Drought responses of forb and grass communities in communal and protected rangelands

J Klem

orcid.org 0000-0003-1644-969X

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Supervisor:	Dr F Siebert
Co-supervisor:	Dr H Van Coller

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In nature there are neither rewards nor punishments; there are consequences.
- Robert Green Ingersoll

Abstract

The structure, growth, dynamics and productivity of herbaceous vegetation in semi-arid savannas are strongly limited by rainfall variability and nutrient availability. These factors interact with other drivers of savanna vegetation structure and function, of which herbivory remains among the strongest disturbance agents. Herbivore pressure is applied through grazing and/or browsing by multiple herbivore guilds of which their effects vary among rangeland types and herbivore densities. The spread of African pastoralism along with the predicted increase in frequency and severity of drought events highlights the need to improve our scientific understanding of herbaceous community responses to changes in rainfall variability and rangeland type. While grasses are generally the principal component in rangeland productivity and herbaceous dynamics studies, forbs are disproportionately underrepresented, whilst hosting the most diverse components of rangeland plant communities. Since African savanna vegetation structure and function have co-evolved with native herbivores, the interactive effects of land-use change towards single-species pastoralism and frequent or extensive drought events are expected to prompt significant changes in the herbaceous layer of semi-arid savannas. Grass community responses to changes in rangeland type and rainfall variability are well documented, although forb community dynamics have largely been neglected in the past. Forbs comprise an important part of the herbaceous layer as they significantly contribute to savanna ecosystem diversity and function. Plant functional traits adapted to tolerate disturbances are considered central to the functioning of herbaceous vegetation. Global climate and land use change necessitate the identification of drought- and herbivore tolerance traits to understand the functioning of the complete herbaceous component. The drought of 2014 – 2016 provided a unique opportunity to investigate the effects of a severe drought event on herbaceous community responses to distinct rangeland land-use practices in a nutrient-poor semi-arid Lowveld savanna of South Africa. The study aimed to evaluate and compare the drought responses of forbs and grasses on community- and functional level within two contrasting rangelands (wildlife and livestock). Sampling of herbaceous vegetation data were conducted towards the end of the drought (October 2016), and repeated several months after significant rainfall (January 2017). Field surveys took place in two different rangelands in the Gazankulu area, South Africa. The two rangeland types included a protected area, hosting a diverse community of large indigenous wildlife, and a communal rangeland with a long history of cattle grazing. Sampling of floristic data was conducted per herbaceous life form, permitting comparisons of forb and grass community responses to rainfall variability and rangeland type. Species abundances, basal cover per species and plant functional traits were recorded in a total of 120 fixed 1m^2 plots across rangeland types. Results revealed life-form specific responses to rainfall and rangeland type. Post-drought herbaceous communities were significantly different from drought-communities, although grass assemblages in the communal rangeland were not affected by drought release. Forbs responded significantly to rainfall variability and rangeland type on community and functional level. For all the species richness and diversity indices forbs responded significantly within the protected area, except for species evenness. The communal rangeland did not respond significantly for either life form in any of the richness and diversity indices. Grasses responded significantly in species abundance and Shannon-wiener diversity index, however forbs had the greatest interaction with rainfall variability and rangeland type. Plant functional types did not respond as expected. In the drought year perennial forb and grass plant functional types dominated the herbaceous layer. Post-drought conditions were characterised by unpalatable perennial forbs dominated and palatable perennial grass plant functional types. Forbs had higher functional diversity with the most plant functional types within both rainfall years. The communal rangeland functional and compositional characteristics remained constant across rainfall years which could indicate drought-tolerance for this community. However, the protected area did show resilience through high plant functional type abundance.

Key words: *communal; herbaceous; herbivory; plant functional types; resilience; African savanna; livestock; nutrient-poor savanna; diversity*

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Declaration

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

JKlem

Jana Klem (student)

Siebert

Dr. F. Siebert (Supervisor)

HvanColler

Dr. H. van Coller (Co-supervisor)

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Chapter 1

Introduction

1.1 Background and Rationale

African savannas cover approximately 40% of the continent's land surface and provide resources and ecosystem services not only for a high diversity of native biota, but specifically for human livelihoods (Higgins *et al.*, 1999; Shackleton *et al.*, 2002; Osborne *et al.*, 2018). Semi-arid sub-tropical savannas of Africa are characterized by a hot season with varying precipitation and a dry, warm, non-growing season (Scholes, 1987). During the hot growing season, the majority of rainfall occurs between October and April (Scogings *et al.*, 2012), which not only drives annual primary production (Scholes, 1987) and fire regimes, but also the migratory behaviour of mammalian herbivores (Venter *et al.*, 2003). The vegetation structure of savannas is unique because plant life form dominance is dependent upon varying environmental perturbations at various spatiotemporal scales (Scholes, 1987). Interactive mechanisms involving bottom-up controls such as nutrient availability, and top-down drivers relating to fire, herbivory and water availability shape these dynamic ecosystems (Skarpe, 1992; Scholes & Archer, 1997; van Wilgen *et al.*, 2000). Interactions among abiotic and biotic drivers maintain spatial and temporal heterogeneity and may change the structure and diversity of savanna ecosystems (Walker *et al.*, 1981; Scholes, 1987; Ellis & Swift, 1988; O'Connor, 1995; Van Wilgen *et al*., 2003; Augustine & McNaughton, 2006; Gertenbach, 2010; Scogings *et al*., 2012; van As *et al*., 2013).

Savanna plant communities are highly seasonal (Ellis & Swift, 1988; O'Connor, 1995) and consist of a discontinuous woody component (consisting of trees and shrubs) and a relatively continuous, and mostly dynamic herbaceous layer (Walker *et al*., 1981; Knoop & Walker, 1985; Belsky *et al*., 1989; Skarpe, 1991; Couteron & Kokou, 1997; Scholes & Archer, 1997; Sankaran *et al*., 2008). Grasses (mainly C_4) and herbaceous dicotyledonous species, non-graminoid monocots and geophytes (collectively termed 'forbs' hereafter), represent the herbaceous layer (Scholes, 1987). The coexistence of the herbaceous and woody layer is based on differences in floristics, morphology and physiology (Turner & Knap, 1996; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015).

Semi-arid African savannas host a unique set of herbivores, but as pastoralism spreads these diverse herbivore guilds are being replaced by single species domestic livestock (Koerner *et al.,* 2014; Daskin *et al.,* 2016). In light of this change of herbivore guild it is important to understand how the herbaceous layer will react to this type of herbivore pressure in systems being exposed to it. The knowledge gained will allow for better predictions on vegetation response to future changes, including global warming. Herbivores transform savanna landscapes and vegetation through trampling, defoliation, dung deposition, urination, and trashing (Skarpe, 1991; Jacobs & Naiman, 2008). Grazing has been reported to cause an increase in species richness in productive habitats (Angassa, 2014), however the opposite has been reported for low-productivity habitats (Olff & Ritchie, 1998). Herbaceous layer response to herbivory has been studied extensively, with most of the focus being on the response of grasses (Trollope *et al.*, 2014). These studies predominantly reported long-lived perennial grasses being replaced by forbs, short-lived perennial and annual grasses when the system was exposed to heavy grazing and drought conditions (Milchunas *et al.*, 1993; O'Connor; 1995; Illius & O'Connor, 1999; Fynn & O'Connor, 2000; Gao *et al.*, 2009). Light to moderate grazing pressure generally results in an increase in species richness and cover (Porensky *et al.*, 2013; Treydte *et al.*, 2013; Angassa, 2014), whereas heavy grazing pressure reduces species richness, diversity and cover (Gao *et al.*, 2009; Hanke *et al.*, 2014). Studies comparing the effect of different herbivore guilds (livestock; mesoherbivores; livestock and mesoherbivores; mesoherbivores and megaherbivores;) reported that livestock grazing alone had stronger effects on the herbaceous layer in terms of species composition, richness, diversity and cover than any other combination of herbivores (Du Toit & Cumming, 1999; Porensky *et al.*, 2013; O'Connor, 2015).

Soil (based on the underlying geology) is considered a significant driver of savanna vegetation composition and structure. The Lowveld Savanna Bioregion is particularly known for species composition contrasts on nutrient-rich versus nutrient-poor soils (Venter, 1986; Mucina *et al.,* 2006). Rainfall variability and herbivory remains the strongest driver of savanna vegetation dynamics (Venter *et al.*, 2003; Rowntree *et al.*, 2004). In turn, vegetation and primary production of an area drives the movement of mammalian herbivores (Frank *et al.*, 1998). Fire is another important savanna ecosystem driver due to its key role in maintaining vegetation structure, especially in mesic savannas (Bond & Keeley; 2005; Sankaran *et al.,* 2005; Bond & Parr, 2010; Casillo *et al.*, 2012; Hempson *et al.*, 2015). Dry seasons in savannas provide optimum conditions for regular fires, a necessary driver of tree-grass coexistence as it clears large patches of biomass, which allows for ecological rejuvenation (Scholes & Walker, 1993; Higgins *et al*., 2000; Van Wilgen *et al*., 2003; Sankaran *et al*., 2004; Farina, 2007; Higgins *et al.,* 2007).

Understanding the dynamic character of savannas as a result of interactions between climate and local-scale drivers, such as nutrients, herbivory and fire has been the focus of savanna studies over many decades (Knoop & Walker, 1985; Scholes, 1990; O'Connor, 1995; Bergström & Skarpe, 1999; Fynn & O'Connor, 2000; Augustine, 2003; Bardgett & Wardle, 2003; Van Langevelde *et al.*, 2003; Augustine & McNaughton, 2006; D'Odorico *et al.*, 2007; Abdallah & Chaieb, 2012; Porensky *et al*., 2013; Hanke *et al.*, 2014; Koerner *et al.*, 2014; Trollope *et al.*, 2014; Burkepile *et al.*, 2017). Yet predicting plant community changes in response to these drivers remains challenging (Scholes, 1987; Osborne *et al.*, 2018), especially for subordinate life forms in herbaceous communities.

Forbs are often neglected in range condition assessments due to their perceived low forage value (Trollope *et al.*, 2014). Although forbs are generally considered an important source of biodiversity in grasslands and savannas (Uys, 2006; Buitenwerf *et al*., 2011; Trollope *et al*., 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015), their ecological value, especially in terms of their contribution to ecosystem resilience, remains poorly known. More recent studies, however, infer that forbs are ecologically more significant than previously acknowledged (Odadi *et al.*, 2007; Odadi *et al.*, 2013; Siebert & Scogings, 2015). Forbs are often perceived negatively by land managers due to their dominance over grasses under certain environmental conditions, especially on nutrient-rich soils (Reich *et al.*, 2003; Van Coller & Siebert, 2015), when grazing pressure is moderate to high (Scholes, 1987; Hejcmanová *et al.*, 2010; Cowley *et al.*, 2014) or after drought events (Fynn & O'Connor, 2000; Buitenwerf *et al.*, 2011). High species richness and functional adaptability (conveyed through the dominance of forbs over grasses under stressed conditions) suggest high functional redundancy, which is expected to improve resilience of ecosystems constantly exposed to environmental disturbances. Consequently, there is an increased awareness among ecologists of the significance of forbs in the maintenance of ecosystem resilience (Pokorny *et al.*, 2004; Bond & Parr, 2010; Kotschy, 2013; Scott-Shaw & Morris, 2015; Shackleton, 2000; Jacobs & Naiman, 2008; Masunga *et al*., 2013; Van Coller *et al.,* 2018). The implied importance of forbs (e.g. provision of goods and services) in African savannas indicate the need for further research on this plant functional group. Due to their dynamic response to environmental disturbances (Scott-Shaw & Morris, 2015), it is expected that forbs and grasses will respond differently in terms of abundance and functional trait composition.

Drought is considered one of the main threats to the livelihood of people who depend on ecosystem services provided by savannas (Martin *et al.*, 2016). The predicted increase in drought events due to climate change will challenge rangeland owners and managers to find methods for reducing the ecological and environmental impacts of drought, making research on this topic particularly relevant (Vetter, 2009; Porensky *et al.*, 2013; Koerner & Collins, 2014; Swemmer *et al.*, 2018). The recent drought of 2014 - 2016 affected most parts of southern Africa (Baudoin *et al.*, 2017). The drought did not only cause livestock and wildlife mortality across South Africa, but also led to observable changes in vegetation composition (Baudoin *et al.*, 2017; Swemmer *et al.*, 2018). Previous research investigating drought effects on herbaceous vegetation in savannas focussed on the agriculture sector due to the importance of crop- and livestock production. As a result, most studies focused almost exclusively on grass productivity and plant community structure (Milchunas *et al.*, 1989; O'Connor, 1995; Fuhlendorf & Smeins, 1997; Fynn & O'Connor, 2000; Fuhlendorf *et al.*, 2001; Vetter, 2009). In general, these studies reported droughts to cause dieback and declines in cover of tufted perennial grasses, allowing annual forbs to increase in abundance (Fynn & O'Connor, 2000; Milton & Dean, 2000; Hodgkinson & Müller, 2005; Munson *et al.*, 2016; Swemmer *et al.*, 2018). Droughts furthermore caused a turnover of species in certain areas (Fynn & O'Connor, 2000) with several annual and perennial grass species being recorded for the first time after the drought (O'Connor, 1995). In contrast to drought effects, increased precipitation in semi-arid grasslands stimulated an increase in species richness and diversity (Porensky *et al.*, 2013; Koerner & Collins, 2014; Zerbo *et al.*, 2016), as well as an increase in perennial grasses (O'Connor, 1995; Buitenwerf *et al.*, 2011). Moreover, higher rainfall has been associated with higher species evenness (Porensky *et al.*, 2013; Zerbo *et al.*, 2016).

Previous studies on combined effects of drought and herbivory in savannas generally emphasise the productivity of grasses due to their importance in providing forage stability for grazers (Uys, 2006; Zimmerman *et al.*, 2010; Trollope *et al.*, 2014). Following a drought event, a turnover from palatable perennial grasses to unpalatable weakly tufted perennials and ephemeral or annual grasses and forbs is commonly reported under moderate to heavy grazing pressure (i.e. Weaver & Albertson, 1936; Milchunas *et al.*, 1989; O'Connor, 1995; O'Connor, 1998; Fynn & O'Connor, 2000; Morecroft *et al.*, 2004; Vetter, 2009; Porensky *et al.*, 2013; O'Connor, 2015). Although forbs drive community diversity (Koerner & Collins, 2014), they demonstrate weaker responses under combined pressure of drought and herbivory in systems where grasses dominate as the functional group. Understanding the interactions between drought and grazing is important for conservation and management as heavy grazing may exacerbate the effects of drought on the vegetation composition (O'Connor, 1995; Illius & O'Connor, 1999; Fynn & O'Connor, 2000; Vetter, 2009; Zimmerman *et al.*, 2010; Ruppert *et al.*, 2015).

Studies on the effects of drought are mostly carried out in highly productive and nutrient-rich systems (i.e. O'Connor, 1995; Van Coller *et al.*, 2018). Consequently, there is a lack in research on drought effects in nutrient-poor savanna rangelands (Swemmer *et al.*, 2018). The 2014 - 2016 drought provided a unique research opportunity to address this knowledge gap through assessing the response of grasses and forbs, as separate life forms to drought within a nutrient-poor Lowveld granitic savanna. Since the Lowveld savanna of South Africa is home to varying rangeland types hosting different herbivore guilds (i.e. domestic livestock of rural rangelands and wild ungulate herbivores of protected areas), its geographical setting was furthermore in support of potential improved understanding of drought effects in African landscapes. For the purpose of this study the term 'rangeland' refers to "land carrying natural or semi-natural vegetation which provides a habitat suitable for herds of wild or domestic ungulates" as defined by Pratt *et al.* (1966).

1.2 Aims and Objectives

Considering the knowledge gap pertaining to drought response patterns of grasses and forbs respectively, the primary aim of this study was to evaluate and compare community–and functional-level responses of grasses and forbs to drought within two contrasting rangeland systems (i.e. a protected area that hosts indigenous free roaming wildlife, and a communal rangeland with a long history of livestock grazing). Knowledge gained from this study is envisaged to contribute to our understanding of the resilience of all components of the herbaceous layer to drought and herbivory in semi-arid African savannas.

Results were presented in two respective chapters, which were designed to report on drought responses of the herbaceous layer at species– (Chapter 5) and functional (Chapter 6) levels, respectively.

The objectives which dealt with community (species) level responses (i.e. Chapter 5), were to test (i) the effects of rainfall variability (drought versus post-drought rainfall conditions) on herbaceous community composition, structure and diversity, and (ii) how these effects interact with differences in rangeland type (i.e. herbivore guild).

Objectives at functional level (i.e. Chapter 6), included to (i) evaluate patterns in forb and grass functional trait composition in response to rainfall variability, and (ii) link response patterns in functional traits to differences in rangeland type (i.e. herbivore guild).

Specific objectives will be presented in the Introduction section of each of the respective results chapters.

1.3 Hypotheses

The broad hypothesis of the study was that responses to rainfall variability are strongly dependent upon herbaceous life form and rangeland type as it is expected that grasses and forbs will not respond similarly to drought conditions, neither will intensely grazed communal rangelands and protected areas display equal vegetation responses.

It was hypothesised that:

1. The response of the herbaceous layer to drought will differ between two contrasting rangeland types: as a result of higher stocking densities, the communal rangeland is

expected to undergo more severe changes in vegetation composition compared to the protected area.

2. The community structure (species composition), diversity (species richness and evenness) and function (functional traits and plant functional types) will differ between grasses and forbs, i.e. palatable perennial grass species will decline in response to drought whereas annual forb species and short-lived perennial grass species are expected to increase in abundance and diversity.

1.4 Format of the study

This dissertation conforms to the guidelines set for a standard dissertation at the North-West University (See section 2.1 of the manual for Post Graduate Studies available at: www.nwu.ac.za/library/documents/manualpostgrad.pdf). It encompasses eight chapters. Cited literature is included as a single list of references at the end of the dissertation.

Chapter 2: Literature Review

This chapter provides an overview of the existing literature related to the research topic. The description of semi-arid African savanna characteristics provides background information on the locality of the study. It also reports on soil nutrients, herbivory and rainfall variability as important savanna ecosystem drivers. Lastly, it highlights the need to incorporate forbs into existing ecological models based on the limited information available on this plant functional group.

Chapter 3: Study Area

A detailed description of the study area including information on the location, climate, geology, history and vegetation description is provided in this chapter. It furthermore provides information on the two different land use types investigated in this study.

Chapter 4: Materials and Methods

This chapter provides a description of the experimental design and elaborates on general methodology followed to acquire floristic and trait data, as well as statistical analyses that were applied for which the results are presented in chapters 5 and 6.

Chapter 5: Forb and grass community responses to drought

This chapter provides visual and tabular results and descriptive reports on the responses of forb- and grass communities to drought in a protected area and communal rangeland. Shifts in life form cover, species composition and species diversity of grasses and forbs are reported for each respective life form.

Chapter 6: Plant functional attributes related to rainfall and rangeland type

This chapter presents descriptions and discussions on plant functional trait assemblages and plant functional types (PFT) for each rainfall year for forbs and grasses, respectively.

Chapter 7: Discussion

In this chapter, results are discussed and brought into context with existing knowledge and literature on drought and herbivore effects on herbaceous communities in semi-arid savannas.

Chapter 8: Conclusions

This chapter culminates all findings and highlights the contribution of this study towards existing knowledge and understanding of drought and herbivore effects on herbaceous layers in savanna ecosystems. The combined effects of these drivers on semi-arid savanna function and structure is articulated and recommendations for future research and reference are also presented.

Chapter 2

Literature Review

2.1 Semi-arid savannas

Savannas cover approximately 20% of global land surface and represent more than half of the terrestrial areas of the southern hemisphere (Mordelet & Menaut, 1995). African savannas comprise ~40% of the continent (Higgins *et al.*, 1999; Shackleton *et al.*, 2002; Osborne, *et al.*, 2018). Many people in Africa are dependent on this biome for livestock farming (Scholes & Archer, 1997; Augustine *et al.*, 2003; Shackleton, 2004) and crop production (Van Der Merwe, 2010), both commercially and in rural areas.

A characteristic feature of African savannas is the rich diversity of animals which they support (Du Toit, 2003). Trees, shrubs, grasses and forbs sustain vast numbers of grazers, browsers and mixed-feeders (Van As *et al.*, 2013). The diversity of large mammalian herbivores that dominate semi-arid African natural savanna landscapes include browsers such as giraffe (*Giraffa camelopardalis*), black rhino (*Diceros bicornis*), bushbuck (*Tragelaphus sylvaticus*) and greater kudu (*Tragelaphus strepsiceros*), grazers (e.g. Cape buffalo (*Syncerus caffer*), hippopotamus (*Hippopotamus amphibius*), blue wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*), and mixed feeders (e.g. impala (*Aepyceros melampus*), African elephant (*Loxodonta africana*), grey duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*)) (Gertenbach, 1983; Du Toit & Cumming, 1999; Scogings *et al.*, 2012; Treydte *et al.*, 2013). General carnivorous species include lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*), wild dogs (*Lycaon pictus*) and leopard (*Panthera pardus*) (Augustine & McNaughton, 2006). In African rural villages most of the households that can afford livestock own cattle whereas goats and sheep are not as common (Teague & Smit, 1992; Shackleton, 2000; Dovie *et al.*, 2006; Baumgartner *et al.*, 2015; Veblen *et al.*, 2016).

Tree-grass co-existence

The absence of a single dominant plant growth form distinguishes savannas from other terrestrial biomes (Scholes, 1987; Scholes & Archer, 1997). Savannas are characterised as ecosystems with a discontinuous woody layer consisting of trees and shrubs of different heights spread out among a continuous herbaceous layer of graminoids and forbs (Walker *et al.*, 1981; Knoop & Walker, 1985; Belsky *et al.*, 1989; Weltzin & Coughenour, 1990; Skarpe, 1991; Couteron & Kokou, 1997; Scholes & Archer, 1997; Sankaran *et al.*, 2008; Eckhardt, 2010).

The woody and grass layer coexist and interact with abiotic and biotic factors giving rise to the well-known vegetation structure of savannas (Knoop & Walker, 1985; Skarpe, 1992; Scholes & Archer, 1997; Jeltsch *et al.*, 2000; Eckhardt, 2010). Grasses, which belong to the Poaceae family, are considered as one of the most important plant families on Earth (Van Oudtshoorn, 2002). Grasses provide important ecosystem services which include the provision of forage to herbivores and fuel for fires, stabilisation and protection of soil, whilst certain grass species form a fundamental part of rangeland condition assessment (Trollope *et al.*, 1989; Van Oudtshoorn, 2002; Uys, 2006; Trollope *et al.*, 2014; Van Coller, 2018). In savannas, grasses and woody plants co-exist through dynamic interactions and competition for resources (Walker *et al.*, 1981; Jeltsch *et al.*, 2000; Ward *et al.*, 2013; Wiegand *et al.*, 2006). Grasses may regulate woody plant recruitment, either directly, by competing for light, water and nutrients, or indirectly, by producing large amounts of aboveground biomass influencing fuel loads and fire frequency and intensity (Frost & McDougald, 1989; Scholes & Archer, 1997; Abdallah & Chaieb, 2012; Cowley *et al.*, 2014). In some systems the negative effect of grasses on trees are evident, where woody seedlings are trapped within the flame zone of a distinct grass layer, limiting the number of seedlings that grow past the flame zone to reach maturity (Scholes & Archer, 1997; Bond & Midgley, 2000; Bond & Parr, 2010). However, in systems where grazing, browsing and fire is absent, shifts from open- to closed-bush savannas may occur within a relatively short period (San José & Fariñas, 1991). Increased density of grasses as a result of average or above-average rainfall (February *et al.*, 2013) leads to increased competition for soil moisture, which might suppress the establishment and growth of shrubs and small trees (Knoop & Walker, 1985; Vetaas, 1992; Scholes & Archer, 1997; Eckhardt, 2010).

An increase in woody species, termed bush encroachment (Smit *et al.*, 1996), often leads to a decrease in palatable perennial grasses and woody plants (Wiegand *et al.*, 2006; Eckhardt, 2010), thus lowering the browsing and grazing value of the system (Smit, 2004). Moreover, bush encroachment enhances the effects of erosion through increasing patches of bare soil and increasing volumes and speed of runoff water (Smit, 2004; Eckhardt, 2010). Bush encroachment furthermore decreases aboveground grass biomass, inherently lowering fire fuel loads (Trollope, 1980), further promoting the establishment and encroachment of woody species (Scholes & Archer, 1997; Eckhardt, 2010).

Forbs as a component of the herbaceous layer in savannas

Forbs, a collective term for a life form containing herbaceous dicotyledonous species, non-graminoid monocots and geophytes, comprise an essential part of semi-arid African savanna systems through a diverse set of families (Kallah *et al.*, 2000;). Yet, forbs are often being neglected as a plant functional group in veld condition assessments and vegetation studies (Hayes & Holl, 2003; Pokorny *et al.*, 2004; Hempson *et al.*, 2015; Scott-Shaw & Morris, 2015) as they are commonly lumped into a ‘non-grass’, increaser II category (for southern African rangeland studies), or simply referred to as ‘forbs’ without sufficient information on their species diversity (Scott-Shaw & Morris, 2015). The general reasoning behind this disregard of forbs in vegetation studies is the challenging task of sampling and identifying this plant group (Bond & Parr, 2010). The noticeable absence of forbs in savanna ecological models is surprising, since forbs account for ~70% of species richness in semi-arid savannas (Siebert & Scogings, 2015) and ~80% in grasslands (Hayes & Holl, 2003; Pokorny *et al.*, 2004; Scott-Shaw & Morris, 2015). Uys (2006) found consistent results, indicating that forbs are the largest contributor to species richness in the savanna grasslands of South Africa. Despite their perceived low forage value, evidence from African savannas suggest that forbs are a particularly nutritious food source and form an important part of native and domesticated herbivore diets (Kallah *et al.*, 2000; Du Toit, 2003; Odadi *et al.*, 2013). Disturbances such as herbivory (Scholes, 1987), fire (Bond & Parr, 2010) and drought (Buitenwerf *et al.*, 2011) are often perceived as natural stimulants of forb dominance in the herbaceous layer. Forbs are valuable indicators of ecosystem change which make forbs an important functional entity with greater ecological value than previously acknowledged, but more research is needed at the species level.

Significant attributes of forbs

Forbs are known contributors to herbaceous species richness in African grassland (Pokorny *et al.*, 2004; Bond & Parr, 2010; Scott-Shaw & Morris, 2015) and savanna ecosystems (Shackleton, 2000; Jacobs & Naiman, 2008; Masunga *et al*., 2013; Van Coller *et al.,* 2013). Forbs comprise between 50% and 80% of the wet-season diet of three savanna mesoherbivores (i.e. greater kudu, impala and steenbok) (Du Toit, 1988). In the semi-arid and sub-humid savannas of West Africa, forbs are widely used to supplement livestock forage, especially during the dry season (Kallah *et al.*, 2000). Forbs are not only valuable dry season forage but their forage potential also varies across topographic positions in the landscape. Siebert and Scogings (2015) studied browsing intensity of herbaceous forb species across a semi-arid savanna catenal sequence in the Kruger National Park, South Africa and concluded that forbs were utilised at varying intensities along the catena, but that forbs were preferentially browsed on the nutrient-rich sodic bottomlands.

Most forb species can tolerate shading effects better than grasses, making tree islands or dense tree stands favourable habitats for the establishment of forbs (Ludwig *et al.*, 2001, 2004; Abdallah & Chaieb, 2012; Linstädter *et al.*, 2016). As global CO_2 levels rise it is expected that bush encroachment could increase whilst grass dominance could decrease (Bond & Parr, 2010). These predictions may imply greater abundance and enhanced competitive vigour of forbs over grasses, especially the C3 forbs, which necessitates further research on the ecology of forbs at the species level (Trollope, 1980; Scholes & Archer, 1997; Oba *et al.*, 2000; Ward, 2005; Britz & Ward, 2007; Angassa, 2014; Wigley *et al*., 2010; Buitenwerf *et al*., 2012).

The dominance and abundance of forbs following fires (Cowley *et al.*, 2014) may be ascribed to the presence of underground storage organs or dormant seeds present in the seed bank, which allow these species to rapidly resprout following a fire disturbance (Uys, 2006; Bond & Parr, 2010; Scott *et al.*, 2010). Enhanced forb species diversity has been found to be associated with medium to intensely grazed systems (Van Coller, 2014), which may be attributable to trampling effects by herbivores which decreases aboveground biomass and increases the occurrence of bare soil, in turn facilitating the establishment of forb species with prostrate and rosette growth forms (Burkepile *et al.*, 2017).

Forbs are considered resilient to different environmental conditions due to their diverse morphologies, regeneration strategies, and a variety of eco-physiological attributes (Turner & Knapp, 1996; Lavorel *et al.,* 1999). Forbs are furthermore important host plants for pollinating insect species (Uys, 2006; Van Oudtshoorn, 2015). African rangeland forbs also have great cultural significance and may potentially benefit all of humankind (Uys, 2006). Throughout history many of these rangeland forbs have been used in traditional medicines (Botha, 1998) and also formed part of the local people's diet (Fox & Norwood Young, 1982; Hutchings, 1996; Arnold *et al.*, 2002). Despite being a flora valued for its many uses in traditional medicines, where a rich diversity of phytochemical characteristics exists between families, the alpha family diversity of forbs could potentially hold extensive pharmaceutical potential (Arnold *et al.*, 2002) which has yet to be explored and incorporated.

The perceived negative association of forb dominance

Managers often perceive forbs negatively due to their dominance over the grass component - an important source of forage stability in savannas (O'Connor, 2015). The dominance of forbs occurs under particular environmental conditions i.e. under moderate to heavy grazing pressure (Scholes, 1987; Hejcmanová *et al.*, 2010; Cowley *et al.*, 2014), after a drought event (Fynn & O'Connor, 2000; Buitenwerf *et al.*, 2011), on nutrient-rich soils (Reich *et al.*, 2003; Van Coller & Siebert, 2015) and beneath tree canopies (Linstädter *et al*., 2016). This negative perception of forbs is mostly based on the dominance of forbs as life form group in general, but these associations fail to identify certain valuable forb species and functions which form part of this dominance of forbs over grasses.

The ecology of grassland forbs needs to be studied extensively to form a better understanding of this unique plant group and its interaction with the environment and other plant life forms (Uys, 2006). It is suggested that forbs increase functional redundancy due to their high species richness and functional adaptability (Kotschy, 2013) which is expressed through their dominance over grasses under stressful conditions. The resilience of a system exposed to sustained disturbance is expected to improve as the level of functional redundancy increases (Kotschy, 2013). The need for research on forbs at a level lower than the collective functional group or life form, is validated by the high functional redundancy that this group displays.

2.2 Heterogeneity of African savannas

Picket *et al.* (2003) defines heterogeneity as the degree of difference between a set of factors. In the context of savannas, heterogeneity can be expressed as the collection of plant communities and habitat assemblages present in space and time, which is furthermore determined by fluctuations in environmental factors such as soil conditions, topography, competition, fire regimes, distribution of soil moisture, and herbivory (Baker, 1992; Bergström & Skarpe, 1999; Van Wilgen *et al.*, 2003; Scogings *et al.*, 2012). Fragmentation and disturbance enhance heterogeneity at different scales (Farina, 2007).

Scale may affect the ecological patterns being observed or studied (Wiens, 1989). Biodiversity is dependent on scale (McCann, 2000), which is why observed changes in diversity patterns at larger scales may be the result of changes at smaller scales (Farina, 2007). Local-scale topographical variance, such as catenal sequences on granitic landscapes with their associated distinct turnover in savanna vegetation assemblages, is one such example of a source of heterogeneity at the landscape scale (Scholes, 1987). Landscape heterogeneity is known to enhance biodiversity (Pickett *et al.*, 2003) since spatially heterogeneous environments provide diverse microclimates and microhabitats, creating niche partitioning able to host a greater diversity of functionally different species (Mouquet *et al*., 2002; Begon *et al.*, 2006). Increased heterogeneity will generally lead to increased species richness and diversity (Mouquet *et al*., 2002). Ecosystems with greater heterogeneity and thus greater species diversity are more resilient to the dynamic interactions between savanna drivers (Vitousek *et al.*, 1997; Bullock *et al.*, 2011; Mori *et al.*, 2013). Vegetation dynamics in savannas are driven by various factors such as climate (particularly rainfall variability), herbivory, soil characteristics, fire (Augustine & McNaughton, 1998; House *et al*., 2003; Augustine & McNaughton, 2004; De Knegt *et al*., 2008; Sankaran *et al.*, 2008; Joubert, 2010), and life history traits of plants (Eckhardt, 2010). Fire is often implemented as management regime in protected areas but not in communal rangelands.

Climate as source of heterogeneity

Rainfall in the semi-arid savannas of the Lowveld (500-700 mm MAP) occurs mainly during warm moist summer months (between October and April) (Venter *et al.*, 2003; Scogings *et al.*, 2012), and decreases from South to North, and from East to West. Savanna winters are mostly dry with mild to cold temperatures with little or no frost (Scholes, 1987; Teague & Smit, 1992; Scholes & Walker, 1993; Venter *et al*., 2003; Mucina & Rutherford, 2006; Gertenbach, 2010). In the summer, hot temperatures and elevated radiation levels lead to evapotranspiration rates that exceed annual precipitation (Scholes, 1987).

Seasonality and variability of rainfall characterises savannas (Tolsma *et al.*, 1987; Fynn & O'Connor, 2000; Mucina & Rutherford, 2006), and their vegetation structure is determined by the stochastic nature of rainfall events (Venter *et al.*, 2003; Rowntree *et al.*, 2004). Rainfall in southern Africa varies significantly at both spatial and temporal scales, which affects the economy as well as the environment (Vetter, 2009; Phakula *et al.*, 2018). The highly variable rainfall patterns in semi-arid savannas (Belay & Moe, 2012) over space and time interact with other factors such as soil nutrients and herbivory (Augustine, 2003; Augustine & McNaughton, 2006) which drive changes in vegetation dynamics such as species assemblages and biomass production (Fynn & O'Connor, 2000). In southern Africa, there decadal return periods for severe droughts seem to be common (Roualt & Richard, 2003), although less severe droughts may also be a common phenomenon across the region (Le Houerou, 1984; Schulze, 1997), especially in the semi-arid parts. Rainfall variability affects ecosystems in various ways of which the movement of large mammalian herbivores are relevant to the management of protected areas (Bergström & Skarpe, 1999; Venter *et al.*, 2003). The intensity of a rainfall-shower determines the degree of soil erosion from runoff water (Venter *et al.*, 2003). Plant physiology is strongly affected by rainfall events where plants can be physiologically active for days or even weeks following rain, whilst becoming dormant before the next rainfall event (Venter *et al.*, 2003).

South African arid and semi-arid rangelands experience droughts on a regular basis (Vetter, 2009). Drought effects are most pronounced in herbaceous layers, because grasses and forbs are dependent on the moisture in the top layers of the soil, which is the first layer to become dry during dry periods (Gertenbach, 2010). Another adverse effect of drought in grasslands is the loss of species diversity in the herbaceous layer, especially when combined with overgrazing (O'Connor & Pickett, 1992), and when grazing pressure is low (Du Toit & Cumming, 1999). Given the predicted increase of severe drought events in African savannas as a result of global climate change (Du Toit & Cumming, 1999; Batisani & Yarnal, 2010; Van Wilgen *et al.*, 2016; Swemmer et al., 2018), there is a growing need to understand responses of grasses and forbs to drought, particularly in terms of species richness and diversity.

