Global change drivers and their impact on herbaceous, ant, and grasshopper assemblages in an African semi-arid savanna

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January 2020

Thesis Presented for the Degree of

DOCTOR OF PHILOSOPHY

In the Department of Biological Sciences

UNIVERSITY OF CAPE TOWN

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Abstract

Assessments of the anthropogenic threats to savanna ecosystems are primarily focussed on land use change, bush encroachment, and biological invasions. There is, however, very little understanding as to the threats from atmospheric pollution. South Africa is the major emitter of CO_2 on the African content while the Mpumalanga region bordering the Kruger National Park (KNP) is among the leading regions for nitrous oxide pollution in the world. It is not only increasing atmospheric pollution, but rainfall intensity is also predicted to increase for southern Africa. As savannas are nutrient limited, an increase in nitrogen deposition will have major consequences for vegetation structure and this can only be exacerbated by increased rainfall amounts. Current research suggests that these predicted increases in water and nutrients will result in increasing grass biomass and decreasing herbaceous species richness. The effects of global change drivers on savanna vegetation are also likely to propagate through to multiple trophic levels, with changes in vegetation structure cascading down to invertebrate assemblages. As invertebrates are ubiquitous, form the bulk of metazoan species diversity and biomass on earth, and play a pivotal role in many ecosystems, I discuss in the introductory chapter of this thesis why the influence of global change on these assemblages should not be ignored.

In my first data chapter, Chapter 2, I examine the effect that increases in available nutrients and water may have on vegetation structure, and how this may cascade down to grasshopper and ant assemblages. I do this using a fully factorial experiment in KNP with nutrient and water additions where I assessed both herbaceous (forb and grass) and insect (ant and grasshopper) assemblages five years after resource additions began. My results show that there was a substantial increase in grass biomass while plant and insect species richness declined with water addition alone and that a combination of nutrients and water resulted in the greatest increases in grass biomass and concomitant decreases in plant and insect species richness. The effects of nutrient and water additions on the insect community assembly was primarily driven by a decrease in grasshopper species and ant abundance respectively. An analysis of ant functional traits showed that the rare ant species mediated the impact of the resource additions on the ant assemblage.

Fire is inherent to savanna systems with profound effects on vegetation structure. There has, however, been relatively little research on the effects of fire on savanna invertebrate fauna. In Chapter 3 I look at the effect that fire may have on the vegetation and insect community assembly at my study site between five and eight months after the site had been burned. These results show an increase in grass biomass and decrease in plant and insect species richness with a combination of nutrients and water. My results also show that grasshopper biomass, abundance, and species richness decreased as herbaceous biomass decreased. While ant species richness decreased, ant abundance increased post-fire, primarily related to an increase in patches of bare ground.

With global change, drought frequency is also expected to increase. The insect and grass assemblages, both on and off *Macrotermes* mounds, at two sites in the southern section of KNP had been sampled in a separate study in 2012. In Chapter 4 I describe a study where I resampled these mounds during the peak of the most severe drought in 30 years. The two sites differed in drought severity, one where the drought severity was very high and the other where severity was much lower. The objective was to determine the effects that drought may have on the grass and associated insect assemblages both on and off termite mounds. My results show that at the high severity site grass cover and biomass and grasshopper abundance decreased both on and off mounds. The overall reduction in habitat structure resulted in an increase in both ant abundance and species richness but the mound and matrix ant assemblages diverged during drought. Where the drought was less severe there was an increase in large mammal herbivores as animals moved out of the more affected areas. This increase in mammal herbivory was more evident on rather than off mounds resulting in grass biomass being lower on rather than off mounds. The cascading effect saw grasshopper abundance decrease on and increase off mounds. The mound and matrix ant assemblages did not respond to the comparatively smaller change in habitat structure.

Finally, in the synthesis chapter I discuss my results in the broader context of how global change drivers such as increased nitrogen deposition may cascade down from plant to insect community assembly. At present there is very little understanding of the amounts of nitrogen being deposited in KNP or the effect that this may have. The results of my study would suggest that this increase in nitrogen deposition will have major consequences for vegetation structure and that this will cascade down to the insect assemblage. In mitigating for this, it is therefore essential that management in KNP adapt a monitoring protocol for nitrogen deposition, especially when considering that where N deposition is really high fire may not volatilise everything to allow the system to reset itself back to its original state. It is not only nitrogen deposition, but drought frequency is also likely to increase. In mitigation for this there should also be monitoring programmes to consider the effects of drought as animals may move from areas of high drought severity to areas where severity is lower. Such movement will increase grazing pressure on both low and high nutrient environments with cascading effects on vegetation structure and insect assemblages.

