The effects of experimental drought, grazing, and seasonality on ant and spider diversity in an arid region of South Africa

By

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DECLARATION

I **RATSHIBVUMO TSHIKAMBU,** hereby declare that the dissertation for the degree of Masters of Science at the University of Venda, hereby submitted by me, had not been previously submitted for a degree at this university or any other university, that it is my own work in design and execution and that all reference material contained has been duly acknowledged.

1 September 2020

Signature (student): R.Tshikambu .... Date: ....

DEDICATION

"I would like to dedicate my thesis to my beloved mother, you are the best"

ABSTRACT

Coupled with irreversible shifts, climate-driven disturbance of ecosystems will probably be the largest impact of climate change on humans. With higher rainfall variability and more intense events, separated by extended dry periods, semi-arid rangelands will be severely altered. Adding to these climatic events, livestock grazing is one of the most common land use practices globally, which will increase as human populations grow. The magnitude of these synergies between drought and grazing could also vary with season. Our understanding of faunal response to the interaction of both drought and grazing is limited. This study investigated the response of ants and spiders, two dominant components of epigeal invertebrate assemblages, to a long-term drought and grazing experiment. The experiment consisted of four 40 x 40 m blocks, each with nine 10 x 10 m plots. Drought was simulated using rainout shelters, whilst grazing was manipulated by excluding livestock from the plots using ~ 1 m high fence around the plots. Ants and spiders were collected seasonally in a blocked and two-way crossed experiment using a total of 96 pitfall traps. Both ant and spider size were assessed using community weighted mean. Grazing treatment had the bigger impact on ants than drought, as they got smaller, functionally less diverse and less active with grazing. The interaction between grazing and drought encouraged the increase in activity of large ants. There was an interesting interaction between grazing and drought, plots with grazing had smaller ants than plots without grazing, but only in plots for which there had been drought. This could be attributed to antlion abundance and how they interact with grazing on the specific plots. Assemblage level analysis confirmed the importance of size in structuring these communities, with larger species of ants associated with open and dry habitats. In contrast, spiders were more responsive to drought than grazing treatments. The spider response to the treatments was in conjunction with seasonality, with spider richness decreasing with cold, dry season (winter) and hot, dry season (spring) respectively. Spiders also became less active during the dry seasons. Interestingly, smaller spider species were more active during cold, dry season, and larger species were more active during the hot, dry season where there is no grazing. At assembly level, grazing and no drought interaction encouraged mobile species that were more of active hunters, as open habitats are ideal hunting ground. Our findings clearly suggest that both long-term drought and grazing have an impact on ants and spiders. How these taxa respond to long-term effects on drought and livestock grazing in semi-arid rangelands in the face of climate change is likely to shed light also on how other invertebrates are likely to be affected, and what it could mean for

the ecosystem as whole. Further studying is needed to uncover other underlying changes, how that affects and shapes the semi-arid rangeland ecosystems in the long-term.

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First and foremost, I thank the God for giving me the strength to come this far. I am truly grateful to Prof Stefan Hendrick Foord. I could not have asked for a better supervisor and mentor. He believed in me and helped me tirelessly. He was very patient with me through the course of this thesis. I am very grateful to my co-supervisor Dr Caswell Munyai for reading and commenting on all the manuscripts and also guiding me.

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CHAPTER 1: INTRODUCTION

Global climate change

Climate-driven change on ecosystems coupled with irreversible shifts of faunal assemblages will have the most impacts on humans. Climate change has altered phenology, ranges of individual species, and community structure across many taxa (Resasco *et al.* 2014), as well as their relative abundances within communities (Walker *et al.* 2006). It will also have a profound impact on the terrestrial animal species in South Africa (Erasmus *et al.* 2002) where it is already posing a significant threat to South Africa's water resources, food security, biodiversity and ecosystem services (Ziervogel *et al.* 2014).

Global climate change models generally predict higher rainfall variability, with more intense rainfall events separated by extended dry periods in the arid and semi-arid regions of Southern Africa (IPCC 2007). It is also predicted that reductions in mean annual rainfall, increased inter-annual variation, and more frequent droughts in the Savanna semi-arid rangelands will lead to disproportionately large negative consequences for assemblage structure, and species distribution (Lohmann *et al.* 2012), and these changes are expected to have a profound negative impact on ecosystem processes and biodiversity.

Drought in southern Africa's semi-arid rangelands

Much of southern Africa lies within semi-arid or arid climatic regions, which experience a high degree of variability in rainfall (Manson and Joubert 1996), where droughts occur frequently and can have severe ecological and economic consequences (Vetter 2009). Drought is a naturally occurring phenomenon and it mostly causes hydrological imbalance which has consequences for the natural resource production systems (Williams and Bailling 1994).

Drought is a change trigger, which acts in synergy with other kinds of triggers such as grazing regime. Thus drought can lower the transition state of the ecosystem such that a particular amount of perturbation, like grazing, becomes sufficient to trigger change (Vetter 2009). Droughts are extreme climatic events that are likely to change more rapidly than the mean climate (Trenberth *et al.* 2003). The potential for large increases in these extreme climate events under global warming is of concern (Trenberth *et al.* 2004).

Livestock grazing in southern Africa's semi-arid rangelands

Rangelands constitute about 30% of South African land surface, with livestock farming being the most dominant land use (Milton and Dean 2003). South Africa's rangelands were reported to be the main source of fodder for more than 42 million livestock (DAFF 2011). The growing human population density and redistribution of people is contributing to the intensifying use of rangelands in south Africa. The intensification of land-use practices for the past 200 years has resulted in changes that are destroying the rangeland ecosystem services, which benefits both rural and urban based South Africans.

In the arid and semi-arid ecosystems especially in the Savanna, mismanaged livestock grazing is reported to be the biggest driver of land degradation, and biodiversity loss (Sala *et al.* 2000). Land degradation is due to grazing regimes that allow insufficient time for vegetation recovery and regeneration (Beinart 2003). Adeel *et al.* (2005) defined land degradation as the decrease in the land's productivity. Poor management and changes in the use of land on a regional and even global scale is decreasing the value of rangelands to people through the loss of palatable plants, firewood, and clean water (Milton and Dean 2003). The effects of livestock grazing in rangelands have been addressed by several studies.

Hanke *et al.* (2014), who tested the impact of grazing intensity, found that heavier grazing reduced total plant cover and altered the species and functional composition. Eldridge *et al.* (2016) observed that the vegetation structure and function declined more when grazed by both sheep and cattle, than sheep alone. Furthermore, in the same study, grazing effects on plant and animal richness and composition declined with increasing aridity, with the negative effect of grazing being more profound in drier environments. The decrease in vegetation cover as a result of grazing intensifies during dry periods and partly recovers after a good rainfall season (Dube and Pickup 2001).

The rangeland livestock carrying capacity can be negatively influenced by variability in rainfall; as prolonged interannual variation in precipitation and temperature can severely decrease the carrying capacity (Lohmann *et al.* 2012). Grazing will likely also interact with climate change to alter ecosystem function in other unforeseen ways (Altwegg *et al.* 2014). Heavy and continuous livestock grazing is thought to be a major factor which increases the likelihood of drought. This is further supported by Vogel (1993) who suggested that land use practices can create or worsen agricultural and/or hydrological drought. Agricultural drought is takes place when the lack of precipitation leads to a decline in soil moisture affecting pastures and hydrological drought occurs when there is a significantly reduction in the availability of water in the hydrological system, rivers, lakes and underground.

Seasonality and precipitation across southern Africa

The southern African rainfall is more variable than temperature, both in space and time. During summer the Namibian coast and western parts of South Africa experience very dry conditions while there is higher precipitation in the north and eastern parts (Daron 2014). A northwest-to-southeast gradient is observed during winter with Namibia and Botswana typically receiving little to no rainfall (Daron 2014). The coast of South Africa and Mozambique receives some winter rainfall, particularly in the winter rainfall region of South Africa. The variation between driest and wettest summers is quite significant (Daron 2014). The rainfall variation between arid and semi-arid areas of central and south-eastern Botswana ranges from less than 100 mm to more than 300 mm between the driest and wettest year (Daron 2014).

Precipitation variability, which is the driving force behind primary productivity, affects species directly or indirectly because it controls habitat productivity (Delsinne 2010, Hawkins *et al.* 2003). On average, precipitation explains 60% of variation on a wide range of plants and animals (Hawkins *et al.* 2003). Schwinning *et al.* (2004) illustrated that the seasonal timing of rain can fundamentally alter its role in the ecosystem function and can influence patterns of species diversity. As a result, seasonality is a key factor to consider when studying variation in species assemblages (Mineo *et al.* 2010).

The variations in seasonal climatic changes in addition to drought continues to change the structure and function of communities. However, the changes to the structure and function of communities are also dependant on geographic location (Stuble *et al.* 2012, Hawkins *et al.* 2003) and aridity (Ruppert *et al.* 2014, Zeppel *et al.* 2014). Evaporation and evapotranspiration are likely to increase throughout the year as a result of warming temperatures but will be more pronounced in autumn, spring and summer as a result of anthropogenic climate change. Moreover, evapotranspiration is greater under arid relative to mesic conditions (Hawkins *et al.* 2003).

Biodiversity monitoring

Biodiversity is a fundamental component for ecosystem functioning and subsequently a key for ensuring ecosystem stability (Tiede *et al.* 2017). Understanding biodiversity and its underlying processes has been a major focus in ecological research (Segev 2009). This calls for continuation in monitoring the status of biodiversity, which not only focuses on the presence or absence of certain (keystone) species but monitors functional changes in species assemblages and their effects on food webs and ecosystem processes (Tiede *et al.* 2017).

Using arthropods as bioindicators

Bioindicators are key stone species that are used in the monitoring of the status of biodiversity and ecosystem (Tiede *et al.* 2017). Numerous types of bioindicators have been described (Andersen 1999). However, for them to be effective they should be distributed over a wide geographic area and be taxonomically and ecologically known (Rainio and Neimala 2003). Ideally, indicators should perform several biodiversity functions within the same ecosystem (Landres *et al.* 1988). Generally, bioindicators show a negative response to ecosystem transformation, and their responses vary between species, sites (Hess *et al.* 2006) and a wide range of other factors including timing and intensity of disturbance. Arthropods have been used as indicators as they contribute most to species richness in any ecosystem (Hoffmann 2000). They are ideal indicators of ecosystem changes and habitat modification due to their high sensitivity to microclimate changes in temperature and moisture content (Schowalter *et al.* 2003). Given their functional importance, monitoring arthropod response patterns to habitat transformation and disturbance, might help to better predict and understand how other species and the ecosystems at large will be affected. A wide variety of arthropods have been used as indicators of ecosystem changes and habitat transformation in numerous studies.

Beetles are cost-effective as they are easy to sample and they are excellent bioindicators of forest disturbance caused by fragmentation (Osawa *et al*. 2005, Nicholas *et al.* 2007). Forest fragmentation decreases the numbers of large-bodied carabid species with poor dispersal, making them ideal indicators of forest disturbance and fragmentation (Osawa *et al.* 2005). Adult cerambycid beetles are plant-feeders and occasional pollinators in diverse forest ecosystems, thus have become a target group for forest biodiversity monitoring (Maeto and Makihara 1999, Maeto *et al.* 2002).

Butterflies and moths have been used to monitor the health of the grassland ecosystems (Grill *et al.* 2005) and its recovery after disturbance (New 2004). Butterfly abundance, species richness and diversity can be indicative of a healthy ecosystem as it reflects vegetation diversity (Halder *et al.* 2008, Grill *et al.* 2005). This might be because the species richness of butterflies is associated with the richness of nectar and herbaceous plants (Grill *et al.* 2005). Moths have been used as indicators in environmental disturbance recovery (New 2004). However, their response to disturbance varies between families. Some moths respond positively whilst others respond negatively (Kitching *et al.* 2000).

Ants have also been used extensively as indicators of ecosystem change (Anderson 1997, Anderson 1999, Ellison 2012, Tiede *et al.* 2017). Moreover, their simple and cost-effective sampling has made them suitable bioindicators (Folgarait 1998). Ants are widely used to assess landscape disturbance (Andersen & Majer 2004, Arcoverde *et al.* 2016) and ecological functioning (Stuble *et al.* 2014). These insects constitute an important fraction of the animal biomass in terrestrial ecosystems and respond to stress on a much finer scale compared to vertebrates (Bhati *et al.* 2016). Moreover, ants are present at almost all the trophic levels of the food web (Pfeiffer *et al.* 2013), making them indispensable for the propesr functioning of most terrestrial ecosystems and the resulting ecosystem services (Del Toro *et al.* 2012). Habitat disturbance and transformation affect ant communities in many ways, either by changing habitat structure, microclimate (Lach *et al.* 2010) or resource availability (Philpott *et al.* 2010).

Like ants, spiders have been used successfully as bioindicators of natural and anthropogenic disturbances (Pearce and Venier 2006), and they are also known to be very sensitive to changes in the environment on a fine scale (Foord *et al.* 2008). Spiders have been used in previous studies (Horváth *et al.* 2015, Mineo *et al.* 2010, El keroumi *et al*. 2012, Whitmore *et al.* 2002) to monitor microclimate changes. They have a strong potential as ecological indicators as they are readily surveyed in adequate numbers for important conclusions to be drawn and they have a stable taxonomy (Pearce and Venier 2005). Furthermore, grassland spiders are the most abundant generalist predators and they are sensitive to habitat change making them ideal in the detection of microclimatic changes (Horváth *et al.* 2015). Spiders have been reported to be good indicators of habitat disturbance resulting from forest fragmentation (Pearce and Venier 2005).

Response of ants to grazing and drought

Previously, studies (Hoffman 2000, Hoffman 2010, Bestelmeyer and Wein 2001, Arcoverde *et al.* 2016) have suggested that ants respond predictably to habitat transformation and disturbance. Grazing has a secondary influence on variation in ant communities, with such variation primarily driven by soil and vegetation (Hoffman 2000). Clay soil is associated with low ant diversity as compared to other soil types, which might be due to the difficulty in building nests and seasonal waterlogging (Arcoverde *et al.* 2016) and Bestelmeyer and Wein 2001).

Although grazing modifies ant species composition, it often does not change ant species richness and overall abundance (Hoffmann 2010). There was no direct relationship found between grazing and the three indices, *viz.* ant richness, activity and overall abundance in the arid Savanna ecosystems. This suggests that any impact of grazing is primarily through species turnover (Hoffman 2000, Hoffmann 2010) where species that prefer open and bare habitats (grazed) are replaced by species that prefer structurally complex grass layers (ungrazed) (Arcoverde *et al.* 2017). However, how species respond to grazing varies, and many responses are context dependent (Hoffmann 2010). Thus, the challenge now is to provide a predictive understanding of this context dependency, as well as to improve the precision of the predictive responses.

After studying the impacts of rainfall exclusion on ants for six months, Delsinne *et al.* (2013) observed that the overall species richness was not changed by drought, however, the species composition was modified. Additionally, species that were nesting in suspended branches started nesting under drought shelters which suggest that drought provided better nesting sites and that the latter could be more limiting than food. Convergence of ant communities and optimum nesting conditions has been positively correlated with drought stress caused by low precipitation (Rizali *et al.* 2013). Temperature was found to have a strong association with ant diversity in dry treatments (Sanders *et al.* 2007).

In the Indonesian agroforestry system, no effect of precipitation on species richness were observed, however, high precipitation had a negative impact on nests and nesting site availability (Rizali *et al.* 2013). High precipitation may influence ant communities because of its negative relationship to ant nesting site availability, which is an important stressor for ants in agroforestry system (Rizali *et al.* 2013). In addition, seasonality influences ant assemblages; high precipitation can decrease the size of colonies and the activity of ants (*Delsinne et al.* 2013).

Purdon *et al.* (2019) predicted that in semi-arid savannah seasonality, in the presence of grazing, would affect the speed at which ants discovered resources and the intensity of resource monopolization and found that ants in winter monopolized more baits and discovered resources at a slower rate since activity is generally reduced due to changes in temperature, but only at certain times within the experiment. Grazing in conjunction with the season thus had a significant effect on ant diversity and foraging behaviour, with dominant ants promoted where habitat complexity was simplified during winter (Purdon *et al*. 2019).

Response of spiders to grazing and drought

Various studies (Gibson *et al.* 1992, Churchill and Ludwig 2004, Jansen *et al.* 2013) have reported a negative impact of grazing on the diversity of spiders, with ungrazed areas having a greater species richness. Spider diversity gradually increases with plant succession in the absence of grazing, suggesting that the impact of grazing on spiders is generally through the change of plant architecture, as this affects web-building for foliage dwelling spiders (Da Silva and Ott 2017). Ungrazed sites tend to have more spiders due to unchanged plant architecture and harbors web-building species in families such as Theridiidae, which are positively correlated with increasing numbers perennial plants (Gibson *et al.* 1992).

On the contrary, in Swedish grasslands grazed plots were reported as having more species richness compare to ungrazed plots (abandoned plots) (Dupre and Diekmann, 2001). In highland grasslands no measurable effect of grazing intensity on the diversity of ground-dwelling spiders were observed (Jansen *et al.* 2013). Furthermore, in the same study, ungrazed areas were observed to have spider communities with fewer individuals. Suggesting that plant architecture may not affect ground-dwelling spiders as it does with plant-dwelling species.

A long-term (14 years) study on the effects of fire and seasonality of rainfall on spider assemblages reported rainfall seasonality as the major driving force in structuring seasonal spider assemblages (Langlands and Pearson 2006). Furthermore, favorable weather during mating and juvenile development increased recruitment~~s~~ for the following seasons. The seasonal variation in climate continues to change the structure and function of spider communities. However, the changes to the community structure and function depend also on geographic location (Lensing *et al.* 2005) and aridity (Ruppert *et al.* 2014, Zeppel *et al.* 2014).

Collembola species declined by 60 % in the overall activity-density (mean number trapped on each sampling date) in drought plots than in plots receiving increased precipitation (Lensing *et al.* 2005). Interestingly the overall spider activity-density was 1.6 times greater in the drought plots. Furthermore, in the same study, the spatial stratification in response to rainfall was different for the prey (Collembola) and predator (spiders). Wandering spiders from the family Gnaphosidae accounted for this response (Lensing *et al.* 2005).

Study aim and justification

We lack a mechanistic understanding of the impacts of changes in rainfall seasonality, grazing, and drought on ant and spider diversity in the arid and semi-arid regions of Africa. Most studies focus mainly on impacts of drought (Delsinne 2013, Buchholz 2010, Churchill and Ludwig 2014, Lensing *et al.* 2005), grazing (Andersen 1995, Hoffman 2010, Boulton *et al.* 2005, Churchill and Ludwig 2004) and seasonality (Rizali *et al.* 2013, Lensing *et al.* 2005) with no real understanding of how these processes interact and how biodiversity responds to this interaction. More extensive sampling through spring, summer, and winter might uncover dynamic shifts in abundance and diversity not detected by short-term studies (McDonald 2007).

The effect of climate change could be modelled at biome or species level but can also be studied through experimentation. The former approach is largely observational and based on statistical modelling and must be complemented with experimentation if we are to establish cause and effect (Altwegg *et al.* 2014). Field experiments that simulate projected climate change scenarios can provide a bridge between observational, correlative studies and potential mechanisms that underlie any observed patterns (Resasco *et al.* 2014). These studies increase the ability to assign causation of biotic changes to abiotic variables.

Considering these knowledge gaps and our need to understand and predict the response of these ecosystem components to climate and land-use change, this study is aimed at experimentally evaluating the response of ant and spider diversity to three important drivers of biological processes; precipitation, seasonality in precipitation, and grazing. The interaction between these processes was also explored focusing on both taxonomic and functional responses of ants and spiders at a long-term experimental site in an arid, summer rainfall region of South Africa.

CHAPTER 2: METHODS

Study Area and Site Selection

The study was conducted at the Syferkuil experimental farm (S 22, 97760°, E 030, 44347°) (University of Limpopo), east of the city of Polokwane in the Limpopo province of South Africa (Figure 1). The farm is situated within the savanna biome, one of the world's major terrestrial biomes, comprising a dynamic mixture of trees and grasses that encompasses open woodland and grassland (Figure 2). Savannas are inhabited by one-fifth of the world's population and subject to intense human exploitation as they are mostly converted into agricultural and grazing land (Mauda *et al.* 2017).