Herbivory as source of heterogeneity

Herbivores act as ecosystem modifiers and are particularly important in semi-arid African savannas where they influence the structure, function, dynamics, stability and resilience of these ecosystems (Bucher, 1987; Jacobs & Naiman, 2008; Waldram *et al.,* 2008; Cassidy *et al.*, 2013). Grazers have the ability to influence ecosystem processes and diversity by changing the spatial heterogeneity of the vegetation (Adler *et al.,* 2001; Riginos & Grace, 2008). At the start of the rainfall season, there is an increase in available forage and water, which drives the annual long-distance migration of ungulates (Bergström & Skarpe, 1999). This migratory behaviour exhibited by ungulates is essential in the functioning of savanna grazing systems (Fynn *et al.*, 2005; Augustine & McNaughton, 2006).

Herbivores influence the spatial heterogeneity and cycling of nutrients in savannas, either directly (defoliation and trampling) or indirectly (decomposition or defecation) (Augustine & McNaughton, 1998; Fynn *et al.*, 2005; De Knegt *et al*., 2008). Herbivores reduce canopy cover and biomass of certain dominant herbaceous and woody species, creating grazing patches, game paths and wallows, which in turn increases system heterogeneity (Olff & Ritchie, 1998; Jacobs & Naiman, 2008).

Herbivore effects on vegetation structure and spatial heterogeneity are driven by herbivore density (Waldram *et al*., 2008). Large mammalian herbivore densities which are either too high or too low may have major non-trophic impacts on the ecosystem (Augustine *et al.*, 2003; Van Langevelde *et al.*, 2003) i.e. transformation of the vegetation structure which alters the fire regime (Waldram *et al.*, 2008). Depending on the intensity, grazing pressure maintains the structure of the herbaceous layer, whilst browsing pressure maintains the structure of the woody layer (Augustine & McNaughton, 2004; Levick *et al*, 2009). However, overgrazing and human-induced shifts in herbivore guilds may cause changes in the vegetation composition of both the herbaceous and woody layers (Augustine & McNaughton, 2004; Baumgartner *et al.*, 2015).

The long history of coexistence and coevolution between plants and herbivores make African savannas ideal ecosystems in which to study plant-animal interactions (Scholes & Walker, 1993). In many African savannas indigenous wild herbivores are being replaced by domestic livestock (Teague & Smit, 1992; Du Toit & Cumming, 1999; Daskin *et al*., 2016; Veblen *et al.*, 2016; Riginos *et al.*, 2018), which may negatively affect ecosystem structure and function. Intensive livestock farming often leads to disturbance in the balance of standing crop biomass, especially perennial grass species, reduction of ecosystem heterogeneity, and an increase of bare soil patches and soil erosion (O'Connor, 1991; Du Toit & Cumming, 1999). Studies examining the overall response of plant communities to herbivore loss or herbivore guild change are lacking in semi-arid systems (Veblen *et al.*, 2016).

Soil nutrient status as a source of heterogeneity

Soil is an important driver of savanna ecosystems (Frost *et al.*, 1986), which affects and shapes the vegetation of an area through its texture, nutrient status, moisture content and variability on spatial and temporal scales (Scholes & Archer, 1997; Jeltsch *et al.*, 2000; Venter *et al.*, 2003;

Sankaran *et al.*, 2004). Most African savannas are classified as 'dystrophic' due to their association with broad-leaved vegetation on nutrient poor soil covered by a thin top layer of organic material (Van As *et al.*, 2013). The distribution of nutrients can, however, be irregular in semi-arid savannas which allows an area to have both nutrient-poor and nutrient-rich soil, depending on their position on the catenal sequence (Scholes, 1987; Scholes, 1990**;** Petersen, 2006; Siebert & Scogings, 2015). The underlying geology of an area determines the type of derived soil, which in turn will determine the composition of vegetation and fauna (Venter, 2010). Eutrophic or nutrient-rich savannas of arid and semi-arid regions are characterised by low bulk biomass of high-quality forage that support high densities of smaller grazing herbivores. In contrast, dystrophic or nutrient-poor savannas are characterised by high standing biomass of low-quality forage that host large herbivores in low densities (McNaughton & Georgiadis, 1986; Teague & Smit, 1992).

The Lowveld region of South Africa with its underlying granitic-derived soil has a characteristic catenary sequence which provides the area with a source of heterogeneity (Scholes, 1987). The catena phenomenon is common in savanna systems and describes an undulating landscape with broad, rounded, convex crests, mostly straight midslopes and defined concave footslopes (Alard, 2010). In the context of this area, catenas refer to predictable soil profile sequences and associated soil forms and vegetation communities (Alard, 2010). Most savannas are located on nutrient poor soil, with some areas exposed to alluviation having deeper, clay soils (Scholes, 1987; Van As *et al.*, 2013). Consequently, the soil type on ridge crests is shallow and sandy supporting broad-leaved (i.e. 'dystrophic') savanna vegetation, whereas bottomlands on deeper, clayey soil are characterised by fine-leaved vegetation (i.e. 'eutrophic' savanna vegetation) (Scholes, 1987; Venter *et al.*, 2003; Venter, 2010). Although widely recognized that variable annual rainfall is a significant driver of savanna vegetation composition and structure (Ellis & Swift, 1988), the importance of soil nutrients as a determinant of plant productivity remains important to acknowledge (Donaldson *et al.*, 1984; Snyman, 2002). Studies on semi-arid savanna vegetation has mostly been conducted in systems with nutrient-rich soil underlain by basalts or gabbros (Riginos & Young, 2007; Jacobs & Naiman, 2008; Burns *et al.*, 2009; Kotzé *et al.*, 2013; Porensky *et al.*, 2013; Baumgartner *et al.*, 2015). Despite the fact that most rural villages occur in nutrient-poor areas underlain by granite, only a few ecological studies have been conducted in these areas (Swemmer *et al.*, 2018). Other studies on nutrient-poor landscapes have been conducted in the Miombo woodlands (i.e. Gambiza *et al.*, 2000; Daskin *et al.*, 2016) and the Kalahari (i.e. Scholes *et al.*, 2002; D'Odrico *et al.*, 2007) and a few in Mopaneveld, which can be both nutrient-poor and nutrient-rich (Gertenbach, 1983; O'Connor, 1998; Macgregor & O'Connor, 2002).

2.3 Vegetation structure and community responses

Savanna dynamics are dependent upon interactive mechanisms involving various drivers (Augustine, 2003; De Knegt *et al*, 2008). Large herbivores can affect primary productivity and nutrient cycling either positively or negatively (Augustine & McNaughton, 2006; Cassidy *et al.*, 2013), or not at all (Fleischner, 1994; Hiernaux, 1998; Milchunas *et al*., 1988), depending on each ecosystem's unique characteristics. Large herbivores migrate across landscapes tracking soil nutrients and the associated productivity, consequently also distributing soil and grass nutrients across the landscape over time through dung and urine deposits (Frank *et al.*, 1998; Du Toit & Cumming, 1999; Augustine *et al.*, 2003; Fynn *et al.*, 2005). Inter-annual rainfall variability creates patches of high productivity across the landscape also driving the migratory behaviour of African mammalian herbivores (Bergström & Skarpe, 1999).

Herbivores drive savanna ecosystem functioning through their influence on species diversity (Adler *et al.*, 2001; De Knegt *et al.*, 2008; Jacobs & Naiman, 2008). Grazing pressure significantly affects plant communities, causing discernible shifts both in vegetation structure and composition (Archer, 1989; Angassa, 2014; Fynn; 2012). Increased grazing intensity generally suppresses herbaceous species richness and diversity (Porensky *et al.*, 2013; Wesuls *et al.*, 2013; Eby *et al.*, 2014). Only a few grazing-adapted species will increase in numbers when subjected to heavy grazing (Angassa, 2014) through grazing-adapted functional traits such as a prostrate growth form (Wesuls *et al.*, 2013). The effects of grazing may become apparent only after several years of exposure and sustained intensities, which alter vegetation composition and heterogeneity (Fynn & O'Connor, 2000; Adler *et al*., 2001; Burns *et al*., 2009). In some cases, herbaceous species richness decreases in the absence of herbivory and increases where herbivores are present due to lower biomass and decreased abundance and competition for light, water and nutrients within the herbaceous layer (Jacobs & Naiman, 2008; Asner *et al.*, 2009; Burns *et al.*, 2009).

Studies on herbivore effects suggest that an increase in plant diversity should occur in high-productivity habitats and a decrease in low-productivity habitats (Olff & Ritchie 1998; Bakker *et al.*, 2006). Habitats with limited resources may benefit from herbivore exclusion, since plant recovery and colonization may increase in the absence of herbivory, enhancing species richness (Olff & Ritchie 1998; Osem *et al.*, 2002). In high productivity habitats plant diversity is increased when plant-plant competition is alleviated and the establishment of species are constrained by herbivore presence (Eskelinen *et al.*, 2005; Bakker *et al.*, 2006; Young *et al.*, 2013).

Areas exposed to heavy grazing, such as sites near water points generally supports a lower species richness and herbaceous communities dominated by unpalatable annuals (Andrew, 1988), compared to lightly to moderately grazed sites (Angassa, 2014). At such sites, species richness is higher than heavily grazed sites, although the dominance and assemblages of herbaceous plants remain dependent on rainfall and its variability throughout the year (Ellis & Swift, 1988; Oba *et al.*, 2001; Bhattarai *et al.*, 2004; Roxburgh *et al.*, 2004; Catford *et al.*, 2011). Literature supports this since various studies have proven increased grazing pressure may also have significant effects on individual species, which will inherently alter the composition of herbaceous layers (Angassa, 2014). Combined effects of herbivory and drought therefore have profound effects on the composition and production of the vegetation (O'Connor, 1995). Combined effects of these two drivers may furthermore lead to rapid and significant plant community changes, opposed to the stand-alone effects of either one of these disturbances (Fuhlendorf & Smeins, 1997; Loeser *et al*., 2007; Stubbendieck & Tunnell, 2008; Dreber & Esler, 2011). In an experiment spanning over eight years, O'Connor (1995) observed drought as the primary driver of vegetation change, with herbivory causing additional change. Porensky *et al.* (2013) observed low species diversity during droughts with a marked increase in species diversity in the wet season following a drought event in areas under moderate livestock grazing pressure. The combined effect of herbivory and drought could in the short term cause a decrease in diversity and an increase in dominance of undesirable species i.e. unpalatable species (Milchunas *et al***.,** 1989; Gao *et al.,* 2009). Drought and herbivory have similar effects on herbaceous life forms and several studies found that their combined effects tend to release forbs, weeds, and annual grasses which replaces perennial grasses (Weaver & Albertson, 1936; Heady, 1966; Dunnett *et al.*, 1998; Sternberg *et al.*, 1999; Morecroft *et al.*, 2004; Stampfli & Zeiter, 2004; Renne & Tracy, 2007; Dreber & Esler, 2011).

Comparing the dynamics of grasses to forbs

In savanna systems palatable perennial grasses are important for livestock production (Uys, 2006; Trollope *et al.*, 2014), because they supply grazers with an essential source of forage stability (O'Connor, 2015). The distribution of mammalian herbivores has been linked to the rise in dominance and diversity of grasses (Scholes *et al.*, 2003), indicating the importance of grasses as forage for indigenous herbivores**.** Extreme droughts tend to increase perennial herbaceous species mortality (O'Connor, 2015) and when combined with heavy grazing, may lead to the extinction of certain desirable perennial grass species (Scholes *et al.*, 2003). Ecosystem responses to drought can be predicted to a certain extent by examining the life history traits of dominant species (O'Connor, 1995). For instance, palatable perennial grass species are sensitive to rainfall variability (Scholes *et al*., 2003; Buitenwerf *et al*., 2011; O'Connor, 2015), showing marked increases in years with above average rainfall and decreases significantly during years with below average rainfall (O'Connor, 2015; Tessema *et al.,* 2016). In semi-arid southern African savannas drought episodes may favour annual grasses (O'Connor, 1998; Buitenwerf *et al*., 2011). Furthermore, sustained heavy grazing with no rest favours annual grasses and unpalatable perennial grasses, as well as annual and perennial forbs, all of which may lead to a decrease in palatable perennial grasses (Milchunas & Lauenroth, 1993; Lavorel *et al*., 1997; Fynn & O’Connor, 2000; Buitenwerf *et al*., 2011; O’Connor, 2015; Tessema *et al*., 2016). However, herbivory and rainfall are not the only factors effecting vegetation compositional changes; soil as an environmental gradient interacts with herbivory and rainfall which could aid in explaining vegetation responses (Young *et al.*, 2013). Soil properties (e.g. fertility and water holding capacity) are important in moderating grass layer compositional responses (O’Connor, 2015). Heavy textured fertile soil is more prone to changes in perennial grass composition than sandy infertile soil (O’Connor, 2015).

Forb cover and density are highly affected by seasonal rainfall (Nicolai *et al.*, 2008), with the emergence of certain forb species being driven by the first precipitation after a dry season or a drought event (Uys, 2006; Casillo *et al.*, 2012). Uys (2006) found that forb richness declined sharply in areas with a MAP of below 800 mm with monocotyledonous species richness showing a sharper decline than that of dicotyledonous species. Small environmental changes are known to prompt strong responses from forbs (Shackleton, 2000; Lettow *et al*., 2014) as is evident in the increases of both annual and perennial forb species during and after drought events (O’Connor, 1998) and under heavy grazing pressure (Fynn & O’Connor, 2000; Buitenwerf *et al.,* 2011). Forbs are suggested to benefit from elevated atmospheric CO_2 levels (Bond & Parr, 2010), reinforcing the importance of studying this life from since forbs are the greatest contributors to herbaceous species diversity and richness in savannas and grasslands (Turner & Knapp, 1996; Uys, 2006; Jacobs & Naiman, 2008; Van Coller *et al.,* 2013; Trollope *et al.,* 2014; Siebert & Scogings, 2015; Van Oudtshoorn, 2015). Results from several studies on herbaceous layer dynamics suggest that species richness and diversity of certain forb species are favoured by light to moderate grazing intensity (Fynn & O'Connor, 2000; Nicolai *et al.*, 2008; Hejcmanová *et al.*, 2010; Wesuls *et al.*, 2013; Cowley *et al.*, 2014; Siebert & Scogings, 2015). When exposed to high grazing intensities, forb communities will generally shift from palatable perennial native species, to annual and often exotic species (Jacobs & Naiman, 2008; Nicolai *et al.*, 2008). In ecosystems which evolved through moderate grazing controls, grasses and forbs coexist leading to an increase in herbaceous species richness and diversity (Bakker *et al.*, 2003; Hayes & Holl, 2003; Jacobs & Naiman, 2008; Van Coller & Siebert, 2015). In contrast, forb abundance and diversity tend to decline when exposed to heavy grazing, although this is more common in mesic grasslands (Scott-Shaw & Morris, 2015).

Protected areas and communal rangelands: two contrasting rangeland types

Effects of herbivory on plant species richness is largely dependent on the herbivore guild as well as the abundance of the herbivores hosted by a particular system (Olff & Ritchie, 1998; Smet & Ward, 2005). The diverse assemblage of indigenous wild herbivores which roam the grasslands and savannas of southern Africa have in many regions been replaced by single-species domestic livestock (Du Toit & Cumming, 1999; Pollard *et al.*, 2003; Augustine & McNaughton, 2004; Koerner *et al*., 2014; Baumgartner *et al.*, 2015; Charles *et al.*, 2017). Such changes in herbivore guilds could be meaningful for production, considering that wild herbivores comprise a more diverse set of species compared to livestock – which, in Africa is for the most part limited to cattle, sheep and goats (Baumgartner *et al.*, 2015; Veblen *et al.*, 2016). Despite apparent similarities in their diet, the effect on productivity and spatial structure may differ with each herbivore guild and species involved (Olff & Ritchie, 1998; Smet & Ward, 2005; Charles *et al.*, 2017). Porensky *et al.* (2013) suggested that grazing by livestock, compared to indigenous wild herbivores, may have a significantly larger effect on savanna plant community structure and function, even if the system has a long history of grazing. Small browsers such as goats, impala and kudu limit the growth of trees shorter than 2 m, whilst the African elephant and other large browsing herbivores have larger effects on taller trees (Augustine & McNaughton, 2004; Owen-Smith & Cooper, 1985; Prins & Van Der Jeugd, 1993). The density of woody species, especially those prone to cause bush encroachment is therefore expected to be greatest under mono-specific grazing (Augustine & McNaughton, 2004; Baumgartner *et al.*, 2015) where important natural bush control agents, such as elephant, impala and kudu are absent. Higher stocking densities of livestock exert more strain on the vegetation than the lower stocking densities of indigenous wild herbivores (Du Toit & Cumming, 1999; Charles *et al.*, 2017). Overstocking of livestock will generally lead to a decrease in herbaceous layer species diversity and an increase in a few grazing-tolerant species (Hanke *et al.*, 2014). In most cases, indigenous wild herbivore guilds comprise of a greater species diversity than livestock, which increases the range of foraged species and, consequently spreading the strain on the vegetation across a wider range of species (Fynn, 2012; Kartzinel *et al.,* 2015). Diverse methods of defoliation such as differences in cropping height preferences, foraging time, frequency and duration, as well as certain plant species being preferentially browsed by each herbivore guild and species (Burkepile *et al.*, 2017, Owen-Smith & Cooper, 1985) bring forward distinct physiological and demographic effects (Charles *et al.*, 2017). Grazers feed mainly on graminoid monocots (grasses and sedges), whereas browsers feed on herbaceous forbs and the twigs and leaves of woody plants and mixed feeders forage on both food types (Odadi *et al.*, 2013). Despite being classified as grazers, cattle will also feed on forbs, depending on the season and location (Ralphs & Pfister, 1992; Beck & Peek, 2005; Odadi *et al.*, 2007; Roba & Oba, 2009). A study by Odadi *et al.* (2007) observed that forbs constituted up to 15% of the intake of cattle, providing further evidence that forbs are an important part of livestock diets. Studies comparing the effects of wildlife versus livestock grazing/browsing are limited, but it has been suggested that these herbivore guilds could coexist (Odadi *et al.*, 2011; Charles *et al.*, 2017). Despite the assumed forage value of forbs, the effect of livestock and wildlife grazing/browsing on forbs at both functional trait and species levels remains less explored.

Herbivore exclosures in the Kruger National Park, South Africa, has been used in many studies to determine the different effects of herbivory on the herbaceous community. In general, the exclusion of all herbivores on low productivity sites caused increased herbaceous species richness, whereas the species richness decreased on high productivity sites (Jacobs & Naiman, 2008; Van Coller, 2014; Burkepile *et al.*, 2017). The exclusion of small/medium herbivores caused a significant change in species richness on high productivity sites, with increased forb species richness being most notable (Burkepile *et al.*, 2017). Van Coller (2014) reported highest species richness in areas exposed to herbivores and lowest species richness in areas excluding herbivores. The exclusion of herbivores leads to an increase in dominance by certain plant species, which ultimately changes the ecological mechanisms through which plants interact. Such system modifications lead to plant species richness declines (Eby *et al.*, 2014; Burkepile *et al.*, 2017).

The impacts of herbivore loss on ecosystems are highly context dependent and various factors might affect the outcome, i.e. herbivore guild that is lost, the plant functional type involved, as well as the local environmental context (Waldram *et al.*, 2008; Goheen *et al.,* 2013; Van Der Plas *et al.,* 2016). Most studies on the combined effects of herbivory and drought have concentrated on domestic herbivores, consequently studies that compare the effects of indigenous wild herbivores with livestock during drought are limited and necessary (Porensky *et al.*, 2013).

Plant functional trait and -group assemblages

A functional trait is any measurable characteristic of an individual plant that is likely to affect its fitness or performance (Lavorel *et al.,*1997; Mokany *et al.*, 2008; Cadotte *et al.*, 2011; Lavorel *et al.,* 2011). The characteristics can be biochemical, physical, temporal, or phenological, hence providing support towards determining where species can live, how they interact as well as their how they contribute to ecosystem functioning (Lavorel *et al.,*1997; Mokany *et al.*, 2008; Cadotte *et al.*, 2011; Lavorel *et al.,* 2011). Ecologists generally lump together species with similar functions and disturbance responses. Functional trait assemblages and dominance is more commonly being used in ecological studies (Cadotte *et al.*, 2011). The use of functional traits in the description of vegetation, instead of floristic composition alone, or the use of these measures in concert is considered useful to scientists. Such approaches allow for the comparison of taxonomically distinct floras, as well as providing a summary of the underlying biodiversity of particular ecosystems (Lausi *et al.*, 1989; Díaz *et al.*, 1999; McIntyre *et al.*, 1999). Recently, the importance of dominant plant traits in ecosystem functioning has also been observed (Díaz *et al.*, 1999; Lavorel & Garnier, 2002; Cadotte *et al.*, 2015). Trait-based studies of ecosystems may improve our understanding of the link between vegetation structure and ecosystem processes and function (Díaz *et al.*, 1999; Cadotte *et al.*, 2015), which would be difficult without the use of plant traits. In understudied areas rich in diversity, traits could offer a way to predict and understand the response of the system to various land management regimes, which would be challenging to observe at species level alone (Díaz *et al.*, 2001). Plant traits suitable to be used in these instances must be ecologically relevant and simultaneously easy to measure (Lavorel *et al.*, 1997, Weiher *et al.*, 1999). Species richness and/or composition may show changes as a result of various climatic factors or disturbances after long time periods, whereas trait diversity, ecosystem structure and function could potentially show such changes much quicker (Meyer *et al.*, 2010). Analyses of functional traits allow for the detection of these changes which could be obscured by apparent species composition stability (Díaz *et al.*, 1999, Cadotte *et al.*, 2011; Hanke *et al.*, 2014). Significant progress has been made in the description of functional assemblages and diversity of plant communities, but the ability to predict the composition and diversity of communities in response to a disturbance have only recently been developed (Cadotte *et al.*, 2015).

Plant functional types or –groups (also referred to as 'beta guilds' Wilson (1999)) comprise species which group together based on their similar response to changes in environmental conditions, their capacity to fulfil the same function within the ecosystem, and the way in which they affect major ecosystem processes (Díaz *et al.*, 1999, Meyer *et al.*, 2010). Species that possess similar functional traits will therefore be classified within the same plant functional type. Several studies have highlighted the importance of considering the biotic and abiotic environment when studying an ecosystem on functional level, because these factors interact and thus influence species response to disturbance (Díaz *et al.*, 1999, Linstädter *et al.*, 2014; Kimball *et al.*, 2016; Lohmann *et al.*, 2017).

Plant traits that have been identified as good predictors of grazing response, include plant height (maximum height to grazer), small stature (prostrate, scrambler, erect), tender leaves, and high specific leaf area (SLA) (Díaz *et al.*, 1999; McIntyre *et al.*, 1999). Shorter plants with small leaves resist grazing through their traits which conveys grazing avoidance (Noy-Meir *et al.*, 1989; Díaz *et al.*, 2001). Other traits associated with grazing avoidance include leaf toughness, prostrate growth form and low palatability (Coughenour, 1985; Grime *et al*. 1996; Cornelissen *et al*. 1999; Van Coller, 2018). Local climatic variation also determines the role played by large herbivores in ecosystems (Augustine & McNaughton, 2006). Certain traits allow plants to resist the effects of drought. Such traits usually also enable plants to tolerate herbivory, as seen in defoliation tolerance traits in plant communities of arid ecosystems (Coughenour, 1985; Milchunas *et al.*, 1988).

Savanna vegetation has evolved and developed mechanisms to resist the effects of drought (Uys, 2006). Some of these adaptations include short spinescent branches, small leathery leaves, flaky bark, and multi stemmed growth forms (Coetzee, 2010). In the absence of heavy grazing, the extreme change observed in herbaceous layer highlights the unmistakable effect of rainfall on the vegetation of semi-arid savannas (O'Connor, 1998). Describing and understanding the responses of individual forb species and trait groups is extremely important in forming an improved picture of forb responses to climatic aridity. In arid areas with reduced moisture, typical plant traits include reduced leaf size (ericoid and sclerophyllous leaves), succulence, crassulacean acid metabolism (CAM) and C_4 photosynthetic pathways and xeromorphic roots (fibrous, shallow or adapted for storage) (Dudley, 1996). Clonality allow plants to regenerate through vegetative strutures called ramets, which allow the plant to expand horizontally following a disturbance (Pérez-Harguindeguy *et al*., 2013).

Functional traits and functional classification allow ecologists to understand and describe the mechanisms and processes that are responsible for changes in vegetation in response to disturbances such as rainfall variability and drought (McIntyre *et al.*, 1999; Weiher *et al.*, 1999; Lohmann *et al.*, 2017). When using traits to study and describe vegetation it is crucial to take the local conditions i.e. location, topography, herbivore guild, etc. into account when compiling the trait list to be used for the particular study (McIntyre *et al.*, 1999).

2.4 Summary

African savanna ecosystems are well known for their faunal diversity and associated flora that are maintained by landscape heterogeneity and numerous natural disturbance events. Many people across the continent depend on savannas for their livelihood, not only through crop production and livestock farming (commercial or communal), but also through tourism in nature reserves and protected areas. Inter-annual rainfall variability, herbivory and soil nutrient status are important drivers of savanna ecosystem structure, diversity and function. A sound knowledge of these drivers and their impact on savanna structure and function is paramount to understand and conserve the rich biodiversity and dynamic ecosystem functions of these systems. The co-existence of trees and grasses under various biotic and abiotic disturbances have been studied in detail, although studies on the dynamics of the herbaceous layer other than grasses are generally lacking. Forbs are suggested to play an important role in savanna ecosystem functioning and resilience, reinforcing the importance of studying this generally neglected herbaceous life form further.

Chapter 3

Study Area

3.1 Locality

The study was conducted at two rangeland types in the Gazankulu area along the Klaserie-Orpen (R531) road in Mpumalanga, South Africa (Figure 3.1).

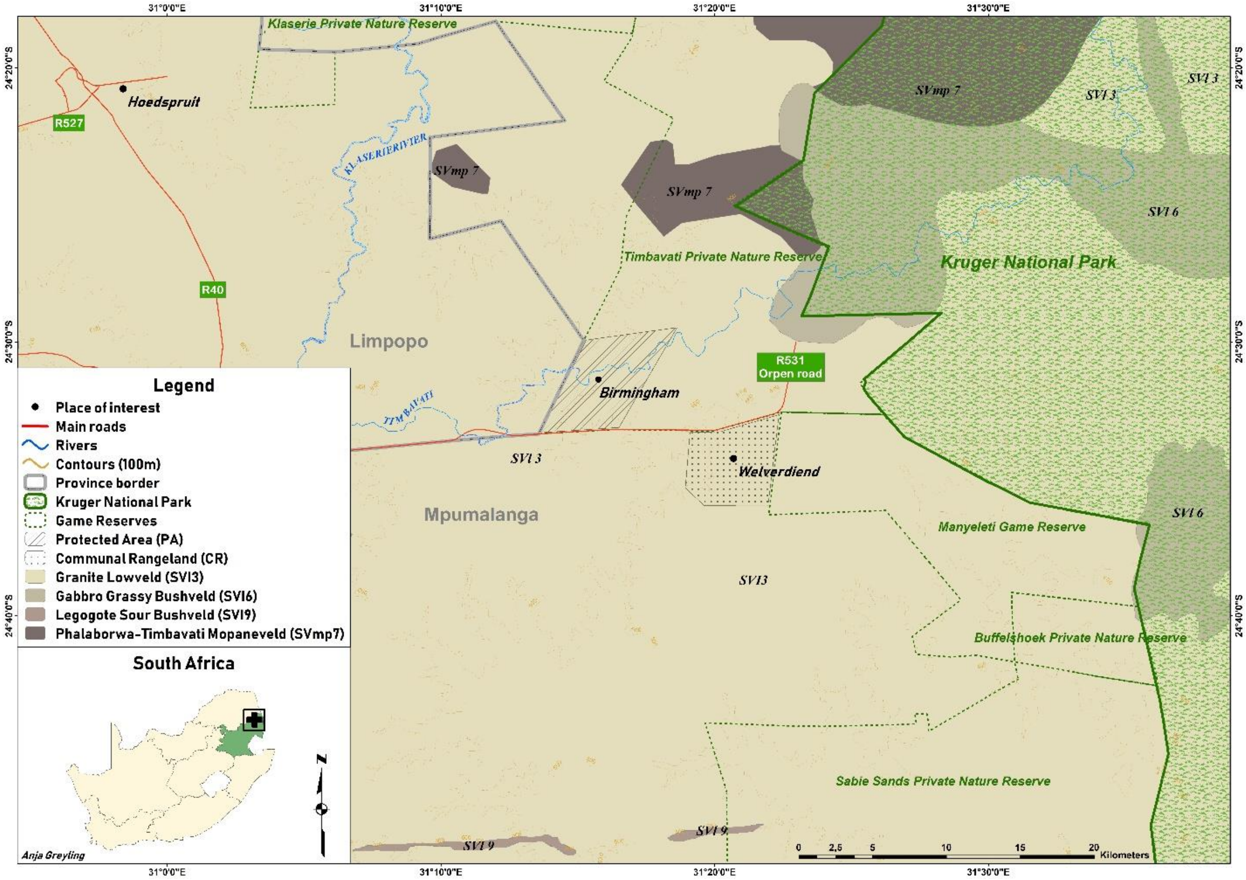

Figure 3.1: Map of the two study sites, with an inset map of South Africa indicating the position of the broader study area (Map prepared by A. Greyling).

The Birmingham section of the Timbavati Private Nature Reserve (TPNR) is located North of the Klaserie-Orpen (R531) road and served as the Protected Area (PA) rangeland type (i.e. indigenous wildlife site), whereas Welverdiend, a rural village South of the R531 represented the Communal Rangeland (CR) livestock site (Figure 3.2). The two sampling sites are separated by a distance of approximately 7 km, although they are both located within similar geology, rainfall and broad topography and soil types. Please refer to Chapter 4 for a detailed description of the experimental design and sampling techniques followed within these two studied sites.

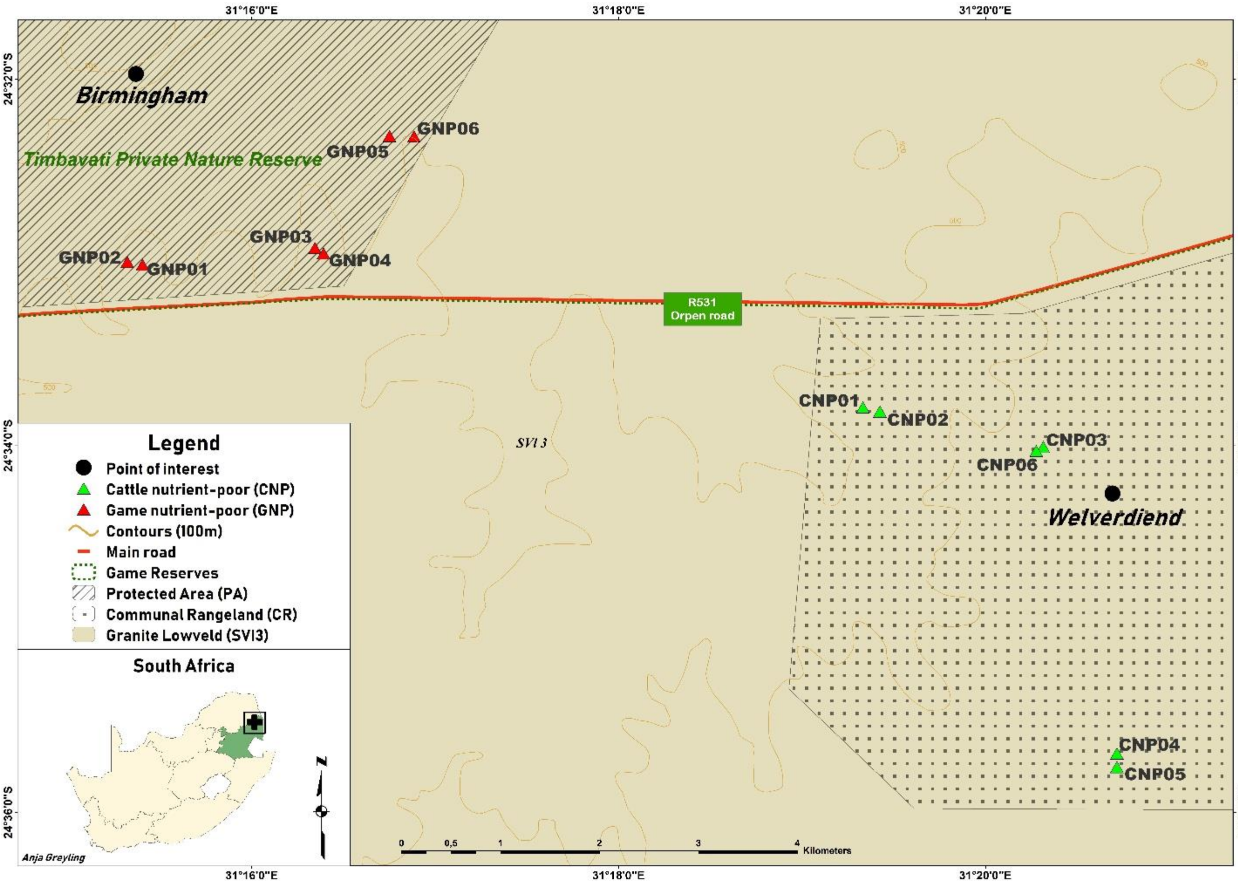

Figure 3.2: Map of the sampling sites within each rangeland type. Sites within the PA (Protected Area) are depicted by red triangles, whilst green triangles indicate sites within the CR (Communal Rangeland) (Map prepared by A. Greyling).

3.2 History and land use

Timbavati Private Nature Reserve (Protected Area)

The Timbavati Association was established in 1956 by a group of landowners with conservation as their main objective (Hirst, 1969; Bornman, 1995; Timbavati Private Nature Reserve, 2016). Prior to the establishment of the Timbavati Association, the area was subjected to increased soil erosion and destruction of indigenous plant species as a result of intensive crop production and cattle farming (Timbavati Private Nature Reserve, 2016) which was prevalent in the reserve for the first part of the twentieth century (Van der Waal *et al.*, 2011). The construction of dams which rerouted natural water sources to water dependent farmers caused further damage to the natural state of the area and declines in wildlife numbers (Timbavati Private Nature Reserve, 2016). Today, the TPNR is owned by more than 50 private landowners and forms part of the Associated Private Nature Reserves (APNR), all of which removed their border fences with the Kruger National Park (KNP) in 1993 to form part of the Greater KNP (Kreuter *et al.*, 2010; Mwakiwa, 2011; Timbavati Private Nature Reserve, 2016).