Acknowledgements

First and foremost, I would like to thank my supervisors Ed February, Kate Parr, and Mike Picker. I could not have asked for a better supervisory team. You showed your commitment and dedication to my research from the outset when all of you converged on Satara for my first season of data collection. Ed, I walked into your lab in 2013 and expressed my desire to further my scientific training. Your positive response to my request meant more to me than I will ever be able to verbalise. You allowed me to follow my own research direction, only questioning and guiding me when I was tempted to stray down the wrong path. Kate, you have motivated me to work harder and think deeper about my work. The opportunity to visit your lab in Liverpool and attend the Ant Course will be fondly remembered. I will always thank you for introducing me to the world of funky ants. Mike, your love for and knowledge of the insect world is incredible and infectious. Working in the field with you was awesome, every insect would have its own story told. I must thank you all for your patience and for your endless support. Thank you for your contributions to my thesis and for enriching my life.

I would like to acknowledge Lars Hedin, Leigh-Ann Woolley, and Navashni Govender. My PhD was made possible by your complete dedication to the Satara study site. Thank you for initiating and managing the experiment and allowing me to join in. Thank you for the data collection, data sharing, countless discussions, and valuable guidance. I would also like to thank Faith Jumbi for all the time and effort she put in at the study site. Lastly, my time at Satara would not have been the same without the extended family of Ryan, Drew, Zoe, Jo, and Jason. You made the fieldtrips beyond enjoyable. Because of you, Satara always felt like home. A particular highlight was playing for the Satara Black XI with Jason. Thanks must also go to Andrew Davies and Monica Leitner. Your work on the termite mounds of Kruger in 2012 made it possible for me to take advantage of the 2014-16 drought. Your willingness to share ideas and data and your comments on the termite chapter improved my understanding and my PhD.

I have developed a deep love for Kruger. A big thank you to South African National Parks for allowing me to work in Kruger. To Patricia Khoza, Samantha Mabuza, Tercia Strydom, and Judith Botha, thank you for dealing with all my requests and making my fieldtrips substantially easier. Furthermore, my data collection would not have been possible without the help of Happy Mangena, Khensani Mkonto, Velly Ndlovu, Renson Thethe, and Thomas Rikombe. Thank you for all the laughs and keeping me safe.

Julia, you are my best friend and have been with me throughout this journey. From undergraduate lectures and camps, to travelling with me in Kruger and beyond- I have loved every minute of our time together. Thank you for putting up with me. The value of your love, support, and guidance, especially over the final months, cannot be overstated. I look forward to many more wild adventures and endless laughs whilst we explore this pale blue dot!

Lastly, I feel very lucky to have the family that I do. From a young age we were encouraged to get outside and explore and the impossible was made possible. Thank you for believing in me, for encouraging me, and for giving me the confidence to reach for my dreams and not give up. Your support has meant the world to me! If not for you, I would never have had the opportunities I have been given. My love for you is unwavering and unconditional.

In addition to funding from the University of Cape Town, funding was provided by the National Research Foundation.

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Abbreviations Used

ANCOVA – Analysis of covariance

ANOSIM – Analysis of similarity

ANOVA – Analysis of variance

CAP – Canonical analysis of principal coordinates

CWM – Community-weighted mean

C:N – Carbon:nitrogen ratio

GCD – Global change driver

GLM – Generalised linear model

KNP – Kruger National Park

N – Nitrogen

nMDS – Nonmetric multidimensional scaling

P – Phosphorous

PERMANOVA – Permutational multivariate analysis of variance

PROTEST – Procrustean randomization test

SANParks – South African National Parks

SIMPER – Similarity percentage

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centroids are shown. Percentage values indicate the percentage of variation explained by each axis.

Figure 4.4: Mean of mounds and matrix plots ± standard error for grass (a) percentage cover and (b) standing biomass, (c) grasshopper abundance, and (d) ant abundance and (e) ant species richness on and off *Macrotermes* mounds before (2012) and during drought (2016) at Pretoriuskop. Letters indicate significant differences between sampling years, while asterisks denote significant differences between treatments (mound vs savanna matrix).

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Chapter 1: General introduction

1 | Savannas

Savannas are globally distributed dynamic systems, defined as a continuous layer of C_4 grass with a discontinuous cover of trees (Frost et al. 1986, Lehmann et al. 2011). Roughly eight million years ago C_4 grass species expanded into previously wooded ecosystems and currently dominate more than half of the ~25% of the land surface covered by grassy systems globally (Edwards et al. 2010, Keeley and Rundel 2005, Ramankutty and Foley 1999, Archibald et al. 2020). The C_4 expansion into dry environments was associated with increased aridity and expansion into wetter environments was associated with increased fire and rainfall seasonality (Keeley and Rundel 2005, Osborne and Beerling 2006). Determinants of savannas vary but these systems generally occur where growing season temperatures are above 10°C with intermediate rainfall (Cole 1963, Osborne and Beerling 2006, Sarmiento 1984, Scholes and Archer 1997).

It is now generally well understood that the primary drivers for savanna vegetation structure are a complex interaction between the bottom-up and top-down controls soil nutrients, water, herbivory, and fire (Frost et al. 1986, Weltzin and Coughenour 1990, Staver et al. 2009). The long-term future of these ecosystems is of global relevance and within Africa they form the centre of the African livestock and wildlife conservation industry and are of enormous socio-ecological importance (Scholes and Walker 2004). Savannas arose after the continents separated which has resulted in savannas being structurally similar globally but floristically distinct on different continents (Lehmann et al. 2014). These floristic differences are concerning given that floristically different savannas may respond differently to global change, highlighting the need for a deeper understanding of these systems (Lehmann et al. 2014, Moncrieff et al. 2016).