Climate

The study site has a distinct wet and dry season. The savanna biome typically receives summer rainfall. Some streams and rivers within and around the vicinity of the site also dry up. Annual precipitation ranges from 400 mm to 600 mm. The area is generally a frost-free region. The annual mean temperature of 20.9ºC and a mean monthly maximum and minimum temperature ranges of 38ºC and 3.7ºC respectively. The area has an annual mean potential evaporation of 2007 mm and mean annual soil moisture stress of about 77% (Mucina & Rutherford, 2006). Seasonality follows a precipitation and temperature pattern of hot and wet (December to March), cold and dry (April to August) to hot and dry (September – November).

Dominant vegetation

Important woody plant species include *Senegalia caffra, Senegalia karoo, Ziziphus mucronata, Gymnosporia senegalensis, Lipia javanica, Combretum hereroense, , Aristida congesta, , Pollichia campestris, , Aloe greatheadii greatheadii* and *Aloe marlothii* (Mucina & Rutherford 2006).

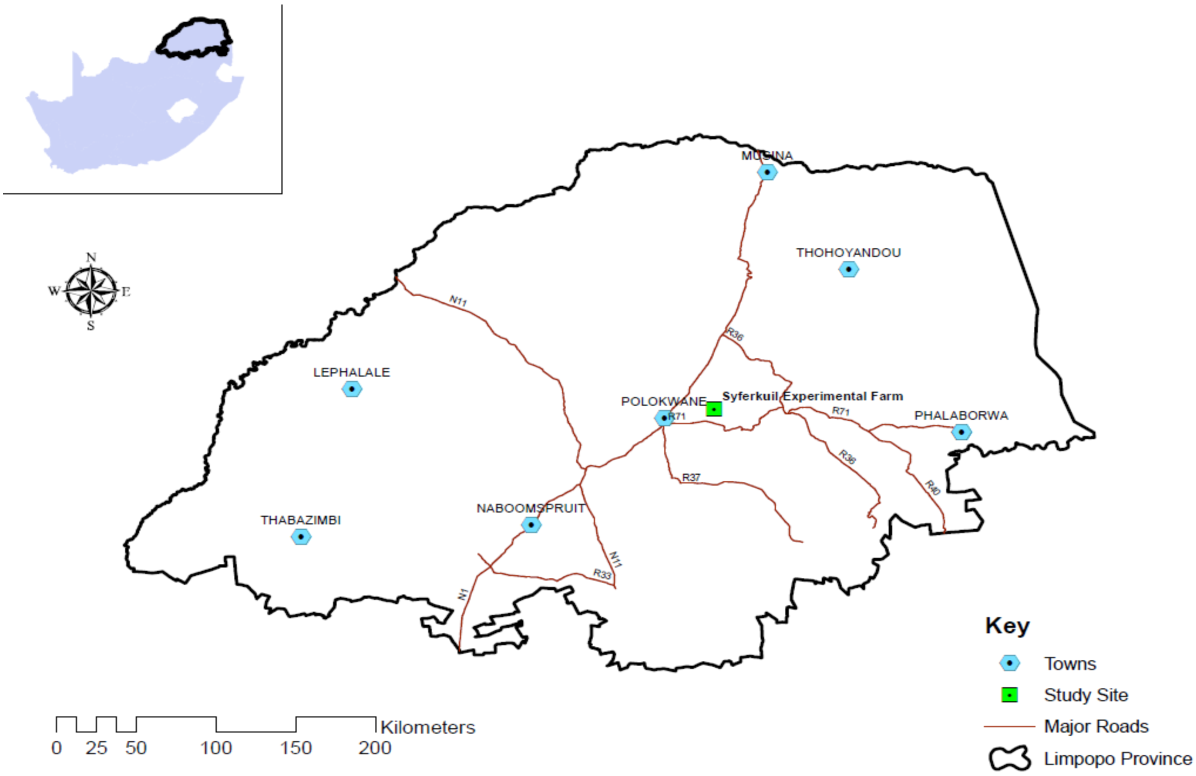

Figure 1. Map of Limpopo province showing the location of the Syferkuil experimental farm (study site).

Figure 15. Picture of the general surrounding environment of the Syferkuil experimental farm (study site).

Background

The Syferkuil drought experiment was established in 2014 at the University of Limpopo experimental farm in Mankweng, a township which is 29 km outside the city of Polokwane. The goal of the experiment was to discern the impacts of livestock grazing and drought on plant and animal biodiversity in the semi-arid regions in light of the global climate changes and growing human populations. Livestock grazing is one of the most commonly practiced land uses in the semi-arid regions (Arcoverde *et al.* 2017) that experience frequent drought and high rainfall variability (Manson and Joubert 1996). The ongoing experiment has been running for the past six years, and the grazing and drought treatment setup has been changed once during the 2016/2017 season.

Experimental design

The experiment is a two-way crossed randomized block design which consists of four (A – D) 40 × 40 m blocks that are at least 40 m apart, each with nine 10 × 10 m plots and 5 m corridors between the plots (Fig. 3). Treatments included drought simulation (D^+) and grazing exclusions (G^+) (Fig. 4). The drought was simulated using a rainfall exclusion shelter with a polycarbonate plastic roof, which filters approximately 75% of the rainfall, which runs off and is then collected by the gutter at the end of the plastic roof which is then carried away through the pipe connected to the gutter (Fig. 4a). The roof does not filter sunlight. Grazing was manipulated by excluding cattle from plots using ~1m high fences (Fig. 4b). The four treatment combinations (Table S1) included grazing and drought (G^+ x D^+) (Fig. 4a), no drought and no grazing (G^- x D^-) (Fig. 4b), no grazing and drought (G^- x D^+) (Fig. 4c) and finally the control, grazing and no drought (G^+ x D^-) (Figure 4d). Treatments were replicated twice in each block and the two replicates were randomly allocated in each block (Fig. 3).

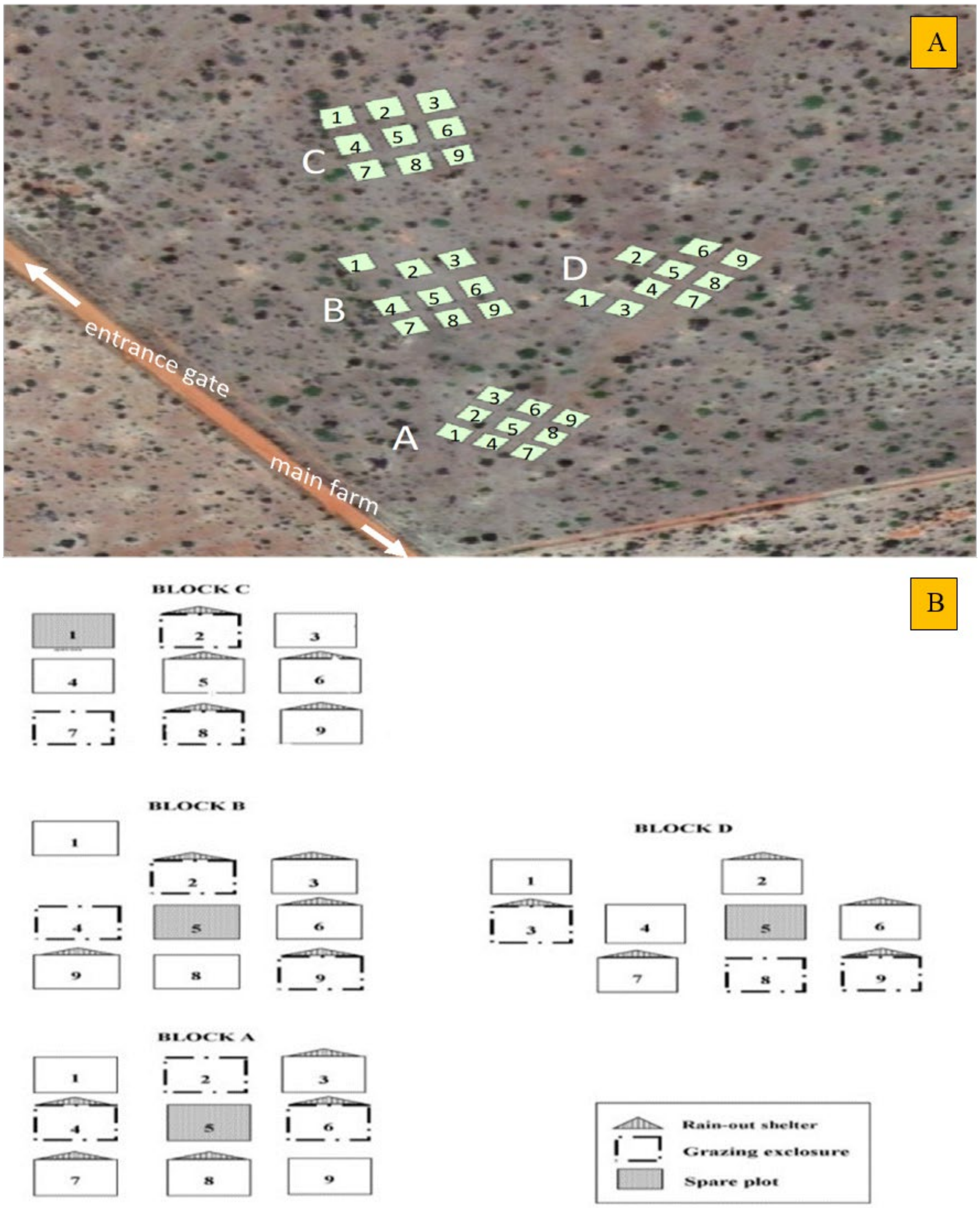

Figure 16. The layout of the study site. A) location of each of the blocks and nested plots and B) treatment plot allocation within each of the blocks.

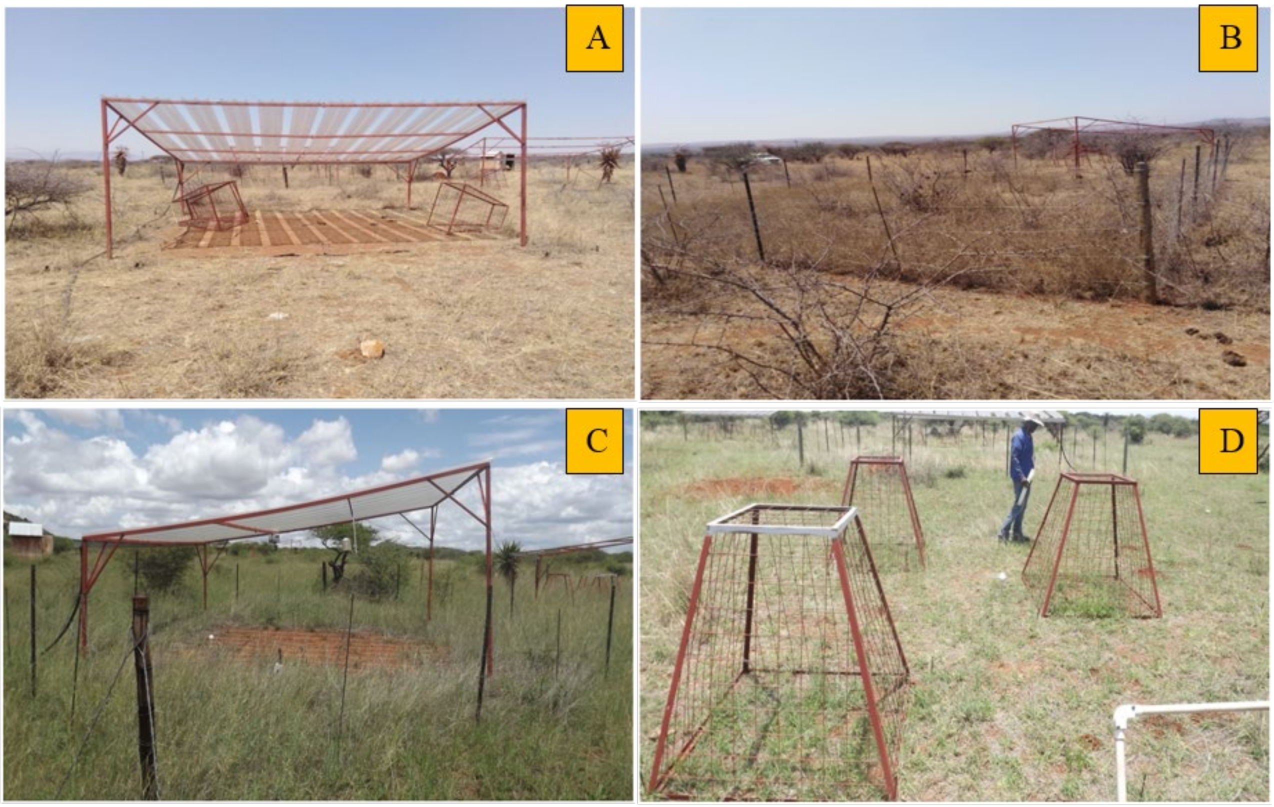

Figure 4. Treatment combinations. A) Grazing and drought ($G^+ \times D^+$), B) no grazing and no drought ($G^- \times D^-$), C) no grazing and drought ($G^- \times D^+$), and D) grazing and no drought – $G^+ \times D^-$ control.

Ant and spider sampling

Sampling

Ants and spiders were sampled using pitfall traps which were 40 mm in diameter and 60 mm in depth and left open for five days. Three pitfall traps arranged in a triangular grid containing propylene glycol were set up within each plot (Figure 5), for a total of 96 pitfall traps for each sampling survey.

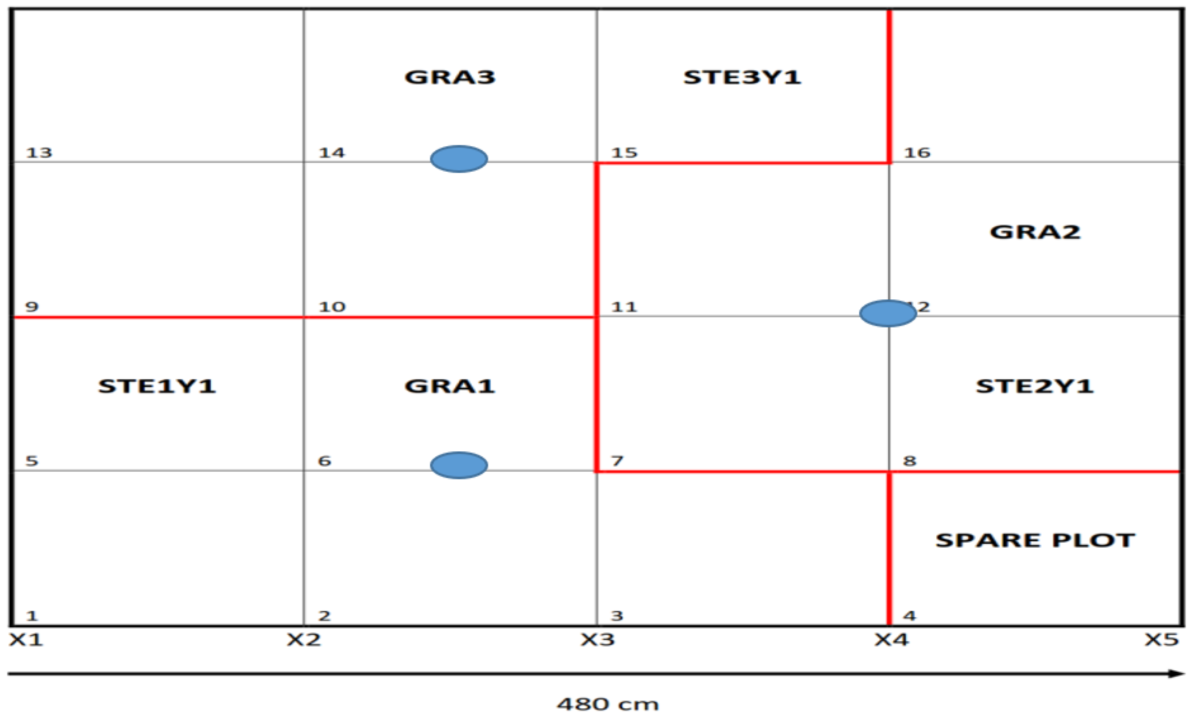

Figure 17. The triangular arrangement format used for setting up of pitfall traps within each of the treatment plots. Codes: GRA = grazed plots, STE = short term exclosures (cages), Y = year**.** The blue ovals are the positions for the pitfall traps.

The treatment plots were 10 × 10 m in size, and rain exclusion shelters were 6 × 6 m, Only the central 4 × 4 m~~,~~ was used to avoid the edge effect. The long-term impact of drought and grazing was assessed over a period of four years from December 2014 to January 2019 (Table S2). For this part of the study, ants were sampled each year in December and February during the hot and wet period when the ants were most active. The effect of seasonality was studied by sampling during summer (hot and wet season, December and February), winter (cold and dry sseason, June) and spring (dry and hot season, October) in 2018 (Table S2). Ants caught were washed, sorted in the laboratory and preserved in 90 % ethanol and then identified to species and/or morpho-species level by T.C. Munyai, School of Life Sciences, University of KwaZulu-Natal. Spiders were identified by AS Dippenaar-Schoeman from the Agricultural Research Council (ARC).

Ant and spider functional traits

Five morphological traits which are ecologically related to resource acquisition and use by ants were selected to describe species traits (Yates *et al.* 2014; Sommer and Wehner 2011; Schofield *et al.* 2016) (Table 1). Standard measurements for each individual specimen were taken in millimetres (mm) using a calibrated ZEISS Discovery V12 Modular Stereo Microscope with Motorized 12x Zoom Module with a Zeiss Application Suite V3.024. Only species that had five or more individuals were included. A minimum of five individuals were measured per species. Only size was included as a trait for spiders. Sexual dimorphism is common among spiders and therefore, only measurements of females were included which had the largest size recorded for a species (Table 2). Size is related to foraging strategies and resource acquisition (Joseph *et al.* 2017).

Table 1. Five morphological traits measured (in millimetres) to test for correlation.

Morphological traits	Abbreviation	Hypothesized functional significance
Weber's length	WL	Indicative of body size (Weber 1938), correlated with metabolic function and habitat complexity (Yates *et al.* 2014)
Mandible length	ML	Indicative of diet; longer mandible could allow predation of larger prey (Fowler *et al.* 1991, Weiser and Kaspari 2006)
Eye width	EW	Correlated with ability to see laterally (Baker *et al.* 2017). Wider eyes are typical of predatory species (Weiner and Kaspari)
Scape length	SL	Related to perception; length correlates to simplified environments (Weiser and Kaspari 2006).
Hind femur length	FL	Leg length increases locomotion speed for species in simple habitats allowing them rapid exploration of the habitat, whereas those that are in complex habitats have smaller leg length which allows them maneuverability (Gibb and Parr 2013).

		Longer legs lift the body away from the hot ground surface to cooler levels of the air, avoiding desiccation (Sommer and Wehner 2011) (full stop) Longer legs are also indicative of foraging speed, which reflects habitat complexity (Feener *et al*. 1988)

Table 2. The two morphological traits for spiders that were selected and measured (in millimetres) from Josephs *et al.* (2017).

Morphological traits	**Units**	**Hypothesized functional significance**
Maximum body length (tip of the cephalothorax to tip of the abdomen)	mm	Indicative of body size (Weber 1938) which is correlated with metabolic function and habitat complexity (Yates *et al.* 2014)
Maximum leg length to body ratio (longest leg length)	mm	Indicative of speed, which aids in hunting, enhanced dispersal and evading predators (Malumbres-Olarte *et al.* 2014)

Data analysis

Statistical analysis

All analyses were done using R version 3.6.1 (Core Development Team 2018). The three pitfalls in a plot were pooled for analysis as these could not be considered independent. The analysis, therefore, included a total of 8 plots × 4 blocks × 10 surveys = 320 communities for the grazing and drought impact study, and 8 plots × 4 blocks × 3 surveys = 96 communities for the seasonality component. Richness, activity and the community weighted mean of traits (CWM) were calculated for each community. Species richness was the total number of species in a community, while activity was the total number of individuals in the community. It is often not possible to identify juvenile spiders to species level. To maximize the number of spider specimens included in the analysis, generic richness was also calculated. There was a highly significant ($\beta = 1.09$, $R^2 = 0.98$, $p < 0.001$) linear relationship between species and generic richness (Fig. 6), and generic richness was used as a surrogate for spider species richness in the analysis. Functional diversity (FD) was only calculated for the ants.