The reserve hosts a variety of indigenous wildlife including mixed feeders (elephant , impala and steenbok), browsers (greater kudu, giraffe, black rhino and bushbuck), and grazers (Cape buffalo, blue wildebeest and plains zebra (*Equus burchelli*) (Hirst, 1975; Van der Waal et al., 2011; Timbavati Private Nature Reserve, 2016). Predators residing in the study site include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), hyena (*Crocuta crocuta*), as well as the critically endangered African wild dog (*Lycaon pictus*) (Hirst, 1975; Van der Waal et al., 2011; Timbavati Private Nature Reserve, 2016). Since the removal of the border fences between TPNR and the KNP, some of the specialist rare antelopes, such as roan (*Hippotragus equinus*), eland (*Taurotragus oryx*) and tsessebe (*Damaliscus lunatus*) have returned to the area, although not in substantial numbers (Timbavati Private Nature Reserve, 2016). Permission was granted by TPNR management for sampling to take place in Birmingham, a privately-owned farm in the south-western corner of TPNR.

Welverdiend (Communal Rangeland)

The Welverdiend village is located in the southern most exclave of Gazankulu, a former homeland for the Shangaan-Tsonga people (Cadman, 1987; Shackleton, 2000). Situated relatively far away from the economic hub of the region (Banks *et al.*, 1996), the people of Welverdiend and surrounding villages largely depend on communal farming, and even more so on natural resources to sustain their livelihoods (Shackleton, 2000; Dovie *et al.*, 2006; Kneidel, 2009). Herbivores are limited to domestic cattle and goats, which are heavily stocked in areas surrounding the village which are zoned off for livestock grazing with no buildings or manmade structures, but due to reduced authority of traditional chiefs in the area, there is little regulation of the use of these communal rangeland zones (Shackleton, 2000, Shackleton & Shackleton, 2004; Kaschula *et al.*, 2005; Petersen, 2006; Matsika *et al.*, 2012). Each household who owns cattle are allocated a piece of the rangeland zone where their cattle can graze during the day.

Cattle are ushered to the rangeland zones early in the morning and returned to the village in the afternoon where they spend the night in a boma or kraal. With this grazing system most of the rangeland zones are grazed continuously during the year with no rest periods. Fenced off areas for crop production are the only areas in and around the village which are not grazed by cattle (Mightyman Mashele, personal communication).

Areas surrounding the village are mainly protected areas (George, 2000) – TPNR to the north, Manyeleti Private Game Reserve and KNP to the east and south-east, and to the west it borders the Timbavati rural village. Grazing and harvesting pressure is significantly higher in Welverdiend and the surrounding villages when compared to the neighbouring nature reserves, mainly because management plans of the protected areas prescribe lower stocking rates as well as the exclusion of local village people (Matsika *et al.*, 2012). In 2009 the South African Environmental Observation Network (SAEON) established a developing long-term ecological research site in Welverdiend to determine the effects of fuelwood harvesting and communal livestock on biodiversity and functioning of this savanna ecosystem. SAEON granted permission to sample their established monitoring sites.

3.3 Topography

The landscape is associated with a flat to undulating topography, giving rise to a catenal sequence which includes a complete series of terrain morphologies (Kaschula *et al.*, 2005). Altitude rarely exceeds 600 m above sea level (Shackleton *et al.*, 1994; Banks *et al.*, 1996). Crests have characteristic shallow, coarse sandy nutrient-poor soil, whereas nutrient-rich soils with high clay content and high water holding capacity characterise footslopes (Kaschula *et al.*, 2005). Nutrient-poor, potassic granites and granodiorite are typical of the underlying Bandelierkop Complex and its complex strata (Kaschula *et al.*, 2005). The area is classified as semi-arid subtropical savanna with characteristic vegetation of Granite Lowveld SVI3 (Mucina & Rutherford, 2006). Woody plants that dominate the tree layer include members of the Combretaceae (*Terminalia sericea, Combretum spp.*) and Mimosaceae families (*Vachellia spp.* and *Senegalia spp.)* (Shackleton, 2000). Dominance of these woody families varies significantly across the area (Kaschula *et al.*, 2005).

Due to the paucity of information on nutrient-poor granitic crests, this study will focus on the herbaceous layer of these topographic land forms. Past studies have mostly been conducted on highly productive nutrient-rich soils i.e. studies in the KNP and Tanzania (Pratt *et* *al.*, 1966; McNaughton, 1985; O'Connor, 1995; Veblen & Young, 2010; Siebert & Scogings, 2015; Swemmer *et al.*, 2018) consequently leading to a knowledge gap on nutrient-poor savanna herbaceous layer responses to disturbances.

3.4 Vegetation

Gertenbach (1983) classified the vegetation of the study area as Mixed *Combretum* spp*./Terminalia sericea* Woodland. This vegetation type is also described as *Combretum*-veld, Mixed *Combretum* Savanna Woodland, *Combretum*-veld on Granite Undulations, Tropical Semi-Arid Granitic Lowveld and Arid Lowveld and broadleaf savanna (Van Der Schijff, 1957; Pienaar, 1963; Van Wyk, 1973; Acocks, 1975; Coetzee, 1983). The uplands or crests of the area are characterised by dense bush savanna vegetation and the bottomlands by open tree savanna (Gertenbach, 1983). Sandy soils of the crests are characterised by *Terminalia sericea/Combretum zeyheri/Combretum apiculatum* communities where few to no trees occur within a dense shrub layer (Gertenbach, 1983; Venter, 1986). The discontinuous woody component is dominated by *Cissus cornifolia, Combretum apiculatum, Combretum zeyheri, Commiphora africana, Dalbergia melanoxylon, Dichrostachys cinerea, Ormocarpum trichocarpum, Peltophorum africanum, Pterocarpus rotundifolius, Sclerocarya birrea, Senegalia burkei, Strychnos madagascariensis, Terminalia sericea* and *Ziziphus micronata*. Two other woody plants, *Albizia harveyi* and *Senegalia nigrescens* are found on steeper slopes (Gertenbach, 1983; Venter, 1986). Dominant graminoids in the discontinuous herbaceous layer include *Aristida congesta* subsp. *barbicollis, Digitaria eriantha, Panicum maximum, Heteropogon contortus, Schmidtia pappophoroides*, *Urochloa mosambicensis, Eragrostis rigidior, Trichoneura grandiglumis, Pogonarthria squarrosa* and *Aristida meridionalis* (Gertenbach, 1983; Venter, 1986). The forb component of crest herbaceous layers is dominated by *Tephrosia polystachya, Commelina bengalensis, Rhynchosia totta, Clerodendrum ternatum, Leucas glabrata, Evolvulus alsinoides, Chamaecrista mimosoides, Waltheria indica, Indigofera filipes, Agathisanthemum bojeri, Kohautia virgata, Chamaecrista absus, Merremia* (syn. *Xenostegia*) *tridentata, Hibiscus micranthus, Tragia dioica, Phyllanthus asperulatus* and *Stylosanthus fruticosa* (Gertenbach, 1983). A complete list of the plants sampled in the study area is presented in Appendix B, Table B1, which is accompanied by species acronyms used for analyses.

3.5 Climate

Rainfall

The Lowveld savannas of South Africa are classified as subtropical with two distinct seasons, a highly variable wet season when rainfall is concentrated in the summer months between October and April/May in the form of convectional thunderstorms (Kaschula *et al.*, 2005, Matsika *et al.*, 2012), and a dry non-growing season associated with high temperatures and water stress (Williams *et al.*, 2009). Mean annual rainfall for the study area ranges between 500 - 700 mm (Kaschula *et al.*, 2005; Matsika *et al.*, 2012), from 700 mm in the west to 500 mm in the east (Gertenbach, 1983; Shackleton *et al.*, 1994; Banks *et al.*, 1996). Drought events occur approximately once every 10 years (Matsika *et al.*, 2012). The summer rainfall region of South Africa experienced a major drought between 2014 - 2016, with the Central Lowveld (north-eastern Mpumalanga and southern Limpopo) experiencing two consecutive years of below long term mean rainfall (Figure 3.3) (Swemmer *et al.*, 2018). The previous major drought episodes in South Africa occurred in the early and late 1990's (Swemmer *et al.*, 2018).

Temperature

The study area has a temperate climate with frost only occurring on the bottomlands (Gertenbach, 1983). A regular phenomenon in the area is temperature inversions, where daytime temperatures are higher at the bottomlands than the uplands, whilst the bottomlands cool down significantly at night (Gertenbach, 1983). The mean annual temperature for the area is 22°C, and rises to a mean daily temperature of 30°C during the hot summers (Shackleton, 1994). Winters are mild and dry, and reach a mean daily temperature of 23°C (Shackleton, 1994). A distinguishing feature of the 2014 - 2016 drought was the extreme temperatures, with an unusually high number of months in 2015 reaching a mean monthly maximum above 30°C (Swemmer *et al.*, 2018).

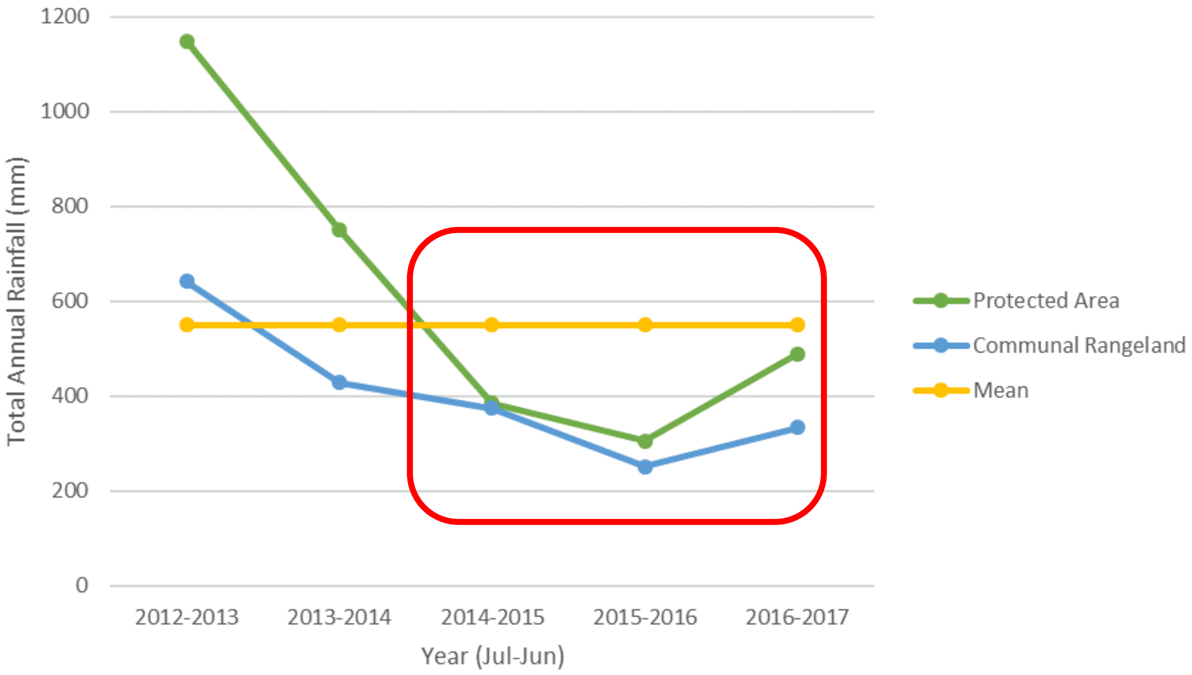

Figure 3.3: Total annual rainfall for the study area from July 2012 to June 2017, long term mean annual rainfall for the communal rangeland rainfall station is indicated in yellow. The drought of 2014 - 2016 is highlighted by a red square (Rainfall data provided by A.M. Swemmer and A. Bosch)

3.6 Geology

Vegetation structure and species composition are strongly correlated with the geology and soil of the area (Timbavati Private Nature Reserve, 2016). The study area is underlain with granite and gneiss, with the occurrence of various dolerite intrusions (Gertenbach, 1983). These parent materials are rich in feldspar and quartzite, which comprise silica and oxygen and limited amounts of iron and magnesium (Timbavati Private Nature Reserve, 2016). The area is characterised by sandy soils derived from weathering of the geological substrata (Timbavati Private Nature Reserve, 2016).

3.7 Soil

Granitic crests are mostly characterised by Hutton and Clovelly sandy soil forms with clay a content of between 6 – 15% (Gertenbach, 1983). Hutton soils consist of weakly structured orthic

A–horizons with a reddish colour, and red apedal (unstructured) B–horizons (Soil Classification Working Group, 2009). Clovelly soils differ from Hutton soils in having a yellow-brown apedal B–horizon (Soil Classification Working Group, 2009), low fertility and water holding capacity when compared to Hutton soil forms with a similar clay content (Merryweather, 2002). Refer to Appendix C Table C1-C3 for soil characteristics of the study area.

Chapter 4

Materials and Methods

4.1 Introduction

This chapter provides a detailed description of the survey methods used to collect floristic and trait data, as well as the statistical analyses that were applied for which results are presented in Chapters 5 and 6.

4.2 Experimental design and sampling

Selection of sampling sites

Sampling sites were located in two rangeland types which represented distinct herbivore communities: i) indigenous free roaming wild herbivores of the Timbavati Private Nature Reserve (hereafter referred to as the Protected Area or PA) and ii) communal livestock of the Welverdiend communal village (hereafter referred to as the Communal Rangeland or CR). A reconnaissance field trip was conducted prior to sampling, to verify the pre-identified homogeneous areas (through Google Earth 2017 images) on the granitic crests of the Lowveld Savanna Biome. Homogenous areas where sampled to ensure any changes detected in vegetation composition and structre could be ascribed to herbivory and rainfall and not to other environmantal factors. Suitability of sampling plots was verified through field observations. Granitic sites in the communal rangeland were selected to overlap with the SAEON long-term vegetation monitoring sites, which were established in 2009. These sites surrounding the village of Welverdiend were established to determine the effects of fuelwood harvesting on the biodiversity and functioning of this savanna ecosystem. SAEON granted permission for the use of the broader area within which their established monitoring sites are located. Care was taken to avoid placing sampling plots directly within or near these sites as to avoid any effects of fuel harvesting on the sampled data. Sampling plots were carefully placed on the upland crest along which represented the environmental gradient as to sample within a homogenous vegetation type (Figure 4.1). During each sampling season (i.e. drought and post-drought) herbaceous floristic and functional data, together with biomass were sampled within each large (50 x 20 m) plot, and the cover for each species was visually estimated.

Experimental layout

An adapted version of the Modified Whittaker sampling technique was applied since it allowed for estimates of mean species cover, analysis of plant diversity patterns at multiple spatial scales, as well as trend analyses from monitoring (Stohlgren *et al.*, 1995). Fixed plots were established on nutrient-poor granitic crests using six Global Positioning System (GPS) coordinates which were furthermore used to locate the plots with 0.9 m accuracy in the following season (see Appendix C for an example of the datasheets used to record sampling data). GPS coordinates were taken on the four outermost corners of the 50 x 20 m plot (i.e. points 1,3,4,6; Figure 4.1) as well as at the starting point (2), and end point (5) of the 50 m transect (Figure 4.1). During the 2016 rainfall year 6 large (50 x 20 m) plots were sampled per rangeland type, i.e. 12 large plots in total for the 2016 rainfall year. Sampling was repeated in 2017, during which 6 large (50 x 20 m) plots were sampled per rangeland type, totalling 12 large plots for the 2017 rainfall year (a total of 24 large plots were sampled across rangeland types and rainfall years).

Vegetation sampling within 1 m^2 sub-plots

Vegetation sampling was conducted in October and November of 2016 at the end of the extended drought period, and repeated in January 2017 after first significant rainfall of the 2016/2017 wet season. Total percentage cover of vegetation, bare soil, leaf litter and debris were recorded within each of the five 1 m^2 sub-plots (Figure 4.1), adding up to 100% per 1 m^2 sub-plot. Furthermore, the percentage basal cover for each individual herbaceous species, together with a browse/graze index was recorded. All herbaceous individuals (forbs, sedges and grasses) rooted within the 1 m^2 sub-plots were counted and identifiedto species level conforming to Germishuizen and Meyer (2003). Above-ground rooted clonal structures were counted as individuals. Unknown species were collected outside the fixed plots from which herbarium specimens were prepared for identification at the A.P. Goossens Herbarium of the North-West University, which holds a comprehensive collection of forbs and grasses from the Lowveld Savanna.

Functional trait selection and sampling

Traits were assigned to species using various sources of literature (Van Oudtshoorn, 2002; Cornelissen *et al.*, 2003; Germishuizen & Clarke, 2003; Germishuizen & Meyer, 2003; Van der Walt, 2009; Manning, 2009; JSTOR, 2016) and through field observations during sampling (hairiness and palatability). Traits were selected for their perceived relevance to disturbance response (i.e. Landsberg *et al*., 1999, Lavorel *et al*., 1999; Díaz *et al.*, 2001; Cornelissen *et al.*, 2003), with specific focus on domestic and wild ungulate grazing and drought. Detailed plant functional trait measurements were recorded per species within the first 1 m^2 sub-plot, which included traits explained in Table 4.1 (see Figure C1 Appendix C for an example of the datasheets used to record sampling data). A browse/graze index between one and five was given based on visual evidence of herbivory, where number one was recorded for signs of light herbivory and number five was recorded for signs of heavy herbivory. The browse/graze index was used to determine palatability in conjunction with available literaure. Hairiness was recorded for individuals if the plant had either hairy stems, hairy leaves or the whole plant was covered in hair. Thereafter, recordings were made only for the species not encountered in the previous sub-plots. Traits were therefore only measured once per species in each 1000 m^2 plot. Each recorded species was defined according to a set of morphological, regenerative and physiological traits (Table 4.1) to determine their responses to variations in grazing and rainfall year. Although many of the selected functional traits were sampled for both grasses and forbs, certain traits were identified as being relevant to a distinct herbaceous life form (Table 4.1). Trait datasets for forbs and grasses were analysed separately since previous studies have shown that certain response patterns may be obscured when the herbaceous layer is analysed as a whole (Lavorel *et al.*, 1997; McIntyre *et al.*, 1999) and life form responses strengthen disturbance effects (Biswas & Malik, 2010; Linstädter & Baumann, 2013). For statistical analyses, each life form database was furthermore separated into annuals and perennials since life history is known to be a strong indicator of disturbance response (Belsky, 1992; Pettit *et al.*, 1995; Díaz *et al.*, 2007; Linstädter *et al*., 2014).

Biomass sampling within the 200 m^2 center plot

Standing herbaceous biomass was collected during both sampling years from a 10 x 10 cm (100 cm^2) square frame which was placed at five randomly selected locations within the 200 m^2 plot (Figure 4.1). Forbs and grasses were separated to estimate the contribution of each life form to total above-ground biomass. Herbaceous biomass was dried at 30 ºC for 24 hours. Dry material was weighed and converted to kilograms per hectare (kg/ha).

Soil nutrient status and particle size distribution

Soil samples were collected during the first sampling season (2016 i.e. drought year) and not during the second sampling season (2017 i.e. post-drought year) to establish soil nutrient status and particle size distribution at each site. Five sub-samples, taken from the top 10 cm of the soil layer in close proximity of each 1 m^2 sub-plot, were pooled for a representative sample per 1000 m^2 plot. Soil samples were placed in brown paper bags and stored for analyses to confirm our assumption that vegetation sampling was conducted on the nutrient-poor granitic substrates. Soil analysis was done by an independent laboratory. Soil particle size distribution (> 2mm, sand, silt and clay) were determined by filtering soil samples through different size sieves. The nutrient content, pH and electrical conductivity was determined using the 1:2 extraction method (Scoggings *et al.*, 2002). Results are presented in Tables C1, C2 and C3 (Appendix C).

Table 4.1: Selected plant functional traits recorded for each herbaceous life form.

Forbs		**Grasses**	
Trait number	**Trait**	**Trait number**	**Trait**
1	Growth habit	1	Growth habit
2	Herbaceous or Woody	2	Growth form
3	Average height	3	Average height
4	Observed hairiness	4	Observed hairiness
5	Leaf size	5	SLA
6	SLA	6	Life history
7	Life history	7	Palatability
8	Palatability	8	Clonality
9	Spinescence	9	Seed dispersal mode
10	Clonality	10	Average tuft basal area
11	Nitrogen fixing ability		
12	Seed dispersal mode		
13	Sun or Shade		
14	Underground Storage Organ		

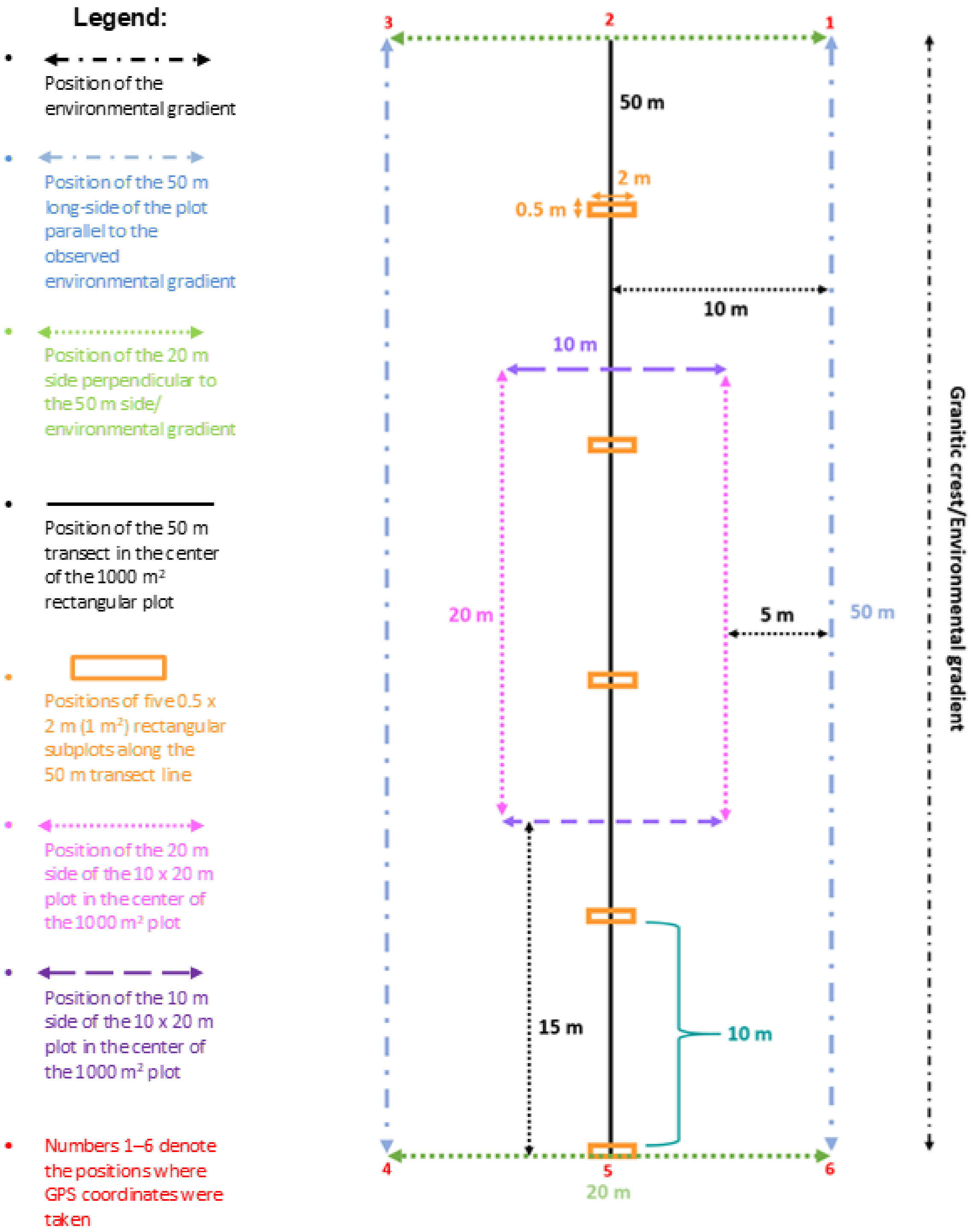

Figure 4.1: Experimental layout of a typical 50 m transect within each 1000 m^2 plot, as well as the position of the 200 m^2 middle plot and five 1 m^2 sub-plots.

Table 4.2: Selected plant functional traits with a short description of the categories and codes, units, definitions of traits and motivation for selecting these particular traits in this study.

Forb functional traits					
Trait	**Category and code score**	**Trait unit**	**Definition**	**Relevance to study**	**References**
Growth habit	1= Erect 2= Prostrate 3= Tussock 4= Climber	Categorical	Mainly determined by canopy structure and height	Reveals plant strategy and adaptations in response to changes in climate and land use	Cornelissen *et al.* (2003)
Herbaceous or Woody	1= Herbaceous 2= Woody	Categorical	Determined as woody when the plant had a woody base (or woody rootstock)	Reveals plant adaptation to remain stable during drought episodes and defence against herbivory	Pérez-Harguindeguy *et al*. (2013)
Average height	1= 0 - 5 cm 2= >5 - 10 cm 3= >10 - 20 cm 4= >20 - 40 cm 5= >40 cm	Categorical	Measured from the top of the photosynthetic tissues to the ground level	Reveals competitive vigour and response to disturbances such as damage and climatic factors and light availability	Cornelissen *et al.* (2003); Pérez-Harguindeguy *et al*. (2013) (measured during sampling)
Leaf size	1= Small (*Evolvulus alsinoides*) 2= Small, long/slender (*Heliotropium strigosum*) 3= Medium (*Waltheria indica*) 4= Medium, long/slender (*Chorchorus asplenifolius*) 5= Medium, round (*Chamaecrista absus*) 6= Large (*Abutilon	Categorical	Measured in mm. For this study reference species were identified and used to determine leaf size. Leaf sizes of the various forb species listed in brackets were used as proxies for each of the respective leaf size categories.	Interspecific variation in leaf size has been attributed to environmental nutrient stress, disturbances or climatic variation (e.g., drought might select for species with small leaves)	Cornelissen (2003); Pérez-Harguindeguy *et al.* (2013)

	angulatum) 7= Large, long (*Stylochiton natalensis*)				
Spinescence	0 = Absent 1 = Present	Binary	Indicates the degree to which a plant is defended by the presence of spines, thorns and/or prickles	Adaptations for anti-herbivore defence and a response to damage	Cornelissen *et al*. (2003); Scholes et al. (2003); Pérez-Harguindeguy *et al.* (2013)
Nitrogen fixing	0 = Absent 1 = Present	Binary	Improves efficiency of plant nutrient uptake, converts atmospheric nitrogen (N) into ammonia (NH_3), the N form utilised by plants	Aids in plant growth and nutrient cycling	Cornelissen *et al.* (2003); Van Oudtshoorn (2015)
Sun or Shade	1= Sun 2= Shade	Categorical	Corresponds with a plant's ability to function in certain light conditions	Plant survival in disturbed areas with high sun exposure	Baker (1967) Valladares and Niinemets (2008)
Underground storage organs	1= None 2= Woody rootstock 3= Tuberous rootstock 4= Woody rhizome 5= Woody taproot 6= Unspecified	Categorical	Linked with clonality, may serve as vegetative reproduction organ and/or as underground storage organ	Provides plant with ability to survive disturbances and damage	Cornelissen *et al.* (2003)
Grass functional traits					
Trait	**Category and code score**	**Trait unit**	**Definition**	**Relevance to study**	**References**
Growth habit	1= Erect 2= Prostrate	Categorical	Based on canopy structure and height	Reveals plant strategy and adaptations in response to changes in climate and land use	Van Wyk and Malan (1998); Kirby (2013); Kotschy, (2013)
Growth form	1= Tuft	Categorical	Stolons provides		

	2= Stoloniferous		the ability to reproduce vegetatively and expand horizontally in disturbed areas		
Average height	1= >0 - 5 cm 2= >5 - 20 cm 3= >20 cm	Categorical	Measured from the top of the photosynthetic tissues to the ground level	Reveals competitive vigour and response to disturbances such as damage and climatic factors and light availability	Cornelissen *et al.* (2003); Pérez-Harguindeguy *et al*. (2013) (measured during sampling)
Average tuft basal area	1= >0 – 3 cm 2= >3 – 10 cm 3= >10 cm	Categorical	Diameter measured at the widest part of the tussock and then calculate tussock area	Determines herbivore preference	O’Reagain (1993)

General plant functional traits					
Trait	**Category and code score**	**Trait unit**	**Definition**	**Relevance to study**	**References**
Average height	1= 0 - 5 cm 2= >5 - 10 cm 3= >10 - 20 cm 4= >20 - 40 cm 5= >40 cm	Categorical	Measured from the top of the photosynthetic tissues to the ground level	Reveals competitive vigour and response to disturbances such as damage and climatic factors and light availability	Cornelissen *et al.* (2003); Pérez-Harguindeguy *et al*. (2013) (measured during sampling)
Observed hairiness	1= Glabrous 2= Hairy stem 3= Hairy leaves 4= Completely hairy	Categorical	Any form of a trichome (Epidermal cells with outgrowths that prevents the plant surface to be classified as glabrous)	Limits water loss through evapotranspiration, may deter herbivory	Payne (1978)
SLA (Specific Leaf Area)	1= <10 2= 10-20 3= 20-30	Categorical	One-sided area of a fresh leaf divided by its	Low values usually correspond with	Garnier *et al*. (2001); Cornelissen *et*

	4- 30-40 5= Unspecified		oven-dry mass (mm^2 mg^{-1})	high leaf defence investment and high values coincides with low stress environments	*al.* (2003); Pérez-Harguindeguy *et al.* (2013)
Life history	1= Annual 2= Perennial 3= Unspecified	Categorical	Period of time from the establishment of the plant until no live part remains	Reveals adaptation to damage and disturbance	Cornelissen *et al.* (2003); Lavorel *et al.* (1997); Kotschy (2013); Pérez-Harguindeguy *et al.* (2013)
Observed palatability	1= Low 2= Moderate 3= High	Categorical	Corresponds with the amount of nutrients in the plant and influences herbivore preference	Provision of food to two different herbivore guilds	Manning (2009); Van der Walt (2009); Van Oudtshoorn (2015); Siebert & Scogings (2015)
Clonality	0 = Non-clonal 1 = Clonal	Binary	A plant's ability to reproduce vegetatively	Provides plants with competitive vigour, and aids in survival after disturbances, may also aid in migration when seed dispersal is poor	Cornelissen *et al.* (2003); Pérez-Harguindeguy *et al.* (2013); Kotschy (2013)
Seed dispersal mode	1= Unassisted 2= Anemochory 3= Exozoochory 4= Endozoochory 5= Exozoochory & Endozoochory 6= Unspecified	Categorical	Ability of a plant to disperse its seed, fruit or spore	Ability of a plant to establish or survive in a specific environment despite disturbances	Cornelissen *et al.* (2003); Pérez-Harguindeguy *et al.* (2013)

4.3 Treatment combinations

Six fixed plots were sampled at each rangeland type (i.e. herbivore treatment), adding up to a total of 12 plots per sampling year, each representing different rainfall conditions: (i) October

2016 as the drought sample, and (ii) January/February 2017 as the post-drought sample. Data analyses were performed on a total of 120 1m^2 plots, each with its own set of floristic and trait data nested within 24 larger plots (50 m x 20 m) across distinct rangeland types (Table 4.3).

4.4 Data preparation

Excel (Windows 2016) spreadsheets were used to capture and consolidate data. The complete data matrix consisted of quantitative floristic (i.e. species and individual counts, physical trait measurements) and literature-based trait data for herbaceous species for each transect across both treatments for the years 2016 and 2017. Data were formatted to be imported into PRIMER 6 software (Clarke & Gorley, 2006), Paleontological Statistics Software (PAST) (Hammer *et al*., 2001), SPSS version 24 (Hancock & Mueller, 2010), Canoco (Ter Braak & Šmilauer, 2002) and Statistica version 13.3 (TIBCO Software Inc., 2007) software packages. Herbarium specimens of unidentified species collected during floristic sampling were kept to aid in identification. Herbarium specimens were collected of species in flower and stored in the A.P. Goossens Herbarium in Potchefstroom for identification and to supplement the existing collection of plant material from the Lowveld Savanna.

4.5. Data analyses

Herbaceous composition of species (Chapter 5) and functional traits (Chapter 6)

Herbaceous species composition and functional trait composition across different rangeland types and rainfall years (drought (2016) vs. post-drought (2017)) were explored using Non-Metric Multi-Dimensional Scaling (NMDS) analyses compiled in PRIMER 6 software (Clarke & Gorley, 2006). Square root transformation was applied to species abundance data and trait abundance data to equalise the contributions of rare and common species or traits as well as to reduce the impact of significant differences in total abundances (Kent, 2012). The data were further analysed using the Bray-Curtis similarity index. Bray-Curtis similarity distance measure is recommended for ordinations and is used together with Permutational Multivariate Analysis of Variance (PERMANOVA) (Scogings *et al.*, 2012; Taylor *et al.*, 2012; Linstädter *et al.*, 2016; Veblen *et al.*, 2016). NMDS is an unrestricted indirect ordination method that is used to evaluate the gradient of diversity between locations (i.e. beta diversity) (Kent, 2012).

A species abundance per plot matrix was analysed with NMDS to determine species composition (Chapter 5). Using the MMult function in Microsoft Excel, a functional trait-plot matrix was compiled by multiplying a functional trait-species matrix (with presence and absence data) with a species-abundance matrix and NMDS analyses was then applied to this data to determine functional trait composition (Chapter 6). NMDS ordinations are based on species space and environmental space and similar sites/species/traits are plotted closer together and dissimilar sites/species/traits further apart on the ordination plot (Gaines & Gratton, 2010; Kent, 2012). Ordination results were presented as two-dimensional plots in the respective results chapters. The measure fit or match between two data points is referred to as the stress value which can be any value ≥ 0 (Kent, 2012). NMDS stress values can be interpreted as follows: (i) a stress value of < 0.05 provides an excellent representation with no chance of misinterpretation, (ii) a stress value of < 0.1 indicates a good ordination with low risk of misinterpretation, (iii) a stress value of < 0.2 could still provide a good two-dimensional picture, and (iv) a stress value > 0.2 is most likely to produce a poor representation and should be interpreted with caution (Clarke, 1993).

To substantiate the NMDS visual representations, PRIMER 6 software was used to apply Permutational Multivariate Analysis of Variance (PERMANOVA; permutations = 999; type III sums of squares) to the data to test for significant variance in floristic (Chapter 5) and functional trait composition (Chapter 6) across rangeland types and rainfall years. PERMANOVA is a preferred tool used to analyse differences in plant community assemblages since it applies permutational methods to test hypotheses in cases where data do not conform to assumptions of normality of the traditional multivariate correspondents of one-way analyses of variance (ANOVA) (Scogings *et al.*, 2012; Taylor *et al.*, 2012; Linstädter *et al.*, 2016). Pairwise comparisons of PERMANOVA allowed for differentiation where treatments differed significantly. A Monte Carlo test was also applied to determine the probability that the NMDS stress was derived by chance (Kent, 2012).

To identify which species contributed most to significant differences among floristic clusters (Chapter 5), Similarity Percentage Analysis (SIMPER) was applied to the species abundance data using PAST (Hammer *et al*., 2001). SIMPER determines and compares the overall percentage contribution of each species to the similarity between two groups (Clarke, 1993, Hunter, 2017).

Species biomass (Chapter 5)

Repeated measures analysis of variance (ANOVA) combined with the Bonferroni *post-hoc* significance test was performed on forb and grass biomass data separately. This was done to determine whether herbaceous life form biomass varied across rainfall years and between rangeland types. T-test for independent samples by groups were applied to determine how biomass of herbaceous life forms changed over time across rangeland types. All analyses were done in STATISTICA version 13.3 (TIBCO Software Inc., 2007) with the standard significance level set at $p < 0.05$ which allowed for confident conclusions based on the statistical results (Lindgren & Sullivan, 2001).