2 | Threats to savanna biodiversity

Changes in land use, climate, nitrogen (N) deposition, invasive species, and increasing atmospheric carbon dioxide concentrations are human-mediated global change drivers (GCDs) threatening biodiversity and ecosystem functioning at both local and global scales (Sala et al. 2000, Loreau et al. 2001, Thomas et al. 2004, Thuiller et al. 2011). In 2004, 65% of the savanna ecosystem types in South Africa were poorly protected or not protected at all (Driver et al.

2004). By 2018, the protected status of savanna ecosystem types had improved but only marginally as about 50% are still poorly protected or not protected at all (Skowno et al. 2019). South Africa's largest National Parks are located in the savanna biome and despite this the highest concentration of threatened mammals and birds occur in this biome (Skowno et al. 2019). There is, therefore, a pressing need to conserve South Africa's savanna biome. Assessments of the anthropogenic threats to South Africa's terrestrial ecosystems, and the savanna in particular, are however primarily focussed on land use change and pressures such as bush encroachment, overgrazing, and biological invasions, with very little understanding as to the threats from atmospheric pollution (Bobbink et al. 2010, Skowno et al. 2019).

South Africa is a major regional source of anthropogenic atmospheric pollutants with a nitrogen dioxide hotspot bordering the Kruger National Park (KNP), South Africa's largest conservation area, in the Mpumalanga Highveld (Lourens et al. 2012, Conradie et al. 2016). Current estimates of combined wet and dry N deposition in KNP resulting from these pollutants vary between 3.1 and 6.1 kg.ha^{-1}.yr^{-1} (Conradie et al. 2016). While there is still very little understanding as to the effects of N deposition on savanna vegetation structure, N deposition of 5 kg.ha^{-1}.yr^{-1} has changed plant species composition in temperate Europe and North America (Bobbink et al. 2010). Models predict N deposition of 13 kg.ha^{-1}.yr^{-1} by 2050 in east Africa and an increase in mean annual precipitation with more intense wet seasons (Phoenix et al. 2006, Shongwe et al. 2011). In southern African savannas the predictions are for an increase in precipitation intensity with no change in mean annual precipitation (Easterling et al. 2000, Frich et al. 2002, Pohl et al. 2017).

Globally savannas are nutrient limited with the vegetation adapted to these low nutrient conditions suggesting an increase in N will have major consequences for vegetation structure (February et al. 2020). It has been suggested that with an increase in rainfall intensity trees rather than grasses may benefit from deeper infiltration of water, changing the vegetation structure dramatically (Kulmatiski and Beard 2013b). It has, however, also been demonstrated that grasses are formidable competitors for resources and that an increase in available resources may instead benefit grasses rather than trees (Bond 2008, February et al. 2013). Experimental additions of N in South African mesic grassland have been shown to increase above-ground net primary production and decrease both grass and forb richness, thereby changing the herbaceous assemblage (Fynn and O'Connor 2005). Furthermore, a global analysis of N addition experiments in grass dominated systems across a substantial rainfall gradient showed a similar pattern of increasing above-ground net primary production and decreasing herbaceous species richness (Grace et al. 2016). An understanding of vegetation responses to elevated N deposition and water availability is, therefore, of pivotal importance for the future management of savannas.

3 | Fire in savanna

There are not only bottom-up consequences for an increase in atmospheric pollution. Changes in vegetation structure resulting from increased nutrient deposition may result in changes to the fire regime. The very strong seasonality of the rainfall in savanna means that many of the trees are deciduous while the grasses cure during the dry season (Higgins et al. 2011). Grass productivity, through rainfall amount, largely determines fire characteristics in savanna systems (O'Connor et al. 2001, Bai et al. 2008). In mesic savanna, grass biomass will increase proportionally to rainfall amount for the first four to five years after fire (Govender et al. 2006). Once cured, it is this dry grass that provides the fuel for the regular fires inherent to the system (Trollope 1984, Stott 2000). Mesic savannas typically burn at annual or 2-year intervals, while xeric savannas burn every 3–10 years (Hempson et al. 2020). It is uncertain, however, how human-mediated impacts on atmospheric properties, global climate, and vegetation distributions can alter fire regimes (Cochrane and Barber 2009, Bowman et al. 2011).

One possibility is that; as grasses are extremely competitive for soil resources an increase in available N derived from an increase in N deposition will result in an increase in grass biomass (Fynn and O'Connor 2005, February et al. 2013). This increase in grass biomass may result in an increase in fuel loads with more intense and frequent fires (Higgins et al. 2000, Higgins et al. 2007, Simpson et al. 2016, Wragg et al. 2018). Alternatively, fire may be used as a management tool to maintain the savanna in the face of growing anthropogenic pressures. For example, increasing atmospheric carbon dioxide concentrations and resultant woody plant encroachment may be mitigated by altering fire regimes (Smit et al. 2016). There is a real need to understand the relationship between increased N deposition, vegetation responses and the effects that his may have on the fire regime.