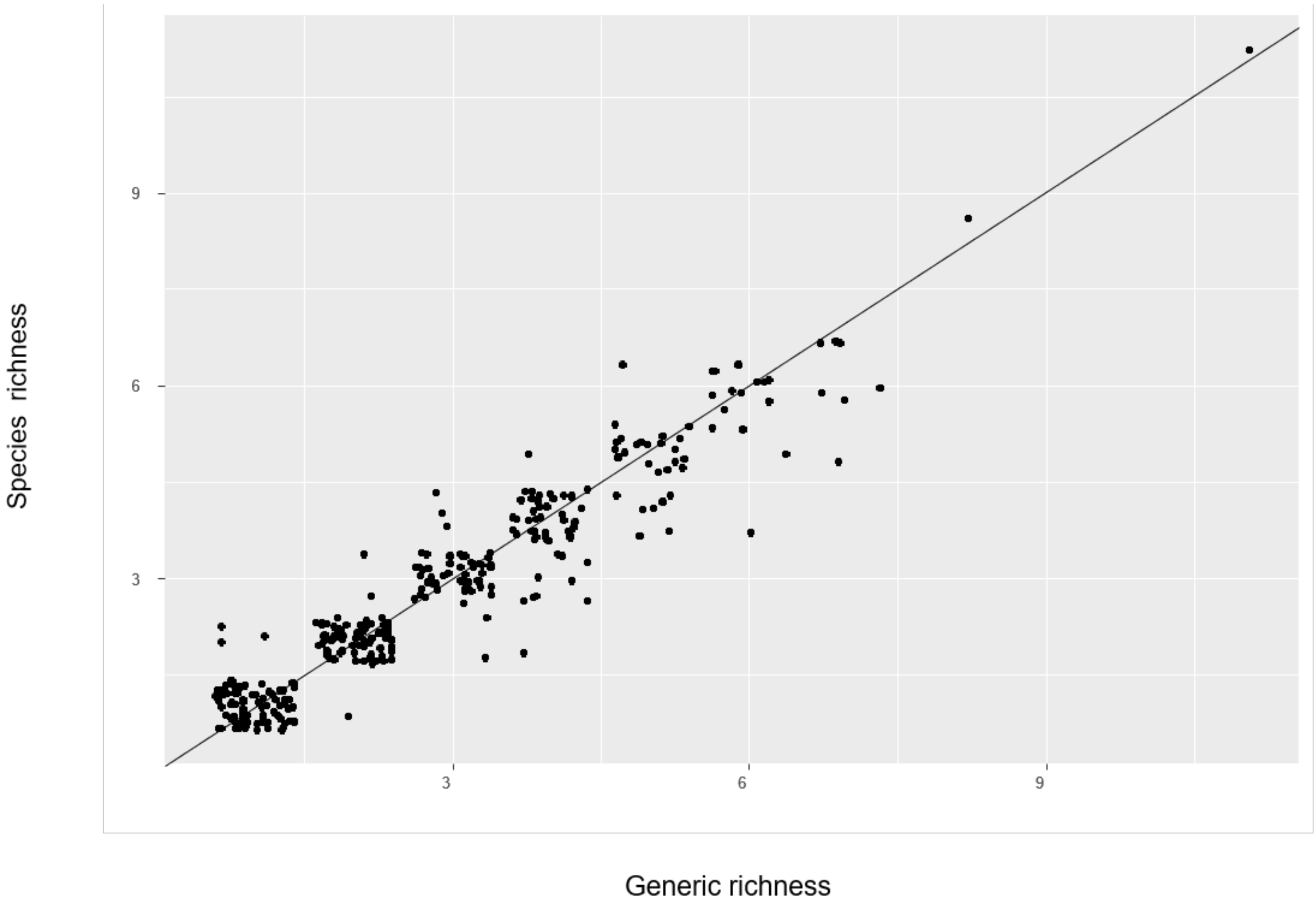

Figure 6. Linear relationship between species richness and generic richness using a linear regression model, showing that genera richness is a good surrogate for species richness. $\beta = 1.09$, $R^2 = 0.98$, $p < 0.001$.

Functional diversity

Relationships between functional traits and species were explored using Principle Component Analysis (PCA) and K-means clustering. Functional diversity (FD) was calculated, from R "FD" package (Laliberte and Legendre 2010), using multivariate dispersion as a multidimensional index of functional diversity (FDis), with FDis being defined as the mean distance of individual species to the centroid of all species in the community (Laliberté and Shipley 2011). The morphological trait mean values for each of the species were computed, and the relative abundance was accounted for by computing the weighted centroid of the **X** = [$\boldsymbol{x_{ij}}$] (species x traits) matrix in the following manner:

$$\boldsymbol{c} = [ci] = \frac{\sum a_j x_{ij}}{\sum aj}$$

where **c** is the weighted centroid in the *i*-dimensional space, *aj* the abundance of species *j*, and x_{ij} the attribute of species *j* for trait *i*. To quantify the functional diversity for each treatment and their combinations, the weighted mean distance $\acute{z}$ to the weighted centroid $\boldsymbol{c}$, is then computed as:

$$FDis = \frac{\sum a_j z_i}{\sum a_j}$$

where a_j is the abundance of species *j* and z_i is the distance of species *j* to the weighted centroid $\boldsymbol{c}$.

Community-weighted mean

Variation in the community-level weighted mean CWM of traits between assemblages is a useful tool for assessing community dynamics and properties (Garnier *et al.* 2004) and it is the mean trait value weighted by the relative abundance of each species. CWM for traits was calculated using the FD package (Laliberte and Legendre 2010).

Modelling of the four univariate measures of diversity

Generalized Linear Mixed Effects Models (GLMM) with Poisson error distributions (Negative Binomial in the case of activity data) and a log-link function were used to analyse the effects of grazing, drought, seasonality and their interaction on the four univariate response variables (semicolon) ant activity, richness, CWM, and functional diversity. The impacts of drought and grazing were analysed in two different ways, firstly by focusing on the impact of drought and grazing treatments in general as well as their interaction and secondly by modelling the impacts of treatment combinations. Blocks nested within a survey were used as a random factor to account for repeated measurements at the same point and the dependence of plots within blocks. Marginal R^2 (R^2m, due to fixed effects only) and conditional R^2 (R^2c, due to fixed and random effects) were calculated to determine how much of the variation is explained by fixed and random effects, respectively (Nakagawa and Schielzeth (space, no comma)2013). Model residuals were inspected for normality, heteroscedasticity, and independence.

Multivariate analysis

The multivariate response of assemblages was modelled using the function 'manyglm' in the package mvbund (Wang *et al.* 2012). The manyglm fits GLM to each species, using a common set of explanatory variables. The treatments grazing and drought were modelled without block and survey to test whether the treatment models explained more variation (marginal R^2), than when modelled with block and survey (marginal R^2). To test for the effect of treatments, survey, and block, we used ANOVA function with the argument p.uni = 'adjusted' so P-values are adjusted to control the family-wise error rate across species, using a resampling-based implementation of Holms step-down multiple testing procedure (Westfall and Young 1993). The function 'anova.manyglm' uses resampling-based hypothesis testing to make community-level and taxon-specific inferences about which factors or environmental variables are associated with the multivariate abundances, while also taking into account correlation between species (Wang *et al.* 2012). In addition to the 'anova.manyglm' function having a block argument that allows for defining a random factor, it is also flexible and handles nested hypotheses and was used to test whether the treatment models for grazing, drought, and their combination explained any additional variation not captured by a block and survey model alone. In all instances, model residuals were inspected for normality, independence and constant mean-variance relationships (Haddad *et al.* 2019). s

CHAPTER 3: RESULTS

Ants

A total of 3 652 ants were collected, representing 58 species, 21 genera and five subfamilies. Myrmicinae (26 species), Formicinae (16 species), Ponerinae (8 species) and Dorylinae (4 species) were the subfamilies with most species (Appendix 3).

Ant functional traits

PCA and K-means clustering of functional traits suggest that there are three main groups of ants and that these groups are largely related to size differences (Fig. 7).

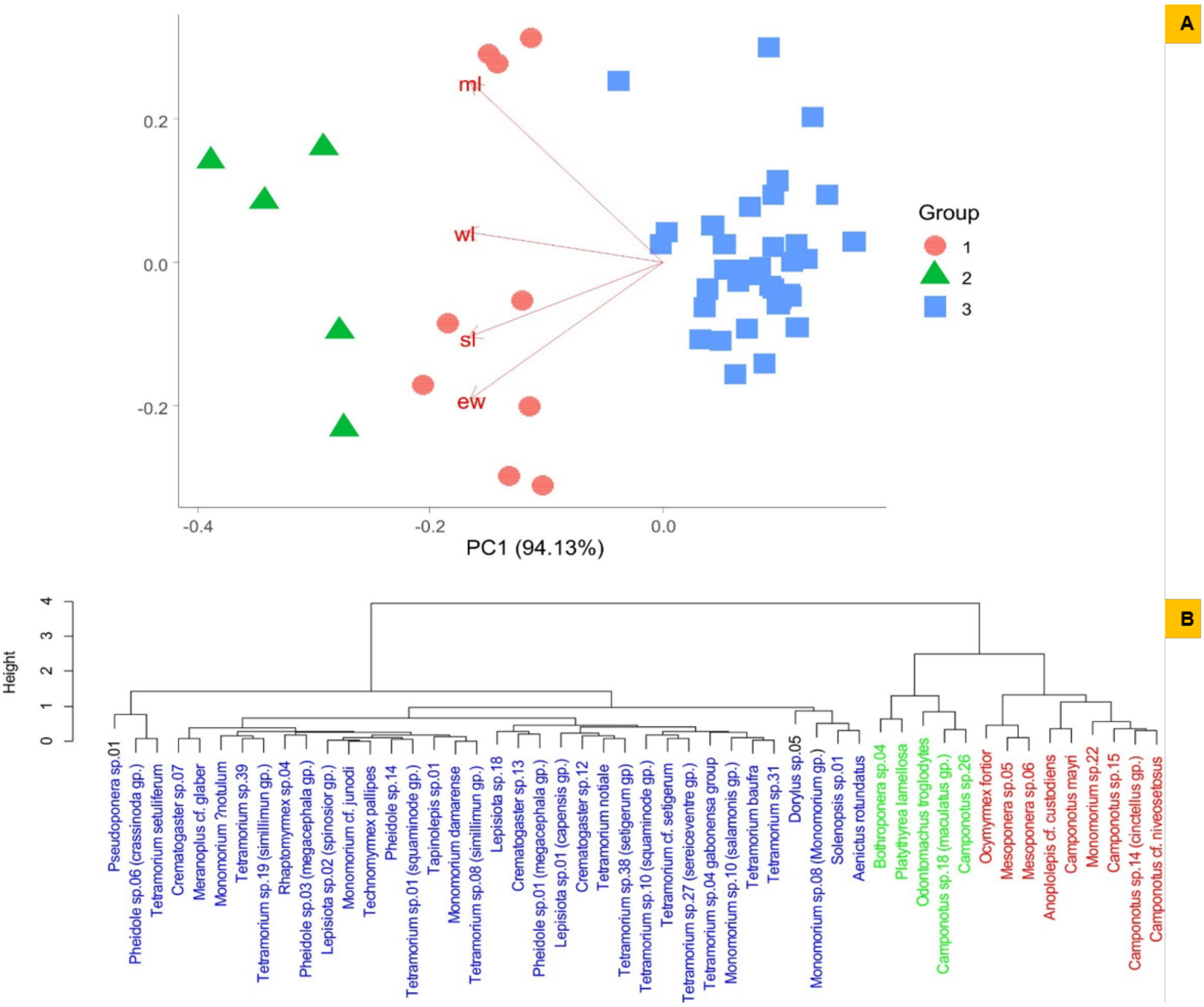

Figure 7. A) PCA results showing relationships between functional traits and the three functional groups identified using B) k-means clustering of ant species based on their functional traits. Code meanings = sl – scape length, ew – eye width, wl – Weber's length, and ml – mandible length.

Long-term experimental impacts of grazing and drought

The control grazing and no drought is the reference for all the results reported on the long-term impacts of experimental grazing and drought. Ant activity significantly decreased under both drought and no grazing treatments. The interaction between the two treatments had a significant increase in activity (Fig. 8a, Table S1 in Appendix C). Ant activity decreased significantly under all treatment combinations (Fig. 8b) with strong evidence that plots where there was no grazing and no drought experienced the greatest decrease in activity.

Drought and grazing treatments and their interactions as well as treatment combinations had no significant impact on species richness (Fig. 8c & d, Table S1 in Appendix C). Ant size decreased under the no grazing treatment and they were up to 1.5 mm smaller in these plots. In a similar way to activity, though, their sizes increased by one mm when treatments interacted (Fig. 8e). Ant size decreased significantly in all grazing exclusion treatment combinations while drought had no impact (Fig. 8f).

Functional diversity only responded to grazing, decreasing when there grazing was excluded (Fig. 8g). Any treatment combination that included drought had no effect on FD (Fig. 8h).

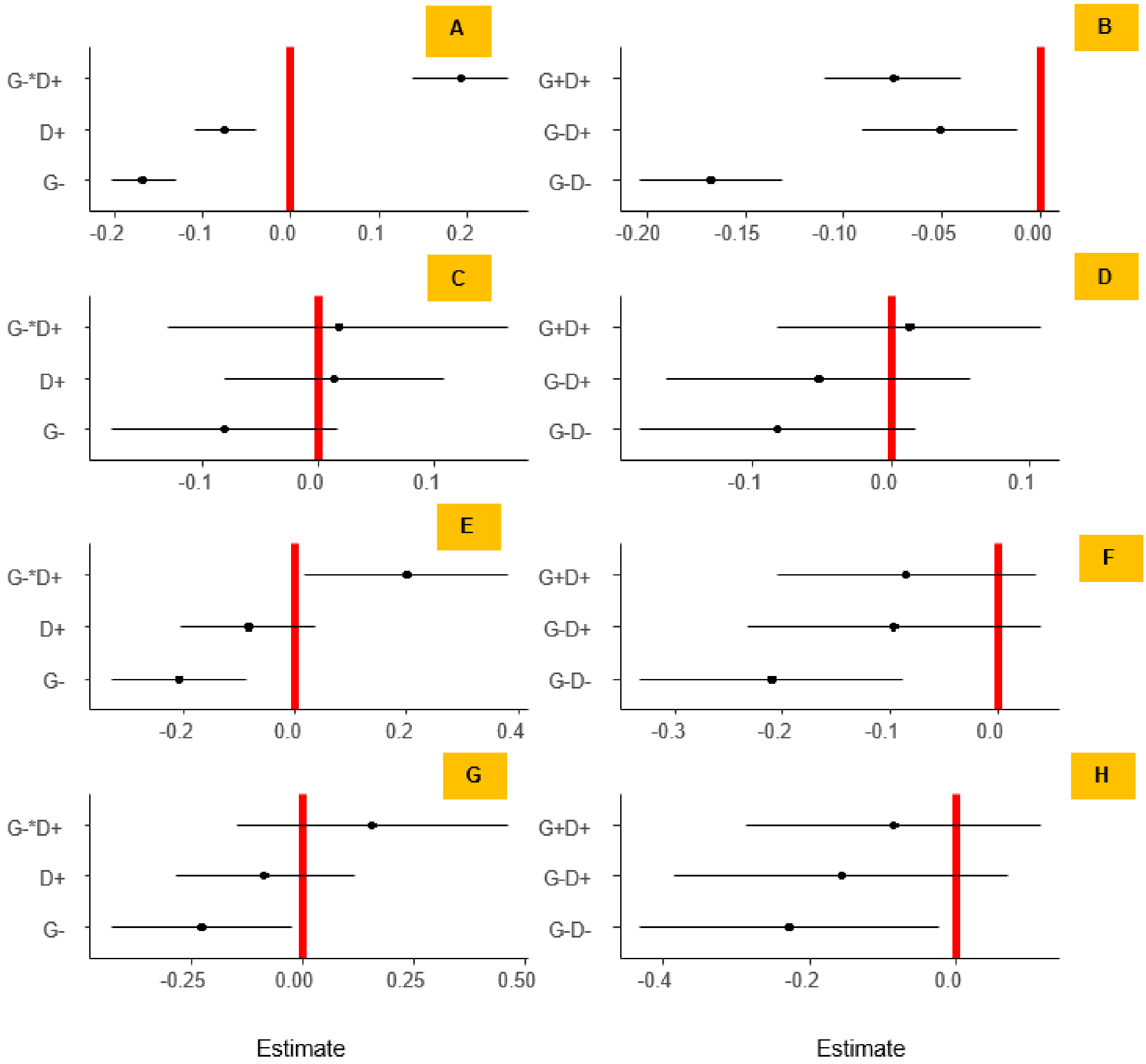

Figure 8. Parameter estimates and plots of predictors for GLMM models of ant activity, richness, Weber's length and functional diversity. The reference is equivalent to the vertical red line. Grazing (G^+), grazing exclusion (G^-), drought (D^+), no drought (D^-). All categorical variables are compared to the control, grazing (G^+) and no drought (D^-). A, B) ant activity, C, D) species richness, E, F) body size, and G, H) functional diversity (FD).

Spiders

A total of 1 230 individual spiders were collected represented by 130 species, 24 families and 71 genera. The four most diverse families were Gnaphosidae (6 genera and 25 species), Salticidae (15 genera and 23 species), Lycosidae (12 genera and 19 species), and Zodariidae (9 genera and 16 species). Families that were most abundant included Lycosidae (372 individuals), Salticidae (304 individuals), Gnaphosidae (223 individuals) and Zodariidae (134 individuals). The most abundant genera were, *Stenaellurillus* (202 individuals), *Evippomma* (171 individuals), *Asemesthes* (116 individuals) and *Oxyopes* (91 individuals).

Long-term experimental impacts of grazing and drought

The control grazing and no drought is the reference for all the results reported on the long-term impacts of experimental grazing and drought. Grazing exclusion, drought and their interaction had no significant impact on spider activity (Fig. 9a, Table S2 in Appendix C), generic richness (Fig. 9b, Table S2 in Appendix C) and body size (Fig. 9e & f, Table S2 in Appendix C). The three indices also did not respond to any of the treatment combinations (Fig 9 a-f (comma) Table S2 in Appendix C).