Species diversity patterns (Chapter 5)

For species diversity analyses, grass and forb data sets were kept separate to establish response differences between these two herbaceous life forms. A separate species abundance-plot matrix was compiled in Excel (Office 2016) for forbs and grasses which was also analysed separately across rangeland type. Calculation of diversity indices (total species (S), total individuals (N), Simpson's index of diversity (1-Lambda), Shannon-Weiner diversity index (H'), Margalef's index (d) and Pielou's evenness index(J')) was done in PRIMER 6 software (Clarke & Gorley, 2006). Using a combination of these indices provided a complete outline of herbaceous species richness and diversity patterns since these indices cover multiple aspects of diversity (Kent, 2012). Species richness is defined as the number of species present in a defined area (e.g. a quadrat or community) (Kent, 2012). Species diversity can be defined as the total number of species combined with their relative abundances (evenness) (Kent, 2012). For this study species richness was considered as the total species (S) calculated as the mean number of species recorded for each rectangular nested sub-plot (1 m^2).

Simpson's diversity index is one of the most widely used diversity indices. This index places emphasis on the most abundant species in a sample and is therefore less sensitive to species richness (Magurran, 2004). In essence this diversity index calculates the variance of species abundance in a sample (Magurran, 2004) using the following equation:

$$1 - \sum \frac{n_i(n_i - 1)}{n(n-1)}$$

where n represents the mean total of individuals per plot and n_i is the number of individuals of the i^{th} species (Peet, 1974).

Shannon-Wiener index of diversity stems from information theory and has been applied with great success in biological sciences (Kent, 2012). This index operates on the assumption that an infinitely large population is randomly sampled and that the sample will include all species present in the relevant community (Kent, 2012). The Shannon-Wiener Index was calculated according to the following equation:

$$H' = \sum_{i=1}^{s} p_i \ \ln p_i$$

where s is the number of species, p_i represents the abundance of the i^{th} species, and ln = log base_n (Kent, 2012).

Margalef's species richness is highly sensitive to sample size and requires data as absolute numbers and not as a density data matrix (Gamito, 2010; Magurran, 2004). Margalef's species richness index was calculated as follows:

$$\mathrm{d} = \frac{S-1}{\ln N}$$

where S is the number of species, and N is the total number of individuals in the sample (Gamito, 2010) and ln = log $\text{base}_{n.}$

Evenness is defined as the distribution of individuals over species (Crowder *et al.*, 2012). This index is not only highly dependent on sample size, but also the inclusion or exclusion of rare species (Crowder *et al.*, 2012). Pielou's evenness was determined as follows:

$$J' = \frac{H'}{\ln S},$$

where H is the observed value of the Shannon-Weiner index and S is the total species in the sample (Zhang *et al.*, 2012).

The normality of the data set was tested before detailed statistical analyses were applied by plotting the distribution of richness, diversity, abundance, and cover estimate data between different rangeland types and rainfall year treatments on histograms, Q-Q plots and the application of Kolmogorov-Smirnov and Shapiro-Wilk normality tests.

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

The nested data structure comprised of three hierarchical levels, which included 1 m^2 sub-plots within 1000 m^2 fixed plots that were established within two rangeland types. To account for the nestedness of transects within treatments, the sampled plots were specified as subjects (ID) with life form, rainfall year and rangeland type as the interactive effects.

Significant differences in forb and grass richness, diversity and cover estimates in response to rangeland type and rainfall year was tested further using effect sizes (Cohen's *d*). Effect sizes were interpreted as: (i) small effect: d =0.2, (ii) medium effect: d =0.5 and (iii) large effect $d \geq 0.8$ (Cohen, 1988; Ellis & Steyn, 2003). Effect sizes were calculated according to the following equation:

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

Whereby *MSE* is the mean square error and $\mathbf{x}_i$ is the sample mean of the ith group.

Only large effect sizes (i.e. highest significance) have been visually presented; whereas medium effect sizes are only reported.

Identification of plant functional types (PFTs) (Chapter 6)

A total number of 95 forb species and 29 grass species were investigated according to type compositions of 14 (forbs) and 10 (grass) pre-selected drought- and herbivore-tolerant traits (Table 4.1). Separate trait databases were compiled for grasses and forbs. A data matrix of species (rows) and traits (columns) was constructed for each life form in which each trait was given a numerical score (binary or categorical) as listed in Table 4.2. The selection and sampling of traits were done according to the procedures and methods described in section 4.2. Trait categories were established according to the cited literature in Table 4.2.

Initial analyses of the combined trait data for grasses and forbs indicated a strong influence of life form as supported by Lavorel *et al.* (1997). Forb and grass trait data sets were subsequently split to conduct separate analyses for forbs and for grasses. Furthermore, each life form database was separated into five different matrices: 1) Full trait data set, 2) Drought (2016) data set, 3) Post-drought (2017) data set, 4) PA data set and 5) CR data set, which delivered ten trait data sets in total. This allowed for detailed analyses within each life form to determine the contribution of traits other than life history (Lavorel *et al.*, 1997) (i.e. clonality, hairniess) and also to allow for the identification of functional types associated with each rangeland type (i.e. herbivore treatment) across the respective rainfall period (i.e. drought and post-drought).

An Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clustering with a hierarchical agglomerative clustering analysis and Gower distance measure was used in PRIMER 6 software (Clarke & Gorley, 2006; Kent, 2012). This method grouped plant species based on their trait scores which were in the form of binary and categorical data (Botha, 2017). Gower’s general similarity coefficient was used as it is suitable for mixed data types – binary or categorical (Kent, 2012; Botha, 2017). The cluster analyses were combined with a Similarity Profile (SIMPROF) test, which is known for being objective in identifying significant groupings (Botha, 2017). Groupings of species obtained from the cluster analyses were filtered based on significance of traits that were well represented and the less significant traits or traits with poor representation were omitted from the next round of analyses (McIntyre *et al.*, 1999). Final clusters on which PFTs were based consisted of strong groupings of species based on significant traits. These clusters delivered various instances of two-trait PFTs, four-trait PFTs and five-trait PFTs.

Linking plant functional type assemblages with rangeland type and rainfall year (Chapter 6)

Similar to the procedures followed to construct a trait-plot matrix, the MMult function in Microsoft Excel was used to compile a functional type-plot matrix for each herbaceous species separately. The treatment-plot matrix for each rainfall year used rangeland type in binary form, which was linked to the environmental data. Environmental gradients consisted of rangeland type treatment (PA and CR) as well as certain soil characteristics (macro elements: Calcium (Ca), Magnesium

(Mg), Potassium (K) and Sodium (N); micro elements: Iron (Fe), Manganese (Mn), Copper (Cu), Zink (Zn) and Boron (B); pH; EC (Electrical Conductivity) and P-Bray 1 (extractable Phosphorus)). Refer to Table C2 and C3 for details on soil characteristics.

Canoco for Windows version 4.5 (Ter Braak & Šmilauer, 2002) was used to investigate associations between functional type assemblages and herbivore and/or rainfall treatments and soil characteristics for both herbaceous life form data sets respectively. To detect gradient length Detrended Correspondence Analysis (DCA) with detrending segments was performed on functional group-plot matrices for both rainfall years (Lepš & Šmilauer, 2003). DCA gradient length estimates the heterogeneity of the community and it indicates the ordination method best suited to the data (Lepš & Šmilauer, 2003). A DCA gradient length larger than 4.0 indicates that the data is unimodal and heterogenous, whereas a DCA gradient length smaller than 4.0 reveals that the data is linearly distributed (Lepš & Šmilauer, 2003; Van Staden, 2016). Unimodal CA (Correspondence Analysis) or CCA (Canonical Correspondence Analysis) is used when DCA gradient length exceed 4.0 and Principal Component Analysis (PCA) or Redundancy Analysis (RDA) is used to analyse linear data (Lepš & Šmilauer, 2003).

PCA was applied to the data sets of forbs and grasses to provide a summary of community variation (Ter Braak & Šmilauer, 2002) and to reveal associations between PFTs, rainfall years and rangeland type. Eigenvalues for each PCA ordination are presented in Table E1 Appendix E. Eigenvalues were used to represent the relative contribution (%) of each component to the explanation of the total variation in the data (Kent & Coker, 1994). Each of the components had one eigenvalue and the magnitude of the value was directly indicative of the importance of that component to the total data variation (Kent & Coker, 1994).

Chapter 5

Forb and grass community responses to drought

5.1 Introduction

Increased population growth in Africa has led to significant agricultural land use expansion and increased livestock densities in savanna ecosystems (Pollard *et al.*, 2003; Koerner *et al.*, 2014; Baumgartner *et al.*, 2015; Veblen *et al.*, 2016; Zerbo *et al.*, 2016). Combined with these anthropogenic perturbations are natural disturbance events, such as drought, which is predicted to increase in frequency and severity due to global climate change (Batisani & Yarnal, 2010; Van Wilgen *et al.*, 2016). Understanding effects of disturbances such as drought and herbivory on savanna vegetation structure and dynamics is essential for the management and conservation of semi-arid rangelands since herbaceous vegetation plays a key role in the functioning of these systems.

Herbaceous communities provide important services to savanna ecosystems including forage for herbivores (Scholes & Walker, 1993; Bailey & Scholes, 1997; Khomo & Rogers, 2005), protection against soil erosion through soil stability, increased water filtration aided by organic litter, cycling of nutrients (Walker *et al.*, 1981; Moretto *et al.*, 2001) and fuel for fires (Skarpe, 1992; Bond, 1997; Govender *et al.*, 2006; Van Wilgen *et al.*, 2011). Grasses and forbs respond differently to drought and herbivory which affects the species composition and diversity of the herbaceous layer (Augustine & McNaughton, 1998; Augustine & McNaughton, 2006; Odadi *et al.*, 2011; Veblen *et al.*, 2016; Van Coller *et al.*, 2018). Since responses by the forb component of herbaceous layers to disturbances such as drought and herbivory remain less explored (Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015), their responses will be compared to grasses which have been studied more extensively (i.e. Morris & Tainton, 1993; Uys, 2006; Treydte *et al.*, 2013; Trollope *et al.*, 2014). Research on the effects of variations in herbivore pressure and severe droughts on herbaceous community dynamics will allow for better predictions of savanna system response to future climate change under different land use regimes which could potentially allow for better management and conservation of savanna ecosystems (O'Connor, 1995; Gao *et al.*, 2009; Vetter, 2009; Porensky *et al.*, 2013; Treydte *et al.*, 2013; Riginos *et al.*, 2018; Swemmer *et al.*, 2018).

This chapter aimed to 1) quantify the effect of rangeland type (i.e. communal rangeland and protected area) on the herbaceous community structure and diversity and 2) assess herbaceous layer responses under different rainfall conditions.

Specific objectives were to:

1. Assess changes in species composition, richness, diversity and biomass across rangeland type and rainfall year for each herbaceous life form, respectively (i.e. forbs and grasses);
2. Identify the herbaceous species that contributed most to compositional changes between rangeland types and across rainfall years.

Studies on semi-arid rangelands with a long history of intensive grazing suggest that other systems with a similar grazing history would show higher resilience to high grazing pressure and drought in terms of grass species composition, than systems with a shorter grazing history (Milchunas *et al.*, 1988; Fynn & O'Connor, 2000; Riginos *et al.*, 2018). Accordingly, it was expected that drought would not significantly affect grass species composition in the communal rangeland, but the protected area was expected to reveal major shifts in species composition. Moreover, various studies have shown that domestic herbivores exert greater qualitative effects on species richness and diversity than native wild herbivores (Shackleton, 2000; Porensky *et al.*, 2013; Zerbo *et al.*, 2016; Riginos *et al.*, 2018). Therefore, changes in species richness and diversity were expected to be more pronounced in the communal rangeland than the protected area. Grass biomass and cover were hypothesised to be lowest during the drought, irrespective of rangeland type as rainfall variability is known to have a larger effect on herbaceous biomass and cover than grazing pressure (O'Connor, 1995; Fynn & O'Connor, 2000). Furthermore, lower biomass and plant cover was anticipated for heavily grazed communal rangeland sites, relative to protected area sites, as suggested by various studies on herbaceous vegetation dynamics (i.e. O'Connor, 1994; Illius & O'Connor, 1999; Treydte *et al.*, 2013; Hanke *et al.*, 2014). Studies on forb responses to herbivory and drought are limited. Considering the diversity of forbs, uniform responses to a specific set of climatic conditions would seem unlikely. Forbs tend to show increased establishment and dominance following environmental disturbances (Scholes, 1987; Buitenwerf *et al.*, 2011). It was therefore hypothesised that annual forbs will be more abundant and dominant after the drought, especially in the communal rangeland.

5.2 Methods

For details on experimental layout and field sampling please refer to Chapter 4, section 4.2 and for details on methods used for statistical analyses refer to section 4.5.

5.3 Results

Results presented in this chapter report on the drought response effects through shifts in species composition and diversity for each (i) rangeland type (i.e. PA and CR) and (ii) herbaceous life form (i.e. forbs and grasses). Significant differences ($p<0.05$; $d > 0.8$) are indicated with an asterisk (*) in all figures and tables. Drought refers to the 2016 rainfall year and post-drought refers to the 2017 rainfall year.

5.3.1 Herbaceous species composition

Non-Metric Multi-Dimensional Scaling (NMDS) results revealed strong evidence of drought and rangeland type effects on herbaceous species composition (Figure 5.1 & Figure 5.2).

Table 5.1: Permutational multivariate analysis of variance (PERMANOVA) results indicating similarity in species composition of forbs and grasses across various combinations of rangeland type and rainfall year.

Treatment combination	***F*-value**	***p*-value**
Forbs		
Drought vs Post-drought	12.233	0.001*****
Protected Area (PA) vs Communal Rangeland (CR)	12.742	0.001*****
PA Drought vs PA Post-drought	12.616	0.001*****
CR Drought vs CR Post-drought	10.579	0.001*****
Grasses		
Drought vs Post-drought	8.813	0.001*****
Protected Area (PA) vs Communal Rangeland (CR)	15.32	0.001*
PA Drought vs PA Post-drought	13.71	0.001*****
CR Drought vs CR Post-drought	1.811	0.101

Drought effects

Rainfall year, irrespective of rangeland type, had a larger effect on the composition of the forb community (*F* = 12.233, *p* = 0.001) than the grass community (*F* = 8.813, *p* = 0.001) (Table 5.1), although forb and grass species assemblages responded significantly to post-drought conditions, the sigificance was only visible for forbs (Figure 5.1) due to a high species turn over for forbs across rainfall years (Table D1 Appendix D).

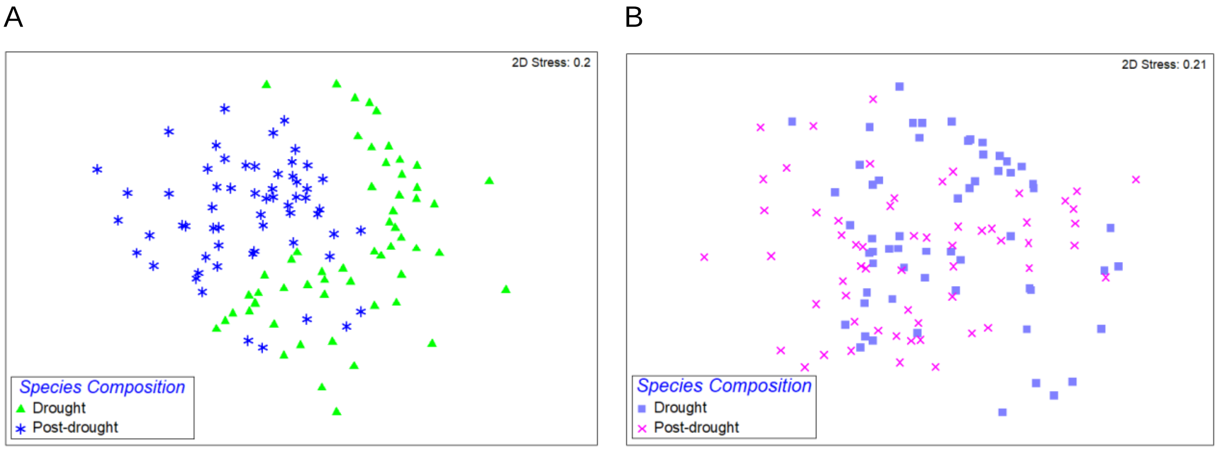

Figure 5.1: Non-Metric Multi-Dimensional Scaling (NMDS) ordination scatter plots illustrating variation in species composition, irrespective of rangeland type between rainfall years for (A) forbs and (B) grasses.

Similarity percentage analysis (SIMPER) identified six forb species (*Tephrosia purpurea, Limeum viscosum, Triumfetta rhomboidea, Hibiscus pusillus*, *Kohautia virgata and Hermannia boraginiflora*) responsible for the shifts in forb species composition, mainly as a result of their absence during the drought surveys and their emergence and dominance after the drought (Table D1 Appendix D). Shifts in grass species composition was mainly due to the post-drought emergence of three species (*Aristida congesta* subsp*. barbicollis, Aristida adscensionis* and *Eragrostis lehmanniana*) which were absent during the drought (Table D2 Appendix D).

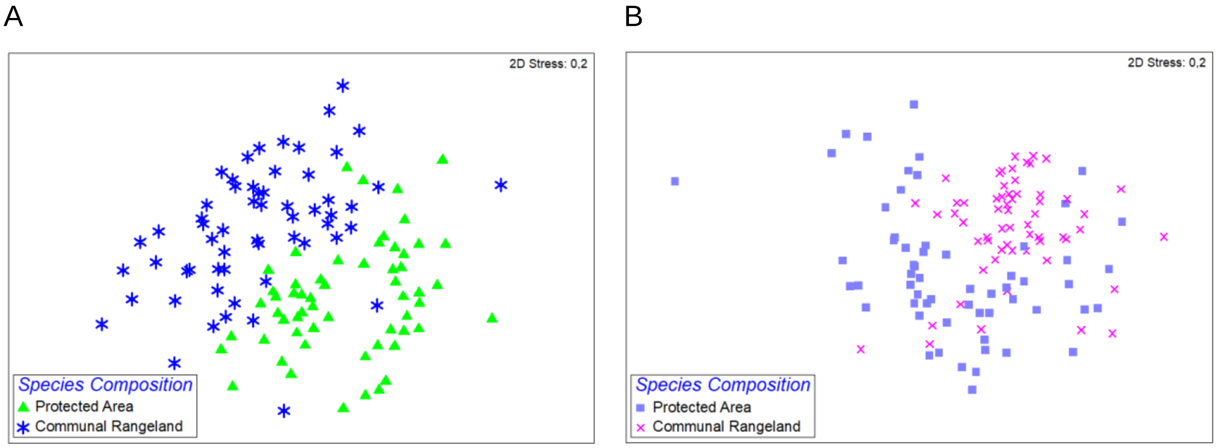

Figure 5.2: Non-Metric Multi-Dimensional Scaling (NMDS) ordination scatter plots indicating differences in species assemblages across rangeland types, irrespective of rainfall year for (A) forbs and (B) grasses.

Rangeland effects

Analyses of the rangeland types, irrespective of rainfall year, provided evidence that a rangeland specific flora exists for both the PA and the CR. Herbaceous species composition varied significantly across rangeland types for both life forms (forbs: F = 12.742, p = 0.001; grasses: F = 15.32; p = 0.001; Table 5.1), although the visual presentation of plots in ordinal space is stronger for forbs (Figure 5.2 A) than for grasses, which revealed some overlap in a two-dimensional space (Figure 5.2 B). Forb species dominant in the communal rangeland included *Kyllinga alba, Cleome macrophylla, Tephrosia purpurea* and *Bulbostylis hispidula*, whereas *Gisekia africana, Chamaecrista mimosoides, Limeum viscosum* and *Cyperus rupestris* (Table D3 Appendix D) characterised the protected area. Differences in grass species composition across rangeland types was mainly due to the dominance of *Panicum maximum, Aristida adscensionis* and *Aristida meridionalis* in the PA, and *Digitaria eriantha, Aristida congesta* subsp. *congesta, Eragrostis rigidior* and *Cynodon dactylon* in the CR (Table D4 Appendix D).

Rainfall effects

NMDS results suggested the presence of a drought-tolerant grass flora in the CR, but not so for the forb component (Figure 5.3 C & D). Grass and forb community composition differed significantly between drought and post-drought sampling years in the PA (Figure 5.3 A & B). Overlapping of plots in a two-dimensional space suggests limited effects of drought on grass species in the CR, which are suggested to be more drought-tolerant (Figure 5.3 D; Table D8

Appendix D). Visual patterns were corroborated by PERMANOVA analyses which indicated that the drought effect was stronger for both grasses (*F* = 13.7, *p* = 0.001; Table 5.1) and forbs (*F* = 12.616, *p* = 0.001; Table 5.1) in the PA. Differences in forb species composition within the PA was mainly driven by the absence of certain species during the drought and the dominance of others after the drought, such as *Limeum viscosum, Chamaecrista absus*, *Hibiscus pusillus, Bulbostylis hispidula, Triumfetta rhomboidea* and *Kohautia virgata* (Table D5; Appendix D). A similar pattern was observed for the CR forb community, where species composition differed significantly between rainfall years (*F* = 10.579, *p* = 0.001; Table 5.1) due to the presence and/or absence of certain species. Although significant, the effect of drought was not as strong on CR forb communities compared to PA forb communities (Table 5.1). In the CR dominant forb species during the drought were *Cleome macrophylla, Monsonia angustifolia, Schkuhria pinnata and Phyllanthus maderaspatensis*, whereas different species were dominant after the drought *Tephrosia purpurea, Triumfetta rhomboidea* and *Limeum viscosum* (Table D7; Appendix D). Variances in grass species composition within the PA was driven by the dominance of a few post-drought species (*Panicum maximum, Urochloa mosambicensis, Aristida adscensionis, Digitaria eriantha and Aristida congesta* subsp*. barbicollis;* Table D6 Appendix D) with only one of these species - *Panicum maximum* - present across rainfall years.

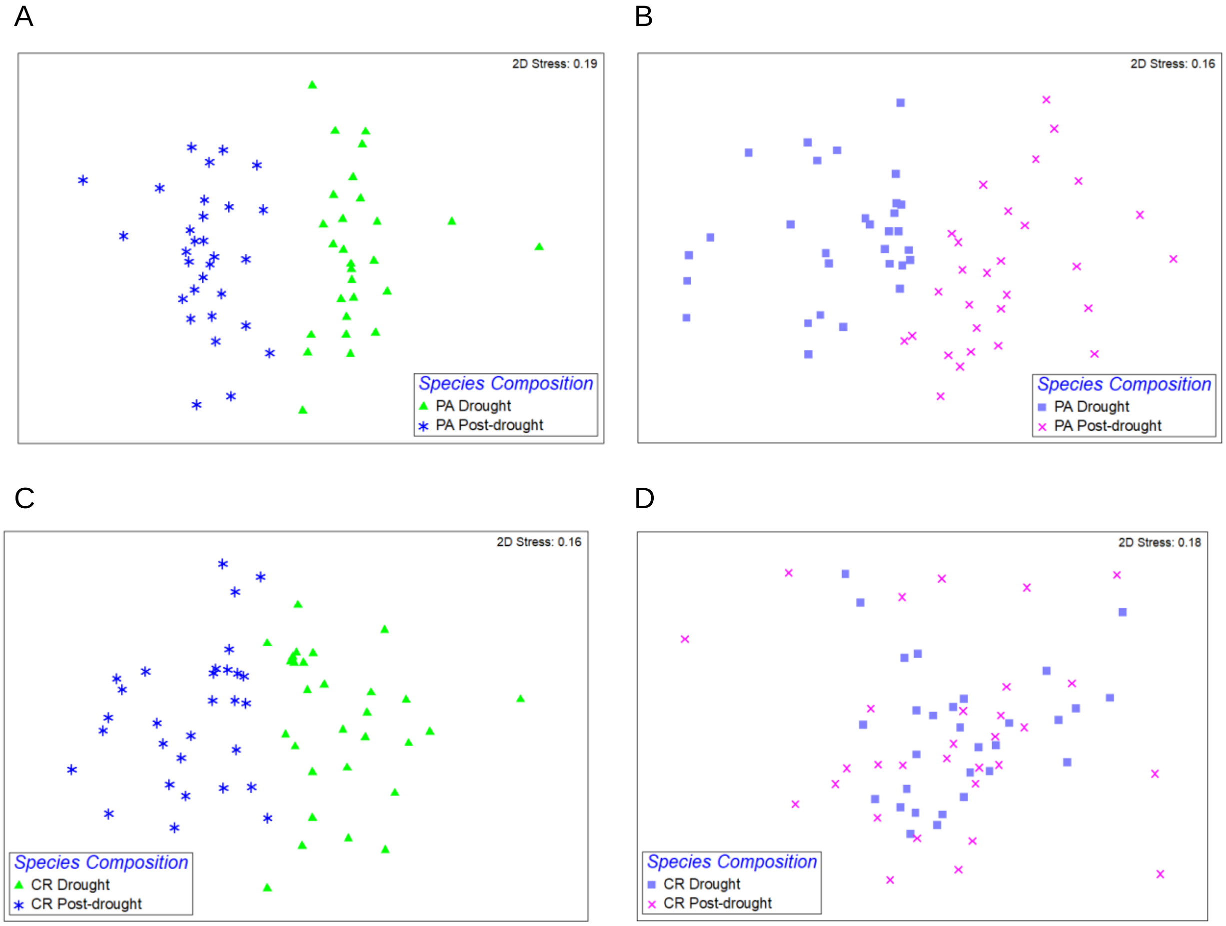

Figure 5.3: Non-Metric Multi-Dimensional Scaling (NMDS) ordination scatter plots of the PA (Protected Area) and CR (Communal Rangeland) for drought and post-drought plots illustrating species composition of forbs (A, C) and grasses (B, D).

Forb species characteristic of the area, irrespective of rainfall year or rangeland type, included *Phyllanthus parvulus, Heliotropium strigosum, Indigofera filipes, Chamaecrista mimosoides* and *Xenostegia tridentata*. These species are mostly palatable perennials of which two had N-fixing abilities (i.e. *Indigofera filipes* and *Chamaecrista mimosoides*) (Table D9; Appendix D). During the drought four annual forb species, namely *Phyllanthus maderaspatensis, Bidens bipinnata, Heliotropium ovalifolium* and *Phyllanthus pentandrus* (Table D9; Appendix D) were present at all the sites across rangeland types. Eleven forb species were associated with the drought, of which four were N-fixing (*Tephrosia purpurea, Tephrosia polystachya, Crotalaria podocarpa* and *Crotalaria sphaerocarpa*) (Table D9; Appendix D).

Grass species characteristic of the area were mostly palatable perennial, clonal and hairy (*Eragrostis rigidior, Panicum maximum, Perotis patens, Pogonarthria squarrosa, Schmidtia pappophoroides* and *Urochloa mosambicensis* (Table D10 Appendix D)). No specific grass species characterised the drought community. Prominent post-drought grasses included perennial, mostly unpalatable species (*Aristida congesta* subsp*. barbicollis, Brachiaria deflexa, Eragrostis lehmanniana* and *Tricholaena monachne*) (Table D10 Appendix D).

5.3.2 Herbaceous life form biomass

Table 5.2: Results from t-tests performed on independent samples by groups indicating differences in biomass per life form across various combinations of rangeland type and rainfall year.

Treatment combination	t-value	*F*-value	*p*-value
Forbs			
PA Drought vs CR Drought	0.678	9.514	0.513
PA Post-drought vs CR Post-drought	1.630	19.697	0.134
PA Drought vs PA Post-drought	-1.638	5.786	0.132
CR Drought vs CR Post-drought	-1.521	2.794	0.159
Grasses			
PA Drought vs CR Drought	0.479	38.194	0.641
PA Post-drought vs CR Post-drought	2.573	106.059	0.027*
PA Drought vs PA Post-drought	-2.778	12.031	0.019*
CR Drought vs CR Post-drought	-4.145	4.332	0.001*

No significant increase in forb biomass in the post-drought sample could be observed (Table 5.2). Above-ground grass biomass varied significantly in three of the four rainfall year and rangeland type treatment combinations (Table 5.2). Following the drought biomass was significantly higher in the PA compared to the CR (*F* = 106.059, *p* = 0.027; Table 5.2). Grass biomass was significantly affected by rainfall, both in the PA (*F* = 12.031, *p* = 0.019; Table 5.2), and the CR (*F* = 4.332, *p* = 0.001; Table 5.2) as biomass was significantly higher in the post-drought sampling year (Figure 5.4 A & B).

Table 5.3: Summary of the Repeated Measures ANOVA type III results for Rainfall year*Rangeland type interaction effects on herbaceous biomass.

Index	***F*-value**	***p*-value**
Fixed effects: Rangeland type*Rainfall year		
Forbs		
Rangeland type	1.9	0.198
Rainfall year	10.575	0.008*
Rangeland type*Rainfall year	4.23	0.066
Grasses		
Rangeland type	4.988	0.049*
Rainfall year	15.909	0.002*
Rangeland type*Rainfall year	8.535	0.015*

Repeated Measures ANOVA revealed a significant effect of rainfall year (F = 10.575, p = 0.008; Table 5.3), although interaction effects between rainfall year and rangeland type did not have a significant effect, on forb biomass (Figure 5.4 A). Forb biomass was higher in the post-drought sampling year; this difference was significant for grass biomass (Figure 5.4 B). Significant interaction effects between rainfall year and rangeland type was observed for grass biomass (F = 8.535, p = 0.015; Table 5.3; Figure 5.4 B). The separate effects of rainfall year and rangeland type were also significant for grass biomass (Figure 5.4 B). During the post-drought sampling year grass biomass was significantly higher in the PA compared to the CR.

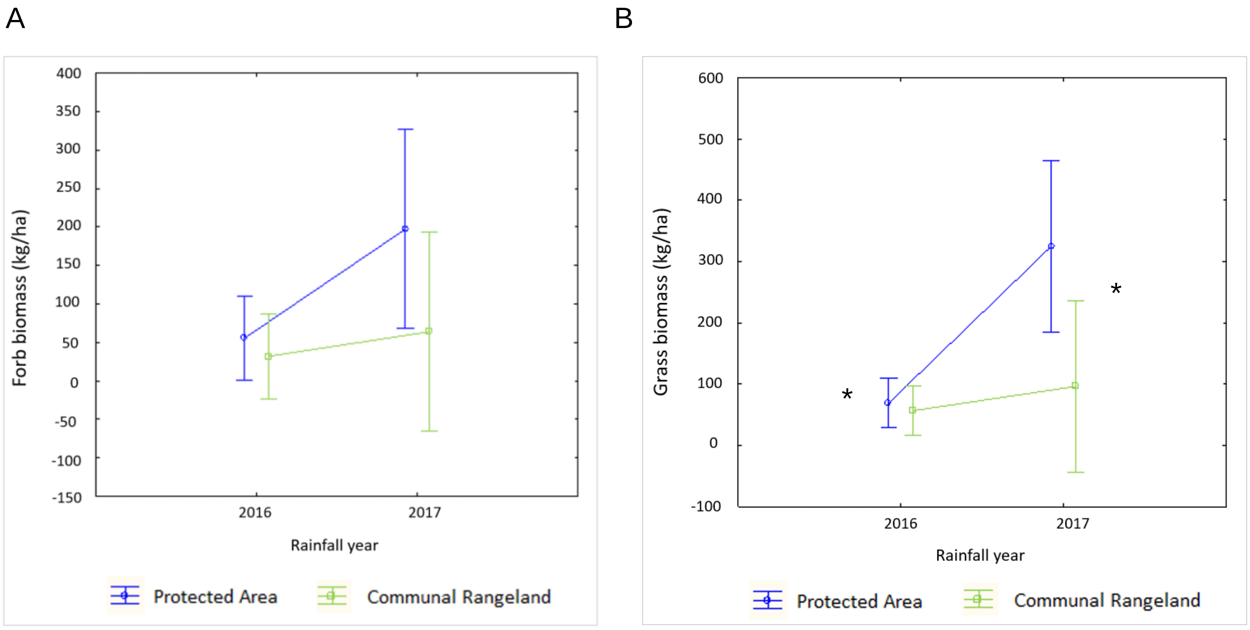

Figure 5.4: Comparisons of mean (±SE) biomass for forbs (A) and grasses (B) for each rangeland type across rainfall years (2016, drought; 2017, post-drought). Significant diferences are indicated with an asterisk (*).

5.3.3 Herbaceous species diversity

Table 5.4: Summary of the two-way ANOVA type Hierarchical Linear Model (HLM) results for variance in forb and grass species diversity indices and basal cover with respect to rainfall and rangeland type.

Index	**df**	***F*-value**	***p*-value**
Fixed effects: Rainfall year*Rangeland type			
Total species (S)	20	10.507	0.004*
Total individuals (N)	20	10.322	0.004*
Margalef's species richness (d)	19.831	7.704	0.012*
Shannon-wiener diversity index (H')	20	6.541	0.019*
Cover estimate (%)	20	8.621	0.008*
Pielou's evenness (J')	19.801	0.626	0.438
Simpson (1-Lambda)	19.857	0.510	0.484

Effect sizes and standard errors (SE) of the HLM results are presented in Tables D11 and D12, respectively (Appendix D).

Rainfall and rangeland type had significant effects on all species diversity indices for both forbs and grasses, except for indices that consider evenness, such as Pielou's evenness (*F* = 0.626, *p* = 0.438; Table 5.3 & Figure 5.10) and Simpson's diversity (*F* = 0.510, *p* = 0.484; Table 5.3 & Figure D1 Appendix D). Rangeland type and rainfall had a significant interaction effect on both forb and grass total species (*F* = 10.507, *p* = 0.004; Table 5.3). Within the PA forb and grass species richness increased significantly between rainfall years (*d* = 1.5; Figure 5.5 A & B), but remained more or less constant in the CR. Grass species richness was significantly higher in the CR compared to the PA during the drought (*d* = 1.53, CR > PA; Figure 5.5 B), whereas grass richness in the CR was significantly higher than that of the PA. In contrast, forb species richness differed significantly in the post-drought sampling year between rangeland types (*d* = 1.79, PA > CR; Figure 5.5 A).

