	Plant strategy directly associated with the plants ability to redistribute its seed during or after environmental disturbances such as herbivory or drought to ensure its future existence.
<i>Height class</i>	Plant strategy directly related to competitive interaction with surrounding plants for resources and serves as good indicator of the plants grazing avoidance ability.

Appendix 2

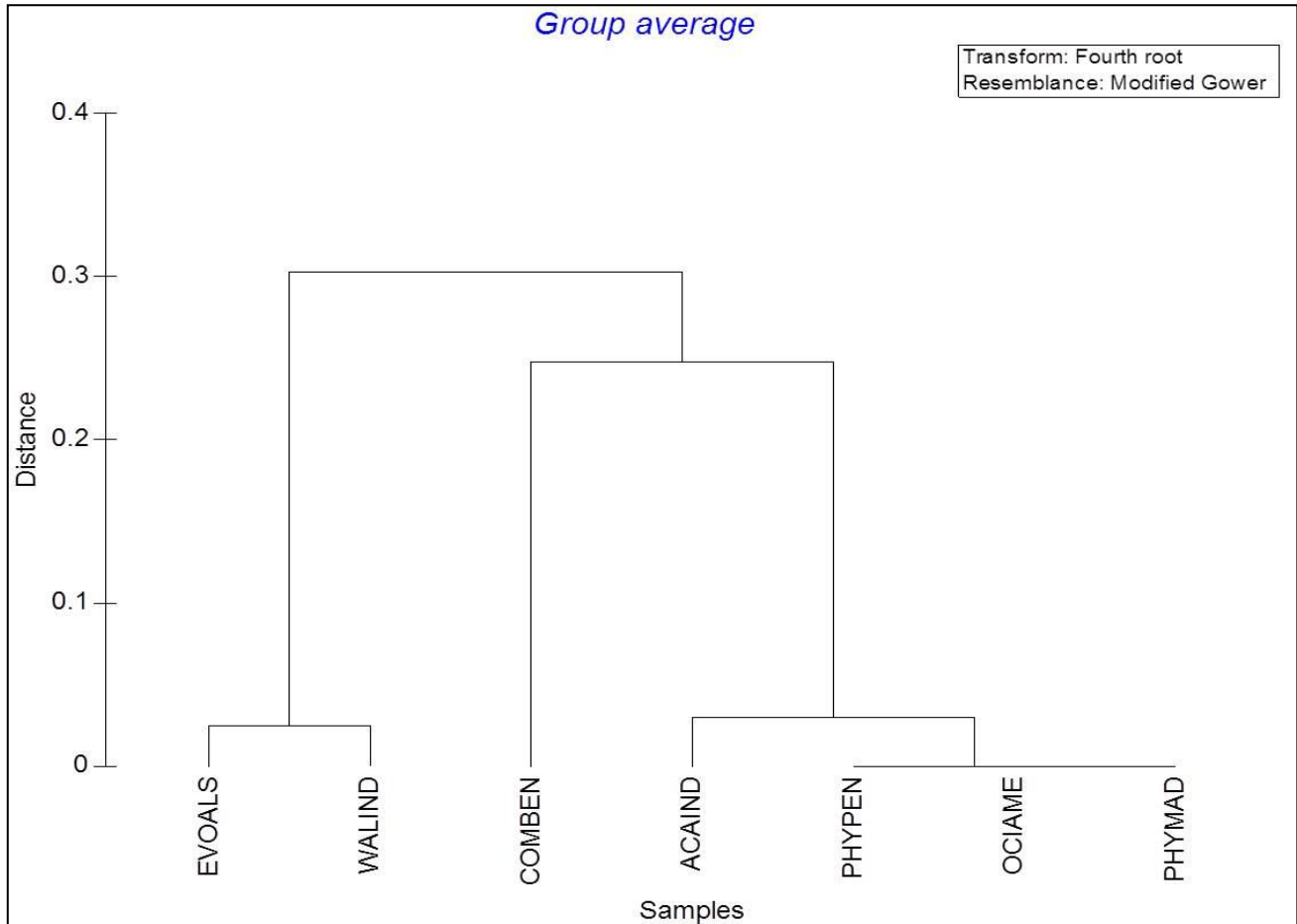
Appendix Table 2.1: List of abbreviations and corresponding species of Appendix Figure 2.1 and 2.2., as well as the major life-form group into which the each specific species was classified.