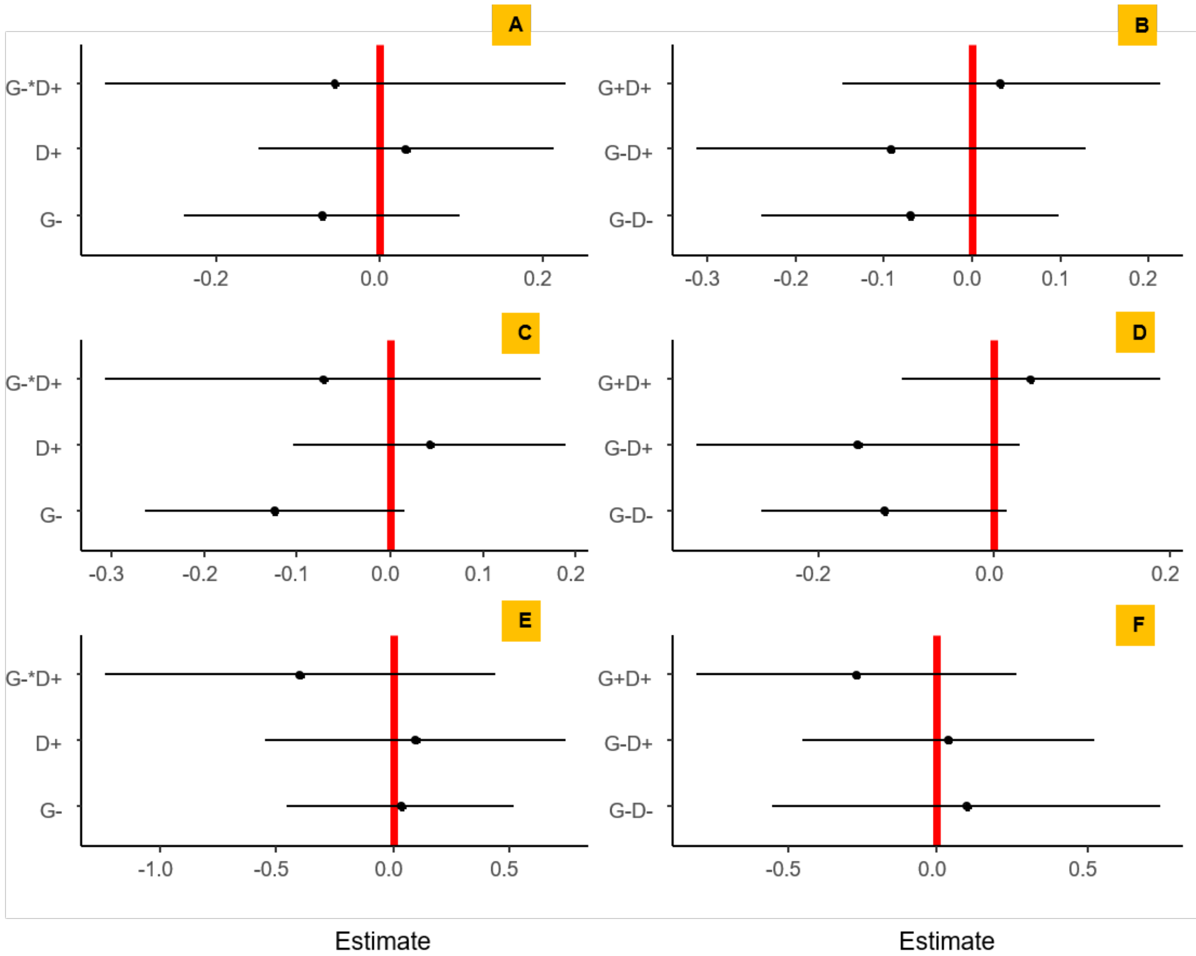

Figure 9. Parameter names and plots of predictors in multiple regression models for spider genera richness, activity, and size. The reference is equivalent to the vertical red line. Grazing (G^{+}), grazing exclusion (G^{-}), drought (D^{+}), no drought (D^{-}). All categorical variables are compared to the control, grazing (G^{+}) and no drought (D^{-}). A, B) generic richness, C, D) activity, E, F) body size.

Seasonal effects on ants

The control grazing and no drought during the hot, wet season (summer) is the reference for all the results reported on the impacts of seasonality. Seasonal patterns were more complex. As expected, ant richness decreased significantly during the cold and dry periods (Table S3 in Appendix C, Fig. S3 in Appendix C). Grazing and drought exclusions resulted in a significant decrease in species richness during the cold, dry season as well as the hot, dry season (Fig. 10a). This was the only treatment combination for which there was a significant effect in any of the seasons though (Table S3 in Appendix C).

Ant activity also decreased significantly during the cold and dry season (Figure10b, Figure S3 and Table S3 in Appendix C). In general ants were less active in grazing treatments and more active under drought treatments (Table S3). During the cold, dry season ant activity decreased in grazing treatments, while hot, dry conditions decreased activity in drought treatments (Figure10b, Table S3). Under the no grazing and no drought, and grazing and drought treatment combinations, activity increased during the cold, dry season (Fig. 10b, Figure S3 in Appendix C). Furthermore, activity decreased significantly under no grazing and no drought, and grazing and drought treatment combinations during hot, dry season (Figure 10, Figure S3 in Appendix C). Ant body size did not respond to changes in seasonality under the treatments and their combinations (Figure 10c, Figure S3 in Appendix C).

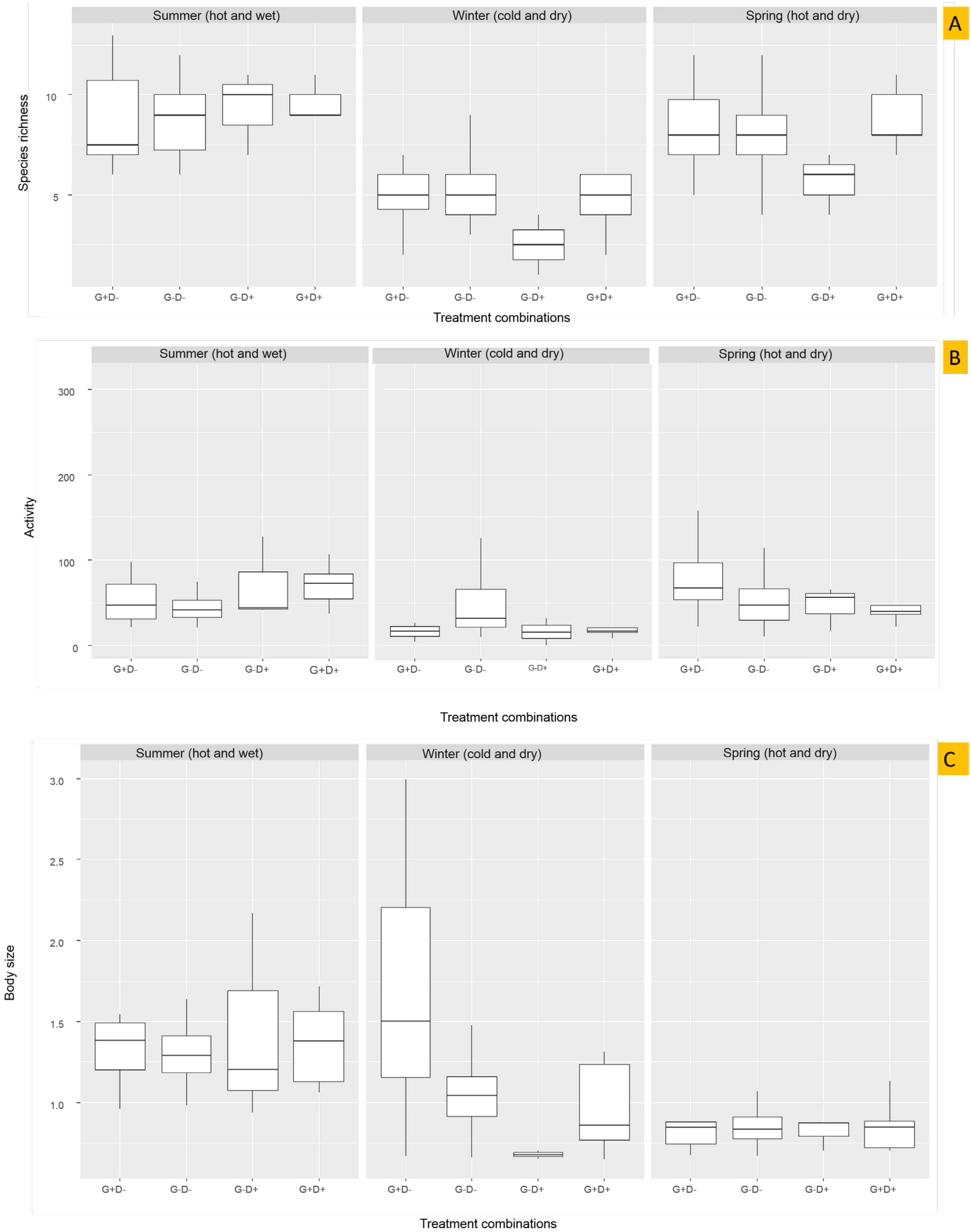

Figure 10. a), Seasonal changes in ant richness, b) ant activity, c) body size, and their interaction with treatments and treatment combinations.

Seasonal effects and their interactions on spiders

The control grazing and no drought during the hot, wet season (summer) is the reference for all the results reported on the impacts of seasonality. As expected, generic richness during the cold and dry season and during the hot, dry season decreased significantly (Fig. 11a & b, Table S4 in Appendix C). A similar effect was observed for the different treatments (Table S4 in Appendix C). However, the treatments and their combinations did not seem to have any impact during the different seasons.

Spider activity also decreased significantly during the cold, dry and the hot, dry seasons (Fig. 11b, Table S4 in Appendix C). This effect was more profound for activity than it was for richness during both seasons. Activity was also not impacted significantly by treatment combinations in the different seasons.

Overall, there were smaller spider species during the two dry periods (Fig. 11b, Table S4 in Appendix C), but there were significantly larger spider species during the hot, dry season. During the cold, dry season under no grazing and drought treatment (G^{-} x D^{+}) there was an increase in large spider species(Fig. 11c, Table S4 in Appendix C).

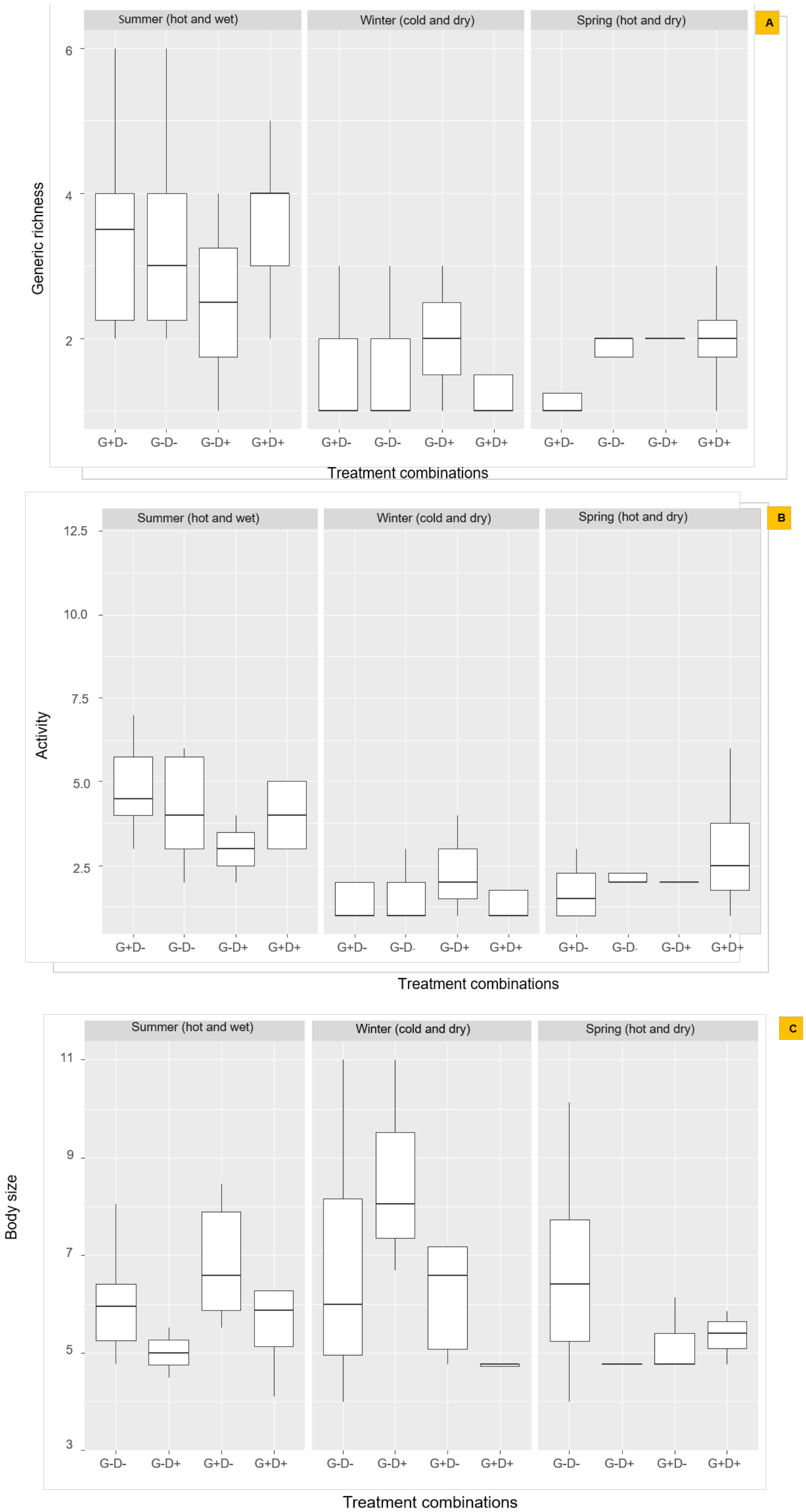

Figure 11. a) Seasonal changes in spider generic richness, b) spider activity, c) body size, and their interaction with treatments and treatment combinations.

Ant community composition

Species composition was significantly modified by both grazing and drought treatments (Table 3). Larger and medium-sized species such as *Camponotus* sp.26, *Camponotus* sp.15 and *Technomyrmex pallipes* were more active in drought treatments together representing a proportion of 69.99 % (Fig. 12a). *Camponotus* sp.26 also increased under drought treatments, while *Camponotus* sp.24 increased in plots with no drought (Figure 12a). (Table 3). Large species, *Bothroponera* sp.05, *Camponotus* sp.26, and *Ocymrymex flaviventris* together representing a proportion of 81.6 % (Fig. 12b), were more active under grazed treatments, while smaller species such as *Pheidole* sp.05 and *Pheidole* sp.06, were most active in grazing exclusions (Figure 12b).

Table 3. Conditional and marginal compositional variation explained by treatments and their combinations.

Conditional variation			**Marginal variation**		
Parameters	**Wald value**	**P-value**	**Parameters**	**Wald value**	**P-value**
D+	7.64	0.014 *	**D+**	7. 05	0.01 **
G+	5.89	0.229	**G-**	6.33	0.05 ·
G+ ^{x} D+			**G+ ^{x} D+**	4.74	0.05 ·
G-D+	6.30	0.012 *	**G-D+**	5.93	0.004 **
G+D-	5.02	0.204	**G+D-**	5.41	0.080 ·
G+D+	5.61	0.074 .	**G+D+**	5.91	0.006 **

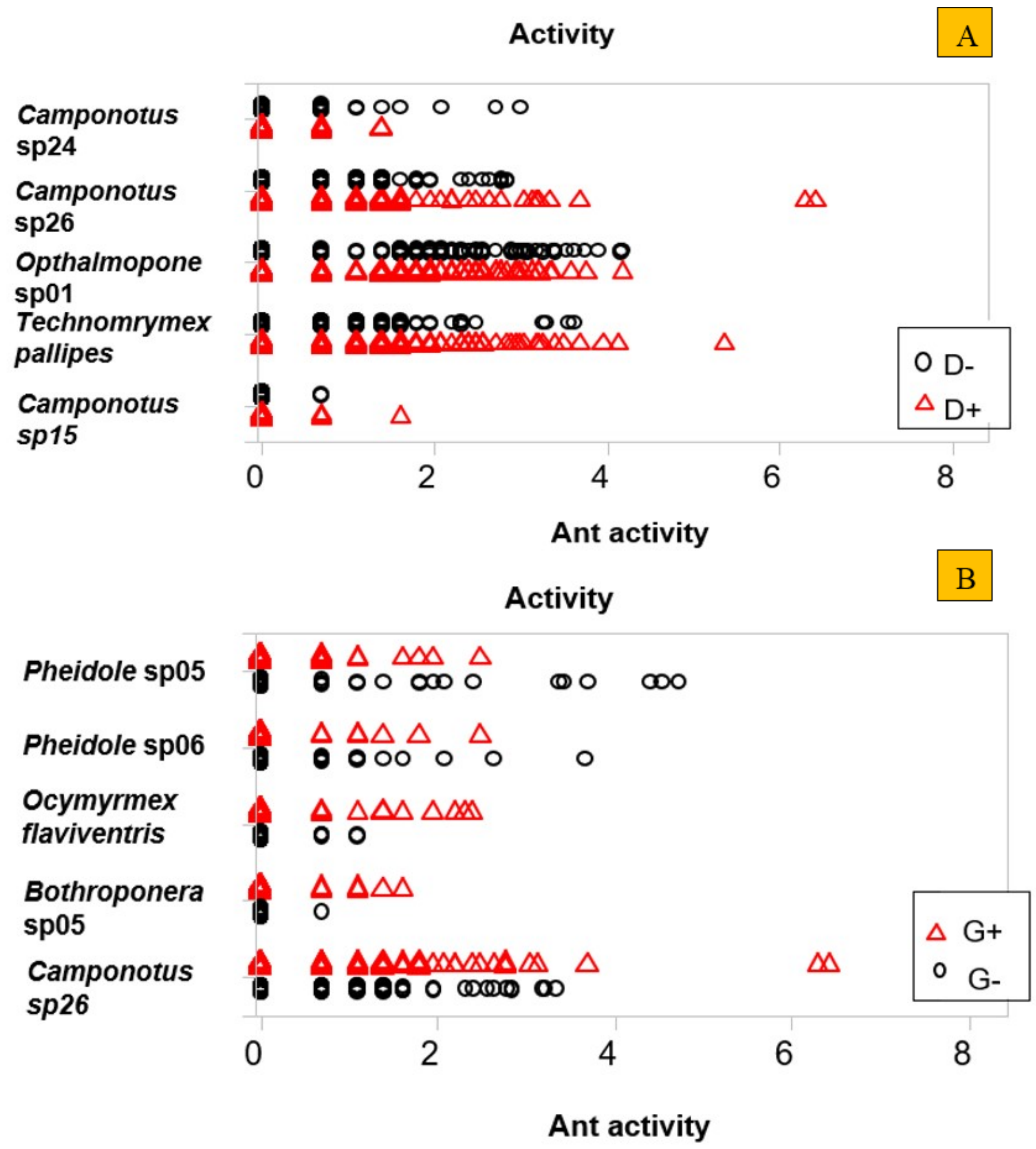

Figure 12. Ant activity for species that accounted for most of the variation in ant assemblages observed in A) drought (D^+) and no drought (D^-) treatments, and B) grazing (G^+) and no grazing (G^-) treatment.

Spider community composition (Genera)

Generic composition changed significantly in response to drought treatments, whilst grazing seemed to have no effect (Table 2). The genera that accounted for most of the variation explained under drought treatments were; *Psammorygma, Ozyptila, Evippomma*, and *Platnickina* (Fig. 13a). Under the treatment combinations, *Ammoxenus, Trabea, Oxyopes* and *Evippomma* were the most responsive genera (Fig. 13b). Drought had a negative impact on the activity of *Evippomma, Psammorygma,* and *Platnickina* (Fig. 13). *Ozyptila* was the only genus that had an increase in activity under drought treatments. *Ammoxenus*, *Trabea*, and *Evippomma* were more active under treatment plots with no drought. Only genus *Ozyptila* showed an increase in activity under drought while other genera displayed an opposite response to drought. Despite Gnaphosidae being the most abundant family with second most genera, genera from this family were not as responsive.

Spider species level community composition

At the species level, grazing and drought treatments and their combinations had a significant impact on the community composition of spiders (Table 5, Fig. 14). *Zelotes radiatus* and *Oxyopes* sp.14 were most active under treatment plots experiencing no grazing, whilst *Oxyopes schenkeli* and *Zenonina albocaudata* were active under grazing treatment (Table 5, Fig. 14b). Treatment plots experiencing no drought favored *Psammorygma aculeatum* and *Evippomma squamularum. Rastellus kariba* was mostly active under treatment plots that were experiencing no grazing and no drought (Table 5, Fig. 14b).

Table 4. Genus level multivariate results for testing whether the multivariate model that includes the drought (D^+), grazing (G^+) and treatment combinations (no grazing no drought ($G^- \times D^-$) , grazing and drought ($G^+ \times D^+$), grazing and no drought ($G^+ \times D^-$), and no grazing and drought ($G^- \times D^+$)) explains a significantly more variation than date and block.

Generic level Community composition					
	Marginal			Conditional	
	Wald statistic	**Pr(>wald)**		**Wald statistic**	**Pr(>value)**
Drought D+	7.992	0.008 **	**Drought D+**	7.057	0.009 **
Grazing G+	6.173	0.160	**Grazing G+**	6.33	0.060 ·
G-D+	6.308	0.013 *	**G-D+**	5.933	0.004 **
G+D-	5.020	0.176	**G+D-**	5.471	0.058 ·
G+D+	5.613	0.079 **.**	**G+D+**	914	0.006 **

Table 5. Species level multivariate results for testing whether the multivariate model that includes the drought (D^+), grazing (G^+) and treatment combinations (no grazing no drought ($G^- \times D^-$) , grazing and drought ($G^+ \times D^+$), grazing and no drought ($G^+ \times D^-$), and no grazing and drought ($G^- \times D^+$)) explains a significantly more variation than date and block.