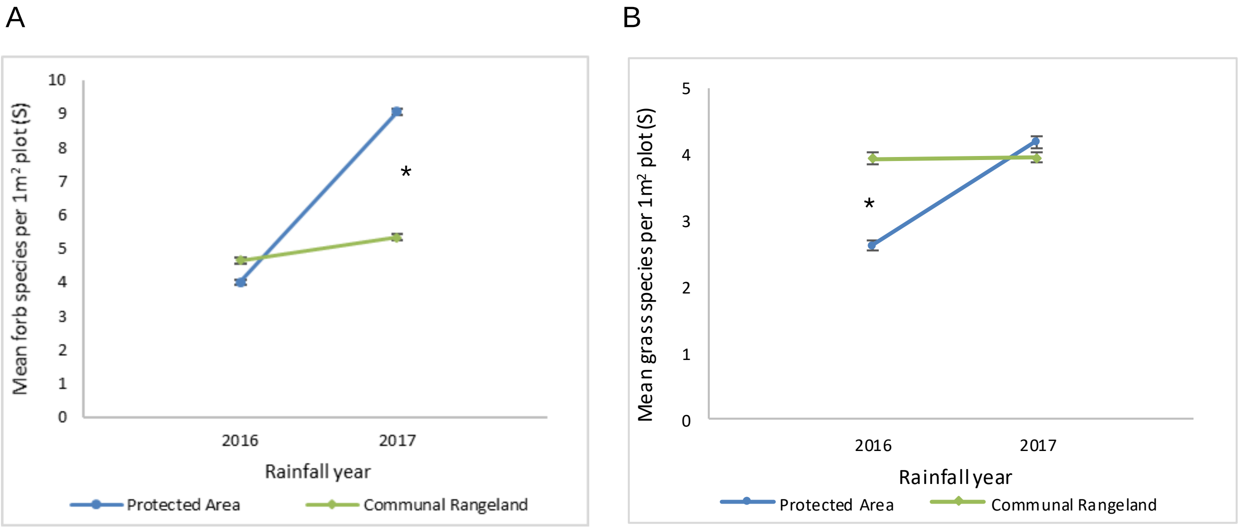

Figure 5.5: Mean (±SE) species (S) per 1 m^2 plot across rainfall years (2016, drought; 2017, post-drought) and rangeland type for forbs (A) and grasses (B). Significant diferences are indicated with an asterisk (*).

Rangeland type and rainfall significantly affected forb and grass abundance (*F* = 10.322, *p* = 0.004; Table 5.3). In the PA, forb and grass abundances increased significantly in the post-drought year (*d* = 1.14; Figure 5.6 A & B). Conversely, forb abundances decreased in the CR in 2017 (i.e. post-drought) (*d* = 0.05; Figure 5.6 A), whilst grass abundances increased, although these changes were not significant (*d* = 0.05; Figure 5.6 B). Mean species abundance for forbs and grasses differed significantly between rangeland type during the drought (*d* = 2.42, CR > PA; Figure 5.6 A & B) with the CR hosting significantly more individuals of forbs during the drought sampling year.

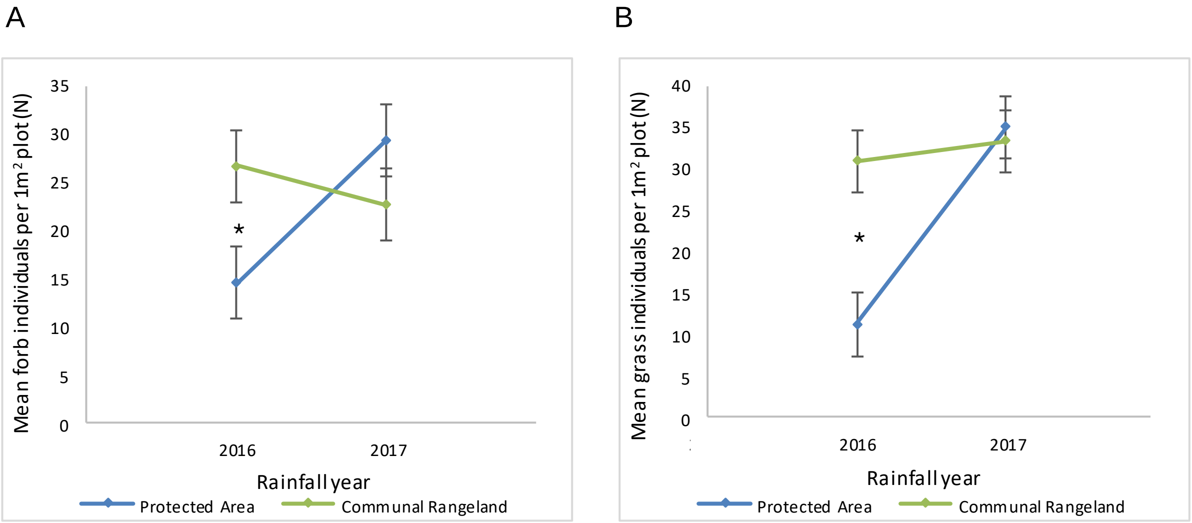

Figure 5.6: Mean (±SE) number of individuals (N) per 1 m^2 plot across rainfall years (2016, drought; 2017, post-drought) and rangeland type for forbs (A) and grasses (B). Significant diferences are indicated with an asterisk (*).

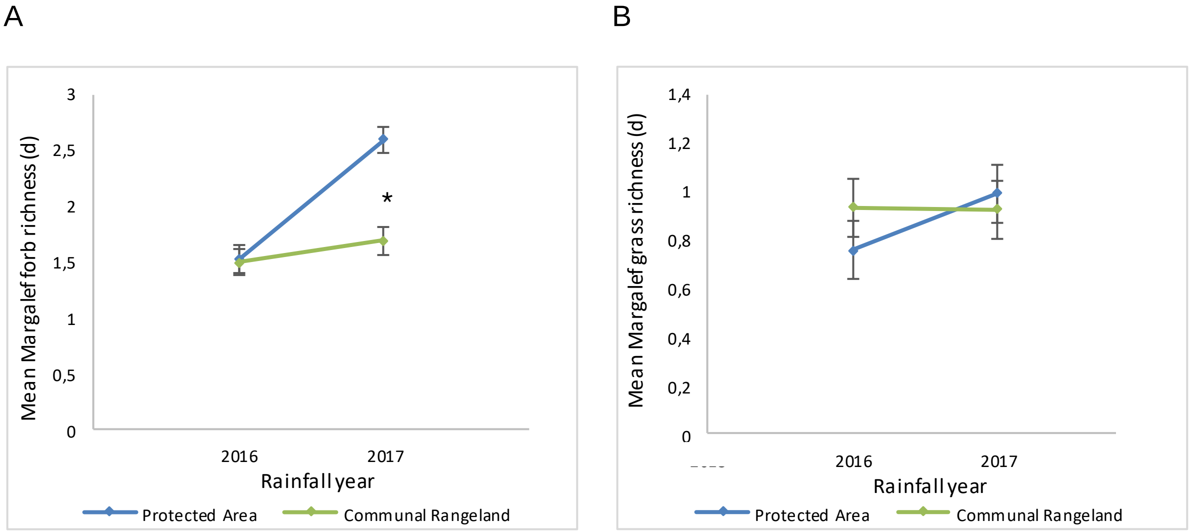

Figure 5.7: Mean (±SE) Margalef's species richness (d) per 1 m^2 plot across rainfall years (2016, drought; 2017, post-drought) and rangeland type for forbs (A) and grasses (B). Significant diferences are indicated with an asterisk (*).

Margalef species richness was affected by an interaction between rainfall year and rangeland type (F = 7.704, p = 0.012; Table 5.3), although only forbs responded significantly. Margalef forb species richness increased significantly in the PA (d = 1.27; Figure 5.7 A & B) in response to rain (i.e. post-drought, 2017 sampling year). Post-drought conditions significantly favoured forb richness in the PA (d = 2.39, PA > CR; Figure 5.7 A). Grass species richness was not significantly affected by either post-drought conditions or rangeland type (Figure 5.7 B).

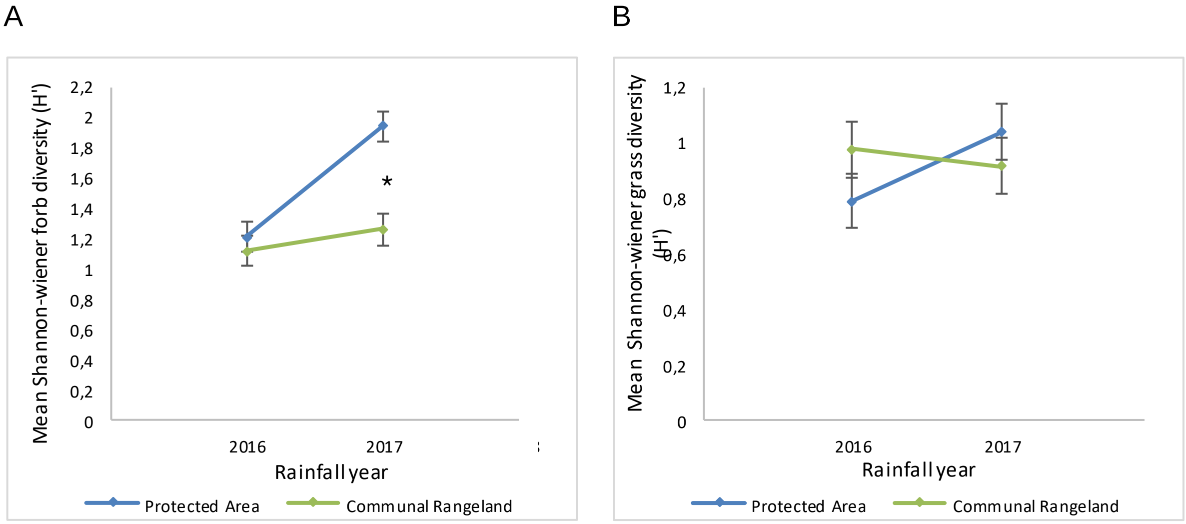

Figure 5.8: Mean (±SE) Shannon-wiener species diversity per 1 m^2 plot across rainfall years (2016, drought; 2017, post-drought) and rangeland type for forbs (A) and grasses (B). Significant diferences are indicated with an asterisk (*).

Shannon-Wiener diversity responded similarly to Margalef's species richness for both forbs and grasses, although weaker effects were revealed (F = 6.541, p = 0.019; Table 5.3) (Figure 5.8 A & B).

Herbaceous species basal cover was significantly affected by rainfall and rangeland type (F = 8.621, p = 0.008; Table 5.3). Both life forms showed a significant increase in cover after the drought (PA: d = 2.64; CR: d = 1.35; Figure 5.9 A & B). Grass basal cover differed between rangeland types with significantly higher grass basal cover in the CR during the drought year (d = 2.42; Figure 5.9 B).

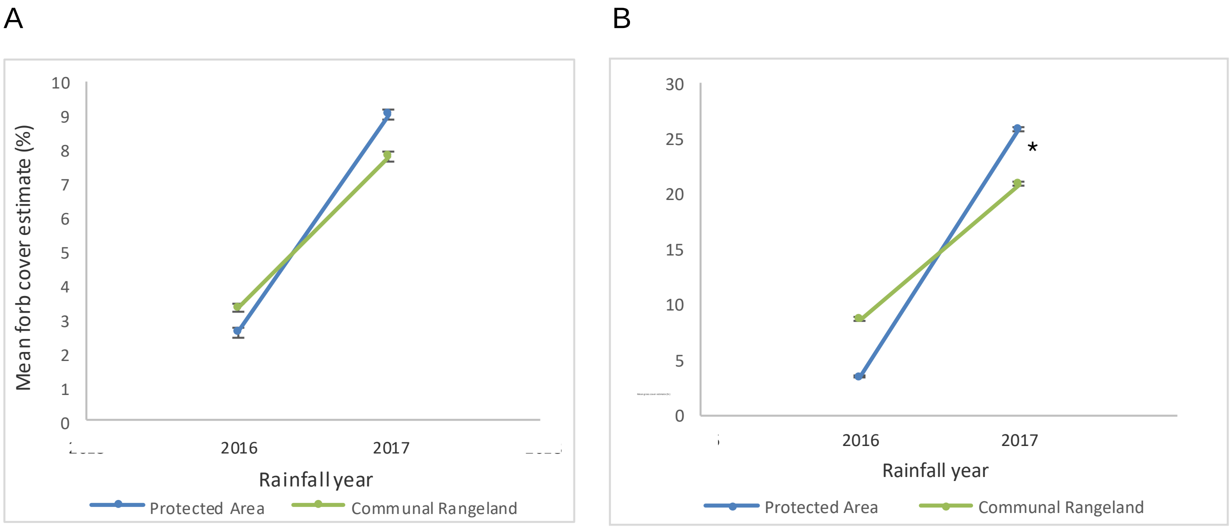

Figure 5.9: Mean (±SE) species basal cover per 1 m^2 plot across rainfall years (2016, drought; 2017, post-drought) and rangeland type for forbs (A) and grasses (B). Significant diferences are indicated with an asterisk (*).

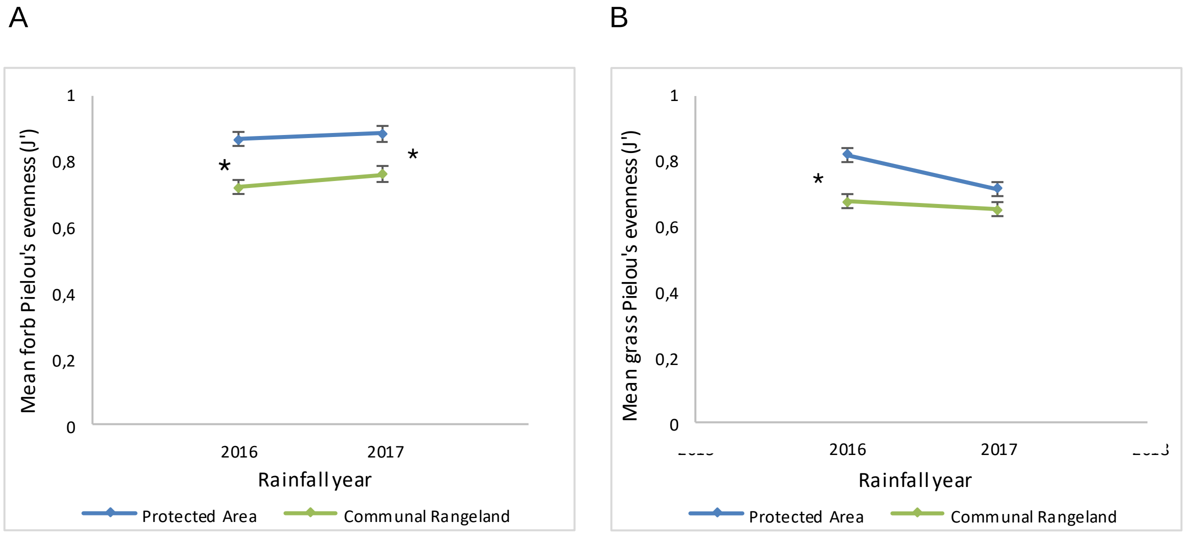

Figure 5.10: Mean (±SE) Pielou's evenness per 1 m^2 plot across rainfall years (2016, drought; 2017, post-drought) and rangeland type for forbs (A) and grasses (B). Significant diferences are indicated with an asterisk (*).

Pielou’s evenness was not significantly affected by the interaction between rainfall year and rangeland type (F = 0.626, p = 0.438; Table 5.3). Herbaceous species evenness did not change significantly in response to rainfall for either of the rangeland types (PA: *d* = 0.25; CR: *d* = 0.04; Figure 5.10 A & B). However, forb and grass species evenness were significantly higher in the PA during the drought year (*d* = 2.07; PA > CR; Figure 5.10 A & B). Post-drought forb species evenness was also significantly higher in the PA (*d* = 1.33; Figure 5.10 A) whereas grass evenness remained stable between both rangeland types (Figure 5.10 B).

Chapter 6

Plant functional attributes related to rainfall and rangeland type

6.1 Introduction

Functional ecology has increased in relevance to ecology research as it assists with the assessment of ecosystem functioning through measures of community-level responses and adaptations to environmental perturbations. In plant ecology, plant functional attributes are commonly explored to better understand ecosystem dynamics (Lavorel *et al*., 1997; Díaz *et al.*, 1999; McIntyre *et al.,* 1999; Lavorel & Garnier, 2002, Díaz *et al.*, 2007; Linstädter *et al.*, 2014). Functional trait-based approaches rely on the presumption that key chemical, physiological, behavioural and morphological traits affect vegetation response to environmental change and/or disturbance (Lavorel *et al.,*1997; Mokany *et al.*, 2008; Cadotte *et al.*, 2011; Lavorel *et al.,* 2011; Wright *et al*., 2017).

Functional traits have been used to predict how plants respond to changes in the environment (Lavorel & Garnier, 2002: Cadotte *et al.*, 2011; Linstädter *et al.*, 2014; Wright *et al.*, 2017) under natural experimental settings as well as under manipulated experimental settings (Kimball *et al.*, 2016). The use of functional trait assemblages to predict changes in community composition and diversity following a disturbance event is a relatively new approach in ecological research, which inevitably creates knowledge gaps pertaining to this topic (Cadotte *et al.*, 2015). Plant functional types describe groups of species with similar features in ecosystem functioning, or species which are likely to respond similarly to climatic variability and/or disturbances such as grazing (Lavorel *et al.*, 1997; Díaz *et al.*, 2001; Linstädter *et al.*, 2014). Ecosystems and the resilience of processes which maintain them are shaped by functional groups, the trait assemblages within these groups and their distribution within and across scales (Peterson *et al.*, 1998; Osborne *et al.*, 2018).

African savanna vegetation is characterised by distinctive plant functional trait assemblages which convey both vulnerability and resilience to anthropogenic and environmental disturbances (Peterson *et al.*, 1998; Garcia *et al.*, 2014; Ruppert *et al.*, 2015; Osborne *et al.*, 2018). In the light of continuous global climate and land use change, ecological research should focus more on understanding the interaction among savanna ecosystem drivers and how these interactions influence the dynamics and functioning of these systems (Peterson *et al.*, 1998; Ruppert *et al.*, 2015; Osborne *et al.*, 2018). Few studies have considered the combined effects of herbivory and rainfall variability on the herbaceous layer of savanna ecosystems (Ruppert *et al.*, 2015, Koerner & Collins, 2014), with even fewer considering forbs and grasses as separate functional entities (Van Coller *et al.*, 2018).

Plant species assemblages are a result of biotic (competition, facilitation, herbivory) and abiotic (disturbance, resource availability, climatic variability) filters that progressively determine which species with their respective response traits can tolerate and survive environmental conditions at a certain site (Lavorel *et al.*, 2002). Functional measures are largely dependent upon a specific research question and the scale at which research is conducted (McIntyre *et al.*, 1999; Osborne *et al.*, 2018). McIntyre *et al.* (1999) developed a site-specific, inductive and hierarchical methodological approach which takes both plant structure and function into account. Linstädter *et al.* (2014) applied this hierarchical methodological approach in combination with multivariate statistics and model selection procedures. A modified combination of the methods used by McIntyre *et al.* (1999) and Linstädter *et al.* (2014) were applied to obtain results presented in this chapter.

This chapter aimed to determine the functional response of herbaceous vegetation to 1) rainfall variability (i.e. drought and post-drought) and 2) rangeland type (i.e. communal rangeland and protected area).

Specific objectives for each herbaceous life form were to:

1. determine whether and how trait composition would change in response to differences in rangeland type and rainfall;
2. identify and describe plant functional types associated with rainfall year irrespective of rangeland type;
3. identify and describe plant functional types associated with each rangeland type during and after the drought.

Studies on grazing effects on herbaceous layers of savanna systems suggest that increased grazing pressure would favour short-lived and fast-growing perennial and annual grasses as well as forbs, whilst causing increased dominance of unpalatable grasses (Fynn & O'Connor, 2000; Díaz *et al.*, 2007; Guo *et al.*, 2016). From this, it is hypothesised that the CR would have a higher number of annual grass and forb PFTs, as well as a greater number of unpalatable grass PFTs when compared to the PA. Additionally, prostrate growth forms, rather than erect growth forms, are more common under grazing pressure (Díaz *et al.*, 2007; Landsberg *et al.*, 1999). Accordingly, it was expected that PFTs composed of prostrate growth forms would dominate the CR more so than the PA. Inter-annual rainfall variability is considered an important driver of savanna herbaceous vegetation structure and function, since the relative abundance of perennial grasses increases after substantial rainfall (Buitenwerf *et al.*, 2011; O'Connor, 2015). Accordingly, it was hypothesised that post-drought PFTs would consist mainly of palatable perennial grasses due to their ability to out-compete forbs (Bond &Parr, 2010; Jacobs & Naiman, 2008; Savadogo *et al*., 2008; Van Coller *et al.*, 2013). Furthermore, it was anticipated that the combined effect of below average rainfall and high/long-term grazing pressure would cause decreases in perennial PFTs, which would lead to an increase in annual and weakly tufted perennial grass PFTs (O'Connor, 1995; Fynn & O'Connor, 2000; Riginos *et al.*, 2018). Under conditions of heavy grazing pressure and high rainfall, annual plants and creeping perennial grasses have been shown to increase in relative abundance (Fynn & O'Connor, 2000). It was therefore hypothesised that the CR would have a greater number of PFTs consisting of annuals and creeping perennial grasses following the drought after substantial rainfall.

6.2 Methods

For details on experimental layout and field sampling please refer to Chapter 4, section 4.2 and for details on methods used for statistical analyses refer to section 4.5.

6.3 Results

Results presented in this chapter report on drought response effects through assessing potential shifts in functional trait composition and plant functional types (PFTs) across rainfall years for each (i) rangeland type (i.e. protected area and communal rangeland) and (ii) herbaceous life form (i.e. forbs and grasses), and linking different PFTs to each rangeland type.

6.3.1 Trait assemblages

Rangeland type

NMDS ordination analyses of functional trait composition did not reveal strong clustering according to rangeland type (Figure 6.1). However, results from PERMANOVA analysis revealed significant differences in functional trait composition across rangeland types for both herbaceous life forms, irrespective of rainfall (forbs: *p* = 0.002; Table 6.1; Figure 6.1 A; grasses: *p* = 0.001; Table 6.1; Figure 6.1 B). The effect was weaker for forbs (*F* = 4.581 Table 6.1) than for grasses (*F* = 15.409 Table 6.1).

Table 6.1: Permutational Multivariate Analysis of Variance (PERMANOVA) indicating significance of differences in functional trait composition for forbs and grasses across rangeland types and rainfall years.

Treatment combination	***F*-value**	***p*-value**
Forbs		
Protected Area (PA) vs Communal Rangeland (CR)	4.581	0.002*
PA Drought vs PA Post-drought	19.342	0.001*
CR Drought vs CR Post-drought	3.755	0.010*
Grasses		
Protected Area (PA) vs Communal Rangeland (CR)	15.409	0.001*****
PA Drought vs PA Post-drought	28.386	0.001*****
CR Drought vs CR Post-drought	0.461	0.819

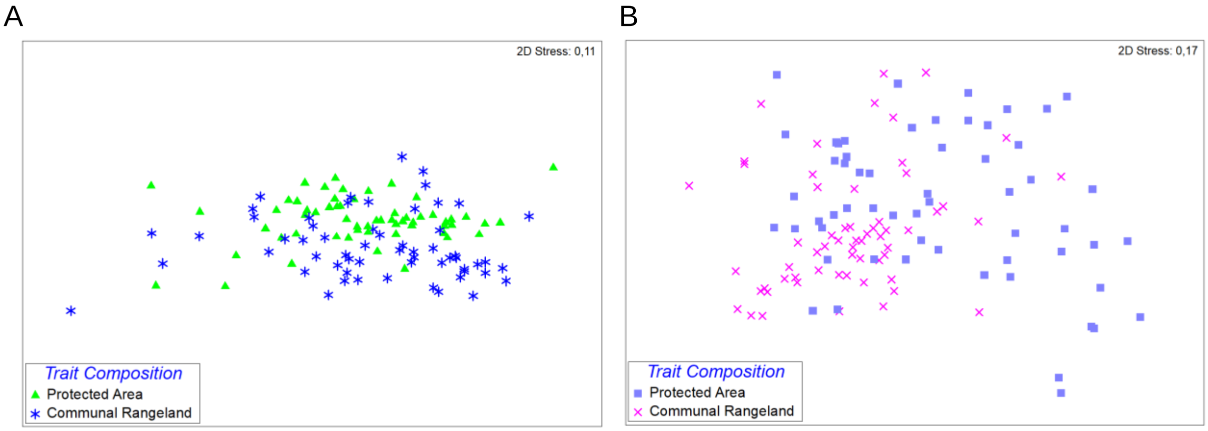

Figure 6.1: Non-Metric Multidimensional Scaling (NMDS) ordinations of A) forb and B) grass functional trait composition across rangeland types, irrespective of rainfall.

Rainfall

Differences in trait assemblages among rangeland types prompted further investigation into rainfall effects on forbs and grasses for each respective rangeland type.

Protected area

Clustering in a two-dimensional space and PERMANOVA results revealed significant rainfall effects on the functional trait composition in the PA for both forbs (p = 0.001; Table 6.1; Figure 6.2 A) and grasses (p = 0.001; Table 6.1; Figure 6.2 B).

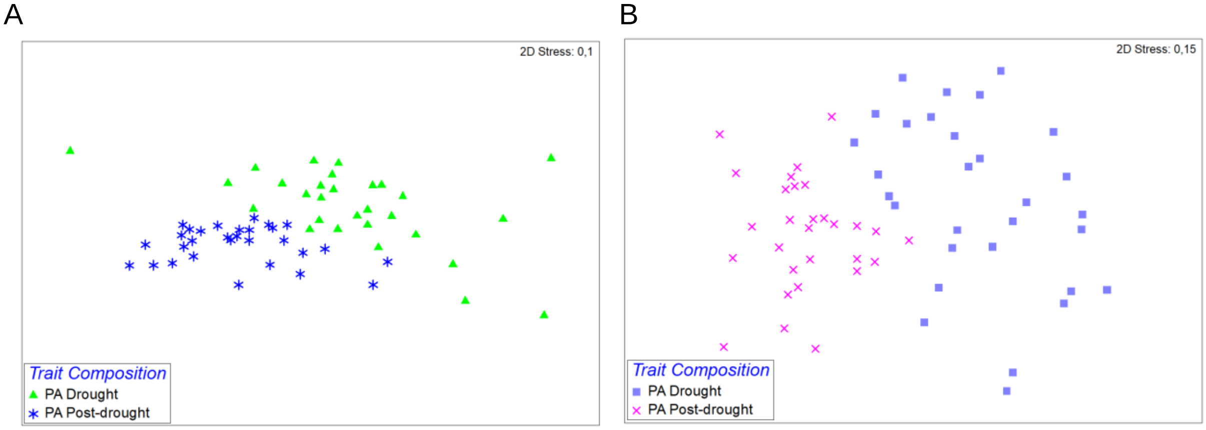

Figure 6.2: Non-Metric Multidimensional Scaling (NMDS) ordinations illustrating variation in A) forb and B) grass functional trait composition across rainfall years within the PA.

Communal Rangeland

Similar to the PA, rainfall in the CR (p = 0.10; Table 6.1; Figure 6.3 A) revealed significant effects on trait assemblages, but only for forbs. Grass trait composition was not significantly affected by the drought (p = 0.819; Table 6.1), as no discernible clustering in the NMDS ordination (Figure 6.3 B) was revealed across rainfall years for the CR.

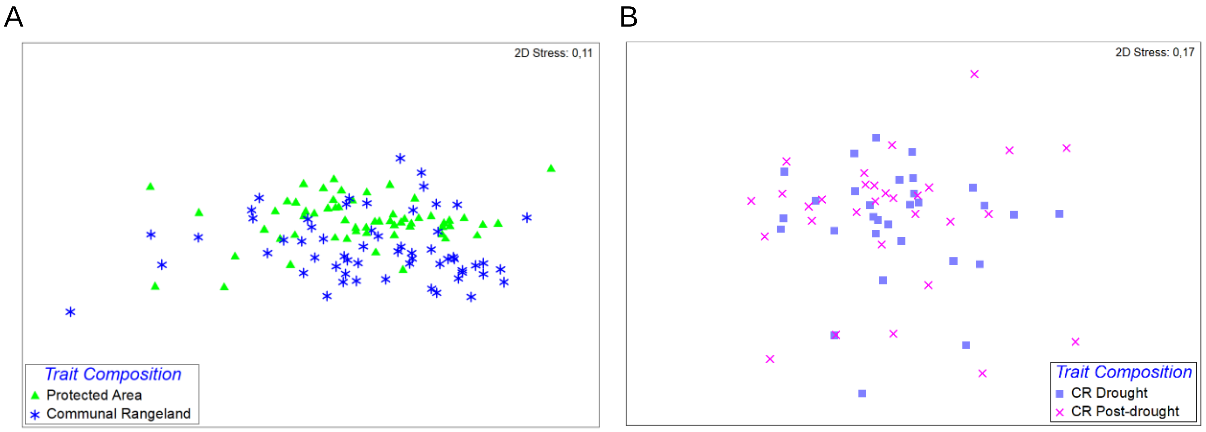

Figure 6.3: Non-Metric Multidimensional Scaling (NMDS) ordinations illustrating variation in A) forb and B) grass functional trait composition across rainfall years within the CR.

6.3.2 Plant functional types

Drought responses

The initial PCoA analysis of species-trait matrices, which included life form and life history traits revealed strong clustering based on life history. These results were obtained for both rainfall years and for each life form separately (Figure 6.4 A-D). Several studies have suggested the importance of life history as a functional trait when explaining the response of herbaceous species to grazing (McIntyre *et al.*, 1999; Díaz *et al.*, 2007; Linstädter *et al.*, 2014). Using UPGMA-cluster analyses (Unweighted Pair Group Method with Arithmic Mean), each life history group was therefore analysed separately to identify, describe and discuss the PFTs for each rainfall year.

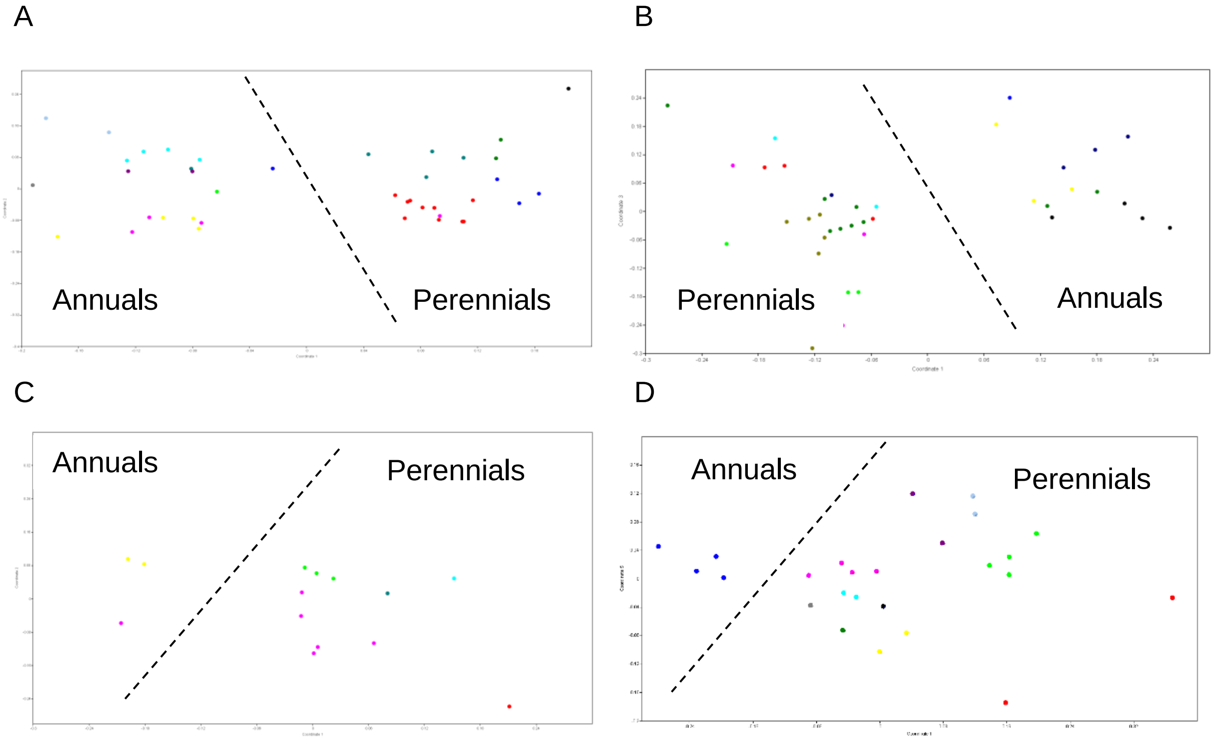

Figure 6.4: Principal Co-ordinate Analysis (PCoA) scatter diagrams illustrating clustering of forbs (A: Drought; B: Post-drought) and grasses (C: Drought; D: Post-drought) based on plant functional traits across sampling years with varying rainfall.

A summary of all PFTs (classified per life form) across rainfall years is presented in table form (Table 6.2) after the UPGMA cluster diagrams (Figure 6.5- Figure 6.8). For a list of acronyms and full species names refer to Table B1 Appendix B. Please note that the numbering of PFT is specific to life form, rainfall year, and life history. PFTs were named according to life form, rainfall year and life history i.e. the PFTs for annual forbs during the drought were named ‘PFT **FDA i** (**F** = Forbs; **D** = Drought; **A** = Annuals’ **i**= PFT number). For the post-drought rainfall year PFT names will be indicated with a **P** instead of a **D** i.e. PFT **FPA i** (**F**= Forbs; **P** = Post-drought; **A** = Annuals). Grass PFTs during post-drought conditions were named ‘PFT **GPP i**’ (**G**= Grasses; **P** = Post-drought; **P** = Perennials; **i** = PFT number). Refer to Table 6.2 and Table 6.3 for details on each PFT.

Annuals: Drought

During the drought, annual herbaceous PFTs were dominated by species with low palatability (Figure 6.5 A & B; Table 6.2). Annual forbs aggregated into five terminal groups or PFTs ranging from single-trait PFTs (i.e. PFT FDA i) to four-trait PFTs (i.e. PFT FDA v) (Figure 6.5 A). PFT FDA v was the dominant annual forb type, which consisted of 12 species separated at four hierarchical trait-levels (i.e. non-spinescent (1st level), erect (2nd level), low to moderately palatable (3rd level) and non-nitrogen (N_2) fixing (4th level)). The forb drought community was dominated by non-spinescent, erect forbs and most of these species were non-N_2-fixing species with low to moderate palatability. Annual grasses were weakly represented during the drought (Figure 6.5 B). The four species were divided into two single-trait PFTs based on hairiness which differed in palatability.