Abbreviation	Species	Major Life-Form Group
ACAIND	<i>Acalypha indica</i> L.	Annual Forbs
AGABOJ	<i>Agathisanthemum bojeri</i> Klotzsch	Perennial Forbs
ARIBAR	<i>Aristida congesta</i> subsp. <i>barbicollis</i> Roem & Schult.	Perennial Graminoids
BOTRAD	<i>Bothriochloa radicans</i> (Lehm.) A.Camus	Perennial Graminoids
BRADEF	<i>Brachiaria deflexa</i> (Schumach.) C.E.Hubb. Ex Robyns	Annual Graminoids
BULBUR	<i>Bulbostylis burchellii</i> (Ficalho & Hiern) C.B.Clarke	Perennial Graminoids
COMBEN	<i>Commelina benghalensis</i> L.	Annual Forbs
CYPIND	<i>Cyperus indecorus</i> Kunth	Perennial Graminoids
DIGERI	<i>Digitaria eriantha</i> Steud.	Perennial Graminoids
ERARIG	<i>Eragrostis rigidior</i> Pilg.	Perennial Forbs
ERASUP	<i>Eragrostis superba</i> Peyr.	Perennial Graminoids
ERATRI	<i>Eragrostis trichophora</i> Coss. & Durieu	Perennial Graminoids
EVOALS	<i>Evolvulus alsinoides</i> (L.) L.	Annual Forbs
HIBMIC	<i>Hibiscus micranthus</i> L.f. var. <i>micranthus</i>	Perennial Forbs
KYLALB	<i>Kyllinga alba</i> Nees	Perennial Graminoids
MELACU	<i>Melhania acuminata</i> Mast. var. <i>acuminata</i>	Perennial Forbs
MELFOR	<i>Melhania forbesii</i> Planch. Ex Mast.	Perennial Forbs
MICCAF	<i>Microchloa caffra</i> Nees	Perennial Graminoids
OCIAME	<i>Ocimum americanum</i> L.	Annual Forbs
PANCOL	<i>Panicum coloratum</i> L.	Perennial Graminoids
PANMAX	<i>Panicum maximum</i> Jacq.	Perennial Graminoids
PHYINC	<i>Phyllanthus incurvus</i> Thunb.	Perennial Forbs
PHYMAD	<i>Phyllanthus maderaspatensis</i> L.	Annual Forbs
PHYNEO	<i>Phyllanthus neopolycnemoides</i> Pax & K.Hoffm	Perennial Forbs
PHYPEN	<i>Phyllanthus pentandrus</i> Schumach. & Thonn.	Annual Forbs
POGSQU	<i>Pogonarthria squarrosa</i> (Roem. & Schult.) Pilg.	Perennial Forbs
SCHPAP	<i>Schmidtia pappophoroides</i> Steud.	Perennial Graminoids
SIDALB	<i>Sida alba</i> L.	Perennial Forbs
SIDCOR	<i>Sida cordifolia</i> L.	Perennial Forbs
TRABER	<i>Tragus berteronianus</i> Schult.	Annual Graminoids
UROMOS	<i>Urochloa mosambicensis</i> (Hack.) Dandy	Perennial Graminoids
WALIND	<i>Waltheria indica</i> L.	Annual Forbs