Species level community composition					
	Marginal			Conditional	
	wald value	**Pr(>wald)**		**wald value**	**Pr(>value)**
Drought D+	8.998	0.039 *	**Drought D+**	7.924	0.0196 *
Grazing G+	8.218	0.078	**Grazing G+**	6.33	0.060 ·
G-D+	5.676	0.039 *	**G-D+**	5.521	0.058 ·
G+D-	5.895	0.137	**G+D-**	5.713	0.098 ·
G+D+	7.133	0.039 *	**G+D+**	6.046	0.058 ·

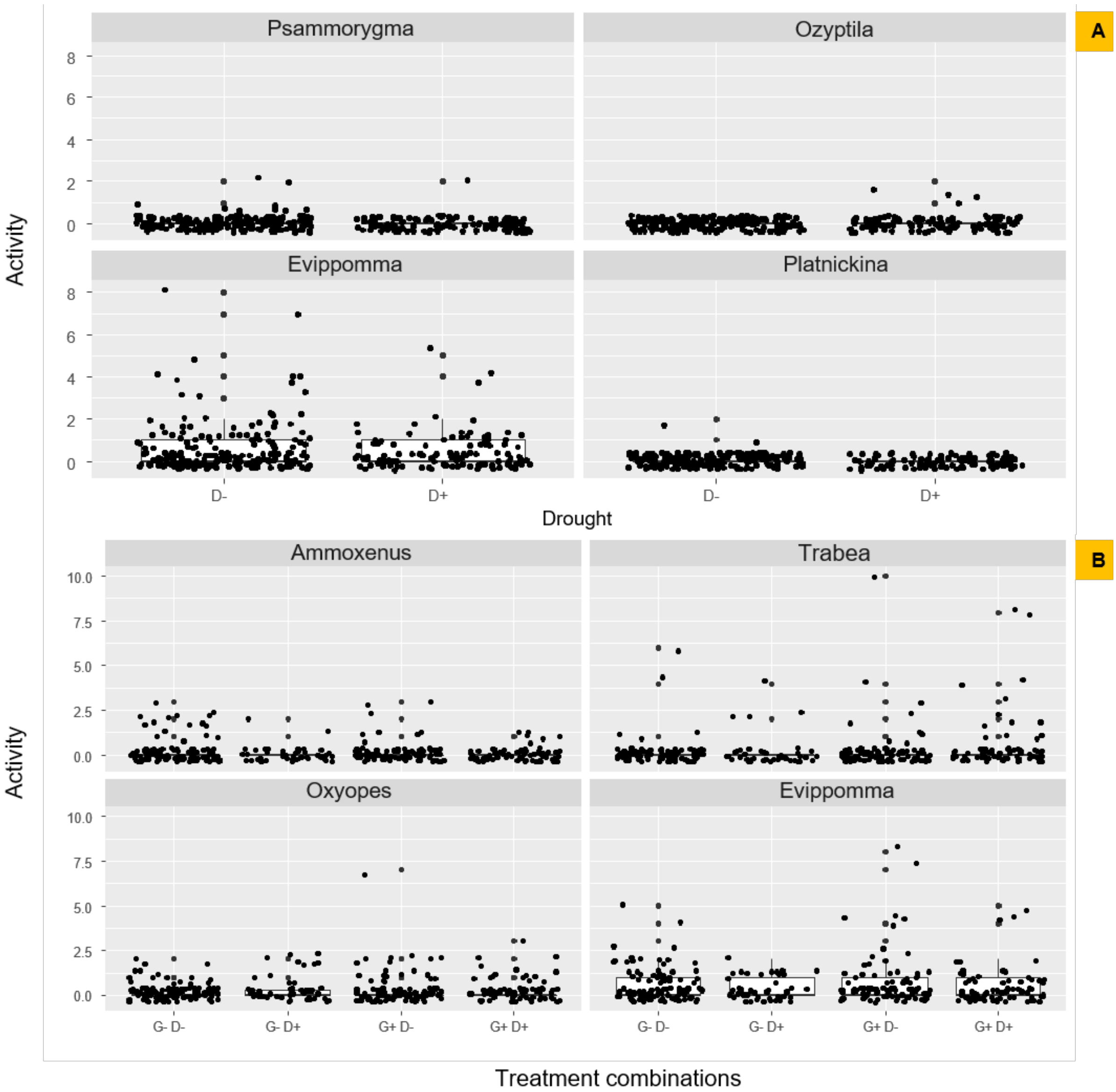

Figure 13. Indicator genera that accounted for most of the variation under drought (D^+) and treatment combinations (no grazing no drought (G^- x D^-), grazing and drought (G^+ x D^+), grazing and no drought (G^+ x D^-), and no grazing and drought (G^- x D^+)).

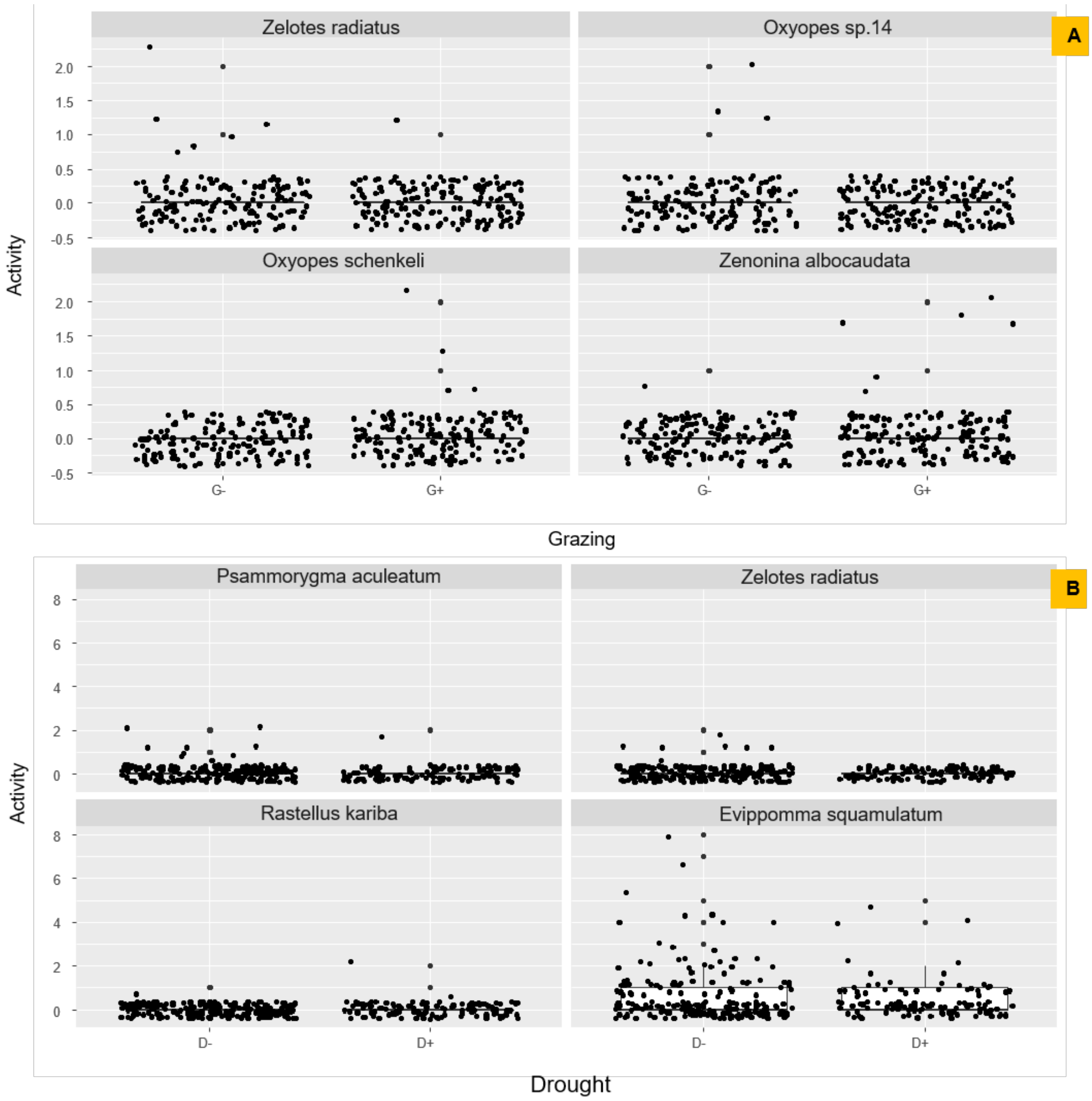

Figure 14. Indicator species that accounted for most of the variation under grazing (G^+) and drought (D^+) treatment.

CHAPTER 4: DISCUSSION

Our study is one of the first to investigate the long-term effects of both experimental drought and grazing together on ants and spiders in the semi-arid region of South Africa. The findings suggest that ants and spiders responded differently to the long-term subjection to both disturbances at a species level and community level. Ants were most responsive to the treatments and the season-treatment interaction than spiders.

Ants

Interestingly, grazing exclusions reduced ant diversity to a greater and significant extent than drought. This was true for all univariate measures except for species richness. In general, it seems that excluding grazers resulted in smaller, functionally less diverse ants, with lowered activity. While drought seemed to mitigate the impact of excluding grazers. Contrasting responses of ant size is observed in drought treatments with and without grazing, with ants getting smaller in drought treatments without grazing and larger in those with grazing. *Effects of drought*

Delsinne *et al.* (2013) in his drought simulation study, found that the ant composition was modified by drought and there was increased activity of *Camponotus* species in drought treatments. Furthermore, in the same study, *Camponotus* species which initially nested on suspended and standing deadwood later started nesting in drought simulation plots where rainfall was completely excluded. This suggests that drought provided ideal foraging and nesting conditions for *Camponotus* species.

Effects of grazing

Several authors have found no impact of grazing on ant diversity in the Australian semi-arid rangelands (Hoffman 2000, Andersen 1995, Hoffman 2010, Boulton *et al.* 2005, Arcoverde *et al.* 2017). Grazing could not relate to either ant species richness or abundance and suggested that impacts of grazing is primarily through species turnover (Arcoverde *et al.* 2017). According to Andersen (1995) and Hoffman (2010) grazing impacts ants indirectly, influencing the suitability and resource availability by modifying soil and vegetation. Hoffman (2010) concluded that soil has a greater impact on ant community modification than grazing, because soil is a major determinant of vegetation composition and structure which influences ant community composition. Grazing was found to be less important in explaining the overall ant species richness and abundance compared to soil attributes, this was attributed to the lack of a relationship between grazing and ant species (Boulton *et al.* 2005). Furthermore, in the same study, soil attributes were consistently associated with ant species richness and abundance of three-dominant ant species. Arcoverde *et al.* (2017) also found this to be the case, as ant diversity was lower in land systems associated with clay soil which is associated with seasonal waterlogging compared with those that had loam soil. Nesting is a major limiting factor ant species even more so than food, making soil type a major determining factor. Ants find it easier to nest in sandy soil rather than clay soil (Boulton *et al.* 2000, Calcaterra *et al.* 2010). Soil type did not vary in the current across the entire study site.

Effect of seasonality on ants

Seasonality seemed to have a bigger impact on richness than drought and grazing. Dry seasons interacted with grazing exclusions and drought to decrease ant richness in particular, but also selected for smaller ants, particularly during cold and dry periods. During dry, cold seasons, ant activity decreased in grazing treatments, while it increased under drought treatments. In contrast, drought treatments experienced a decrease in ant activity during dry, hot seasons. This suggests that the effect of drought varies with temperature. Moreover, with combinations of no grazing and drought treatments, ant activity generally increased. Ant activity decreased during dry seasons, winter and spring, suggesting a negative synergistic effect by drought and the dry seasons on ant activity. However, the impact of grazing and drought varies from winter to spring, as it promotes an increase in ant activity when it is cold and dry during winter but decreases during the hot and dry season i.e. in spring. Though ant size did not show much response to treatments and their combinations, it seems, like richness and activity, during the cold and dry season the size decreases under no grazing and drought combinations.

Grazing and drought in conjunction with seasonality indirectly influenced ant foraging behaviour through changing the habitat structure and increasing temperature; high ground surface temperature prevents foraging by all but the most thermophilic species and this explains the increase in large ants during summer (Purdon *et* al. 2019).In contrast, small ant species, even if they are active under these conditions, tend to be more prone to desiccation, putting them at a disadvantage.

During the sampling period there were antlion traps under drought treatments during the dry, hot seasons, particularly in plots where there is grazing (Fig. 15). The high number of antlion cone pit traps might be correlated with the increase in the activity of *Camponotus* sp.26 and *Camponotus* sp.15 observed under open and dry drought plots during the hot, dry season (spring). Lucas and Brockmann (1981) in a study done in the USA suggest that during spring and summer when antlions are feeding most actively, about 75% of their diet is composed of ants, 50% of which are either *Camponotus* or *Conomyrma*. Heinrich and Heinrich (1981) observed a relationship between prey size and pit diameter; pits that were smaller in diameter (< 5cm) caught small prey, while successively larger pits (> 6 cm) captured both small and larger prey. This might account for the large cone traps size (Fig. 15) under drought treatments where large species of *Camponotus*, amongst others, increased in activity. This is supported by Humeau *et al*. (2015) who observed a positive relationship between pit size and prey-capture probability. Smaller and larger ants escape capture more often than intermediate sized ants, suggesting that there is a lower and upper limit to prey size and consequently an optimal prey size. Thus, the existence of optimal prey size would account for why most prey captures were around 3mm (Humeau *et al*. 2015). Since species from genus *Camponotus* measured in the current study were between 3.9 mm and 4 mm in size which suggests that they fall within the optimal prey size range of the antlion which might explain what Lucas and Brockmann (1981) observed, that about 50% of their diet is either *Camponotus* or *Conomyrma.*

Figure 15. Antlion cone traps colonizing the bare ground under no grazing and drought ($G^- \times D^+$) treatment combination plots.

Community composition

Both grazing and drought treatments changed the species community composition of ants, by influencing activity of different groups of ant species. These treatments promote the increase in the activity of larger ants such as *Camponotus* sp.26, *Camponotus* sp.15, *Bathroponera* sp.05, and *Technomyrmex pallipes*. In the absence of grazing and drought, when habitats are structurally complex, the small-sized group such as *Pheidole* sp.05 and *Pheidole* sp.06 increases in activity. Species from the latter group can manoeuvre through the structurally complex habitats. This suggests that an increase in grazing and drought is likely to result in the environment promoting species from the large and medium-sized ants, replacing smaller short legged ants. This agrees with the findings of several studies (Gibb and Parr 2010, Gibb and Parr 2013, Arcoverde et al. 2017) which show that the impact of grazing was mainly through species turnover. Arcoverde *et al.* (2017) observed that the impact of grazing was mainly through species turnover, where species like *Pheidole* sp.1 in the current study which prefer complex habitat structures were replaced by a thermophilic species, *Iridomyrmex sanguineus*, that strongly prefers open habitats. Variation in the scaling of body size and leg length is also driven by the complexity of the habitat in which a species dwells and that affects the species foraging success (Gibb and Parr 2010). Further explained, in the same study, as the habitat structure becomes more complex the body size and leg length decrease. The *Pheidole* species are generally smaller ants that can manoeuvre with ease through structurally complex habitats, and their foraging success and resource acquisition would be greater than in simplified habitats. The two functional groups, large-sized (WL= 3 – 3.9 mm) and medium-sized (WL= 2 – 2.8 mm), favoured by grazing and drought were large species *Camponotus* sp.26, *Camponotus* sp.15, *Batheroponera* sp.05 and *Technomyrmex pallipes*. Smaller ant species, such as in genus *Pheidole*, discovered resources much quicker in structurally complex habitats as their body size allowed them to move through gaps that tend to impede the movement of larger species (Gibb and Parr 2013). This suggests that *Pheidole* sp.05 and *Pheidole* sp.06 in the current study would have a competitive advantage in the absence of grazing and drought given their body size. As locomotion speed increases with body size in ant species, it is likely that it gave larger species a competitive advantage over smaller ones in open and simple habitats (Gibb and Parr 2013). According to Sommer and Wehner (2011), as the surface temperature increases under drought treatments, long legs might have aided species that were most active under the drought treatments to avoid desiccation since long legs provide thermophilic ants in the genus *Camponotus* with the advantage of carrying their bodies higher into cooler levels of the air away from the hot surface. Leg length and heat tolerance were positively correlated with surface temperature and vapor pressure deficit and negatively correlated with ground cover (Wiescher *et al.* (2012). Moreover, fast locomotion through long legs not only allowed these species rapid exploration of the habitat, quick resource discovery and reduced foraging time but it also aided in further cooling of the body (Sommer and Wehner 2011).

Spiders

Effect of grazing

Overall, spiders size decreased during the cold, dry season (winter) and during the hot, dry season (spring). There were larger bodied spider species in the absence grazing (under the no grazing treatment). Grazing impacts became particularly acute during cold and dry periods and when exposed to drought conditions. Richness only responded to treatments within the context of seasonality, and mainly in response to grazing exclusions and drought conditions during the drier periods. Changes in spider species richness, abundance and community composition are influenced more by vegetation structure (Horvath *et al.* 2008, Horvath *et al.* 2015, Spears and Mchone 2002) over vegetation diversity (Gibson *et al.* 1992). As architectural diversity increases through succession or with relaxation of grazing pressure, a variety of other species colonize areas (Gibson *et al.* 1992). Hunting spiders and web-builders are very sensitive to the vegetation complexity of their habitats, as it provides more shelter, higher prey density, alternative food sources and decreasing intra-guild predation (Horvath *et al.* 2008, Horvath *et al.* 2015). Salticidae decreased with changing vegetation resulting from grazing, as salticids stalk their prey through vegetation (Churchill and Ludwig (2004). Furthermore, in the same study, species from the families Theridiidae and Lycosidae increased with the grazing.

Pitfall trapping has been widely used because it catches a good number of mobile spiders including larger species (Gibson *et al.* 1992). However, it would be ideal to use more than one sampling method such as suction sampling devices (DVACs), visual observation and sweep-netting to include plant dwellers, web-builders, and species living under stones. There are several studies that have used more than one sampling method, with fewer treatment replications and/or smaller ($> 10 \times 10$ m) treatment plots, and a shorter sampling duration than ours to investigate spider response to grazing (de Keer et al. 1989, Webb & Hopkins 1984, Warui *et al.* 2005).

Prey availability seems to be more of a limiting factor than vegetation structure and complexity and consequently influences the diversity of spiders. In the Australian semi-arid rangeland, Churchill and Ludwig (2004) observed that the activity of species from the family Gnaphosidae decreased with the decrease in activity of their prey, springtails, in grazed sites. In Swedish boreal forest moose grazing decreased the activity of spiders through depressing the abundance of flying prey for spiders (Suominen *et al.* 2008). General feeding patterns of common agroecosystem of web-weaver and hunting spiders show that both groups feed on the same prey orders, however, the feeding proportions differ between the groups, Diptera and Hymenoptera prey constituted on average 33 % of hunting spider diet, and 40 % of web-building spiders (Nyffeler 1999). Haddad *et al.* (2016) reported the activity of *Ammoxenids* and their mating seasons were correlated with population size increase of their prey *Hodotermes mossambicus* termites in the Free State grasslands. This suggests that the abundance of *Ammoxenus amphalodes* might be driven by prey availability and not so much the environmental conditions.

Effects of seasonality on spiders

Heavy autumn grazing decreases the proportion of sheet-web builders, whereas spring-and-autumn grazing produce more of this foraging type (Gibson *et al.* 1992). seasonality was observed to modify spider assemblages and as a result they differed between wet and dry seasons both in savanna and grassland (Churchill and Ludwig 2004). The difference was due to seasonal changes rather than habitat, with species in family Salticidae increasing in abundance with changes in vegetation structure in the late wet season.