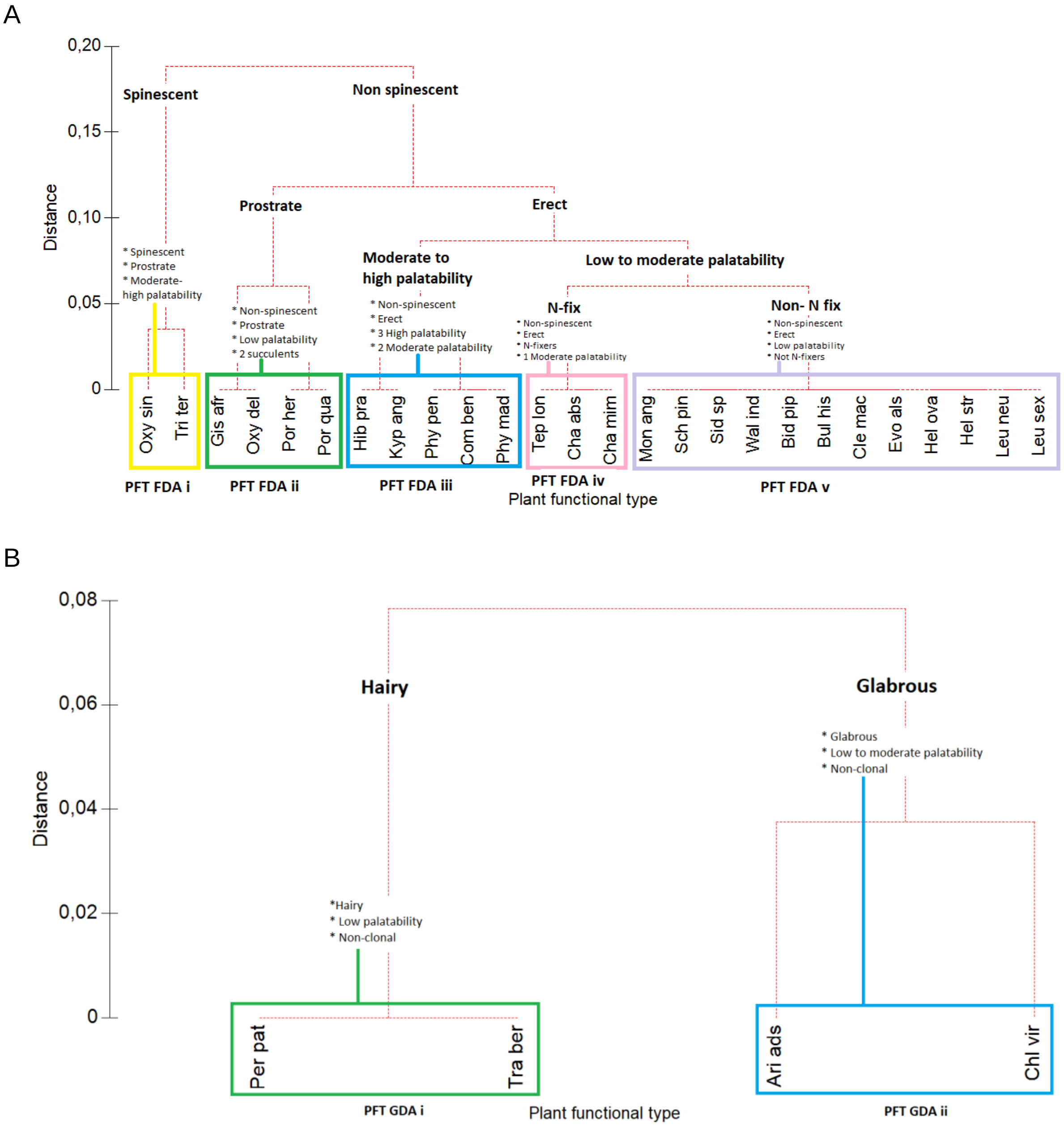

Figure 6.5: Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis based on Gower distance measure indicating annual plant functional types (PFTs) during the drought for A) forbs and B) grasses

Annuals: Post-drought

Similar to the drought, post-drought annual herbaceous PFTs were mostly dominated by unpalatable species (Figure 6.6 A & B; Table 6.3). Post-drought annual forbs grouped into five PFTs (Figure 6.6 A; Table 6.2). However, hierarchical trait-level separation had a different order than that observed during the drought with spinescence (1st level), palatability (2nd level), N_2-fixing ability (3rd level), and growth habit (4th level) being the most important traits in post-drought annual forb communities (Figure 6.6 A). PFT FPA v represented the largest group of annual species, which consisted of erect unpalatable non-spinescent forbs with low to moderate palatability of which most were non-N_2-fixing species. Cluster analysis identified two single-trait PFTs for annual grasses with a variation in palatability and hairiness (Figure 6.6 B; Table 6.2).

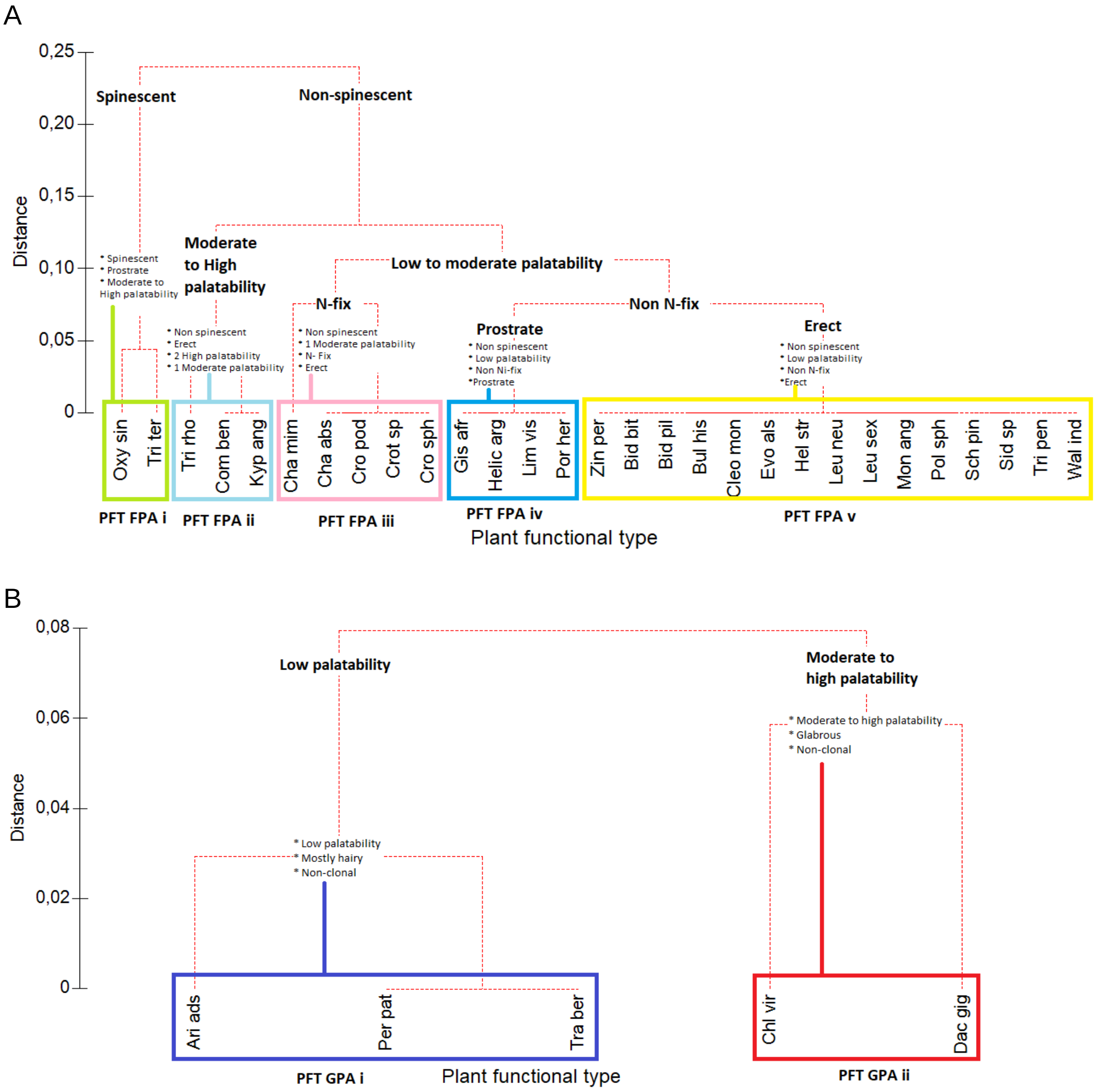

Figure 6.6: Post-drought year cluster analysis with Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on Gower distance measure indicating annual plant functional types (PFTs) for A) forbs and B) grasses.

Perennials: Drought

Hierarchical cluster analysis in combination with SIMPROF analysis revealed more complex results for perennial forbs and grasses during drought than for annual herbaceous species. PFTs revealed that perennial forb species were distributed relatively evenly (Figure 6.7 A). Perennial forbs clustered into two- (PFT FDP vi to PFT FDP viii) and four-trait PFTs (PFT FDP ix to PFT FDP xi) during the drought. These forb PFTs were dominated by clonal, non-N_2-fixing species with low palatability (Figure 6.7 A), whereas palatable species dominated perennial grass PFTs (Figure 6.7 B). For annual forbs, the main trait-level was based on spinescence both during and after the drought, whereas perennial forb types separated primarily on clonality (Figure 6.7 A). Similarly, clonality prompted clustering at the highest hierarchical level for perennial grasses (Figure 6.7 B). During the drought, hairiness was revealed to be an important grass trait with perennial grasses clustering into four two-trait PFTs based on clonality (1st level) and hairiness (2nd level) (Figure 6.7 B).

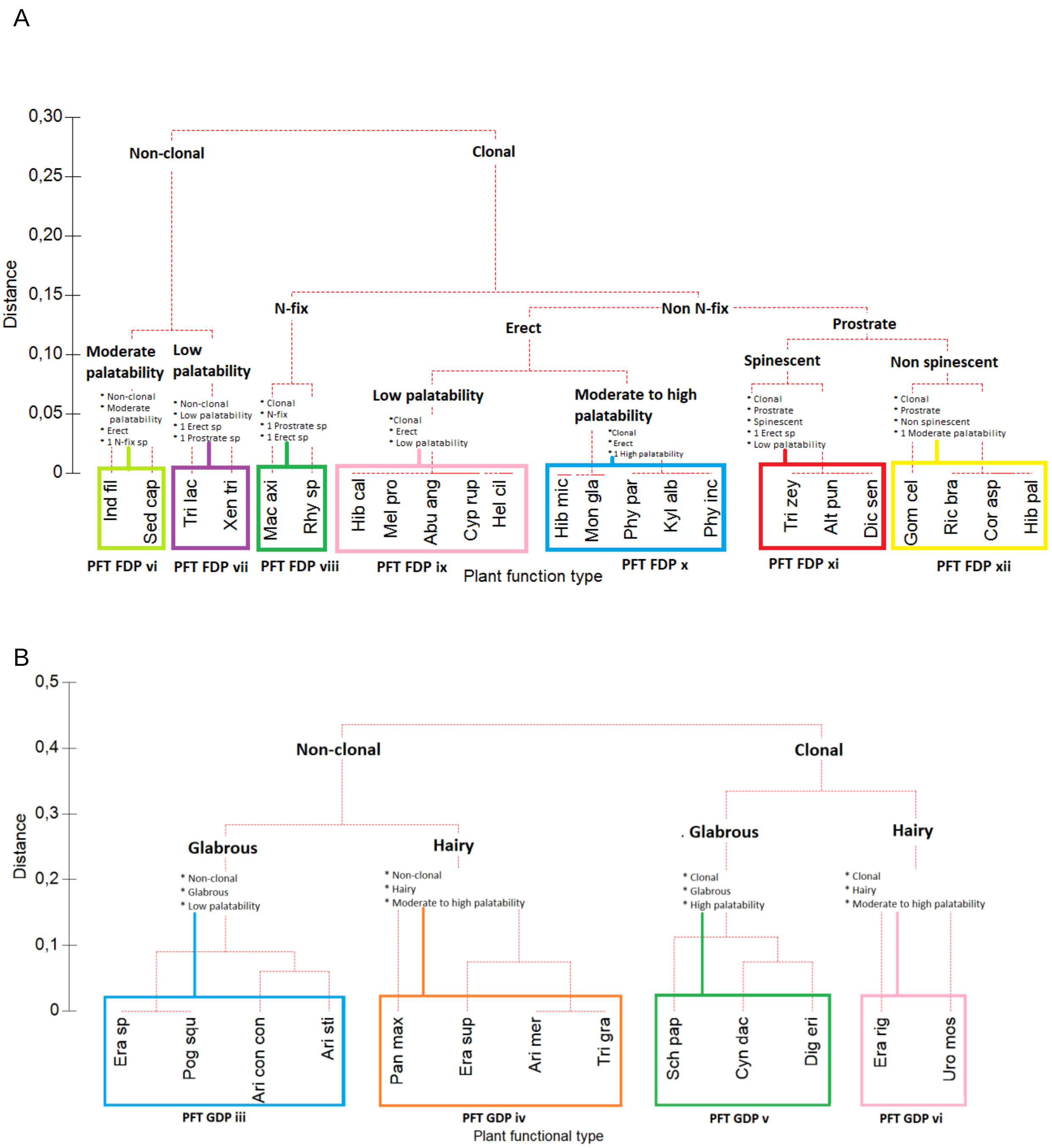

Figure 6.7: Drought year cluster analysis with Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on Gower distance measure indicating perennial plant functional types (PFTs) for A) forbs and B) grasses.

Perennials: Post-drought

As expected, post-drought perennial herbaceous communities were diverse as illustrated through hierarchical trait aggregation, which clustered into a total of 23 PFTs compared to the 18 PFTs for the drought community (Table 6.2 & 6.3). Post-drought perennial forbs assembled into 11 PFTs ranging from two-trait PFTs (PFT FPP vi to PFT FPP ix) to five-trait PFTs (PFT FPP xvi & PFT FPP xvii) (Figure 6.8 A). The majority of forb species belonging to the seven clonal PFTs (PFT x to PFT xvi) had belowground regenerative traits (23 out of 34 species) and most of these species were also non-spinescent. Perennial grasses comprised five PFTs following the drought (Figure 6.8 B). Clonality and hairiness were once again important traits for the grouping of perennial grasses. Most of the grass PFTs consisted of moderately to highly palatable species, which is in contrast with the dominance of unpalatable post-drought perennial forb species.

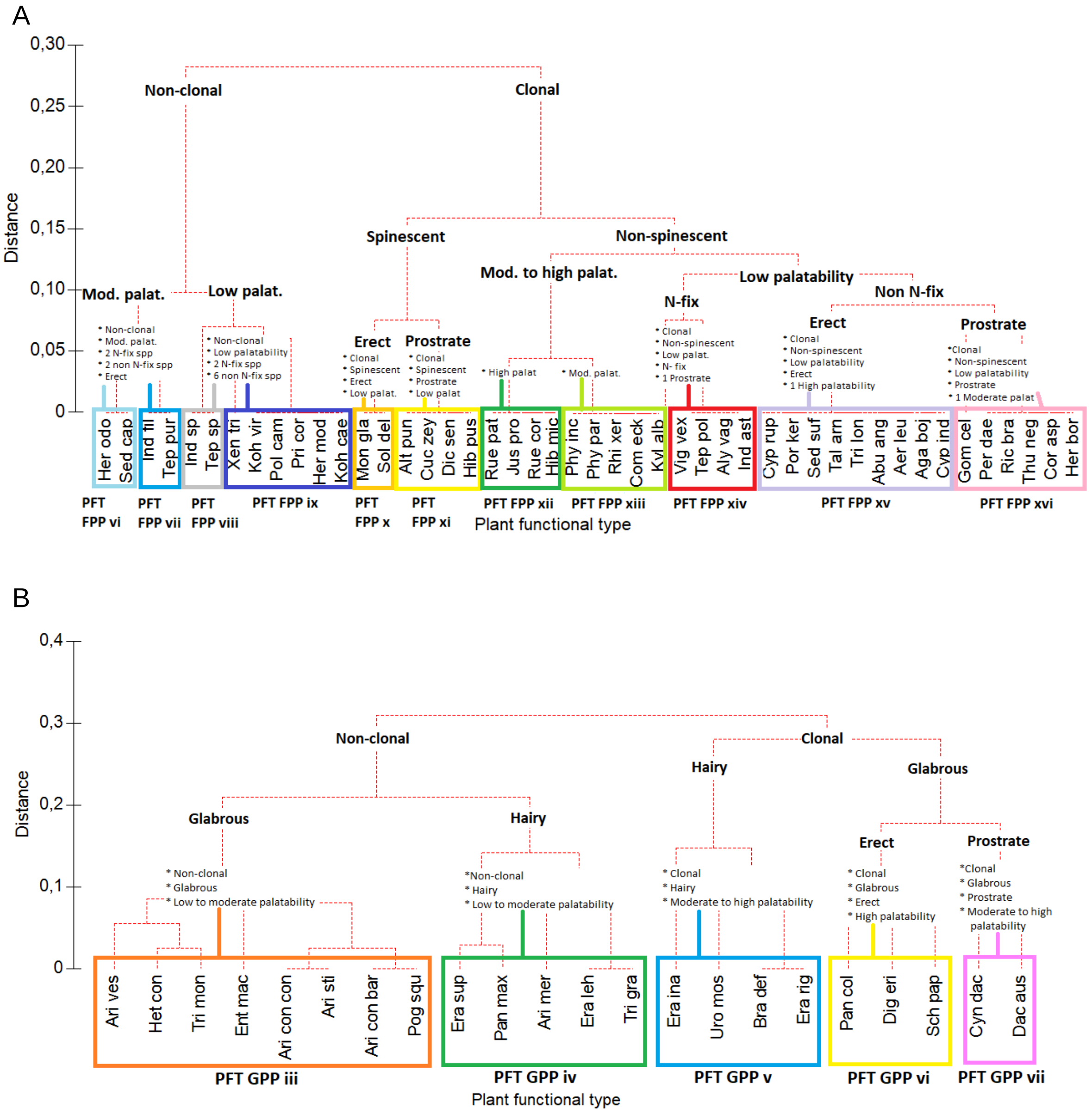

Figure 6.8: Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis based on Gower distance measure indicating post-drought perennial plant functional types (PFTs) for A) forbs and B) grasses.

Summary

Contrary to what was expected, perennial PFTs were more abundant than annual PFTs for both life forms during the drought (Figure E1 & E2 Appendix E). Post-drought forb communities revealed the highest diversity of PFTs, which clustered into 16 groups (of which 11 were perennial). Conversely, drought-tolerant grass traits clustered into only six PFTs, which was the lowest number of PFTs recorded for either life form across rainfall years (Table 6.2).

Table 6.2: Summary of drought plant functional types (PFTs) and their definitions.

PFT	**Forbs: Drought**
FDA i	Annual spinescent prostrate forbs with moderate to high palatability
FDA ii	Annual non-spinescent prostrate forbs with low palatability
FDA iii	Annual non-spinescent erect growing forbs with moderate to high palatability
FDA iv	Annual non-spinescent erect growing and N_2-fixing forbs with low to moderate palatability
FDA v	Annual non-spinescent erect growing and non-N_2-fixing forbs with low palatability
FDP vi	Perennial non-clonal erect growing forbs with moderate palatability
FDP vii	Perennial non-clonal forbs with low palatability
FDP viii	Perennial clonal N-fixing forbs with low palatability
FDP ix	Perennial clonal non-N_2-fixing erect growing forbs with low palatability
FDP x	Perennial clonal non-N_2-fixing erect growing forbs with moderate to high palatability
FDP xi	Perennial clonal non-N_2-fixing prostrate and spinescent forbs with low palatability
FDP xii	Perennial clonal non-N_2-fixing prostrate and non-spinescent forbs with low palatability
PFT	**Grasses: Drought**
GDA i	Annual non-clonal hairy grasses with low palatability
GDA ii	Annual non-clonal glabrous grasses with low to moderate palatability
GDP iii	Perennial non-clonal glabrous grasses with low palatability
GDP iv	Perennial non-clonal hairy grasses with moderate to high palatability
GDP v	Perennial clonal glabrous grasses with high palatability
GDP vi	Perennial clonal hairy grasses with moderate to high palatability

Table 6.3: Summary of post-drought plant functional types (PFTs) and their definitions.

PFT	**Forbs: Post-drought**
FPA i	Annual spinescent prostrate forbs with moderate to high palatability
FPA ii	Annual non-spinescent erect growing forbs with moderate to high palatability
FPA iii	Annual non-spinescent erect growing and N_2-fixing forbs with low to moderate palatability
FPA iv	Annual non-spinescent prostrate and non-N_2-fixing forbs with low palatability
FPA v	Annual non-spinescent erect growing and non-N_2-fixing forbs with low palatability
FPP vi	Perennial non-clonal erect growing and non-N_2-fixing forbs with moderate palatability
FPP vii	Perennial non-clonal erect growing and N_2-fixing forbs with moderate palatability
FPP viii	Perennial non-clonal N_2-fixing forbs with low palatability
FPP ix	Perennial non-clonal non-N_2-fixing forbs with low palatability
FPP x	Perennial clonal spinescent erect growing forbs with low palatability
FPP xi	Perennial clonal spinescent prostrate forbs with low palatability
FPP xii	Perennial clonal non-spinescent forbs with high palatability
FPP xiii	Perennial clonal non-spinescent forbs with moderate palatability
FPP xiv	Perennial clonal non-spinescent and N_2-fixing forbs with low palatability
FPP xv	Perennial clonal non-spinescent erect growing and non-N_2-fixing forbs with low palatability
FPP xvi	Perennial clonal non-spinescent prostrate and non-N_2-fixing forbs with low palatability
PFT	**Grasses: Post-drought**
GPA i	Annual non-clonal hairy grasses with low palatability
GPA ii	Annual non-clonal glabrous grasses with moderate to high palatability
GPP iii	Perennial non-clonal glabrous grasses with low to moderate palatability
GPP iv	Perennial non-clonal hairy grasses with low to moderate palatability
GPP v	Perennial clonal hairy grasses with moderate to high palatability
GPP vi	Perennial clonal glabrous erect growing grasses with high palatability
GPP vii	Perennial clonal glabrous prostrate grasses with moderate to high palatability

Rangeland type responses

This section reports on the forb and grass plant functional types and soil macro elements, pH and extractable P that were associated with each rangeland type. Soil data is only available for the drought year (2016) and was only included in the drought year PCAs since rainfall could affect soil nutrients (Fatubarin & Olojugba, 2014) and no post-drought soil data are available for the post-drought PCAs.

Drought: Forbs

The first two axes (Principal Components) of the PCA explained 30.96 % of variance observed in forb PFT data (Axis 1= 0.172; Axis 2= 0.137; Figure 6.9). The largest contribution of the variance within forb PFTs during drought (17.2 %) was explained by the first Principal Component (Axis 1; Figure 6.9), which was mainly correlated with higher levels of the macro soil element Ca (strong correlation) to the left and Na (weaker correlation) to the right. PA plots clustered tightly to the left of the triplot and CR plots scattered across the triplot axes. PFT FDP xii had a strong correlation with Axis 1. Most of the plots sampled in the PA were strongly associated with PFT FDA iii, PFT FDP vii and PFT FDP vi. Plots sampled in the CR had an association with PFT FDP x and PFT FDP xii. Only a few of the CR plots were correlated with PFT FDA i and PFT FDP viii.

Several of the plots sampled in the PA as well as PFT FDP vi were associated with higher extractable P (P-BRAY1) present in the soil during the drought. In the CR a few plots were associated with higher levels of the macro elements Mg and Na, which were present in the soil during the drought year in various exchangeable cation and salt concentrations. The macro element Mg was associated with PFT FDP viii and PFT FDP xi. Two PFTs were correlated with the macro element Na – PFT FDA i and PFT FDP xii. A number of plots sampled in the PA and the CR were associated with mesotrophic soil base status. PFT FDP x had a moderate association with dystrophic soil base status. Plots sampled in the PA were correlated with higher soil pH during the drought.

During the drought the PA area was characterised by annual, erect, non-spinescent and unpalatable forb PFTs (Table 6.2 & 6.4). The PA perennial PFTs were dominated by non-clonal, unpalatable species. In contrast to the PA the CR was mostly associated with perennial, clonal forbs which were mostly non-N-fixing and unpalatable (Table 6.2 & 6.4). Annual PFTs did not dominate but consisted of annual, spinescent and palatable forbs.

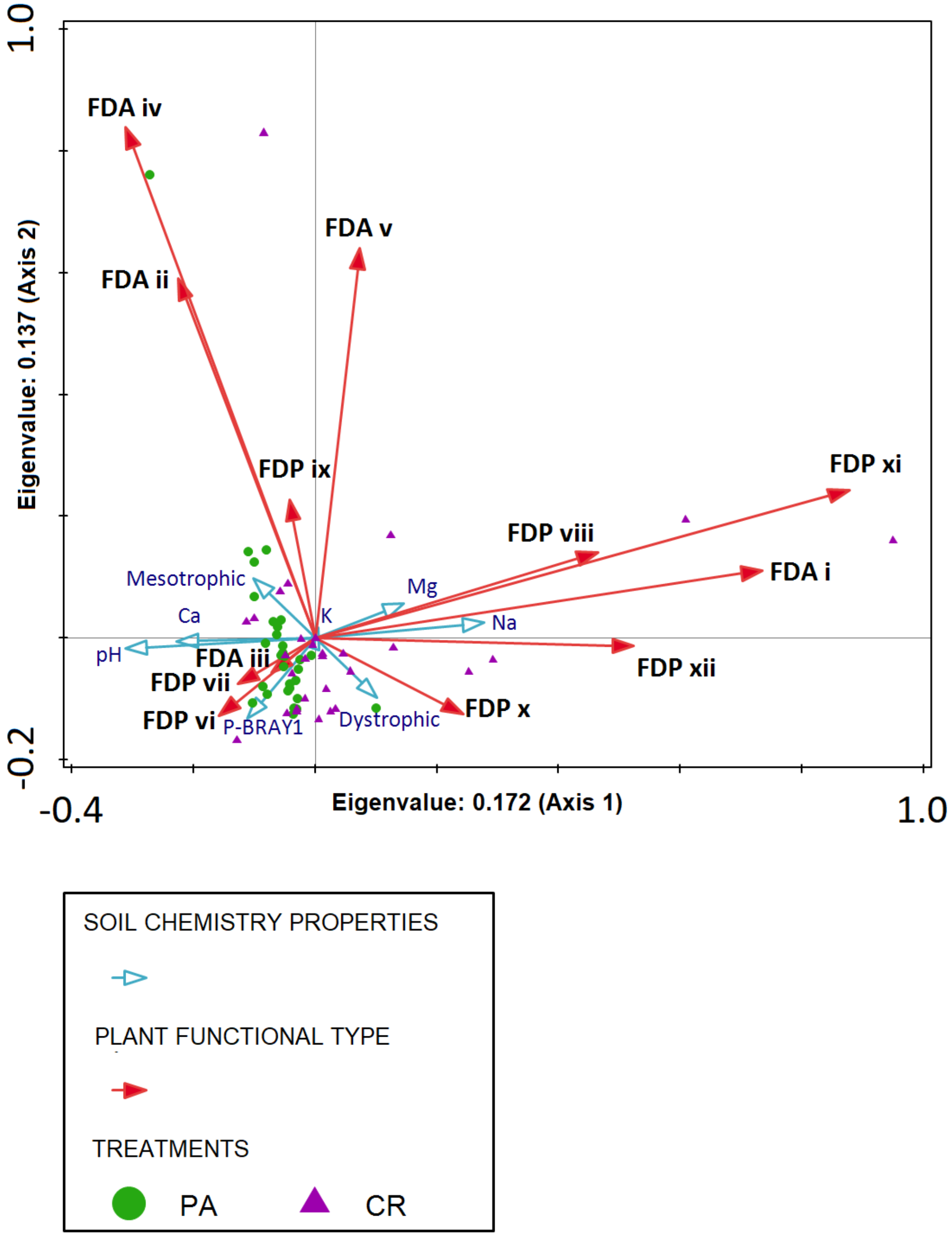

Figure 6.9 Principal Component Analysis (PCA) of forb plant functional type (PFT) data with soil chemistry properties during the drought.

I - XII, Plant functional type; *PA*, Protected area (wildlife); *CR*, Communal rangeland (livestock); *Ca* (Calcium); *Mg* (Magnesium); *K* (Potassium); *Na* (Sodium); *pH* (acidity or alkalinity); *P-Bray 1* (extractable Phosphorus)

Drought: Grasses

Axis 1 and Axis 2 (Principal Components) of the PCA explained 48.41 % of variance observed in the grass PFT data during the drought (Figure 6.10). The first Principal Component (Axis 1; Figure 6.10) was mainly correlated with higher levels of the macro soil element Na to the left and explained 27.91 % of the variance within drought grass PFTs (Figure 6.10). Grass PA plots clustered to the left of the triplot and CR plots mostly to the right during the drought. During the drought a strong correlation existed between most of the plots sampled in the PA and PFT GDA ii and PFT GDP iv. In the CR only a few of the sampled plots showed a strong correlation with PFT GDP iii and PFT GDP v, the correlation was weaker with PFT GDA i.

Most of the plots sampled within the PA had a strong association with Ca and higher soil pH. Extractable P and dystrophic base status were correlated with only a few PA sampled plots. The macro elements Na and Mg was strongly correlated with plots sampled in the CR and a weaker correlation with mesotrophic base status occurred between CR sampled plots.

The grass layer in the CR was characterised by perennial non-clonal grass PFTs in drought conditions. Annual PFTs consisted of non-clonal unpalatable grasses. In the PA duringthe drought PFTs consisted of perennial non-clonal mostly unpalatable glabrous grasses (Table 6.2 & 6.4).

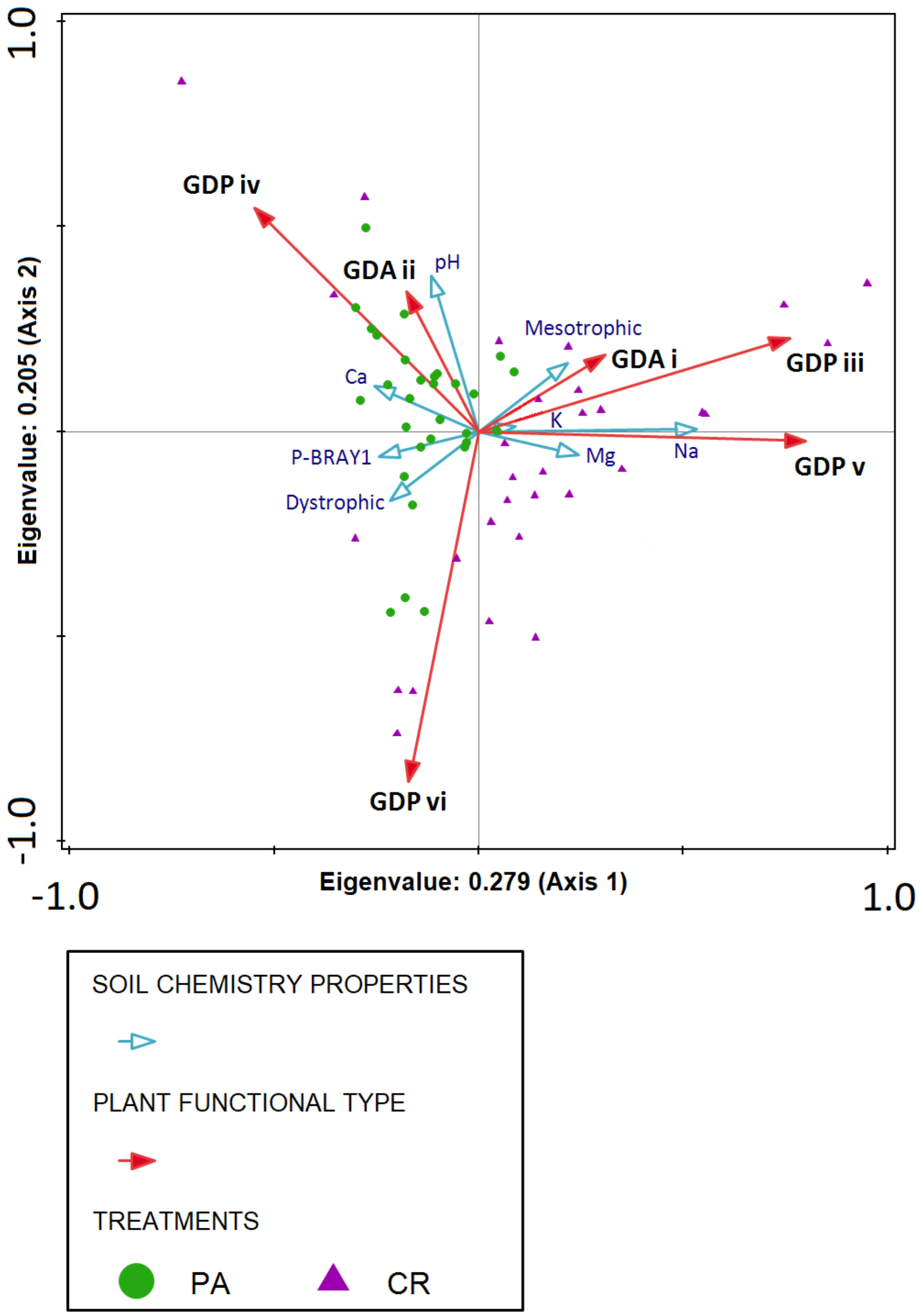

Figure 6.10 Principal Component Analysis (PCA) of grass plant functional type (PFT) data with soil chemistry properties during the drought.

I - VI, Plant functional type; *PA*, Protected area (wildlife); *CR*, Communal rangeland (livestock); *Ca* (Calcium); *Mg* (Magnesium); *K* (Potassium); *Na* (Sodium); *pH* (acidity or alkalinity); *P-Bray 1* (extractable Phosphorus)

Table 6.4: Summary of forb and grass plant functional types (PFTs) associated with each rangeland type during the drought. Strong correlation indicated with an asterisk (*).

FORB PFTs	**GRASS PFTs**
Protected Area	
FDA iii *	GDA ii *
FDP vi *	GDP iv *
FDP vii *	GDP vi
FDA ii	
FDA iv	
FDP ix	
Communal Rangeland	
FDP x *	GDA i
FDP xii *	GDP iii *
FDA i	GDP v *
FDP viii	
FDP xi	

Post-drought: Forbs

The first and second Principle Components (Eigenvalue Axis 1= 0.180; Eigenvalue Axis 2= 0.114; Figure 6.11) of the PCA explained 29.53 % of the variability which was observed in post-drought forb PFT data (Figure 6.11). The first Principle Component (Axis 1) explained 18.07 % of variance in post-drought PFTs. Clustering of sampling plots was similar to the patterns observed in the drought year PCAs – plots sampled in the PA clustered to the left of the triplot and CR sampled plots clustered to the right. Axis 1 had a strong correlation with PFT FPA iii. Several of the plots sampled in the PA had a strong association with PFT FPA iii, PFT FPP iv, PFT FPP xi. The association effect was weaker between PA plots and PFT xv and PFT ix and PFT FPP x. A strong correlation between various plots sampled in the CR and PFT FPP vii and PFT FPP viii was observed. PFT FPP vi and PFT FPP xii had a weaker correlation with several of the plots sampled in the CR.

The post-drought forb community in the PA was dominated by perennial, clonal and unpalatable PFTs. There was an equal split between erect and prostrate growth forms as well as spinescence. Perennial, palatable and non-clonal grasses characterised the CR and the PFTs with the stronger correlation effect were N_2-fixing (Table 6.2 & 6.5).