4 | Ants and grasshoppers

The effects of GCDs on vegetation structure are likely to propagate through to multiple trophic levels. Despite very clear trophic links, roughly 85% of studies examining the effects of climate change between 1980 and 2012 focused on plant responses alone (Jamieson et al. 2012). As invertebrates are ubiquitous, form the bulk of metazoan species diversity and biomass on earth, and play a pivotal role in many ecosystems (Andersen and Lonsdale 1990, Hölldobler and Wilson 1990, Wilson and Hölldobler 2005), they cannot be ignored when addressing effects of GCDs (Underwood and Fisher 2006, Parr et al. 2012, van der Plas and Olff 2014). Plant-insect interactions are notoriously complex (Price et al. 1980), but changes in vegetation structure have been shown to cascade down to influence savanna insect community assembly (Parr et al. 2012, van der Plas and Olff 2014, Andersen 2019).

In grass-dominated ecosystems, grasshoppers are the most abundant herbivore and substantial consumers of biomass (Gibson 2009). In South African savannas grasshoppers can account for 93% of phytophagous insects with an average biomass of 2.28 kg.ha^{-1} (Gandar 1982b). Grasshopper biomass peaks in the wet season and decreases by roughly 50% in the dry season. Estimates for grasshopper consumption indicate that a grasshopper biomass of 0.73 kg.ha^{-1} can consume 94 kg.ha^{-1} of plant material per year with a further 36 kg.ha^{-1} wasted during feeding (Gandar 1982b). Grass can account for 92% of the consumed material and grasshoppers can remove as much as 24% of the annual grass production (Gandar 1983). It has been demonstrated that in the Serengeti grasshopper consumption can be up to 456 kg.ha^{-1} per year (Sinclair 1975). Grasshopper assemblages are primarily controlled by vegetation structure rather than predation (Brock et al. 1992, Joern 1992, Andersen et al. 2001), with these assemblages likely to be directly influenced by GCDs. While the influence of vegetation structure on grasshopper assemblages cannot be overemphasised, N content and protein-carbohydrate ratios of plants are important for determining grasshopper diets (Simpson and Raubenheimer 1993, Behmer 2009). The effects of GCDs such as increases in N deposition and rainfall amount on grass biomass and nutrient content and how this may affect grasshopper community assembly have, as yet, not been quantified.

Changes in grass biomass resulting from global change drivers may affect more than one invertebrate assemblage. Ants are important for many ecosystem functions and they perform a number of roles as tenders of aphids, seed harvesters, omnivores, and predators (Hölldobler and Wilson 1990, Lach et al. 2010). The ants in African savanna systems can constitute between 53% and 70% of all ground-active macroinvertebrate individuals (Parr et al. 2016). In savannas, ants are important ecosystem engineers, suppressing the abundance and activity of termites, millipedes, and beetles and influencing levels of herbivory and decomposition rates (Parr et al. 2016). Changes to the structural complexity of the vegetation resulting from GCDs may influence ant assemblages, as complex habitats benefit smaller ant species filtering out larger bodied species (Farji-Brener et al. 2004, Parr et al. 2012, Gibb and Parr 2013). It is, therefore, important to understand the relationship between vegetation structural complexity and how this may influence ant assemblages.

As fire is inherent to savannas, resident fauna should be either fire-dependent or fire-adapted. There has, however, been very little research on the effects of fire on savanna invertebrate fauna (Parr and Chown 2003, Pausas and Parr 2018). What little research there has been is not conclusive, with results showing that after fire, insect populations may decrease, match the control, or become more abundant (Swengel 2001). The literature regarding grasshoppers specifically in relation to biomass, species richness, and total abundance after fire is likewise contradictory with these results changing with fire frequency (Gandar 1982a, Swengel 2001). Fire effects on ants are typically indirect through its effects on habitat structure, with habitat openness being a key driver of variation in ant assemblages (Andersen 2019). In savannas, ant assemblages have been shown to be highly resistant and resilient to fire, with comparisons made between burned and unburned or between frequently and infrequently burned areas (Izhaki et al. 2003, Parr et al. 2004, Andersen et al. 2014). What remains unexplored is the response of invertebrates to fire with multiple GCD drivers.

5 | Drought

The warming of the Pacific Ocean associated with the El Niño Southern Oscillation is often concomitant with drought in the tropics. These El Niño associated droughts are predicted to increase in frequency and severity (Fauchereau et al. 2003, Dai 2013, Cai et al. 2014). Drought can alter ecosystem functioning (Breshears et al. 2005), by changing vegetation structure and/or plant and animal community assembly. It is, therefore, pertinent to develop an understanding as to how resistant and resilient savanna assemblages are to drought.