Compositional effects: generic

Drought had a larger and more significant impact on generic composition than grazing. Drought promoted the activity of the genus *Ozyptila* but had a negative impact on the activity of *Psammorygma, Evippomma*, *Ammoxenus,* and *Trabea*.

Species composition was strongly modified by drought. Only the activity of *Ozyptila* (Thomisiidae) increased with drought, whilst *Evippomma* (Lycosidae), *Psammarygma* and *Platnickina* decreased with drought. *Ammoxenus* (Ammoxenidae) and *Evippomma* (Lycosidae) were most active in treatment plots without drought, suggesting that drought had a negative impact on these species indirectly through prey availability. Species from the genus *Ammoxenus* are monophagus and are known to feed only on termites. Haddad *et al.* (2016) observed that seasonal population changes of the species *Ammoxenus amphalodes* were related to population size and/or activity of one specific termite species, *Hodotermes mossambicus.* Moreover, the reproductive period of *A. amphalodes* coincides with the high seasonal activity of *H. mossambicus*. This is further supported by Pretrakova *et al.* (2015) who also confirmed, through sequencing the contents of the gut, that *A. amphalodes* is a monophagous termite-eater which feeds only one species of termites, the *H. mossambicus.* Furthermore, not only were different prey types refused, but other sympatrically-occurring termite species were rejected by *A. amphalodes*. Even spiderlings of this species that just hatched fed on the *H. mossambicus* (Pretrakova *et al.* 2015).

Compositional effects: species

Grazing, drought and their combined interactions changed species community composition of spiders. *Zelotes radiatus, Oxyopes* sp.14*, Oxyopes schenkeli* and *Zenonina albocaudata* were more active in grazed plots. Drought promotes an increase in activity of *Zelotes radiatus, Psammorygma aculeatum, Rastellus kariba*, whilst treatment combinations resulted in an increase in activity of *Psammorygma aculeatum, Zelotes radiatus, Hogna spenceri* and *Pellenes cingulatus. Zelotes radiatus* preferred ungrazed habitats with no drought. This is also evident under the no grazing and no drought combination. This suggests that this species is negatively affected by both treatments and their interaction. *Psammorygma aculeatum* was mostly active in grazed areas but without drought. This is also true for *Oxyopes* sp. 14 which is mostly active in ungrazed areas. *Hogna spenceri* is the only species that prefers areas with drought. Drought treatment had the most profound effect on the structure and composition of spider communities compared to grazing treatment.

Grazed areas tend to have an increase in the activity of spiders from the family Lycosidae (Saikkonen *et al.* 2019). These wolf spiders chase their prey at ground level, thus making open habitats the optimal foraging ground. This suggests that lower numbers of Lycosidae species in ungrazed areas is correlated with the absence of suitable prey and a physically demanding, complex habitat structure. Since the impact of grazing is mainly through species turnover (Arcoverde *et al.* 2017), grazed sites favour active hunters over species such as those of the Lyniphiidae family that sit and wait using webs for catching their prey. Grazing also compromises the anchoring of Lyniphiidae web structures (Saikkonen *et al.* 2019). Lyniphiidae was observed to increase with different plant successional stages which provided suitable conditions (Gibson *et al.* 1992 and McDonald 2007). Species are likely to change from high activity of web builders to increasing activity of active hunters as habitats become simplified.

In conclusion, our findings clearly suggest that both long-term drought and grazing have an impact on ants and spiders at both species and community level. Spiders were not as responsive to treatments and their combination as ants were. The current study used only pitfall traps to sample both ants and spiders and therefore findings may be attributed to one reason, the sampling methodology. It would be useful to employ various sampling methods (Gibson *et al*. 1992) which would account for web-builders, plant-dwelling species and those that hide under substrates such as rocks. Employing bigger plots and corridors will prove to be helpful in avoiding species that have big foraging ranges from easily moving from one plot to the next. Some species might respond to food shortage under treatments by foraging outside the plot (Delsinne *et al.* 2013). Employing irrigation systems to better control the timing and frequency of rainfall for seasonality purposes would allow for better monitoring, enabling more accurate conclusions and projections of the effect of grazing, drought and seasonality of precipitation on ant and spider diversity in light of climates change. How ants and spiders respond to long-term effects on drought and livestock grazing in semi-arid rangelands in the face of climate change is likely to shed light also on how other invertebrates are likely to be affected by changes in food webs resulting changes in community structures and functions. Further studying is needed to uncover other underlying changes and dynamics, and how that affects and shapes the semi-arid rangeland ecosystems in the long-term.

REFERENCES

Adeel, Z., U. Safriel, U. Niemeijer, D. and White, R. 2005. Ecosystems and human well-being: desertification synthesis. Millennium Ecosystems Assessment. World Resources Institute, Washington, D.C., USA.

Altwegg R, West, A, Gillson, L. and Midgley G. 2014. Impacts of climate change in the Greater Cape Floristic Region. Fynbos: Ecology, evolution, and conservation of a megadiverse region. In book: Fynbos: pp.299-320

Andersen, A.N. 1997. Using Ants as bioindicators: Multiscale Issues in Ant Community Ecology. *Conservation Ecology*, 1:8-19

Andersen, A.N. 1997. Using Ants as bioindicators: Multiscale Issues in Ant Community Ecology. *Conservation Ecology*, 1: 8-21

Andersen, A.N. 1999. My indicator or yours? Making the selection? *Journal of Insect Conservation* 3: 61–64.

Andersen, A.N. and Majer, J.D. 2004. Ants show the way down under invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment*, 2: 291-298.

Andresen, E. 2005. Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. *Biotropica* 37: 291–300.

Arcoverde, G.B., Andersen A.N and Setterfield, S.A. 2016. Is livestock grazing compatible with biodiversity conservation? Impacts on savanna ant communities in the Australian seasonal tropics. *Biodiversity Conservation*, 26:883–897.

Barton, B. T. 2011. Local adaptations to temperature conserve top-down control in a grassland food web. *Proceedings of the Royal Society of Biological Sciences*, 278:3102–3107.

Baker, D.H., Meese, T.S. and Georgeson, M.A., 2007. Binocular interaction: Contrast matching and contrast discrimination are predicted by the same model. *Spatial Vision*, 20:397-413.

Beinart, W. 2003. *The rise of conservation in South Africa: Settlers, livestock and the environment,* 1770-1950. New York: Oxford University Press.

Bestelmeyer, B. and Weins, J.A. 2001. Ant biodiversity in semiarid landscape mosaic: the consequences of grazing vs natural heterogeneity. *Ecological Applications*, 11: 1123-1140.

Bharti, H., Bharti, M. and Pfeiffer, M. 2016. Ants as bioindicator ecosystem health in Shivalik Mountain of Himalayas: assessment of species diversity and invasive species. *Asian Myrmecology*, 8:1-15.

Boulton, A.M., Davies, K.F. and Ward, A.P. 2005. Species Richness, Abundance, and Composition of Ground-Dwelling Ants in Northern California Grasslands: Role of Plants, Soil, and Grazing. *Environmental. Entomology*, 34: 96-104.

Buchholz, S. 2010 simulated climate change in dry habitats: do spiders respond to experimental small-scale drought? *The Journal of Arachnology*, 38: 280-284.

Calcaterra, L.A., Cabrera, S.M., Cuezzo, F., Perez, I.J. and Briano, J.A. 2010. Habitat and grazing influence on terrestrial ants in Subtropical Grassland and Savanna of Argentina. *The Annals of the Entomological Society of America,* 103:10:0635-0646.

Churchill, T.B. and Ludwig, J.A. 2004. Changes in spider assemblages along grassland and Savanna grazing gradient in north Australia. *The Rangeland Journal*, 26:3-16.

Daron, J.D. 2014. 'Regional Climate Messages: Southern Africa'. Scientific report from the CARIAA Adaptation at Scale in Semi-Arid Regions (ASSAR) Project, December 2014.

Da Silva, O.G. and Ott, R. 2017. Short-term spider community monitoring after cattle removal in grazed grassland. *Série Zoologia*, 107, e2017033, 1678-4766

Dean, W.R.J. and Milton and S.J. 2003. Did the flora match the fauna? Acocks and historical changes in Karoo biota. *South African Journal of Botany,* 69:68-78.

Del Toro, I., Ribbons, R.R. and Pelini, S.L. 2012. The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News*, 17:133-146.

de Keer, R., Alderweireldt, M., Decleer, K., Segers, H., Desender, K. and Maelfait, J.-P. 1989. Horizontal distribution of the spider fauna of intensively grazed pastures under the influence of diurnal activity and grass height. *Journal of Applied Entomology*, 107, 455-473.

Delsinne, T, AriaT.P and Leponce, M. 2013 Effects of experimental rainfall exclusion on a diverse ant assemblage along an elevational gradient in the Ecuadorian Andes. *Basic and Applied Ecology*, 14:357-365.

Dube, P.O. and Pickup, G. 2001. Effects of rainfall variability and communal and semi-commercial grazing on land cover in Southern African rangelands. *Climate Research,* 195:195-208.

Dupre, C. and DIekmann, M. 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. *Ecography*, 24:275‑286.

Ellison, A.M. 2012. Out of Oz: the opportunities and challenges of using ants (Hymenoptera: Formicidae) as biological indicators in north-temperate cold biomes. *Myrmecology News,* 17:105-119.

El Keroumi, A., Naamani, K., Soummane, H. and Dahbi, A. 2012. Seasonal dynamics of ant community structure in the Moroccan Argan Forest. *Journal of Insect Science*, 12:1536-2442.

Erasmus, F.N.B., Jaarsveld, V.A., Chown, S.L., Kshatriya, M. and Wesseles, K.J. 2002. Vulnerability of South African animal taxa to climate change. *Global Change Biology*, 8: 679-693

Espadaler, X. and Gomez, C. 2001. Formicine Ants Comply with the Size-Grain Hypothesis. *Functional Ecology*, 15: 136-138.

Feener, D.H., Lighton, J.R.B. and Bartholomew, G.A. 1998. Curvilinear Allometry, Energetics and Foraging Ecology: A Comparison of Leaf-Cutting Ants and Army Ants. *Functional Ecology*, 4: 509-520.

Folgarait, P.J. 1999. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, 7:1221-1244.

Foord, S.H., Mafadza, M.M., Dippenaar-Schoeman, A.S. and Van rensburg, B.J. 2008. Micro-scale heterogeneity of spiders (Arachnida: Araneae) in the Soutpansberg, South Africa: a comparative survey and inventory in representative habitats. *African Zoology*, 43:56‑174.

Fowler, H.G., Forti, L.C., Brandão, C.R.F., Delabie, J.H.C. and Vasconcelos, H.L., 1991. Ecologia nutricional de formigas. *Ecologia nutricional de insetos e suas implicações no manejo de pragas,* 131-223.

Gibb, H. and Parr, C.L. 2013. Does structural complexity determine the morphology of assemblages? An experimental test on three continents. *PLosOne*, 8: e64005.

Gibb, H., and Parr, C.L. 2010. How does habitat complexity affect ant foraging success? A test using functional measures on three continents. *Oecologia*, 164:1061–1073.

Gibson, C.W.D., Hambler, C and Brownd, V.K. 1992 Change in spiders (Araneae) assemblages in relation to succession and grazing management. *Journal of Applied Ecology*, 29: 132-142.

Grill, A., Knoflach, B., Cleary, D. F. R. and Kati, V. 2005. Butterfly, spider, and plant communities in different land-use types in Sardinia, Italy. *Biodiversity Conservation,* 14: 1281–1300.

Hacker, S.D. and Gains, S.D. 1997. Some implication of direct positive interactions for community species diversity. *Ecology*, 78:1990-2003.

Haddad, C.R., Brabec, M., Pekar, S. and Fourie, R. 2016. Seasonal population dynamics of a specialized termite-eating spider (Araneae: Ammoxenidae) and its prey (Isoptera: Hodotermitidae). *Pedobiologia*, 59:105–110.

Halder, I. V., L. Barbaro, E. Corcket and H. Jactel (2008) Importance of seminatural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. *Biodiversity Conservation,* 17: 1149–1169.

Hawkins, B.A, Field, R., Cornell, H.V., Currie, D.J., Guegan G.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O`Brien, E.M., Porter, E.E. and Turner, T.R.G. 2003. Energy, water, and broad-scale geographical patterns of species richness. *Ecology*, 84: 3015-3117.

Heinrich, B. and Heinrich, M. 1984. The pit-trapping foraging strategy of the ant lion, *Myrmeleon immaculatus* DeGeer. *Behavioural Ecology Sociobiology*, 14:151-160.

Hess, G. R., R. A. Bartel, A. K. Leidner, K. M. Rosenfeld, M.J. Rubino, S. B. Snider and T. H. Ricketts (2006) Effectiveness of biodiversity indicators varies with extent, grain, and region. *Biological Conservation,* 132: 448–457.

Hoffmann, B.D. 2000. Change in ant species composition and community organization along the grazing gradient in a semi-arid rangeland of the northern territory. *Range Land Journal*, 22: 171-89.

Hoffman, B.D. 2010. Using ants for rangeland monitoring: Global patterns in the responses of ant communities to grazing. *Ecological Indicators*, 10: 105-111.

Horváth, R., Magura, T., Szinetár, C. and Tothmerez, B. 2008. Spiders aren`t less diverse in small and isolated grasslands, but less diverse in the overgrazed grasslands: a field study (east Hungary, Nyrseg). *Agriculture, Ecosystem and Environment*, 130: 130 16-22.

Horváth, R., Magura, T., Szinetár, C., Eichardt, J. and Kovács, E. 2015. In stable, unmanaged grasslands local factors are more important than landscape-level factors in shaping spider assemblages. *Agriculture, Ecosystems and Environment*, 208:106–113.

Humeau, A., Rouge, J. and Casas, J. 2015. Optimal range of prey size for antlions. *Ecological Entomology*, 40:776–781.

IPCC, Intergovernmental Panel on Climate Change. 2007. *Fourth Assessment Report: Climate Change*. (2007). Online at http://www. ipcc.ch/ipccreports/assessments-reports.

Jensen, R., Makaka, L., Little, I.T. and Dippenaar-Schoeman, A. 2013. Response of ground-dwelling spider assemblages (Arachnida, Araneae) to Montane Grassland management practices in South Africa. *Insect Conservation and Diversity*, 6:572-589. URL: https://doi.org/10.1111/icad.12013.

Joseph, S.G., Mauda, E.V., Seymour, C.L., Munyai, T.C., Dippenaar-Schoeman, A. and Foord, S.H. 2017. Land-use Change in Savannas Disproportionately Reduces Functional Diversity of Invertebrate Predators at the Highest Trophic Levels: Spiders as an Example. *Ecosystems*, 21:930-942. https://doi.org/10.1007/s10021-017-0194-0.

Kitching, R. L., A. G. Orr, L. Thalib, H. Mitchell, M. S. Hopkins and A. W. Graham. 2000. Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology* 37: 284–297.

Lach, L., Parr, C.L. and Abbott, K.L. 2010. *Ant Ecology*. Oxford University Press, Oxford.

Langland, P.R. and Person, D.J. 2006. Spiders, spinifex, rainfall and fire: long term changes in an arid spider assemblage. *Journal of Arid Environments*, 67: 36-59.

Landres, P. B., J. Verner and J. W. Thomas (1988) Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* 2: 316–328.

Lalibert, E. and Legender, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91:299-305.

Laliberte´ E and Shipley B. 2011. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11. http://CRAN.R-project.org/package=FD.

Lensing, J.R., Todd, S. and Wise, D.H.2005. The impacts of altered precipitation on spatial stratification and activity-densities of springtails (Collembola) and spiders (Araneae). *Ecological Entomology*, 30: 194-2000.

Le Houerou and H.N. 1996. Climate change, drought and desertification. *Journal of Arid Environments*, 34: 133–185.

Lohmann, D., Tietjen, B., Blaum, N., Joubert, D.F. and Jeltsch, F. 2012. Shifting threshold and changing degradation patterns: climate change effect on the simulated long-term response of a semi-arid savanna to grazing. *Journal of Applied Ecology*, 49:814-823.

Lucas, J.R. and Brockmann, H.J. 1981. Predatory Interactions Between Ants and Antlions (Hymenoptera: Formicidae and Neuroptera: Myrmeleontidae). *Journal of the Kansas Entomological Society*, 54:228-232.

Mauda, E.V., Joseph, G.S., Seymour, C.L., Munyai, T.C. and Foord, S.H. 2017. Changes in land use alter ant diversity, assemblage composition and dominant functional groups in African savannas. *Biodiversity Conservation*, 27:947-965. https://doi.org/10.1007/s10531-017-1474-x.

McCabe, D.J and Gotelli, N.J. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia*, 124: 270–279.

McDonald, B. 2007. Effects of Vegetation Structure on Foliage Dwelling Spider Assemblages in Native and Non-native Oklahoma Grassland Habitats. *Proceedings of Oklahoma Academy of Science*, 87: 85-88.

Maeto, K. and Makihara, H. 1999. Changes in insect assemblages with secondary succession of temperate deciduous forests after clear-cutting. *Japanese Journal of Entomology (N.S.)* 2: 11–26.

Maeto, K. and Sato, S. 2004. Impacts of forestry on ant species richness and composition in warm-temperate forests of Japan. *Forestry and Ecological Management,* 187: 213–223.

Manson, S.J. and Joubert, A.M. 1996. Simulated changes in extreme rainfall over southern Africa. *International Journal of Climatology*, 17: 291-301.

Malumbres-Olarte, J., Barratt, B.I.P., Vink, C.J., Paterson, A.M., Cruickshank, R.H., Ferguson, C.M. and Barton, D.M. 2014. Big and aerial invaders: dominance of exotic spiders in burned New Zealand tussock grasslands. *Biology Invasions*, 16:2311–22.

Mineo, M.F., Del-Claro, K. and Brescovit, A.D. 2010. Seasonal variation of ground dwelling spiders in Brazilian Savanna. *Zoologia*, 27:353-362.

Mucina, L, and Rutherford, M.C. 2006 The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.

Nakagawa S. and Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4:133–142.

New, T. R. (2004) Moths (Insecta: Lepidoptera) and conservation: background and perspective. *J. Insect*, 8: 79–94.

Nichols, E., Larsen, T., Davis, S. A. L., Escobar, F., Favila, M. and Vulinec, K. 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological Conservation,* 137: 1–19.

Nyffeler, M. 1999. Prey selection of spiders in the field. *Journal of Archnology*, 27: 317-324.

Osawa, N., Terai, A., Hirata, K., Nakanishi, A., Makino, A., Sakai, S. and Sibata, S. 2005. Logging impacts on forest carabid assemblages in Japan. *Canadian Journal of Forestry Research,* 35:2698–2708.

Parr, C.L., Eggleton, P., Davies, A.B., Evans, T.A. and Holdsworth, S. 2016. Suppression of savanna ants alters invertebrate composition and influences key ecosystem processes. *Ecology* 97:1611–1617, http://dx.doi.org/10.1890/15-1713.1.

Pearce, J. L. and Venier, L. A. 2006. The use of beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecological Indicators,* 6: 780–793.

Petrakova, L., Liznarova, E., Pekar, S., Haddad, C.R. and Symodson, W.O.C. 2015. Discovery of a monophagous true predator, a specialist termite-eating spider (Araneae: Ammoxenidae). *Scientific Reports*, 5:14013.

Pfeiffer M, Mezger D and Dyckmans J. 2013. Trophic ecology of tropical leaf litter ants (Hymenoptera Formicidae) - a stable isotope study in four types of Bornean rain forest. *Myrmecological News*, 19: 31 ‐ 41.

Philpott S., Perfecto I., Armbrecht I. and Parr C.L. 2010. Ant diversity and function in disturbed and changing habitats. *Ant Ecology*, Oxford University Press, Oxford: 137 – 156.

Purdon, J., Parr, C.L. and Somers, M.J. 2019. Grazing by large savanna herbivores indirectly alters ant diversity and promotes resource monopolization. *PeerJ*, 7. DOI 10.7717/peerj.6226.

R Core Development Team. 2018. R: A language and environmental for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rainio, J. and Niemelä, J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity Conservation,* 12:487–506.