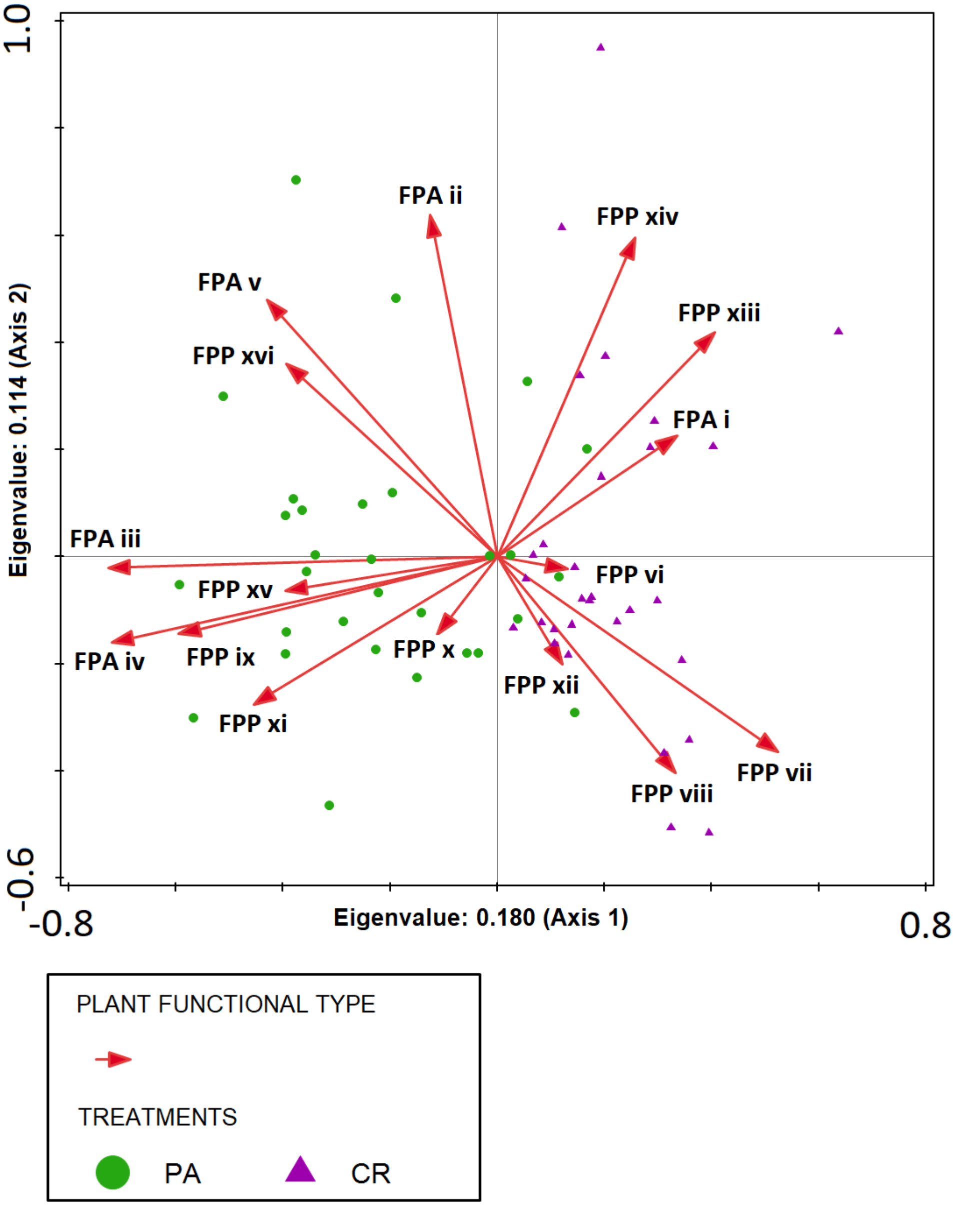

Figure 6.11 Principal Component Analysis (PCA) of forb plant functional type (PFT) data with treatments.

I - XVI, Plant functional type; *PA*, Protected area (wildlife); *CR*, Communal rangeland (livestock); *Ca* (Calcium); *Mg* (Magnesium); *K* (Potassium); *Na* (Sodium); *pH* (acidity or alkalinity); *P-Bray 1* (extractable Phosphorus)

Post-drought: Grasses

Axis 1 and Axis 2 (Principal Components) of the PCA explained 42.96 % of variance observed in grass PFT data following the drought (Figure 6.12). The first Principal Component (Axis 1; Figure 6.12) had a very strong correlation with PFT GPP vi to the right of the triplot and explained 24.17 % of the variance within post-drought grass PFTs (Figure 6.12). Most of the PA and CR plots were clustered to the bottom of the triplot; PA plots to the left and CR plots to the right. The correlation effect was strong between PA sampled plots and PFT GPA i and PFT GPP iv with only a few PA plots correlating with PFT GPA ii. In the CR most of the plots associated with PFT GPP v, PFT GPP vi and PFT vii.

Post-drought conditions in the PA favoured annual, non-clonal and moderately palatable grass PFTs. In contrast, the CR was dominated by perennial, clonal palatable grass PFTs which were mostly glabrous (Table 6.2 & 6.5).

Table 6.5: Summary of forb and grass plant functional types (PFTs) associated with each rangeland type after the drought. Strong correlation indicated with an asterisk (*).

FORB PFTs	**GRASS PFTs**
Protected Area	
FPA iii *	GPA i *
FPP xv	GPA ii
FPP ix	GPP iv *
FPP x	
FPA iv *	
FPA xi *	
Communal Rangeland	
FPP vii *	GPP v *
FPP viii *	GPP vi *
FPP vi	GPP vii *
FPP xii	

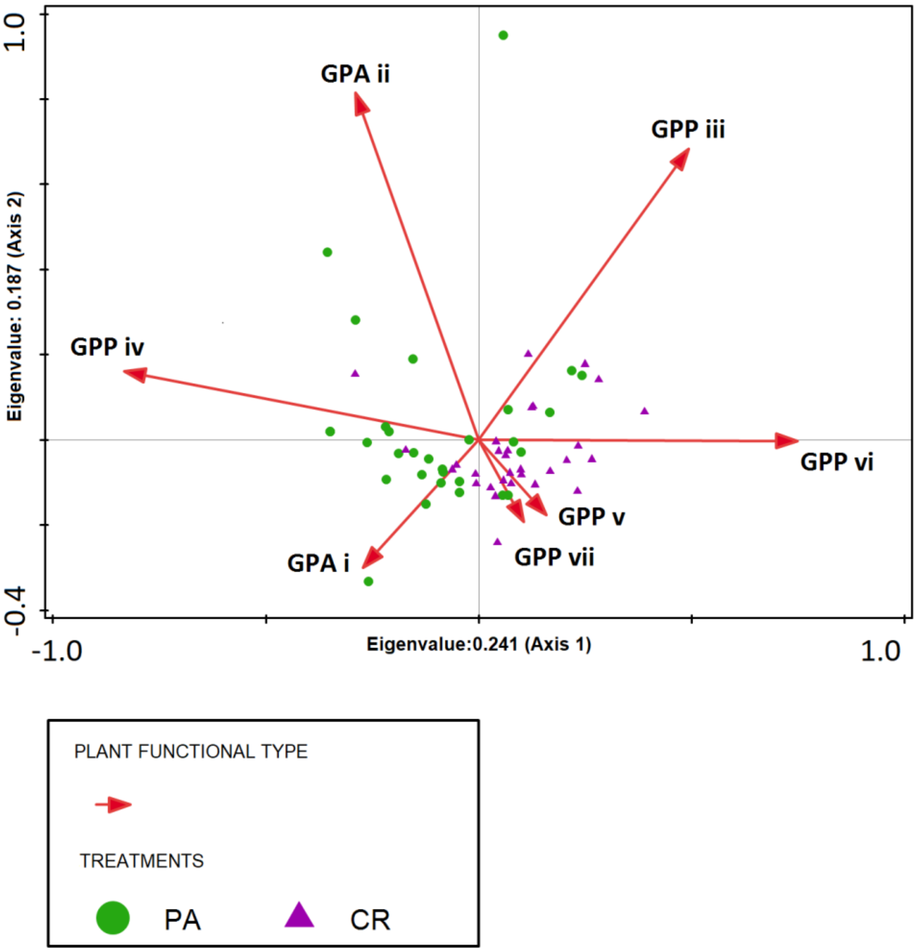

Figure 6.12 Principal Component Analysis (PCA) of grass plant functional type (PFT) data with treatments.

I - XVI, Plant functional type; *PA*, Protected area (wildlife); *CR*, Communal rangeland (livestock); *Ca* (Calcium); *Mg* (Magnesium); *K* (Potassium); *Na* (Sodium); *pH* (acidity or alkalinity); *P-Bray 1* (extractable Phosphorus)

Chapter 7

Discussion

7.1 Contrasting forb and grass community responses to rainfall conditions in savanna rangelands

Herbaceous species composition responded dynamically to rainfall variability and the different rangeland types, which corroborates the findings of similar studies (Shackleton, 2000; Porensky *et al.*, 2013; Ruppert *et al.*, 2015; Zerbo *et al.*, 2016; Riginos *et al.*, 2018). Rangeland type and rainfall variability had synergistic effects on herbaceous species composition (Porensky *et al.*, 2013; Ruppert *et al.*, 2015; Zerbo *et al.*, 2016; Riginos *et al.*, 2018).

Grass species composition only changed significantly in response to post-drought rainfall in the CR. These results correspond with findings by Fynn and O'Connor (2000), who reported very little positive effects of rainfall events on grass community composition in areas with poor rangeland condition as a result of intensive grazing over a long period. Grazing history at Welverdiend dates back to 1929, although the exact change in grazing intensity over the last few decades is not known. However, the long grazing history and the high intensity of grazing, > 400% of the recommended stocking rate for the area (Shackleton *et al.*, 1994; George, 2000), may explain the lack of grass compositional changes observed at the CR site across rainfall years. Studies by Milchunas *et al.* (1988) and O'Connor (1995) further corroborate these findings since they reported that semi-arid rangelands with a long history of grazing are more resistant to grazing pressure due to the establishment of grazing-tolerant communities. In contrast to the weak responses by grasses, forb composition changed significantly after the drought at both rangeland sites, which is similar to previous observations that forbs persist during droughts and emerge and dominate after drought events (Fynn and O'Connor, 2000; Kallah *et al.*, 2000; Buitenwerf *et al.*, 2011). Forbs possess underground storage organs (USOs) that allow them to adapt to and survive disturbances such as below average rainfall and herbivory (Uys, 2006). Traits such as USOs contribute to the resilience of forbs against drought and high herbivore pressure, however USOs did not present as important traits during this study. The lack of a proper definition and sampling technique for USOs may have caused this trait to be filtered out during statistical analyses. Notwithstanding the fact that grasses have also co-evolved with disturbances such as drought and herbivory, results of the current study suggest that forbs are more resilient in semi-arid savannas due to their significantly higher species- and functional richness. High forb species richness is in accordance with Siebert & Scogings (2015) who reported that > 70 % of semi-arid savanna species richness across a catenal sequence is contributed by forbs. Another study in a mesic grassland by Pokorny *et al.* (2004) reported that forbs constitute 83% of species richness in that system. Forbs had unique species assemblages in each rainfall year as well as within each rangeland across rainfall years. For forbs to be resilient and survive disturbances such as drought and herbivory they need special adaptations and traits i.e. nitorgen fixing ability, although further analytical approaches on the plasticity of the forb flora are needed.

Grass biomass was extremely low in both rangelands during the drought, as was expected (Bergström & Skarpe, 1999). An increase in rainfall in semi-arid and mesic savannas normally leads to substantial increases of grass biomass (Fynn & O’Connor, 2000; Koerner & Collins, 2014; Charles *et al.*, 2017) which was observed in the PA, but not in the CR. The lower biomass observed in the CR after the drought corroborates to the findings of previous studies conducted in semi-arid savannas by by O’Connor (1994), Illius & O’Connor (1998) and O’Connor (2015). These studies reported that grass tuft mortality due to very high grazing pressure during drought inhibits regeneration after cessation of the drought event. Non-significant increases in biomass at the CR is also consistent with findings by Koerner & Collins (2014) who reported weak effects of herbivory on forb biomass. Post-drought increases in forb biomass in the PA is in accordance with previous studies that reported that forbs have a preference for low to moderate grazing pressure (Fynn & O'Connor, 2000; Nicolai *et al*., 2008; Hejcmanová *et al*., 2010; Wesuls *et al.,* 2013; Cowley *et al.,* 2014). In the current study the PA was under light foraging pressure compared to the CR. Grass and forb cover increased significantly after substantial rainfall within both rangelands, which is supported by results obtained by Treydte *et al.*, (2013). However, grass cover was higher than forb cover during both rainfall years (Odadi *et al.,* 2013). In contrast to Hanke *et al.* (2014) who reported lower plant cover under heavy grazing pressure, the herbaceous species cover in the current study was higher in the heavily grazed CR than in the PA during the drought. The results from the current study may be due to higher defoliation of forbs in the PA during the drought (Du Toit, 1988; Odadi *et al*., 2007) and the higher occurrence of prostrate and rosette growth forms in the heavily grazed CR whereas the lightly grazed PA was associated with tufted or erect growth forms (Lavorel *et al*., 1997; Landsberg *et al.*, 1999; Díaz *et al*., 2007; Rutherford & Powrie, 2011; Hempson *et al*., 2014; Burkepile *et al.*, 2017).

These results support the suggestion that forbs are resilient and have adapted and acquired traits such as prostrate growth form to survive high grazing pressure, as was evident in the CR. The increase in forb cover and biomass following the drought illustrates the importance of forbs in savanna ecosystems as an additional forage source.

Forbs dominated herbaceous species richness and diversity in both the PA and CR sites, which was expected due to evidence from numerous studies in savanna and grassland ecosystems (e.g. Uys, 2006; Bond & Parr, 2010; Koerner *et al.,* 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015). Uys (2006) ascribes this to various adaptations and strategies in life history and flowering time. Forb species richness and diversity recorded within the drought year were very low, in contrast forb species richness and diversity were significantly higher in the post-drought survey. This finding is in accordance with other studies by Cleland *et al.* (2013), Porensky *et al.* (2013), Koerner & Collins (2014) and Zerbo *et al.* (2016), which reported an increase in herbaceous species richness and diversity with an increase in annual precipitation . This was however only reported in the PA. The significantly higher forb species richness in the PA compared to the CR after the drought contradicted the findings of Shackleton (2000) who observed higher species richness in communal areas adjacent to protected areas following the first rainfall of the season in a semi-arid savanna. On the contrary, grass species richness and diversity remained constant within both rangeland types during the current study. Drought-related grass mortality may have limited post-drought regrowth and seedling recruitment (O’Connor, 1994, Illius & O’Connor, 1998, O’Connor, 2015). Grasses and forbs respond differently to herbivory due to preferential foraging by herbivores and interaction of herbivory with other environmental factors (Augustine & McNaughton, 1998; Augustine & McNaughton, 2006; Odadi *et al.*, 2011; Veblen *et al.*, 2016) and forbs are known to respond dynamically to environmental changes such as increased rainfall (Shackleton, 2000; Uys, 2006; Bond & Parr, 2010). The positive effect of herbivory on forb species richness in the PA is ascribed to the diverse herbivore species assemblages hosted by African savannas because these multispecies herbivore communities forage on both forbs and grasses (Du Toit, 2003; Codron *et al.*, 2007). This foraging pattern allows the total herbivory effect to be distributed across a variety of herbaceous species which reduces competition within the herbaceous layer by creating microenvironments for more species to coexist (Bakker *et al.,* 2003; Jacobs & Naiman, 2008; Van Coller *et al*., 2013; Van Coller & Siebert, 2015).

The significantly higher species evenness within the PA compared to the CR (forbs during and after the drought and grasses during the drought) is in contrast with the findings of Zerbo *et al.* (2016) that reported no significant difference in species evenness between a communal rangeland and protected area within a single sampling season across a rainfall gradient in Burkina Faso. Results from the current study revealed a decrease in grass evenness and a slight increase in forb evenness in the post-drought year for both rangeland types, which partly supports Porensky *et al.* (2013). They reported high species evenness following a drought year but did not distinguish between grasses and forbs. Grass tuft mortality during a drought in a heavily grazed system allows annual forbs to colonise the area (O’Connor, 1995; Fynn & O’Connor, 2000; Porensky *et al.*, 2013) causing a shift in dominance of certain species during post-drought conditions. The CR did not show significant responses to rainfall variability in species richness and diversity suggesting that this system is in an alternate state of stability compared to the PA. This indicates that communal rangelands with long grazing histories may be resilient and able to withstand high grazing pressure as well as drought events.

7.2 Drought and herbivore adapted forb functional types

Previous studies have reported on the combined effects of below average rainfall (drought) and high grazing pressure on vegetation composition change from palatable perennial species to unpalatable annual and perennial species (O’Connor, 1995; Fynn & O’Connor, 2000). The current study deviated from this general pattern in several instances.

In accordance with previous studies, rainfall variability and herbivory caused significant changes in herbaceous functional trait composition (Díaz *et al.*, 1999; Wesuls *et al.*, 2013; Lohmann *et al.*, 2017). Disturbances such as rainfall variability and herbivory have strong filtering effects on the species and traits that colonises a system (Díaz *et al.*, 1999; Mouillot *et al.*, 2013). Studies on changes in trait composition in savanna ecosystems are limited, making it difficult to interpret or predict response of the herbaceous layer to drought and herbivore disturbances in terms of functional trait composition (Lohmann *et al.*, 2017). Through hierarchical clustering of traits this study contributed to the limited knowledge on response traits, and how they aggregate into functional groups which affect ecosystem functioning. Consequently, this will allow for generalisations across different systems with similar biotic and abiotic conditions and disturbances, and how ecosystem functioning will be affected under future conditions of predicted increase in drought events.

Dominance of unpalatable, perennial, clonal forbs and perennial, palatable grasses during the drought in the current study did not support the findings of O'Connor (1995; 2015) who reported a significant reduction in palatable perennial grasses due to high tuft mortality following an extended severe drought event in a semi-arid savanna. The main reason for tuft dieback was ascribed to the drought and heavy grazing pressure acting as an additional effect. Most of the perennial grasses that were recorded during the drought in this study were clonal and hairy which may have allowed these grasses to avoid and/or tolerate herbivory. Van Coller *et al.* (2018) reported co-dominance of palatable perennial forbs and palatable perennial grasses during below average rainfall years in the KNP. Results from the present study along with previous evidence therefore suggest that semi-arid savanna Lowveld systems are resilient to drought and its effects. Although annual forb and grass PFTs did not dominate during the drought, certain annual forb PFTs were prominent during the drought, supporting the results of O'Connor (1995, 2015) that reported an increase in annual forbs and grasses after a severe drought event. Annual forb PFTs consisted of non-spinescent, erect, low to moderately palatable species and mostly non- N_2-fixing species. These annual species could have survived the drought due to their low palatability causing herbivores to forage on other more palatable species. Only three species out of 26 species were erect, low to moderately palatable species were N_2-fixing, which included *Chamaecrista absus, Chamaecrista mimosoides* and *Tephrosia longipes.* This low abundance of N_2-fixing forbs could be an effect of selective foraging during the drought. Ritchie *et al.* (1998) reported that herbivores keep the abundance of N_2-fixing species low. The abundance of these three species following the drought declined in the CR and increased in the PA. The decline in the CR following the drought may be ascribed to over-utilisation during the drought and the high abundance of palatable grass PFTs in the PA following the drought could have shifted herbivore pressure away from these forb species.

During the drought, the dominant perennial forb PFTs were composed of clonal, non- N_2-fixing species which separated equally between erect and prostrate growth forms. Within these PFTs spinescence and palatability emerged as important traits. Spinescence is an anti-herbivory trait which is usually found in areas where herbivore numbers are high, but spines can also assist in reducing stress from heat or drought (Cooper & Owen-Smith, 1986; Cornelissen *et al.,* 2003; Hanley *et al*., 2007; Kotschy, 2013). The species belonging to the spinescent PFT were *Alternanthera pungens* (alien species*), Dicerocaryum senecioides* and *Tribulus zeyheri* which predominantly occurred in the CR during the drought. These species are adapted to resist or tolerate disturbances such as herbivory (Cornelissen *et al.,* 2003; Kotschy, 2013) therefore conveying resilience to the CR. Palatability is a plant functional trait indicating function as possible forage for herbivores (Pérez-Harguindeguy *et al.,* 2013) and unpalatable species are usually linked with savannas under constant grazing pressure (Skarpe, 1992). The only moderate to highly palatable forb PFT consisted of five species i.e. *Hibiscus micranthus, Talinum arnotii, Phyllanthus incurvus, Phyllanthus parvulus* and *Kyllinga alba* which were mostly found in the CR during the drought. However, when the drought was released, their abundance increased markedly in the PA and remained constant in the CR. The presence of these palatable forb species in the heavily stocked CR may be due to their ability to resprout from woody rootstocks, which make these species important sources of forge during drought events. This provides further evidence of the importance of studying forbs at the species level to improve the understanding of savanna ecosystem functioning.

Unpalatable, perennial, clonal forbs and palatable, perennial, clonal grasses dominated the herbaceous layer during the wetter sampling year. Other studies in southern African semi-arid savannas responded similarly with an increase in perennial grasses after substantial rainfall following a drought event (Buitenwerf *et al.*, 2011; O'Connor, 2015; Guo *et al.*, 2016; Tessema *et al.*, 2016). Since the current study was conducted on sandy substrates of granitic crests, the dominance of palatable perennial grasses across rainfall years is in accordance with O'Connor (2015) who suggests that fewer compositional changes in perennial grasses are expected to occur on sandy soils. This is due to the water holding capacity and the nutrient status of sandy soil being lower than that of heavy textured soil, thus the effect of drought does not bring about great change in vegetation composition (O'Connor, 2015). Similar to the drought, clonality was again the main trait on which perennial forb PFTs separated following the drought. Clonality is a functional trait that provides plants with competitive strength and the ability to persist following a disturbance (Cornelissen *et al.,* 2003; Pérez-Harguindeguy *et al*., 2013; Kotschy, 2013). The next split after clonality was based on spinescence, followed by palatability and N_2-fixing ability. Spinescence, palatability and N_2-fixing ability were the important traits of post-drought PFTs. N_2-fixing is usually associated with nutrient-poor systems since it is a plant strategy for nutrient uptake via symbiosis with N_2-fixing bacteria which are present in the soil (Cornelissen *et al.,* 2003). The perennial forb PFT that contained N_2-fixing species included species such as *Alysicarpus vaginalis, Indigofera astragalina, Tephrosia polystachya,* and *Vigna vexillata* which only occurred in the CR in low abundances in post-drought conditions. Their emergence in post-drought conditions are corroborated by studies with similar results (Fynn & O'Connor, 2000; Kallah *et al.*, 2000; Buitenwerf *et al.*, 2011). Fynn and O'Connor (2000) reported a marked increase in forbs following a severe drought event which could be explained by clonality which conveys drought and herbivore resistance to these species (Uys, 2006).

In the drought year the PA was associated with unpalatable and non-spinescent erect forb PFTs, of which three were annual (FDA ii, FDA iii, FDA iv) and three were perennial (FDP vi, FDP vii, FDP ix). The PA had palatable perennial grass PFTs (GDP iii, GDP vi) and one unpalatable annual PFT (GDA ii). The CR was associated with clonal, non-spinescent, non N_2-fixing and palatable forb PFTs, one annual and three perennials (FDA i, FDP x, FDP xi, FDP xii). Two perennial glabrous grass PFTs (GDP iii, GDP v) and one annual, unpalatable PFT (GDA i) were associated with the CR during the drought. Increased grazing pressure from livestock is suggested to reduce the occurrence of palatable perennial species (Angassa, 2014), but the current study did not support these results since grass PFT GDP v is palatable. The occurrence of palatable forb species in the CR during the drought could indicate that this system has drought-adapted PFTs which enhances the resilience of the system. The majority of the total herbaceous layer (forbs and grasses) PFTs during the drought were perennials. Some perennial grass species have been found to be drought-tolerant (O'Connor, 1998, 2015), which could explain the presence of 4 perennial grass PFTs (13 species) versus two perennial grass PFTs (4 species) during the dry year. Unpalatable annual plants are expected to increase and dominate during a drought and under heavy grazing (O'Connor, 1995) but palatable perennials dominated in the current study. This may be due to perennial grasses in this study being mostly clonal and hairy, these traits convey herbivore avoidance to the species.

Forb drought PCA analyses revealed a higher soil pH for the PA and a strong correlation between the macro element Ca and the first axis. Soil pH is involved in many important plant-soil reactions (Draszawka-Bołzan, 2017). The PCA also revealed that higher levels of the macro elements Mg and Na were correlated with the CR plots. These macro elements along with K occur in their various exchangeable cation and salt concentrations which is explained by salination of soil in heavily grazed areas (Zarekia *et al.*, 2012). The drought PCA analyses for the grass component revealed a pattern similar to the forb PCA i.e. the PA was associated with Ca, extractable P and high pH. Heavy grazing in the CR is responsible for soil salination indicted by the very strong association between the CR and the macro element Na as well as weaker associations with Mg and K. The first axis of the grass PCA had a very strong association with PFT GDP v which was correlated with CR plots.

Post-drought forb PFTs associated with the PA were dominated by perennial, unpalatable, clonal PFTs (FPA ii, FPA iv, FPP ix, FPP x, FPP xi). These results support the findings of Van Coller *et al.* (2018) that rainfall increases the abundance of unpalatable, perennial forbs in nutrient-rich semi-arid savannas. These functional types should have traits adapted to herbivore presence. The lack of palatable forb PFTs was compensated for by strong associations with palatable annual PFTs (GPA i, GPA ii) and perennial grass PFT (GPP iv). Other studies of savanna ecosystems have also reported on the positive effect of rainfall on palatable grass abundances (Guo *et al*., 2016; Tessema *et al.,* 2016). Buitenwerf *et al*. (2011). These studies reported an increase in perennial grasses following a wet year in a semi-arid savanna and O’Connor (2015) remarked that palatable, perennial grasses only recovered from a severe drought after four years of above average rainfall. The CR was characterised by clonal, palatable, perennial forb PFTs (FPP vi, FPP xii, FPP vii, FPP viii) the latter two being N_2-fixing. Post-drought grass communities in the CR was also characterised by palatable, perennial PFTs (Buitenwerf *et al*., 2011; O'Connor, 2015; Guo *et al*., 2016; Tessema *et al.,* 2016). Post-drought dominance of palatable perennial grasses is in line with similar studies but the dominance of palatable forb species was somewhat unexpected since Buitenwerf *et al.* (2011) reported that palatable perennial, grasses increase following substantial rainfall at the expense of forbs. The high abundance of palatable forb species in the CR following the drought is a good indicator of adaptation and resilience against sustained grazing and below average rainfall conditions in this system. This could prove to be very valuable as pastoralism and drought events increases in the future.

Chapter 8

Conclusions

Herbaceous life forms were expected to respond inversely to rainfall variability and rangeland type due to obvious differences between forbs and grasses regarding their distinct ecological, morphological and functional differences.

Community level investigations revealed changes in grass assemblages across rainfall years in the protected area only, which support the **first community level hypothesis** stating that grass assemblages remain unaffected by drought in areas with a long history of livestock grazing. Forb species composition, however changed significantly across rainfall years and rangeland types. These results suggest that this particular semi-arid savanna ecosystem hosts a drought-adapted forb flora. Forb species richness and diversity responded positively to post-drought rainfall and increased in the protected area, but not in the communal rangeland. The **second community level hypothesis** stating that the communal rangeland would show greater response to drought due to the perceived larger effects of livestock grazing on herbaceous vegetation is rejected. The drought negatively affected both forb and grass biomass and cover, although these herbaceous productivity measures were higher for forbs compared to grasses during the drought. Post-drought rainfall prompted an increase in both forb and grass biomass and cover, although significant rainfall effects were only evident in the protected area. From this, the **third community level hypothesis** stating that herbaceous biomass would be extremely low irrespective of rangeland type during the drought is supported. The **fourth community level hypothesis** stating that herbaceous cover and biomass would increase significantly following post-drought rainfall is rejected since the communal rangeland did not respond as expected. Forb and grass abundance increased after the drought and forbs dominated both rangelands following the drought which supports the **fifth community level hypothesis** stating that forbs will dominate after the drought, especially in the heavily grazed communal rangeland. From the above the **first main hypotheses of this study** stating that the heavily stocked communal rangeland would undergo more severe compositional changes than the protected area is supported.

Functional level analyses of the herbaceous layer revealed significant changes in functional trait and PFT composition in response to rainfall variability and rangeland type. The protected area was dominated by unpalatable, non-spinescent, erect forbs and palatable, perennial grasses during the drought, which were replaced by perennial, unpalatable, clonal forb PFTs after the drought. In this area of the lowveld palatable, clonal, non-spinescent and non-N_2-fixing forbs and perennial glabrous grass PFTs made way for clonal, palatable perennial forb species. Post-drought grass PFTs in the communal rangeland were palatable, perennial species. From the above the **first functional level hypothesis** stating that the heavily grazed communal rangeland would be dominated by annual grass PFTs as well as unpalatable, creeping grass PFTs is therefore rejected. The **second functional level hypothesis** stating that the communal rangeland would consist of more prostrate PFTs compared to the protected area is rejected because both rangelands hosted both erect and prostrate PFTs in equal abundance. Drought and post-drought conditions were associated with unpalatable, perennial, clonal forbs and perennial, palatable grasses, except that clonality also became an important grass trait after the drought. The **third functional level hypothesis** stating that palatable, perennial grasses will dominate after the drought is supported. The **fourth functional level hypothesis** which stated that drought and grazing will cause perennial PFTs to decrease and allow annual and weakly tufted perennials to establish was rejected based on above mentioned similarity in drought and post-drought PFTs, which consisted of perennial PFTs. From the above the **second main hypotheses of this study** stating that drought will cause a decrease in perennial grass species and in increase in annuals forbs and short-lived grass species is rejected.

Within this nutrient-poor granitic semi-arid savanna the CR herbaceous layer species diversity, richness and evenness was mostly unaffected by rainfall variability. Only small increases or decreases occured in these species indices, except for significant increases in cover for both herbaceous life forms. Similarly, the CR PFTs did not change significantly across rainfall years. The CR of this system appears to be resilient to the effects of drought and herbivory due to the less significant responses to rainfall variability and rangeland type. In the PA dynamic responses were observed in species diversity, richness, evenness and cover across rangeland type and rainfall variability. The PA is adapted to overcome the effects of drought through functional diversity and redundancy in the form of various PFTs within each life form, which can maintain the functioning of the system.

One important limitation of this study was the lack of pre-drought data. More data on pre-drought vegetation could have provided a clearer picture of the system's response to disturbance and ability to recover from a drought event. Rainfall events leading up to the drought could impact the observed patterns during the drought. If the drought was preceded by a single or consecutive wet year the vegetation would have been in a better state going into the drought than if the drought was preded by a series of dry years. A better sense of the resillience of the ecosystem may have been provided by pre-drought data. These responses of the herbaceous layer have a clear impact on the overall community level response to land use and climate change, especially with the spread of pastoralism and predicted increases in rainfall variability and drought events in the future. This study contributed to the knowledge gaps on the response of the herbaceous layer to disturbances such as rainfall variability and rangeland type in nutrient-poor granitic savannas. Results from this study can be compared with similar studies from other areas with different environmental factors or gradients i.e. soil nutrient status, position along the catena or even studies conducted on different continents with other herbivore guilds such as those found in Northern America and Europe. Comparisons of similar studies compared to the current study will lead to better understanding of ecological processes which will allow for better predictions for future disturbances. Land managers could use results obtained in this study as a guideline in making necessary management or conservation decisions.

Recommendations for future research resulting from this study:

- Clearly define plant functional traits that will be recorded during the study and determine best way to sample and record these traits in the field or from literature.
- Sample, analyse and compare results from nutrient-rich sites within this study area.
- Continue monitoring sampling sites on an annual basis to improved understanding of the dynamics of this system.
- Considering commercial livestock land-use as an additional rangeland system and fire as an additional disturbance effect.
- In-depth investigations of underground storage organs and bud-bank regeneration of forbs to better understand forb emergence after drought events.
- Use results from this study in areas where domestic livestock and wild herbivores share the same foraging grounds to better manage these systems for optimal diversity and animal production.

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Appendix A: List of abbreviations relevant to this dissertation

Table A1: List of abbreviations used throughout the dissertation with their meaning

Abbreviation	**Meaning**
ANOVA	One-way Analyses of Variance
APNR	Associated Private Nature Reserves
CA	Correspondence Analysis
CAM	Crassulacean Acid Metabolism
CCA	Canonical Correspondence Analysis
CR	Communal Rangeland
DCA	Detrended Correspondence Analysis
GLMM	Generalized Linear Mixed Model
GPS	Global Positioning System
HLM	Hierarchical Linear Model
KNP	Kruger National Park
MAP	Mean Annual Precipitation
NMDS	Non-Metric Multi-Dimensional Scaling
PA	Protected Area
PCA	Principal Component Analyses
PERMANOVA	Permutational Multivariate Analysis of Variance
PFT	Plant Functional Type
RDA	Redundancy Analysis
SAEON	South African Environmental Observation Network
SIMPER	Similarity Percentage Analysis
SIMPROF	Similarity Profile
SLA	Specific Leaf Area
TPNR	Timbavati Private Nature Reserve
UPGMA	Unweighted Pair Group Method with Arithmetic Mean
USO	Underground Storage Organ

Appendix B: Supplementary tables supporting Chapter 3

Table B1: Acronyms and full species names according to Germishuizen and Meyer (2003) for all herbaceous species recorded in the study area. Alien species are indicated with an asterisk (*). Codes represent unknown species of which no specimen could be sampled due to poor quality of fresh material during the drought year.