Mounds of the termite *Macrotermes* are common features in the savannas of Africa, Australasia, and South America. In African savannas, termite biomass is comparable to that of all ungulates and mega herbivores, and because of competition for resources between colonies, mounds are often spatially over-dispersed (Dangerfield et al. 1998, Korb and Linsenmair 2001, Levick et al. 2010a, Davies et al. 2014a). Both the vegetation and insect assemblages associated with these mounds are distinct relative to that of the surrounding matrix primarily through an increase in available water and nutrients (Davies et al. 2014b, Leitner et al. in revision). As a result, several studies have demonstrated preferential foraging of mound vegetation by both mammal and invertebrate herbivores (Mobæk et al. 2005, Grant and Scholes 2006, Levick et al. 2010b, Davies et al. 2016). There is, however, little empirical evidence of the influence of drought on termite mound vegetation and associated insect assemblages.

6 | Global change: Kruger National Park

My study site is the 19 485 km² Kruger National Park located in the north east of South Africa bordering on Zimbabwe to the north and Mozambique to the east. There is, however, a massive urban population of several million people to the west (Fig. 1.1). The conservation challenges posed by the location of its parks has led to South African National Parks (SANParks) mission statement: "*To develop, expand, manage and promote a system of sustainable national parks that represents biodiversity and heritage assets, through innovation and best practice for the just and equitable benefit of current and future generations.*" SANParks are unlikely to fulfil this mission statement without an understanding of the effects that anthropogenic change may have on vegetation structure as it interacts with fire and cascades down to insect assemblages.

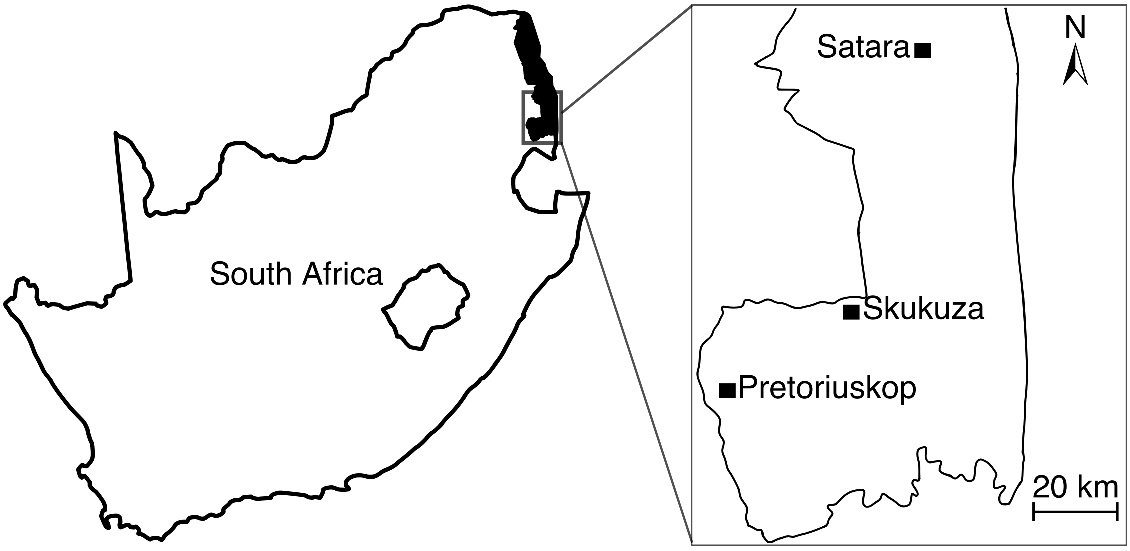

Figure 1.1: Map showing location of Kruger National Park within South Africa. Locations of the three study areas are shown as solid squares: Pretoriuskop, Satara, and Skukuza.

Between 2003 and 2013, 1027 research publications emanated from South Africa's national parks, but less than 1% of all these publications engaged with global change (van Wilgen et al. 2016). In 2016 SANParks released their Global Environmental Change Assessment, an assessment on the state of South Africa's national parks based on the impacts of six GCDs that affect all of the parks (van Wilgen and Herbst 2017). Although useful, this assessment failed to mention N deposition or the potential for increased severe droughts in savanna systems. Considering the commercial and conservation value of African savannas, and KNP in particular, it seems pertinent to develop an understanding of how savanna will respond to these drivers. Considering the recorded levels of N deposition, predicted changes in water availability, and the increasing frequency and severity of drought in southern African savannas, and KNP specifically, it is essential to understand the potential effect of these drivers to better inform current and future conservation effort. In this thesis I explore the relationship between GCDs, vegetation structure and community assembly, and grasshopper and ant community assembly. I examine how these relationships may respond to both fire and drought.