Resasco, J., Pelini, S.L., Stuble, L.S., Sanders, J.N., Dunn, R.R., Diamond, S.E., Ellison5, A.M., Gotelli, N.J. and Levey, D.J. 2014. Using historical and experimental data to reveal warming effects on ant assemblages. *PLOS ONE*, 9: e88029.

Rizali, A., Clough, Y., Buchori, D. and Tscharnutke, T. 2013. Dissimilarities of ant communities increase with precipitation, but not reduced land-use intensity, in Indonesian Cacao agroforestry. *Diversity*, 5: 26-38.

Ruppert, J.C., Harmoney, K., Henkkin, H.A., Snyman, H.A., Sternberg, M., Willmms, W. and Linstadter, A. 2014. Quantifying drylands drought resistance and recovery: the importance of drought intensity, dominant life history and grazing regime. *Global Change Biology*, 23 https://doi.org/10.1111/gcb.12777.

Rypstra, A.L., Schimidt, J.M., Reif, Brant.D., DeVito, J. and Persons, M.H. 2007. Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. *Oikos*, 116: 853-863.

Sala, O. E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloofield, J., Dirzo, Rodolfo., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, Rik., Lodge, M.D., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. and Wall, H.D. 2000. Global biodiversity scenarios for the year 2100. *Science*, 287:1770‑1774.

Sanders N.J., Lessard J.P., Fitzpatrick M.C. and Dunn R.R. 2007 Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, 16: 640–649.

Schofield, S.F., Bishop, T.R. and Parr, C.L. 2016. Morphological characteristics of ant assemblages (Hymenoptera: Formicidae) differ among contrasting biomes. *Myrmecological News*, 23:129-13.

Schowalter, T. D., Zhang, Y. L. and Rykken, J. J. 2003. Litter invertebrate responses to variable density thinning in western Washington forest. *Ecological Application*, 13: 1204–1211.

Schwinning, S., Sala, E.O., Loik, M.E. and Ehleringer, J.R. 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia*, 141:191-193.

Segev, U. 2010. Regional patterns of ant-species richness in an arid region: The importance of climate and biogeography. *Journal of Arid Environments*, 74: 646–652.

Seymour, C.L. and Dean, W.R.L. 1999. Effects of heavy grazing on the invertebrates' assemblages in the Succulent Karoo, South Africa. *Journal of Arid Environments*, 43: 267-286.

Silva, R.R. and Brandão, C.R.F. 2014. Ecosystem-Wide Morphological Structure of Leaf-Litter Ant Communities along a Tropical Latitudinal Gradient. *PLoS ONE*, 9: e93049.

Sommer, S. and Wehner, R. 2011. Leg allometry in ants: Extreme long-leggedness in thermophilic species. *Arthropod Structure and Development*, 41:71-77.

Stuble, K.L., Pelini, S.L., Diamond, S.E., Fowler, D.A., Dunn, R.R. and Sanders, J.N. 2014. Foraging by forest ants under experimental climatic warming: a test at two sites. *Ecology and Evolution*, 3: 482–491.

Spears, L.R. and McMahon, J.A. 2012. An experimental study of spiders in a shrub-steppe ecosystem: the effects of prey availability and shrub architecture. *Journal of Arachnology*, 40:218–227.

Suominem, O., Persson, I., Danell, K., Bergstrom, R. and Pastor, John. 2008. Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. *Ecography*, 31: 636-645.

Tieda, Y., Schlautmanna, J., Donosob, D.A., Wallisa, C.I.B., Bendixc, J., Brandld, R. and Farwiga, N. 2017. Ants as indicators of environmental change and ecosystem processes. *Ecological Indicators*, 83: 527-537.

Trenberth, K.E., Overpeck, J. T. and Solomon, SS. 2004. Exploring drought and its implications for the future. *Ecosystem Transformation American Geophysics Union,* 85:27.

Vetta, S. 2009. Drought. Change and resilience in South Africa's arid and semi-arid rangelands. *South African Journal of Science*, 105.

Vogel, C.H. 1993. Dimension of drought: South Africa case studies. *Geography Journal*, 30.1: 93-98.

Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo.2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, 103:1342‑1346.

Warui, C.M., Villet, M.H., Young, T.P. and Jocque, R. 2005. Influence of grazing by large mammals on the spider community of a Kenyan Savanna Biome. *The Journal of Arachnology*, 33:269-279.

Webb, N.R. and Hopkins, P.J. (1984) Invertebrate diversity on fragmented Calluna heathland. *Journal of Applied Ecology*, 21: 921-933.

Weber, N.A., 1938. The biology of the fungus-growing ants. Part IV. Additional new forms. Part V. The Attini of Bolivia. Biología de las hormigas cultivadoras de hongos. Parte IV. Nuevas formas adicionales. Part V. Las Attini de Bolivia. *Revista de Entomologia (Rio de Janeiro)*, *9*(1/2), pp.154-206.

Weiser, M.D. and Kaspari, M., 2006. Ecological morphospace of New World ants. *Ecological Entomology*, *31*(2): 131-142.

Westfall, P. andYoung, S. 1993. Resampling-Based Multiple Testing. John Wiley & Sons, New York, New York.

Wiescher, T. P., Pearce-Duvet, J.M.C. and Feener, D.H. 2012. Assembling an ant community: species functional traits reflect environmental filtering. *Oecologia*, 169:1063–1074.

Williams, M.A.J. and Balling Jr, R.C. 1994. Interactions of Desertification and Climate. *Geneva: WMO, and Nairobi*: UNEP pp. 230

Yates, M.L., Andrew, N.R., Binns, M. and Gibb, H., 2014. Morphological traits: predictable responses to macrohabitats across a 300 km scale. *PeerJ*, *2*, p.e271.

Zeppel, M. J. B., Wilks, J. V. and Lewis, J. D. 2014. Impacts of extreme precipitation and seasonal changes in precipitation on plants. *Biogeosciences*, 11:3083–3093.

Ziervogel, G., New, M., Van Garderen, E.A., Midgley, G., Taylor, A., Hamann, R., Stuart-Hill, S., Myers, J. and Warburton, M. 2014. Climate change impacts and adaptation in South Africa. *WIREs Climate Change*, 5: 605-620.

Supplementary material

Table S1. Treatment plots. D = drought, G = grazing, (+) = with grazing or drought, and (-) = without grazing or drought.

Treatment codes	Treatment description
LTE ($D^- G^-$)	No grazing and no drought: plots fenced and without a rain shelter
DRO ($D^+ G^+$)	Drought and grazing: plots not fenced and with a rainout shelter
DRO_LTE ($D^+ G^-$)	Drought: plot fenced and with a rainout shelter
CONT ($D^- G^+$)	Grazing and no drought: plot not fenced and without a rainout shelter

Table S2. Survey dates for this long-term monitoring study. Long-term monitoring: December 2014 to February 2017, conducted during the early hot and wet season (December) and late hot and wet season (February). Seasonality sampling: 2017 December to 2018 October.

Survey dates	**Surveys**
2014 December	First survey
2015 February	Second survey
2015 December	Third survey
2016 February	Fourth survey
2016 December	Fifth survey
2017 February	Sixth survey
2017 December (early hot and wet season)	Seventh survey (seasonality survey)
2018 February (late hot and wet season)	Eighth survey (seasonality survey)
2018 June (cold and dry season)	Ninth survey (seasonality survey)
2018 October (dry and hot season)	Tenth survey (seasonality survey)

Appendix B.

Table S1. Species list of all ants caught during the long-term survey from December 2014 to October 2018.

Subfamily	Genus	Species name	Abundance
Dorylinae	*Aenictus*	*Aenictus rotundatus*	1
	Dorylus	*Dorylus* sp.05	209
	Parasyscia	*Parasyscia* sp.05	219
Formicinae	*Anoplolepis*	*Anoplolepis custodiens*	4
Dolichoderinae	*Technomyrmex*	*Technomyrmex pallipes*	103
Formicinae	*Camponotus*	*Camponotus mayri*	10
		Camponotus sp.14 (*cinctellus gp.)*	142
		Camponotus sp.15	139
		Camponotus sp.18 (*maculatus gp.*)	20
		Camponotus sp.26	206
		Camponotus niveosetosus	7
	Crematogaster	*Crematogaster* sp.15	223
	Lepisiota	*Lepisiota* sp.01 (*capensis gp.)*	40
		Lepisiota sp.02 (*spinosior gp.*)	41
		Lepisiota sp.18	150
		Lepisiota sp.21	221
	Polyrhachis	*Polyrhachis* sp.01	218
	Tapinolepis	*Tapinolepis* sp.01	101
Myrmicinae	*Crematogaster*	*Crematogaster* sp.07	183
		Crematogaster sp.12	207
		Crematogaster sp.13	208
	Meranoplus	*Meranoplus cf. glaber*	49
	Monomorium	*Monomorium ?notulum*	55
		Monomorium junodi	58
		Monomorium damarense	59
		Monomorium sp.08 (*Monomorium gp.*)	62
		Monomorium sp.10 (*salamonis gp.*)	63
		Monomorium sp.22	211
		Monomorium sp.23	212
		Monomorium cf emery	224
	Ocymyrmex	*Ocymyrmex fortior*	68

	Pheidole	*Pheidole* sp.01 (*megacephala* gp.)	72
		Pheidole sp.03 (*megacephala gp.*)	74
		Pheidole sp.06 (*crassinoda gp.)*	76
		Pheidole sp.13	172
		Pheidole sp.14	156
		Pheidole sp.15	147
	Tetramorium	*Tetramorium baufra*	104
		Tetramorium cf. setigerum	105
		Tetramorium notiale	106
		Tetramorium setuliferum	108
		Tetramorium sp.01 (*squaminode gp.*)	109
		Tetramorium sp.04 (*gabonense gp.)*	126
		Tetramorium sp.08 (*simillimum gp.)*	111
		Tetramorium sp.19 (*simillimum gp.)*	130
		Tetramorium sp.27 (*sericeiventre gp.)*	141
		Tetramorium sp.31	162
		Tetramorium sp.35	225
		Tetramorium sp.38 (*setigerum gp*)	215
		Tetramorium sp.39	216
		Tetramorium sp.40	226
	Solenopsis	*Solenopsis* sp.01	97
Ponerinae	*Bothroponera*	*Bothroponera sp.04*	205
		Bothroponera sp.05	214
	Hypoponera	*Hypoponera* sp.01	37
	Mesoponera	*Mesoponera* sp.01	220
		Mesoponera sp.02	184
		Mesoponera sp.05	210
		Mesoponera sp.06	217
	Odontomachus	*Odontomachus troglodytes*	70
	Pseudoponera	*Pseudoponera* sp.01	92
		Pseudoponera sp.02	121

Table S2. Species list of all spiders caught during the long-term survey from December 2014 to October 2018.

Family	Genus	Species name	Abundance
Ammoxenidae	*Ammoxenus*	*Ammoxenus amphalodes*	1
		Ammoxenus daedalus	4
		Ammoxenus psammodromus	45
	Rastellus	*Rastellus florisbad*	2
		Rastellus kariba	4
Araneidae	*Argiope*	*Argiope trifasciata*	1
	Hypsosinga	*Hypsosinga lithyphantoides*	1
Atypidae	*Calommata*	*Calommata transvaalica*	2
Corinnidae	*Copa*	*Copa flavoplumosa*	1
Cyrtaucheniidae	*Ancylotrypa*	*Ancylotrypa elongata*	10
		Ancylotrypa brevipalpis	1
Dictynidae	*Dictyna*	*Dictyna sp.01*	3
Eresidae	*Dresserus*	*Dresserus vhembi*	1
		Eresidae sp?	2
	Paradonea	*Paradonea parva*	6
		Paradonea presleyi	1
		Paradonea variegata	2
Gnaphosidae	*Asemesthes*	*Asemesthes flavipes*	2
		Asemesthes ceresicola	50
		Asemesthes lineatus	49
		Asemesthes numisma	3
		Asemesthes pallidus	2
		Asemesthes reflexus	2
		Asemesthes sp.01	8
		Asemesthes sp.08	1
		Asemesthes sp.1	1
	Camillina	*Camillina cordifera*	7
		Camillina pavesii	1
		Camillina procurva	1
		Camillina sp.01	1
	Drassodes	*Drassodes helenae*	1
		Drassodes splendens	2
	Ibala	*Ibala sp.01*	4

		Ibala subtilis	2
	Zelotes	*Zelotes bastardi*	1
		Zelotes caldarius	1
		Zelotes fuligineus	1
		Zelotes humilis	5
		Zelotes natalensis	7
		Zelotes radiatus	8
		Zelotes sclateri	2
		Zelotes tuckeri	1
Hahniidae	*Hahnia*	*Hahnia tabulicola*	2
Linyphiidae	*Agyneta*	*Agyneta prosectes*	2
	Pelecopsis	*Pelecopsis janus*	3
Liocranidae	*Rhaeboctesis*	*Rhaeboctesis trinotatus*	2
Lycosidae	*Allocosa*	*Allocosa gracilitarsis*	4
		Allocosa lawrencei	17
		Allocosa umtalica	2
	Evippomma	*Evippomma sp.01*	5
		Evippomma squamulatum	166
	Foveosa	*Foveosa foveolata*	5
	Hogna	*Hogna bimaculata*	1
		Hogna sp.01	1
		Hogna spenceri	11
	Lycosidae	*Lycosidae sp.06*	1
	Pardosa	*Pardosa crassipalpis*	10
		Pardosa purcelli	1
		Pardosa sp.02	1
	Proevippa	*Proevippa albiventris*	5
		Proevippa biampliata	1
	Trabea	*Trabea heteroculata*	71
		Trabea purcelli	11
	Zenonina	*Zenonina albocaudata*	11
	NA	*Lycosidae sp.01*	4
Oonopidae	*Oonopidae*	*Oonopidae sp.?*	1
Oxyopidae	*Oxyopes*	Oxyopes sp.14	4
		Oxyopes affinis	6
		Oxyopes auriculata	8
		Oxyopes bothai	1
		Oxyopes cornifrons	1
		Oxyopes falconeri	24
		Oxyopes jacksoni	27
		Oxyopes pallidecoloratus	7
		Oxyopes russoi	4

		Oxyopes schenkeli	5
		Oxyopes strandi	7
Oxyopidae	*Oxyopes*	*Oxyopes vogelsangeri*	1
Philodromidae	*Hirriusa*	*Hirriusa variegata*	9
	Philodromus	*Philodromus grosi*	1
	Philodromus	*Philodromus sp.01*	1
	Thanarus	*Thanatus lamottei*	3
Pisauridae	*Charminus*	*Charminus sp.*	2
	Maypacius	*Maypacius roeweri*	1
	Perenethis	*Perenethis simoni*	2
Salticidae	*Salticidae*	*Salticidae sp.01*	1
	Cyrba	*Cyrba sp.*	1
	Heliophanus	*Heliophanus sp.01*	2
	Hyllus	*Hyllus argyrotoxus*	1
		Hyllus brevitarsis	1
		Hyllus dotatus	1
	Icius	*Icius insolidus*	3
	Langona	*Langona bisecta*	1
		Langona hirsuta	2
		Langona? Na charles	1
	Nigorella	*Nigorella hirsuta*	6
	Pellenes	*Pellenes bulawayoensis*	51
		Pellenes cingulatus	4
	Phlegra	*Phlegra cf. procera*	2
		Phlegra karoo	3
		Phlegra long body ?	1
		Phlegra nuda	1
	Pignus	*Pignus simoni*	4
	Stenaelurillus	*Stenaelurillus guttiger*	202
	Tanzania	*Tanzania minutus*	1
	Thyene	*Thyene leighi*	2
		Thyenula fidelis	2
Selenopidae	*Anyphops*	*Anyphos barbertonensis*	1
	Olios	*Olios correvoni*	1
Theridiidae	*Euryopis*	*Euryopis funebris*	1
	Latrodectus	*Latrodectus geometricus*	3

		Latrodectus renovulvatus	1
	Heriaeus	*Heriaeus peterwebbi*	2
	Ozyptila	*Ozyptila caenosa*	5
	Smodicinus	*Smodicinus coroniger*	1
	Stiphropus	*Stiphropus bisigillatus*	7
	Stiphropus	*Stiphropus intermedius*	2
	Synema	*Synema decens*	2
	Tibellus	*Tibellus sp.01*	1
Trohchanteridae	*Platnickina*	*Platnickina mneon*	3
Zodariidae	*Chariobos*	*Chariobas cylindriceus*	1
	Cydrela	*Cydrela schoemanae*	9
		Cydrela spinimana	20
	Diores	*Diores auricula*	8
		Diores magicus	6
		Diores simplicior	1
		Diores triarmatus	1
	Heradida	*Heradida bicincta*	7
		Heradida sp.	16
		Heradida sp.01	1
		Heradida speculigera	6
	Mastidiores	*Mastidiores sp.01*	3
	Microdiores	*Microdiores sp.01*	2
	Psammorygma	*Psammorygma aculeatum*	13
	Ranops	*Ranops caprivi*	5
		Ranops sp.01	1

Appendix C:

Table S1. Parameter name, estimate, lower and upper 95% confidence intervals of predictors in multiple regression models for ant activity, richness, Weber's length and functional diversity. G+ = grazing, G- = grazing exclusion, D+ = drought, D- = no drought. All category variables are compared to the control, grazing (G+) and no drought (D-).

Parameter	Beta	Lower - 95	Upper - 95
		Ant activity	
G-	-0.167*	-0.20	-0.13
D+	-0.07*	-0.11	-0.04
G-*D+	0.19*	0.14	0.24
G-D-	-0.17*	-0.20	-0.13
G-D+	-0.05*	-0.09	-0.01
G+D+	-0.07*	-0.11	-0.04
		Richness	
G-	-0.08	-0.18	0.01
D+	0.01	-0.08	0.11
G-*D+	0.02	-0.13	0.16
G-D-	-0.08	-0.18	0.02
G-D+	-0.05	-0.16	0.06
G+D+	0.01	-0.08	0.11
		Weber's length (Body size)	
G-	-0.21*	-0.33	-0.09
D+	-0.09	-0.21	0.04
G- × D+	0.19	0.02	0.38
SD (intercept) block	0.02		
G-D-	-0.21*	-0.33	-0.09
G-D+	-0.09	-0.23	0.04
G+D+	-0.09	-0.21	0.04
SD (intercept) block	0.03		
		Functional diversity (FD)	
G-	-0.22*	-0.43	-0.02
D+	-0.09	-0.29	0.12
G-*D+	0.16	-0.15	0.46
G-D-	-0.22*	-0.43	-0.02
G-D+	-0.16	-0.38	0.07
G+D+	-0.09	-0.29	0.11

Table S2. Parameter estimates, lower and upper 95% confidence intervals of predictors in multiple regression models for spider activity, generic richness, and body size G+ = Grazing, G- = Grazing exclusion, D+ = Drought, D- = No Drought. All categorical variables are compared to the control, Grazing (G+) and No Drought (D-).

Parameters	Beta	Lower - 95	Upper - 95
		Spider activity	
G-	-0.12	-0.26	0.02
D+	0.04	-0.10	0.19
G-*D+	-0.07	-0.30	0.16
G-D-	-0.12	-0.22	0.02
G-D+	-0.15	-0.34	0.03
G+D+	0.04	-0.10	0.19
		Generic richness	
G-	-0.07	-0.24	0.09
D+	0.03	-0.41	0.21
G-*D+	-0.05	0.33	0.23
G-D-	-0.07	-0.24	0.09
G-D+	-0.09	-0.31	0.13
G+D+	0.03	-0.15	0.21
		Body size	
G-	-0.03	-0.52	0.45
D+	-0.31	-0.85	0.23
G-*D+	0.40	-0.44	1.24
G-D-	-0.03	-0.52	0.45
G-D+	0.06	-0.59	0.72
G+D+	-0.31	-0.85	0.24

Table S3. Parameter name, estimate, lower and upper 95% confidence intervals of predictors in multiple regression models for ant richness and activity. G+ = Grazing, G- = Grazing exclusion, D+ = Drought, D- = No Drought. Seasons, winter (cold and dry) and spring (hot and dry) are compared to summer (hot and wet). All categorical variables are compared to the control, Grazing (G+) and No Drought (D-).