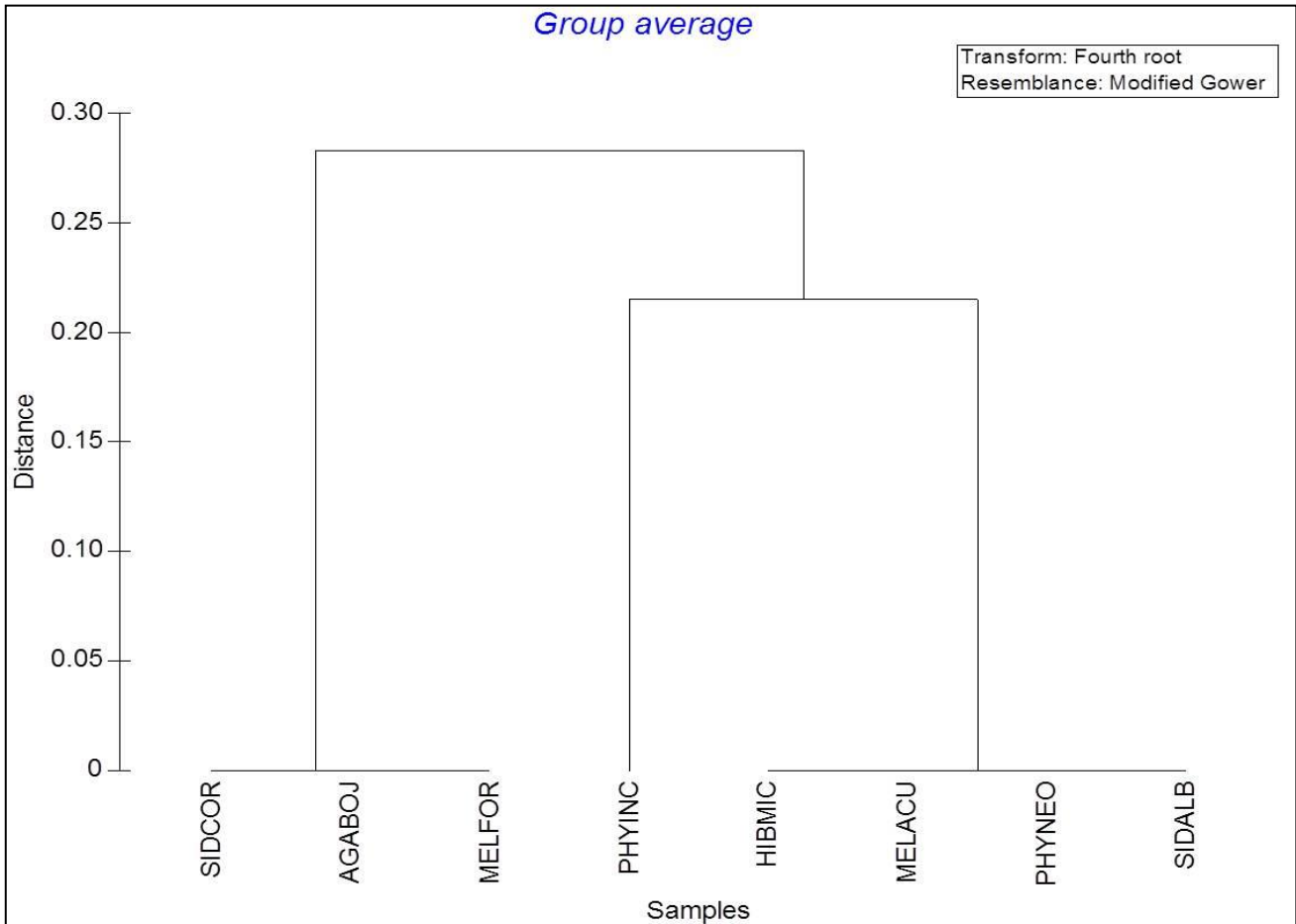


Appendix Figure 2.1: Cluster analysis of proposed Plant Functional Groups (PFG's) inside the four major life form classifications of a) annual graminoids, b) perennial graminoids.

a)



b)



Appendix Figure 2.2: Cluster analysis of proposed Plant Functional Types (PFT's) inside the four major life form classifications of a) annual forbs, b) perennial forbs.

Appendix Table 2.2: The most representative principal components of the Principal Component Analysis (PCA), Eigen Values, percentage of variance and the trait loadings of the most representative traits of the four major life form groups used to identify plant functional groups inside each of the major life forms.

<i>Major Life Form Group</i>	<i>Principal Component</i>	<i>Eigen Value</i>	<i>% Variance</i>	<i>Traits</i>	<i>PCA Trait loadings Axis 1</i>	<i>PCA Trait loadings Axis 2</i>
<i>Annual Graminoids</i>	1	1.5	100	Shade Tolerance	0.5774	0.8165
				Flowering Period Spring	0.5774	-0.4082
				Zoochory	0	0
				Anemochory	-0.5774	0.4082
<i>Perennial Graminoids</i>	1	0.954105	42.996	Shade Tolerance	-0.002562	0.636
	2	0.564978	25.46	Root System	0.8852	-0.1576
	3	0.380174	17.132	Clonality	0.4215	0.3491
				Flowering Period Autumn	-0.02154	-0.2051
				Zoochory	-0.1659	-0.292
				Anemochory	-0.1037	0.567
<i>Annual Forbs</i>	1	1,17209	68,372	Growth Form	0,1897	0,7116
	2	0,343548	20,04	Shade Tolerance	0,882	-0,1792
				Root System	-0,2728	-0,2483
				Clonality	-0,2728	-0,2483
				Flowering Period Spring	-1,93E-01	5,82E-01
<i>Perennial Forbs</i>	1	0,541891	70,572	Growth Form	0	0
	2	0,225966	29,428	Root System	1,33E-16	-1,26E-16
				Clonality	0,9313	-0,3641
				Flowering Period Spring	0,3641	0,9313
				Height Class	0	0