7 | Thesis structure

I explore the abovementioned relationships between GCDs, vegetation, insects, fire, and drought in three chapters after this introductory chapter (Chapter 1). The first of these (Chapter 2) investigates the effects of increased water and nutrient availability on savanna herbaceous vegetation structure, and the cascading effects that this may have on grasshopper and ant community assembly. To do this, both available water and nutrients were experimentally manipulated in the field and the responses of both herbaceous and insect assemblages determined. In the following chapter (Chapter 3), I use a taxonomic approach to evaluate the grass, ant, and grasshopper diversity and biomass responses to fire. Here, each individual plot was burned five years after the initiation of the experiment, with nutrient and water treatments continuing for five to eight months before the grass and insect assemblages were resampled. In Chapter 4 I compare vegetation and associated insect community assembly and biomass on termite mounds relative to the surrounding savanna matrix in the middle of an El Niño induced drought. For this, I compared grass cover and standing biomass, with insect abundance, species richness, and assemblages both on and off *Macrotermes* mounds at two different vegetation types within KNP that also differed in drought severity. I conclude with a Synthesis chapter (Chapter 5).

Chapter 2: **Plant and insect assemblage responses to global change drivers**

1 | INTRODUCTION

Biodiversity loss resulting from human-mediated global change is occurring at both local and global scales (Sala et al. 2000, Thomas et al. 2004, Thuiller et al. 2011). Understanding the contribution of global change drivers (GCDs) to biodiversity loss is, however, complicated by two factors: firstly, there are multiple GCDs (Sala et al. 2000) and secondly, species are connected across multiple trophic levels (Dunne et al. 2002). Changes in land use, climate (temperature and rainfall patterns), nitrogen deposition, and increasing atmospheric carbon dioxide concentrations are human-mediated GCDs threatening biodiversity and ecosystem functioning (Sala et al. 2000, Loreau et al. 2001). The savanna biome in Africa is under significant threat from GCDs, with predicted changes in rainfall, N deposition, and atmospheric carbon dioxide concentrations (Midgley and Bond 2015, Conradie et al. 2016, Pohl et al. 2017). Woody plant encroachment has been documented across continents (Archer 1989, Wigley et al. 2010, O'Connor et al. 2014, Nackley et al. 2017), with several studies implicating increased levels of CO_2 as a major driver (Polley et al. 1997, Bond and Midgley 2000, Leakey et al. 2009, Buitenwerf et al. 2012).

As savannas are nitrogen (N) and phosphorous (P) co-limited, and savanna trees withdraw nutrients before leaf fall and sequester nutrients in woody stems, it is expected that nutrient pools will decrease with woody plant encroachment (Craine et al. 2008, Higgins et al. 2015). This dynamic might change when either water or N is added, as N uptake is determined by water availability (Cramer et al. 2009, Matimati et al. 2014). The loss of soil nutrients to woody plants during bush encroachment might be mitigated by N deposition resulting from air pollution (Binkley and Högberg 1997, 2016). South Africa is a major regional source of anthropogenic atmospheric pollutants with a nitrogen dioxide hotspot over the Mpumalanga Highveld, a region that borders one of South Africa’s premier savanna parks, Kruger National Park (KNP) (Lourens et al. 2012, Conradie et al. 2016). Current estimates of combined wet and dry N deposition in KNP vary between 3.1 and 6.1 $kg.ha^{-1}.yr^{-1}$ (Conradie et al. 2016). Models also predict N deposition of 13 $kg.ha^{-1}.yr^{-1}$ by 2050 in east Africa (Phoenix et al. 2006). Additions of N in South African mesic grassland have been shown to increase above-ground net primary production and a decrease in both grass and forb richness, thereby changing the herbaceous assemblage (Fynn and O'Connor 2005). The effects of N deposition on tropical and sub-tropical African ecosystems are, however, unknown relative to Europe or North America where N deposition of 5 $kg.ha^{-1}.yr^{-1}$ has been shown to result in changes of plant species community assembly (Bobbink et al. 2010).

Global circulation models for southern African savannas predict an increase in precipitation intensity while mean annual precipitation will remain unchanged (Easterling et al. 2000, Frich et al. 2002, Pohl et al. 2017). In the context of KNP, increases in precipitation intensity may increase soil water availability and infiltration (Kulmatiski and Beard 2013b). Global circulation models for east Africa, however, predict an increase in mean annual precipitation with more intense wet seasons (Shongwe et al. 2011). As nutrients and water, along with fire and herbivory, are considered important drivers of savanna vegetation structure and community assembly, and water availability alters ecosystem responses to N addition (Frost et al. 1986, Greaver et al. 2016), it is not clear how savanna grasses and trees will respond to change in available nutrients and water. It has been suggested that trees rather than grasses may benefit from deeper infiltration of water (Kulmatiski and Beard 2013b). It has, however, also been demonstrated that grasses are formidable competitors for resources and that an increase in available resources may benefit grasses rather than trees (Bond 2008, February et al. 2013). An understanding of vegetation responses to elevated N deposition and water availability is therefore of pivotal importance for the management of savannas affected by GCDs.