Seasonality			
Parameters	**Beta**	**Lower - 95**	**Upper - 95**
Species richness			
Treatments			
G-	0.02	-0.22	0.25
D+	0.01	-0.19	0.34
Winter (cold and dry)	-0.51*	-0.83	-0.19
Spring (hot and dry)	-0.02	-0.29	0.25
Winter (cold and dry): G-	-0.06	-0.46	0.35
Winter (cold and dry): D+	-0.16	-0.51	0.18
Spring (hot and dry): G-	-0.34	-0.84	0.16
Spring (hot and dry): D+	-0.14	-0.54	0.26
Treatment combinations			
G-D-	0.03	-0.24	0.31
G-D+	0.07	-0.36	0.49
G+D+	0.09	-0.25	0.45
Winter (cold and dry)	-0.55*	-0.90	-0.21
Spring (hot and dry)	-0.06	-0.36	0.24
Winter (cold and dry): G-D-	0.02	-0.43	0.47
Winter (cold and dry): G-D+	-0.76	-1.78	0.25
Winter (cold and dry): G+D+	-0.18	-0.79	0.42
Spring (hot and dry): G-D-	-0.09*	-0.49	-0.30
Spring (hot and dry): G-D+	-0.43	-1.11	0.23
Spring (hot and dry): G+D+	-0.03	-0.54	0.48
Activity			
G-	-0.36*	-0.45	-0.27
D+	0.15*	0.05	0.25
Winter (cold and dry)	-1.01*	-1.15	-0.88
Spring (hot and dry)	0.07	-0.03	0.16
Winter (cold and dry): G-	0.99*	0.83	1.16
Winter (cold and dry): D+	-0.41	-0.62	0.21
Spring (hot and dry): G-	0.03	-0.09	0.16
Spring (hot and dry): D+	-0.56*	-0.71	-0.40
G-D-	-0.48*	-0.59	-0.37
G-D+	0.16*	0.01	0.32

G+D+	-0.11*	-0.24	-0.24
Winter (cold and dry)	-1.17*	-1.56	-0.79
Spring (hot and dry)	0.11	-0.26	0.49
Winter (cold and dry): G-D-	1.23*	1.04	1.42
Winter (cold and dry): G-D+	-0.27	-0.68	0.13
Winter (cold and dry): G+D+	0.28*	0.02	0.52
Spring (hot and dry): G-D-	0.03	-0.12	0.17
Spring (hot and dry): G-D+	-0.66*	-0.90	-0.41
Spring (hot and dry): G+D+	-0.51*	-0.71	-0.32
	Body size		
G-	-0.02	-0.77	1.42
D+	0.01	-0.68	0.70
Winter (cold and dry)	0.18	-0.49	0.85
Spring (hot and dry)	-0.47	-1.25	0.32
Winter (cold and dry): G-	-0.39	-1.28	0.49
Winter (cold and dry): D+	-0.55	-1.67	0.57
Spring (hot and dry): G-	0.003	-0.97	0.97
Spring (hot and dry): D+	-0.04	-1.16	1.08
G-D-	-0.05	-0.74	0.64
G-D+	0.02	-1.05	1.11
G+D+	-0.03	-0.95	0.87
Winter (cold and dry)	0.17	-0.53	0.88
Spring (hot and dry)	-0.48	-1.35	0.60
Winter (cold and dry): G-D-	-0.38	-1.35	0.06
Winter (cold and dry): G-D+	-0.94	-2.99	1.12
Winter (cold and dry): G+D+	-0.522*	-1.88	-0.84
Spring (hot and dry): G-D-	-0.03	-1.08	1.15
Spring (hot and dry): G-D+	-0.08	-1.86	1.69
Spring (hot and dry): G+D+	-0.017	-1.45	1.49

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table S4. Parameter name, estimate, lower and upper 95% confidence intervals of predictors in GLMM models for spider generic richness, activity and size. G+ = Grazing, G- = Grazing exclusion, D+ = Drought, D- = No Drought. Seasons, winter (cold and dry) and spring (hot and dry) are compared to summer (hot and wet). All categorical variables are compared to the control, Grazing (G+) and No Drought (D-).

	Seasonality		
Parameters	**Beta**	**Lower- 95**	**Upper- 95**
	Generic richness		
G-	-0.09	-0.49	0.29
D+	-0.06	-0.54	0.40
Winter (cold & dry)	-0.87 **	-1.53	-0.29
Spring (hot & dry)	-0.91 **	-1.45	-0.29
Winter (cold & dry): D+	0.32	-0.30	1.12
Spring (hot & dry): D+	0.13	-0.56	1.21
Winter (cold & dry): G-	0.40	-0.34	1.14
Spring (hot & dry): G-	0.23	-0.46	0.93
G-D-	-0.04	-0.47	0.39
G-D+	-0.33	-1.27	0.60
G+D+	0.028	-0.54	0.59
Spring (hot & dry)	-0.81 *	-1.43	-0.19
Winter (cold & dry)	-0.93 **	-1.61	-0.25
Spring (hot & dry): G-D-	-0.12	-0.67	0.92
Spring (hot & dry): G-D+	0.58	-0.75	1.92
Spring (hot & dry): G+D+	-0.06	-1.17	1.04
Winter (cold & dry): G-D-	0.41	-0.42	1.25
Winter (cold & dry): G-D+	0.71	-1.06	2.48
Winter (cold & dry): G+D+	0.34	-0.72	1.42
	Spider activity		
D+	-0.09	-0.5	0.32
G-	-0.11	-0.45	0.22
Spring (hot & dry)	-1.05 ***	-1.58	-0.52
Winter (cold & dry)	-0.93 ***	-1.47	-0.39
Spring (hot & dry): D+	0.21	-0.53	0.96
Winter (cold & dry): D+	0.42	-0.34	1.20
Spring (hot & dry): G-	-0.18	-0.45	0.83
Winter (cold & dry): G-	0.22	-0.44	0.88
G-D-	-0.04	-0.42	0.32
G-D+	-0.42	-1.28	0.42
G+D+	0.02	-0.46	0.51
Spring (hot & dry)	-0.97 **	-1.53	-0.40
Winter (cold & dry)	-0.98 **	-1.57	-0.38
Spring (hot & dry): G-D-	-0.44	-0.69	0.78

Spring (hot & dry): G-D+	0.68	-0.54	1.91
Spring (hot & dry): G+D+	0.04	-1.06	0.97
Winter (cold & dry): G-D-	0.29	-0.46	1.03
Winter (cold & dry): G-D+	0.47	-1.27	2.22
Winter (cold & dry): G+D+:	0.50	-0.41	1.41
	Body size		
G-	-0.91	-2.12	0.29
D+	-0.92	-2.36	0.51
Spring (hot & dry)	-0.7	-2.26	-0.81
Winter (cold & dry)	-1.38	-3.05	-0.28
Spring (hot & dry): G-	2.12	0.26	3.98
Winter (cold & dry): G-	1.94	-0.04	3.94
Spring (hot & dry): D+	0.80	-1.32	2.93
Winter (cold & dry): D+	0.42	-2.01	2.85
G-D-	-0.86	-2.17	0.44
G-D+	-1.96	-4.42	0.49
G+D+	-0.83	-2.56	0.89
Spring (hot & dry)	-0.04	-1.67	-1.59
Winter (cold & dry)	-1.59	-3.32	-0.14
Spring (hot & dry): G-D-	1.02	-1.07	3.11
Spring (hot & dry): G-D+	3.070	0.38	7.01
Spring (hot & dry): G+D+	-1.25	-4.08	1.56
Winter (cold & dry): G-D-	2.23	-2.68	4.38
Winter (cold & dry): G-D+	1.60	-1.94	5.89
Winter (cold & dry): G+D+	0.94	-1.94	3.83

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Appendix D:

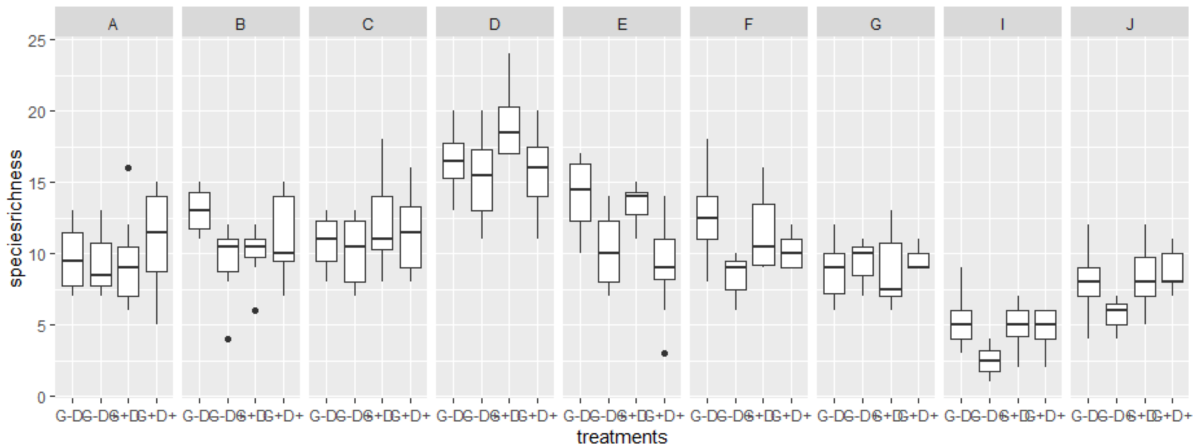

Figure S1. Boxplots for species richness observed under all the treatment and control plots over the four-year sampling period. Grazing and no drought (G^+ x D^-), no grazing and drought (G^- x D^+), no drought and no grazing (G^- x D^-) and grazing and drought (G^+ x D^+).

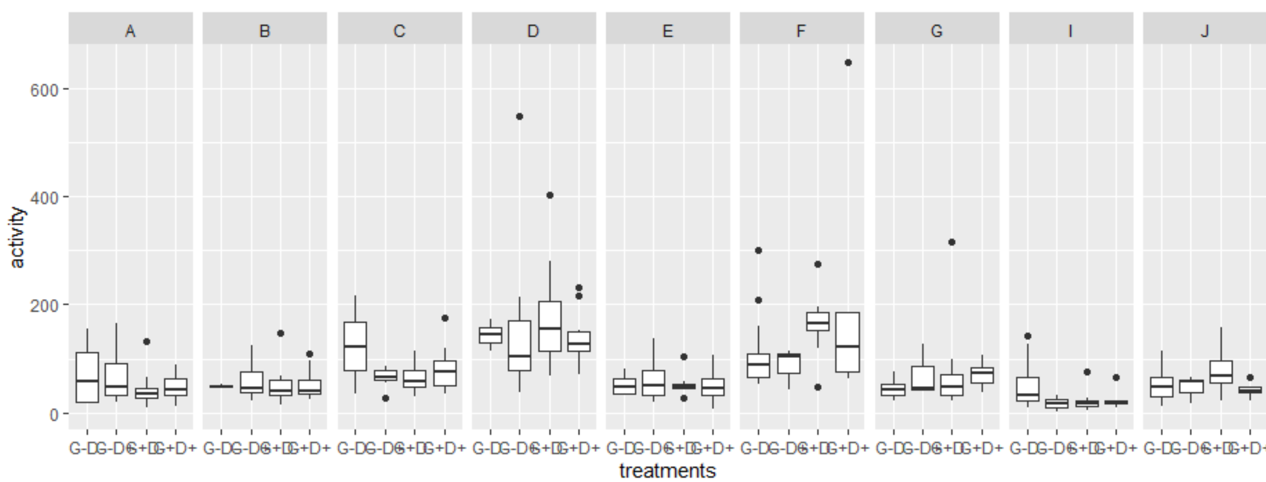

Figure S2. Boxplots for species activity observed under all the treatment and control plots over the four-year sampling period. Grazing and no drought (G^+ x D^-), no grazing and drought (G^- x D^+), no drought and no grazing (G^- x D^-) and grazing and drought (G^+ x D^+).

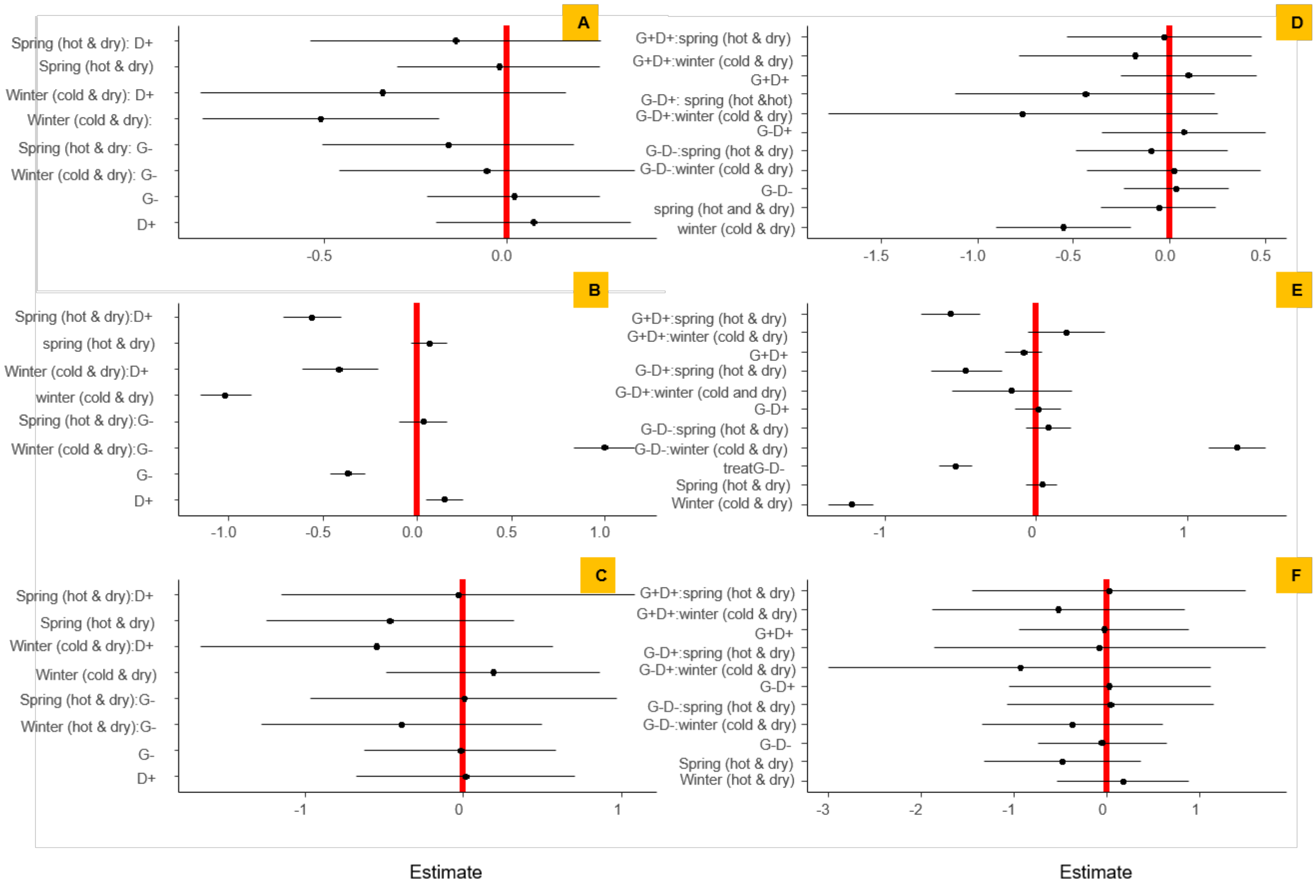

Figure S3. Parameter estimates and plots of predictors for GLMM models of ant activity, richness, Weber's length and functional diversity G^+ = grazing, G^- = grazing exclusion, D^+ = drought, D^- = no drought. All categorical variables are compared to the control, Grazing (G^+) and no drought (D^-). A) ant activity, B) species richness, and C) body size, in different treatments (G^+, G^-, D^-, D^+), and D) ant activity, E) species richness, F) body size (G^- x D^+, G^+ x D^-, G^- x D^-, G^+ x D^+).

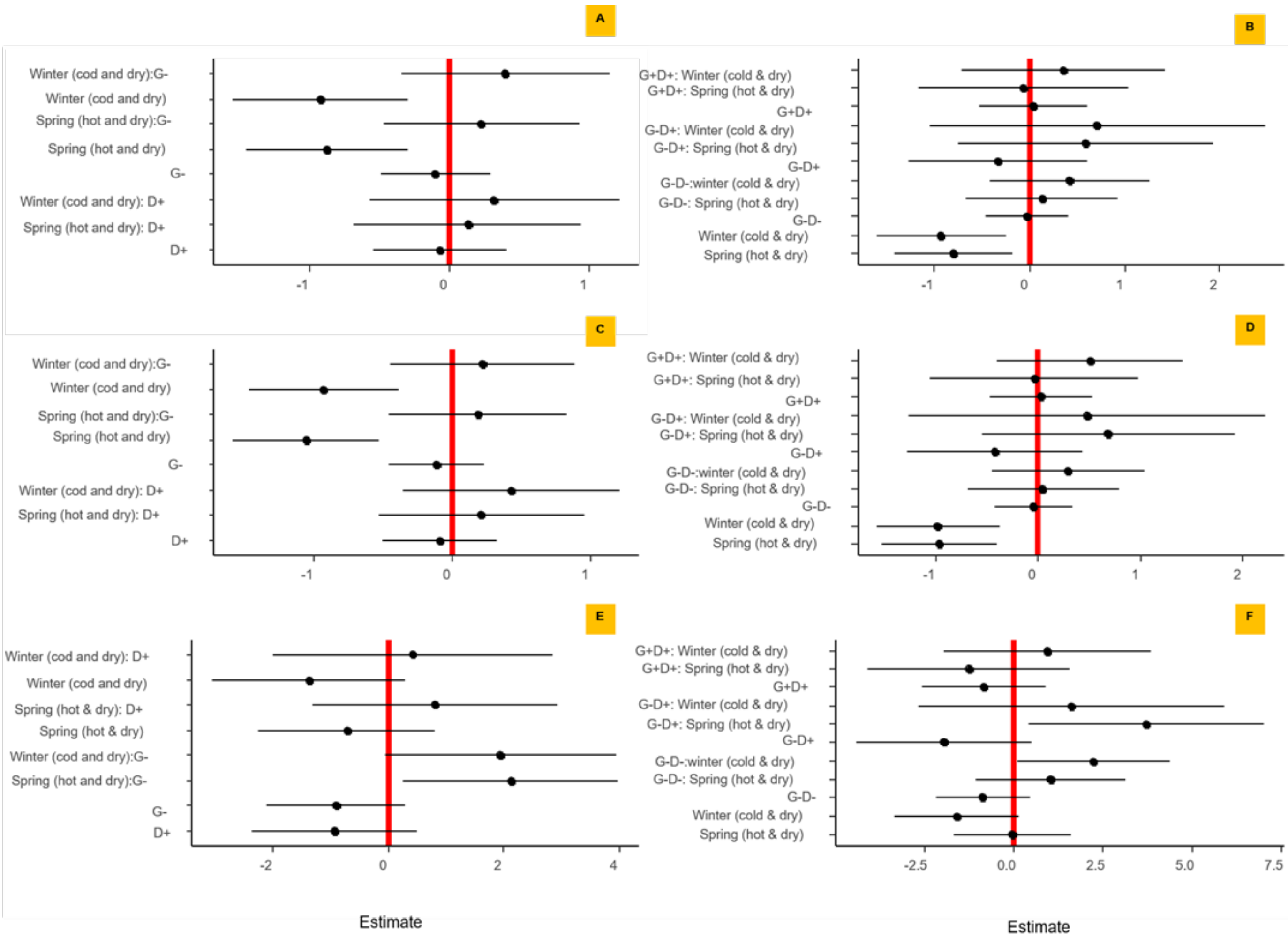

Figure S4. Parameter estimates and plots of predictors for GLMM models of spider generic richness, activity, and body size G^{+} = grazing, G^{-} = grazing exclusion, D^{+} = drought, D^{-} = no drought. All categorical variables are compared to the control, Grazing (G^{+}) and No Drought (D^{-}). A), B) generic richness, and C), D), activity and E), F) body size.