Name	**Species acronym**	**Life form**
Abutilon angulatum Mill.	Abu ang	Forb
Aerva leucara Moq.	Aer leu	Forb
Agathisanthemum bojeri Klotzsch	Aga boj	Forb
**Alternanthera pungens* Kunth	Alt pun	Forb
Alysicarpus vaginalis (L.) DC.	Aly vag	Forb
Aristida adscensionis L.	Ari ads	Grass
Aristida congesta Roem & Schult. subsp. *barbicollis (Trin. & Rupr.) De Winter*	Ari con bar	Grass
Aristida congesta L. Roem & Schult. subsp. *congesta*	Ari con con	Grass
Aristida meridionalis Henrard	Ari mer	Grass
Aristida stipitata Hack.	Ari sti	Grass
Aristida vestita Thunb.	Ari ves	Grass
**Bidens biternata* (Lour.) Merr. & Sherff	Bid bit	Forb
**Bidens pilosa* L.	Bid pil	Forb
**Bidens bipinnata* L.	Bid pip	Forb
Brachiaria deflexa (Schumach.) C.E.Hubb. ex Robyns	Bra def	Grass
Bulbostylis hispidula (Vahl) R.W.Haines	Bul his	Forb
Chamaecrista absus (L.) Irwin & Barneby	Cha abs	Forb
Chamaecrista mimosoides (L.) Greene	Cha mim	Forb
Chloris virgata Sw.	Chl vir	Grass
Cleome macrophylla (Klotzsch) Briq.	Cleo mac	Forb
Cleome monophylla L.	Cleo mon	Forb
Commelina benghalensis L.	Com ben	Forb
Commelina eckloniana Kunth	Com eck	Forb
Corchorus asplenifolius Burch.	Cor asp	Forb

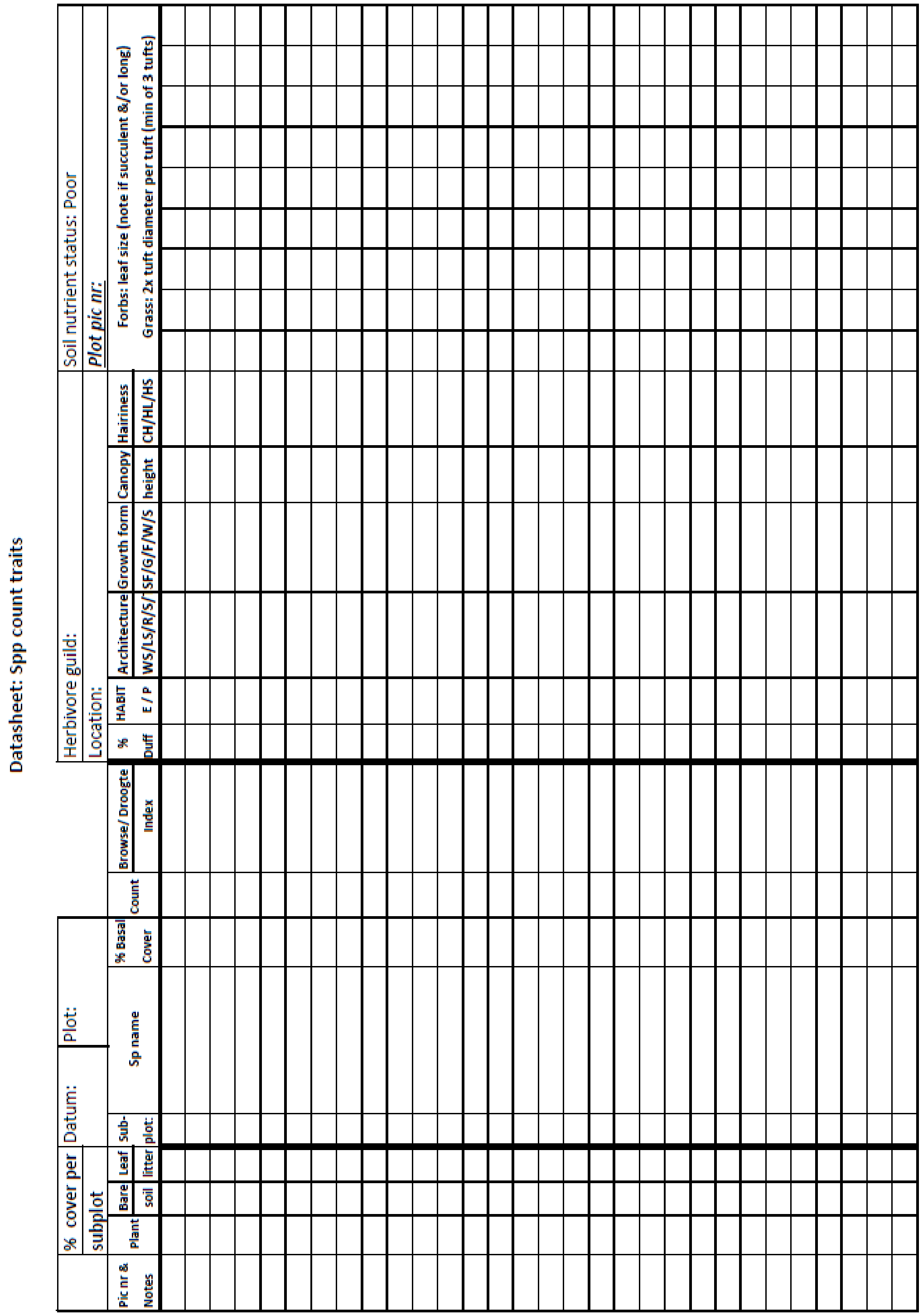
Crotalaria podocarpa DC.	Cro pod	Forb
Crotalaria sphaerocarpa Perr. Ex DC.	Cro sph	Forb
Crotalaria sp L.	Crot sp	Forb
Cucumis zeyheri Sond.	Cuc zey	Forb
Cynodon dactylon (L.) Pers.	Cyn dac	Grass
Cyperus indecorus Kunth	Cyp ind	Forb
Cyperus rupestris Kunth	Cyp rup	Forb
Dactyloctenium australe Steud.	Dac aus	Grass
Dactyloctenium giganteum Fisher & Schweick.	Dac gig	Grass
Dicerocaryum senecioides (Klotzsch) Abels	Dic sen	Forb
Digitaria eriantha Steud.	Dig eri	Grass
Enteropogon macrostachyus (A.Rich.) Benth.	Ent mac	Grass
Eragrostis inamoena K.Schum.	Era ina	Grass
Eragrostis lehmanniana Nees	Era leh	Grass
Eragrostis rigidior Pilg.	Era rig	Grass
Eragrostis sp Wolf	Era sp	Grass
Eragrostis superba Peyr.	Era sup	Grass
Evolvulus alsinoides (L.) L.	Evo als	Forb
Gisekia africana (Lour.) Kuntze	Gis afr	Forb
GNP01-06	GNP01-06	Grass
GNP03-02	GNP03-02	Forb
GNR06-03	GNR06-03	Forb
**Gomphrena celosiodes* Mart.	Gom cel	Forb
Heliotropium ciliatum Kaplan	Hel cil	Forb
Heliotropium ovalifolium Forssk.	Hel ova	Forb
Heliotropium strigosum Willd.	Hel str	Forb
Helichrysum argyrosphaerum	Helic arg	Forb
Hermannia boraginiflora Hook.	Her bor	Forb
Hermannia sp L.	Her sp	Forb
Hermbstaedtia odorata (Burch.) T.Cooke	Her odo	Forb

Heteropogon contortus (L.) Roem. & Schult.	Het con	Grass
Hibiscus calyphyllus Cav.	Hib cal	Forb
Hibiscus micranthus L.f.	Hib mic	Forb
Hibiscus palmatus Forssk.	Hib pal	Forb
Hibiscus praetritus R.A.Dyer	Hib pra	Forb
Hibiscus pusillus Thunb.	Hib pus	Forb
Indigofera astragalina DC.	Ind ast	Forb
Indigofera filipes Benth. ex Harv.	Ind fil	Forb
Indigofera sp L.	Ind sp	Forb
Justicia protracta (Nees) T.Anderson	Jus pro	Forb
Kohautia caespitosa Schnizl.	Koh cae	Forb
Kohautia virgata (Willd) Bremek.	Koh vir	Forb
Kyllinga alba Nees	Kyl alb	Forb
Kyphocarpa angustifolia (Moq.) Lopr.	Kyp ang	Forb
Leucas neuflizeana Courbon	Leu neu	Forb
Leucas sexdentata Skan	Leu sex	Forb
Limeum viscosum (J.Gay) Fenzl	Lim vis	Forb
Macrotyloma axillare (E.Mey.) Verdc.	Mac axi	Forb
Melhania prostrata DC.	Mel pro	Forb
Monsonia angustifolia E.Mey. Ex A.Rich.	Mon ang	Forb
Monsonia glauca R.Knuth	Mon gla	Forb
Oxygonum delagoense Kuntze	Oxy del	Forb
Oxygonum sinuatum (Hochst. & Steud. Ex Meisn.) Dammer	Oxy sin	Forb
Panicum coloratum L.	Pan col	Grass
Panicum maximum Jacq.	Pan max	Grass
Pergularia daemia (Forssk.) Chiov.	Per dae	Forb
Perotis patens Gand.	Per pat	Grass
Phyllanthus incurvus Thunb.	Phy inc	Forb
Phyllanthus maderaspatensis L.	Phy mad	Forb
Phyllanthus parvulus Sond.	Phy par	Forb

Phyllanthus pentandrus Schumach. & Thonn.	Phy pen	Forb
Pogonarthria squarrosa (Roem. & Schult.) Pilg.	Pog squ	Grass
Pollichia campestris Aiton	Pol cam	Forb
Polygala sphenoptera Fresen.	Pol sph	Forb
Portulaca hereroensis Schinz	Por her	Forb
Portulaca kermesina N.E.Br.	Por ker	Forb
Portulaca quadrifida L.	Por qua	Forb
Priva cordifolia (L.f.) Druce	Pri cor	Forb
Rhinacanthus xerophilus A.Meeuse	Rhi xer	Forb
Rhynchosia sp Lour.	Rhy sp	Forb
**Richardia brasiliensis* Gomes	Ric bra	Forb
Ruellia cordata Thunb.	Rue cor	Forb
Ruellia patula Jacq.	Rue pat	Forb
Ruellia sp L.	Rue sp	Forb
Schmidtia pappophoroides Steud.	Sch pap	Grass
Schkuhria pinnata (Lam.) Cabrera	Sch pin	Forb
Seddera capensis (E.Mey. Ex Choisy) Hallier f.	Sed cap	Forb
Seddera suffruticosa Hallier f.	Sed suf	Forb
Sida sp L.	Sid sp	Forb
Solanum delagoense Dunal	Sol del	Forb
Talinum arnotii Hook.f.	Tal arn	Forb
Tephrosia longipes Meisn.	Tep lon	Forb
Tephrosia polystachya E.Mey.	Tep pol	Forb
Tephrosia purpurea (L.) Pers.	Tep pur	Forb
Tephrosia sp Pers.	Tep sp	Forb
Thunbergia neglecta Sond.	Thu neg	Forb
Tragus berteronianus Schult.	Tra ber	Grass
Trichoneurs grandiglumis (Nees) Ekman	Tri gra	Grass
Tricliceras laceratum (Oberm.) Oberm.	Tri lac	Forb
Tricliceras longepedunculatum (Mast.) R.Fern.	Tri lon	Forb

Tricholaena monachne (Trin.) Stapf & C.E.Hubb.	Tri mon	Grass
Triumfetta pentandra A.Rich.	Tri pen	Forb
Triumfetta rhomboidea Jacq.	Tri rho	Forb
Tribulus terrestris L.	Tri ter	Forb
Tribulus zeyheri Sond.	Tri zey	Forb
Urochloa mosambicensis (Hack.) Dandy	Uro mos	Grass
Vigna vexillata (L.) A.Rich.	Vig vex	Forb
Waltheria indica L.	Wal ind	Forb
Xenostegia tridentata (L.) D.F.Austin & Staples	Xen tri	Forb
Zinnia peruviana (L.) L.	Zin per	Forb

Appendix C: Supplementary figures and tables supporting Chapter 4



Datasheet: Spp count traits

Datum:
Plot:
Herbivore guild:
Location:
Soil nutrient status: Poor
Plot pic nr:

	% cover per subplot														
Pic nr & Notes	Plant	Bare soil	Leaf litter	Sub-plot:	Sp name	% Basal Cover	Count	Browse/ Droogte Index	% Duff	HABIT E / P	Architecture WS/LS/R/S/	Growth form SF/G/F/W/S	Canopy height	Hairiness CH/HL/HS	Forbs: leaf size (note if succulent &/or long) Grass: 2x tuft diameter per tuft (min of 3 tufts)

Figure C1: Example of datasheets used to record species information during sampling.

Table C1: Soil particle size for paired transects sampled in the study area. CNP = communal rangeland, CNP01-CNP06 represent the six sampling plots in the communal rangeland. GNP = protected area, GNP01-GNP06 represent the six sampling plots in the protected area. Soil samples form plots located geographically close to each other were pooled before analyses.

Sample site	Sample (plots)	> 2mm	Sand	Silt	Clay	Soil type
		(%)	(% < 2mm)			
Communal Rangeland	CNP01, CNP02	1,8	91,3	4,7	4,1	fine sand
	CNP03, CNP06	3,5	91,2	6,9	1,9	fine sand
	CNP04, CNP05	7,4	90,7	5,0	4,3	fine sand
Protected Area	GNP01, GNP02	1,4	91,6	6,6	1,8	fine sand
	GNP03, GNP04	1,5	93,5	4,6	1,8	fine sand
	GNP05, GNP06	4,0	91,2	7,0	1,9	fine sand

Calculated using Soil Texture Calculator accessed at:
https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/?cid=nrcs142p2_054167

Table C2: Summary of macro elements obtained from soil samples within the study area. CNP = communal rangeland, CNP01-CNP06 represent the six sampling plots in the communal rangeland. GNP = protected area, GNP01-GNP06 represent the six sampling plots in the protected area. Soil samples form plots located geographically close to each other were pooled before analyses.

Sample site	Sample (plots)	Ca	Mg	K	Na	% clay	Base status	
		Centimoles per kg (cmol/kg)						
Communal Rangeland	CNP01, CNP02	0,026	0,1	0,122	0,039	4,1	7,08	mesotrophic
	CNP03, CNP06	0,011	0,008	0,039	0,041	1,9	5,26	mesotrophic
	CNP04, CNP05	0,011	0,011	0,031	0,027	4,3	1,84	dystrophic
Protected Area	GNP01, GNP02	0,023	0,004	0,044	0,012	1,8	4,63	dystrophic
	GNP03, GNP04	0,023	0,01	0,053	0,013	1,8	5,38	mesotrophic
	GNP05, GNP06	0,027	0,011	0,081	0,016	1,9	7,16	mesotrophic

Base status: Calculated by multiplying the sum of the reported basic cations by 100 and dividing by the clay percentage of the sample.

Table C3: Summary of micro elements, pH, soil acidity, EC (electrical conductivity) and P-BRAY1 (extractable phosphorus) of the soil in the study area. CNP = communal rangeland, CNP01-CNP06 represent the six sampling plots in the communal rangeland. GNP = protected area, GNP01-GNP06 represent the six sampling plots in the protected area.

Sample site	**Sample (plots)**	**Fe**	**Mn**	**Cu**	**Zn**	**B**	**pH**	**Soil acidity**	**EC** ***(mS/cm)***	**P-BRAY 1 dpm**
		Millimol per litre (mmol/l)								
Communal Rangeland	CNP01, CNP02	0,02426	0,00315	0,0005	0,00037	0,018	5,77	Acidic	0,25	7
	CNP03, CNP06	0,01822	0,00116	0,00042	0,00042	0,014	5,63	Acidic	0,13	4,66
	CNP04, CNP05	0,02609	0,00166	0,00055	0,00046	0,012	4,96	Acidic	0,11	5,8
Protected Area	GNP01, GNP02	0,02816	0,00307	0,0004	0,00041	0,019	5,91	Acidic	0,12	5,71
	GNP03, GNP04	0,02758	0,00297	0,00044	0,00037	0,018	5,84	Acidic	0,14	5,07
	GNP05, GNP06	0,02493	0,00324	0,00036	0,00054	0,02	6,05	Neutral	0,18	20,66

Appendix D: Supplementary figures and tables supporting Chapter 5

Full species names are provided according to Germishuizen and Meyer (2003). Alien species are indicated with an asterisk (*).

Table D1: Results for similarity percentage analyses (SIMPER) indicating specific forb species contributing > 2 % to compositional differences across rainfall years irrespective of rangeland type. Alien species are indicated with an astrsik (*). Av.dis., Average dissimilarity; Cont. (%); Distance/Similarity measure: Bray-Curtis.

Species	**Av. Dis.**	**Cont. (%)**	**Cumulative %**	**Mean abundance: Drought**	**Mean abundance: Post-drought**
Overall average dissimilarity= 58,65					
Tephrosia purpurea	5,984	10,2	10,2	0	167
Gisekia africana	5,41	9,224	19,43	154	3
Cleome macrophylla	4,837	8,247	27,67	135	0
Limeum viscosum	4,515	7,697	35,37	0	126
Triumfetta rhomboidea	3,046	5,192	40,56	0	85
Kyllinga alba	2,795	4,765	45,33	313	235
Monsonia angustifolia	1,791	3,054	48,38	51	1
Hibiscus pusillus	1,756	2,993	51,37	0	49
Phyllanthus parvulus	1,612	2,749	54,12	19	64
Bulbostylis hispidula	1,469	2,505	56,63	60	101
**Richardia brasiliensis*	1,433	2,443	59,07	1	41
Kohautia virgata	1,326	2,26	61,33	0	37
Phyllanthus maderaspatensis	1,254	2,138	63,47	35	0
Hermannia boraginiflora	1,218	2,077	65,55	0	34

Table D2: Results for similarity percentage analyses (SIMPER) indicating specific grass species contributing > 2 % to compositional differences across rainfall years irrespective of rangeland type. Av.dis., Average dissimilarity; Cont. (%); Distance/Similarity measure: Bray-Curtis.

Species	Av. Dis.	Cont. (%)	Cumulative %	Mean abundance: Drought	Mean abundance: Post-drought
Overall average dissimilarity= 42,11					
Digitaria eriantha	6,852	16,27	16,27	363	590
Panicum maximum	5,373	12,76	29,03	222	400
Urochloa mosambicensis	4,769	11,33	40,36	83	241
Aristida congesta subsp. *congesta*	4,316	10,25	50,61	179	36
Aristida adscensionis	4,256	10,11	60,72	1	142
Aristida congesta subsp. *barbicollis*	3,803	9,032	69,75	0	126
Eragrostis rigidior	2,173	5,161	74,91	205	133
Aristida meridionalis	1,539	3,656	78,57	53	2
Eragrostis lehmanniana	1,509	3,584	82,15	0	50
Schmidtia pappophoroides	1,117	2,652	84,8	43	80

Table D3: Results for similarity percentage analyses (SIMPER) indicating specific forb species contributing > 2 % to compositional differences across rangeland types irrespective of rainfall year. Av.dis., Average dissimilarity; Cont. (%); Distance/Similarity measure: Bray-Curtis.

Species	Av. Dis.	Cont. (%)	Cumulative %	Mean abundance: Protected area	Mean abundance: Communal rangeland
Overall average dissimilarity= 71,69					
Kyllinga alba	18,92	26,39	26,39	10	538
Gisekia africana	5,554	7,746	34,13	156	1
Cleome macrophylla	4,837	6,747	40,88	0	135
Tephrosia purpurea	4,479	6,247	47,13	21	146

Chamaecrista mimosoides	3,26	4,548	51,67	115	24
Limeum viscosum	2,938	4,098	55,77	104	22
Bulbostylis hispidula	2,329	3,248	59,02	48	113
Cyperus rupestris	2,078	2,899	61,92	58	0

Table D4: Results for similarity percentage analyses (SIMPER) indicating specific grass species contributing > 2 % to compositional differences across rangeland types irrespective of rainfall year. Av.dis., Average dissimilarity; Cont. (%); Distance/Similarity measure: Bray-Curtis.

Species	**Av. Dis.**	**Cont. (%)**	**Cumulative %**	**Mean abundance: Protected area**	**Mean abundance: Communal rangeland**
Overall average dissimilarity= 58,65					
Digitaria eriantha	21,64	43,17	43,17	118	835
Panicum maximum	6,52	13	56,17	419	203
Aristida adscensionis	3,833	7,646	63,82	135	8
Aristida congesta subsp. *congesta*	3,35	6,683	70,5	52	163
Eragrostis rigidior	1,992	3,974	74,47	136	202
Cynodon dactylon	1,841	3,672	78,15	4	65
Aristida meridionalis	1,66	3,311	81,46	55	0
Schmidtia pappophoroides	1,298	2,589	84,05	40	83
Aristida congesta subsp. *barbicollis*	1,268	2,529	86,57	84	42
Pogonarthria squarrosa	1,147	2,288	88,86	7	45

Table D5: Results for similarity percentage analyses (SIMPER) indicating specific forb species contributing > 2 % to compositional differences within the Protected area (PA) across rainfall years. Alien species are indicated with an astrsik (*). Av.dis., Average dissimilarity; Cont. (%); Distance/Similarity measure: Bray-Curtis.

Species	**Av. Dis.**	**Cont. (%)**	**Cumulative %**	**Mean abundance: PA Drought**	**Mean abundance: PA Post-drought**
Overall average dissimilarity= 79,62					
Gisekia africana	11,56	14,52	14,52	154	2
Limeum viscosum	7,909	9,933	24,45	0	104
Chamaecrista absus	4,259	5,349	29,8	0	56
Hibiscus pusillus	3,726	4,68	34,48	0	49
Bulbostylis hispidula	3,65	4,585	39,06	0	48
Triumfetta rhomboidea	3,422	4,298	43,36	0	45
Kohautia virgata	2,814	3,534	46,9	0	37
Phyllanthus parvulus	2,738	3,438	50,33	10	46
Hermannia boraginiflora	2,586	3,247	53,58	0	34
**Richardia brasiliensis*	2,433	3,056	56,64	0	32
**Bidens pilosa*	2,357	2,961	59,6	0	31
Phyllanthus incurvus	2,129	2,674	62,27	0	28
Cyperus rupestris	1,673	2,101	64,37	40	18
Tephrosia purpurea	1,597	2,006	66,38	0	21

Table D6: Results for similarity percentage analyses (SIMPER) indicating specific grass species contributing > 2 % to compositional differences within the Protected area (PA) across rainfall years. Av.dis., Average dissimilarity; Cont. (%); Distance/Similarity measure: Bray-Curtis.

Species	**Av. Dis.**	**Cont. (%)**	**Cumulative %**	**Mean abundance: PA Drought**	**Mean abundance: PA Post-drought**
Overall average dissimilarity= 77,63					
Panicum maximum	16,38	21,1	21,1	96	323

Urochloa mosambicensis	11,47	14,78	35,87	1	160
Aristida adscensionis	9,596	12,36	48,23	1	134
Digitaria eriantha	8,514	10,97	59,2	0	118
Aristida congesta subsp. *barbicollis*	6,061	7,807	67,01	0	84
Aristida congesta subsp. *congesta*	3,752	4,833	71,84	52	0
Aristida meridionalis	3,68	4,74	76,58	53	2
Eragrostis rigidior	3,463	4,461	81,04	92	44
Schmidtia pappophoroides	2,742	3,532	84,57	1	39
Eragrostis lehmanniana	2,67	3,439	88,01	0	37

Table D7: Results for similarity percentage analyses (SIMPER) indicating specific forb species contributing > 2 % to compositional differences within the Communal rangeland (CR) across rainfall years. Av.dis., Average dissimilarity; Cont. (%); Distance/Similarity measure: Bray-Curtis.

Species	**Av. Dis.**	**Cont. (%)**	**Cumulative %**	**Mean abundance: CR Drought**	**Mean abundance: CR Post-drought**
Overall average dissimilarity= 53,25					
Tephrosia purpurea	9,892	18,58	18,58	0	146
Cleome macrophylla	9,146	17,18	35,75	135	0
Kyllinga alba	5,962	11,2	46,95	313	225
Monsonia angustifolia	3,184	5,98	52,93	48	1
Triumfetta rhomboidea	2,71	5,089	58,02	0	40
Schkuhria pinnata	2,033	3,817	61,83	30	0
Chamaecrista absus	1,626	3,053	64,89	28	4
Limeum viscosum	1,491	2,799	67,68	0	22
Phyllanthus incurvus	1,355	2,545	70,23	25	5
Phyllanthus maderaspatensis	1,152	2,163	72,39	17	0

Table D8: Results for similarity percentage analyses (SIMPER) indicating specific grass species contributing > 2 % to compositional differences within the Communal rangeland (CR) across rainfall years. Av.dis., Average dissimilarity; Cont. (%); Distance/Similarity measure: Bray-Curtis.

Species	**Av. Dis.**	**Cont. (%)**	**Cumulative %**	**Mean abundance: CR Drought**	**Mean abundance: CR Post-drought**
Overall average dissimilarity= 22,57					
Digitaria eriantha	5,656	25,06	25,06	363	472
Aristida congesta subsp. *congesta*	4,722	20,92	45,98	127	36
Panicum maximum	2,543	11,26	57,24	126	77
Aristida congesta subsp. *barbicollis*	2,18	9,655	66,9	0	42
Cynodon dactylon	1,401	6,207	73,1	19	46
Eragrostis rigidior	1,245	5,517	78,62	113	89
Heteropogon contortus	0,8822	3,908	82,53	0	17
Pogonarthria squarrosa	0,7784	3,448	85,98	30	15
Eragrostis lehmanniana	0,6746	2,989	88,97	0	13
Tragus berteronianus	0,5189	2,299	91,26	14	24

Table D9: Specific forb species characteristic of the forb flora of the Lowveld savanna area, during the drought and after the drought. Values indicate species abundance. Alien species are indicated with an astrsik (*).

Species	**PA Drought**	**CR Drought**	**PA Post-drought**	**CR Post-drought**
Lowveld savanna				
Phyllanthus parvulus	10	9	46	18
Heliotropium strigosum	26	2	13	10
Indigofera filipes	1	8	11	9
Chamaecrista mimosoides	49	17	66	7
Xenostegia tridentata	4	1	4	1
Drought				

Phyllanthus maderaspatensis	18	17	0	0
**Bidens bipinnata*	7	13	0	0
Heliotropium ovalifolium	7	7	0	0
Phyllanthus pentandrus	4	3	0	0
Post-drought				
Tephrosia purpurea	0	0	21	146
Triumfetta rhomboidea	0	0	45	40
Limeum viscosum	0	0	104	22
Pergularia daemia	0	0	4	8
Tephrosia polystachya	0	0	2	5
Agathisanthemum bojeri	0	0	2	4
Helichrysum argyrosphaerum	0	0	6	1
Cucumis zeyheri	0	0	2	1
Polygala sphenoptera	0	0	2	1
Crotalaria podocarpa	0	0	1	1
Crotalaria sphaerocarpa	0	0	1	1

Table D10: Specific grass species characteristic of the forb flora of the Lowveld savanna area and after the drought. Values indicate species abundance.

Species	**PA Drought**	**CR Drought**	**PA Post-drought**	**CR Post-drought**
Lowveld savanna				
Eragrostis rigidior	92	113	44	89
Panicum maximum	96	126	323	77
Perotis patens	6	7	27	8
Pogonarthria squarrosa	4	30	3	15
Schmidtia pappophoroides	1	42	39	41
Urochloa mosambicensis	1	82	160	81
Post-drought				
Aristida congesta subsp*. barbicollis*	0	0	84	42
Brachiaria deflexa	0	0	12	6

Eragrostis lehmanniana	0	0	37	13
Tricholaena monachne	0	0	3	3

Table D11.: Effect sizes of HLM results for comparison between rainfall year, rangeland type and herbaceous species diversity and basal cover. Significant effect sizes at $d \geq 0.8$ are indicated with an asterisk (*).

Variables compared	Treatment	Effect size
Total species (S)		
Rainfall year	Protected Area	1.50*
	Communal Rangeland	0.16
Rangeland type	Drought (2016)	1.53*
	Post-drought (2017)	1.79*
Total individuals (N)		
Rainfall year	Protected Area	1.14*
	Communal Rangeland	0.05
Rangeland type	Drought (2016)	2.42*
	Post-drought (2017)	0.64
Margalef's species richness (d)		
Rainfall year	Protected Area	1.27*
	Communal Rangeland	0.18
Rangeland type	Drought (2016)	0.35
	Post-drought (2017)	2.39*
Shannon-wiener diversity index (H')		
Rainfall year	Protected Area	1.17*
	Communal Rangeland	0.10
Rangeland type	Drought (2016)	0.28
	Post-drought (2017)	2.38*
Basal cover (%)		
Rainfall year	Protected Area	2.64*
	Communal Rangeland	1.35*
Rangeland type	Drought (2016)	2.42*

	Post-drought (2017)	0.72
Pielou's evenness (J')		
Rainfall year	Protected Area	0.25
	Communal Rangeland	0.04
Rangeland type	Drought (2016)	2.07*
	Post-drought (2017)	1.33*
Simpson (1-Lambda)		
Rainfall year	Protected Area	0.35
	Communal Rangeland	0.06
Rangeland type	Drought (2016)	0.60
	Post-drought (2017)	1.33*

Table D12.: Standard errors (SE) of HLM results for comparison between rainfall year, rangeland type and herbaceous species diversity and basal cover.

Life form	**Standard error**
Total species (S)	
Forbs	0.084
Grasses	0.084
Total individuals (N)	
Forbs	3.741
Grasses	3.741
Margalef's species richness (d)	
Forbs	0.119
Grasses	0.118
Shannon-wiener diversity index (H')	
Forbs	0.101
Grasses	0.101
Basal cover (%)	
Forbs	0.140
Grasses	0.140

Pielou's evenness (J')	
Forbs	0.022
Grasses	0.022
Simpson (1-Lambda)	
Forbs	0.048
Grasses	0.047

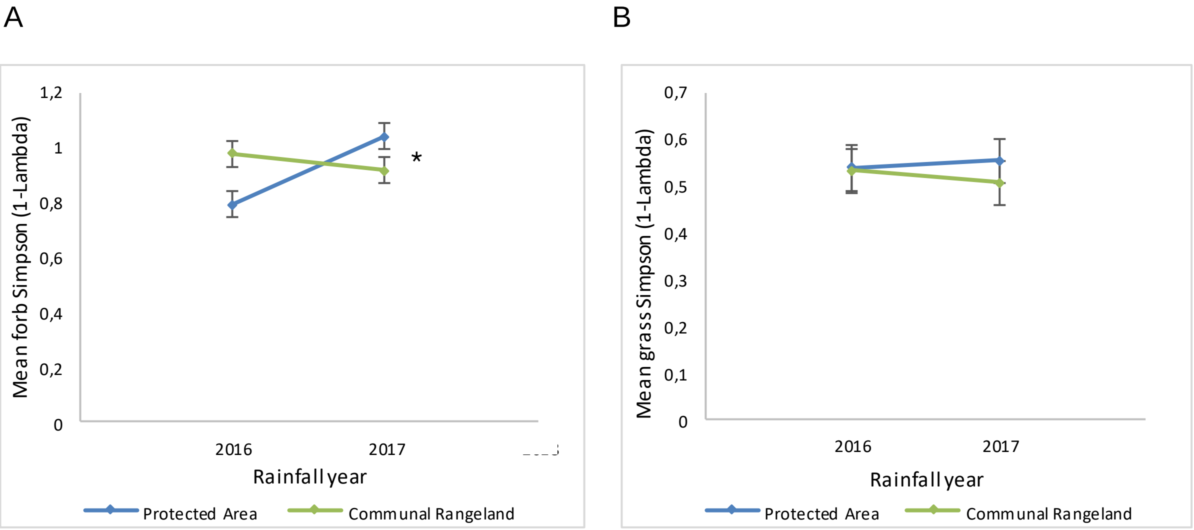


Figure D1: Mean (±SE) Simpson (1-Lambda) per 1m^2 plot across rainfall year and rangeland type for forbs (A) and grasses (B).

Appendix E: Supplementary tables and figures supporting Chapter 6

Table E1: Principal Component Analysis (PCA) eigenvalues and cumulative variance across rainfall years (2016, drought; 2017, post-drought) for forbs and grasses.

Forbs: Drought				
Axes	**1**	**2**	**3**	**4**
Eigenvalues:	0.1720	0.1376	0.1275	0.1106
Explained variation (cumulative):	17.20	30.96	43.71	54.77
Pseudo-canonical correlation (suppl.)	0.3772	0.2412	0.6650	0.5740
Forbs: Post-drought				
Eigenvalues:	0.1807	0.1146	0.0933	0.0828
Explained variation (cumulative):	18.07	29.53	38.86	47.14
Grasses: Drought				
Eigenvalues:	0.2791	0.2050	0.1793	0.1461
Explained variation (cumulative):	27.91	48.41	66.34	80.95
Pseudo-canonical correlation (suppl.)	0.5629	0.5418	0.3812	0.2331
Grasses: Post-drought				
Eigenvalues:	0.2417	0.1879	0.1723	0.1505
Explained variation (cumulative):	24.17	42.96	60.18	75.23

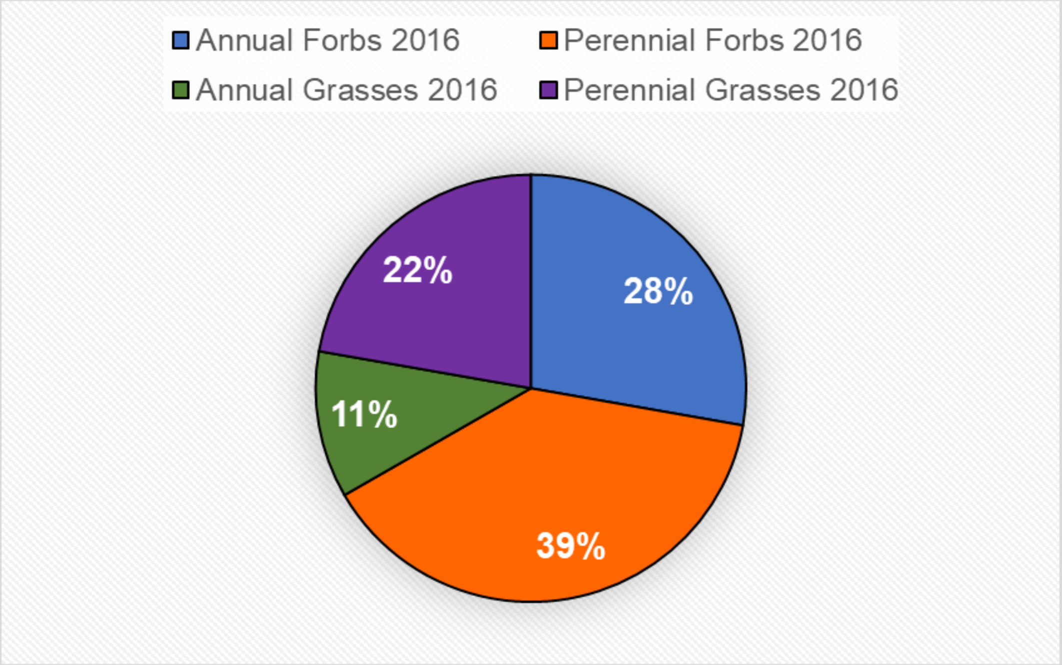


Figure E1: Frequency of plant functional types (PFTs) in the drought (2016) rainfall year.

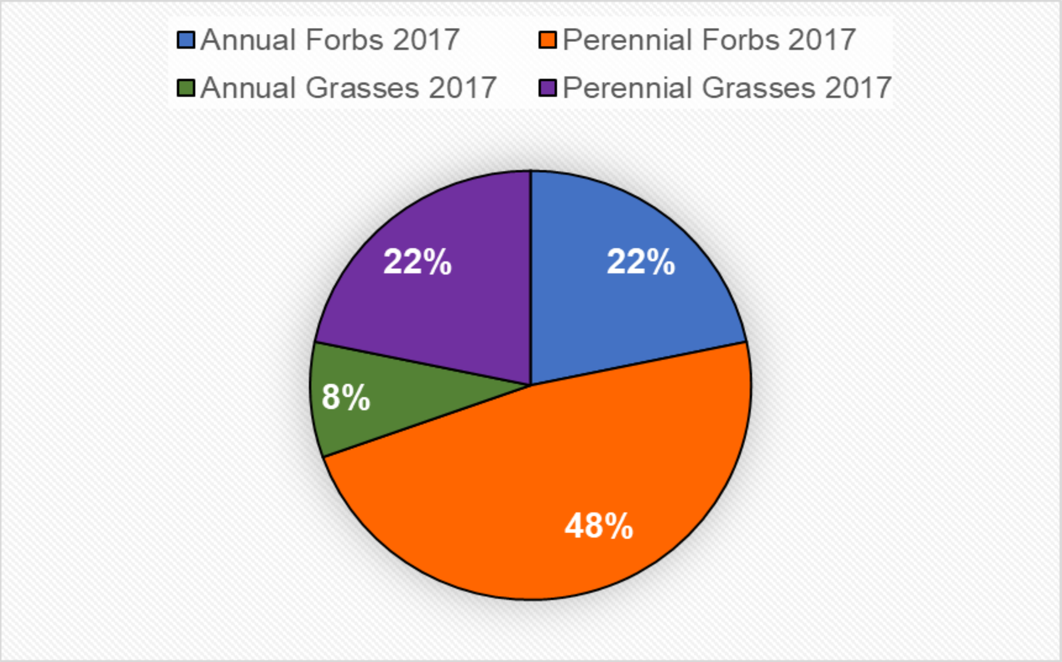


Figure E2: Frequency of plant functional types (PFTs) in the post-drought (2017) rainfall year.