The effects of GCDs on vegetation are likely to propagate through to multiple trophic levels. Plant-insect interactions are notoriously complex (Price et al. 1980), but changes in vegetation structure have been shown to influence community assembly, body size and trophic structure of savanna insect assemblages (Parr et al. 2012, van der Plas and Olff 2014). Shifts from savanna to alternative stable states, such as thicket or forest, result in changes in the diversity and functional composition of both vegetation and insect assemblages (Parr et al. 2012). When considering the effect of N additions on grassland vegetation and insect assemblages, it has been demonstrated that plant biomass increases whilst plant species richness decreases with a concomitant increase in insect population sizes but decrease in insect species richness (Haddad et al. 2000). Several studies have shown that N addition results in an increase in both plant tissue N and seed production as fertilised plants are able to support larger insect populations (e.g. Strauss 1987, Andow 1991, Siemann et al. 1998). Despite these clear trophic links, roughly 85% of studies examining the effects of climate change between 1980 and 2012 focused on plant responses alone (Jamieson et al. 2012). There is, therefore, a growing need to determine how multiple GCDs such as changes in rainfall and N deposition may interact to affect both the vegetation and animal assemblages (Tylianakis et al. 2008).

Community assembly, from regional to local species pools, occurs as a sequence of filters that restrict community membership either through habitat filtering or competition for resources (Diamond 1975, Weiher and Keddy 1995). Community assembly is also concurrently influenced by deterministic and stochastic factors (Dumbrell et al. 2009, Ofiţeru et al. 2010, Langenheder and Székely 2011). The effect of GCDs on ecosystems is stochastic as these are largely unpredictable, however, the effect of added N and water in a savanna may become deterministic if grasses benefit by taking up the nutrients and available water before trees do. The resultant changes to the herbaceous layer will likely affect the insect assemblage through both habitat filtering and competition for resources, selection forces that are both deterministic. In this chapter, my focus is on responses of grasshoppers and ants because savanna ants have a high diversity and biomass, while grasshoppers are substantial consumers of primary productivity (Sinclair 1975, Gandar 1982b, Lach et al. 2010). N content and protein-carbohydrate ratios of plants are pivotal in determining grasshopper diets (Simpson and Raubenheimer 1993, Behmer 2009), while the structural complexity of the vegetation may influence ant body size distributions as complex habitats benefit smaller ant species and tend to filter out larger bodied ones (Farji-Brener et al. 2004, Gibb and Parr 2013).

As discussed above, model predictions are for an increase in N deposition and rainfall intensity in southern African savannas. Here, I investigate the potential effects that such an increase in available water and nutrients may have on the herbaceous vegetation structure. I also determine how this may cascade down to grasshopper and ant assemblages. To do this, I make use of an experiment where both rainfall and nutrients were experimentally manipulated in the field. The field experiment was originally conceived to determine the relative importance of different limiting factors (N, P, and rainfall) on the ecosystem. For the nutrient and rainfall additions to show an ecosystem response in the short duration of the study it was deemed necessary for the applications to be far greater than the predicted inputs. The results presented, however, provide solid evidence on how savanna vegetation and insects may change as a result of changes (that may or may not occur) in nutrient and water inputs. These nutrient additions included both N and P as these are purported to be co-limiting in savanna (Craine et al. 2008). The increase in available water is important, because with transpiration, nutrients are taken up through mass flow (Cramer et al. 2009, February et al. 2013). A taxonomic approach was used to evaluate the vegetation and grasshopper assemblages and a combined taxonomic and functional trait approach to evaluate ant assemblage responses. I do this because a trait-based approach allows for a more quantitative and predictive science when addressing assemblage responses to GCDs (McGill et al. 2006).

There are five major predictions for both vegetation and insect responses to additions of nutrients and water in this study: (1) Grass biomass will increase (Fynn and O'Connor 2005, Bond 2008, Craine et al. 2008, February et al. 2013), and the herbaceous community assembly will alter with reduced grass and forb species richness. (2) Competitively superior grasses will outcompete forbs, such that the herbaceous assemblage becomes dominated by grasses rather than forbs (Bond 2008, February et al. 2013). (3) Grass foliar C:N ratios will decrease and grass seed production will increase (Strauss 1987). (4) Grasshopper species richness will decline as plant species richness declines with increased grass biomass. Alternatively, as plants with high foliar N content are generally preferred food of herbivorous insects and foliar N can increase after fertilisation (Behmer 2009, Phoenix et al. 2012), grasshopper population size will increase as grass biomass increases with increased available nutrients and water (Haddad et al. 2000). (5) With increasing grass biomass and decreasing bare ground, ant assemblages will be dominated by species with shorter legs and smaller body sizes as complex habitats may benefit smaller ants whilst negatively affecting larger bodied ants (Farji-Brener et al. 2004, Sarty et al. 2006, Gibb and Parr 2013).

2 | METHODS

2.1 Study site

The study site is in a semi-arid savanna approximately 10 km north west of the Satara Rest Camp in the central region of Kruger National Park, South Africa (-24.360676, 31.694549). Rainfall for the region is distinctly seasonal resulting in a growing season from October to April. Average summer rainfall at the study site for the five growing seasons of the experiment from 2009/10 to 2013/14 was 534 mm, which is very close to the previous 30 year mean of 518 mm (South African Weather Services). Mean monthly maximum and minimum temperatures for the region are 29.8° C and 16° C respectively. The soil is formed from sedimentary Karoo sequence ecca group sandstones and shales (Venter et al. 2003). Dominant trees are *Senegalia nigrescens* Oliv and *Sclerocarya birrea* (A. Rich) Hochst dominated and dominant grasses are *Bothriochloa radicans* (Lehm) A. Camus, *Digitaria eriantha* Steud, *Panicum coloratum* L., *Urochloa mosambicensis* (Hack) Dandy, and *Themeda triandra* Forssk (Gertenbach 1983, Knapp et al. 2012, van Oudtshoorn 2012).

2.2 Study design

At the study site, rainfall, and nutrients were manipulated in sixteen 30 m diameter circular plots (707 m^2) spaced ± 10 m apart (Fig. 2.1). Treatments were randomly allocated to plots, whilst ensuring that treatment replicates were not neighbours. Two plots were fertilised with N (~12 $g.m^{-2}.yr^{-1}$ as limestone ammonium nitrate (LAN 14 %)), two with P (~5 $g.m^{-2}.yr^{-1}$ as superphosphate), and two with both N and P. Nutrient additions, using a hand-held broadcast spreader (Scotts, USA), began in October 2009 and were repeated every second month from October 2009 to February 2010. The nutrient additions were repeated for all subsequent growing seasons and ended in February 2015. One plot from each pair was irrigated ten times per month from October to April, using a centrally located impact sprinkler, for a total water addition treatment of 210 mm for the growing season. Irrigation began during the 2009/2010 growing season and ended after the 2014/2015 growing season. The treatments were replicated once. There were no manipulations on two control plots (Fig. 2.1). Plots were *c.* 28 times larger than the most extensive resource addition experiment conducted by the Nutrient Network (www.nutneg.org). All plots were accessible to the full complement of indigenous invertebrate and vertebrate grazers.

Replication of the experiment was limited by both logistics and cost. The watering treatments required proximity to a water source where KNP would allow for the installation of an irrigation system. Once a suitable location was identified, the size and number of plots was constrained by the power generated by the water pump feeding the irrigation system. Low replication of large plots was chosen as they are vital for the assessment of insect assemblages. Deductive reasoning was used for the study design and where possible inferential statistics have been used (Oksanen 2001). Despite the low replication, this study is still valuable as it provides the first indication of what GCD impacts might be on savanna vegetation and associated insect assemblages, particularly in KNP where previous research has largely failed to address this issue (van Wilgen et al. 2016).

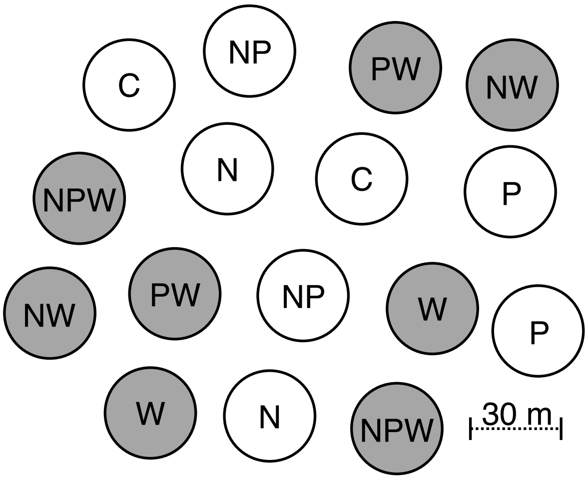

Figure 2.1: Study site layout. Letters correspond to resource additions (C = control, N = nitrogen, P = phosphorous, W = water), grey shaded plots represent water addition.

2.3 Herbaceous assemblage response

The herbaceous community assembly was assessed in April 2014 five years after the initiation of the experiment using five randomly placed 1 x 1 m quadrats per plot (Appendix 1: Fig. 1). The percent cover of bare ground and the percent canopy cover for each grass and forb species rooted in each of the five 1 m^2 quadrats was visually estimated to the nearest 1% (Mueller-Dombois and Ellenberg 1974). All grass and forb species were separated and clipped at the base in six randomly placed 0.25 x 0.25 m quadrats per plot, and total grass and forb biomass was determined after weighing and drying at 80^o C for 24 hours.

Foliar N and C was determined for *U. mosambicensis, D. erianthra, Eragrostis rigidior* Pilg*,* and *Chloris virgata* Sw, as these species had the highest percentage cover on each plot. For each species, on each plot, a minimum of 10 fully extended adult green leaves were oven-dried at 80^o C for 24 hours before grinding to a fine powder using a Retsch MM200 ball mill (Retsch Inc. GmbH & Co KG, Haan, Germany). Percentages of N and C were then obtained using a Flash 2000 organic elemental analyser (Thermo Scientific^{TM}, Bremen, Germany) connected to a Delta V Plus Isotope ratio mass spectrometer at the University of Cape Town (Thermo Scientific^{TM}, Bremen, Germany). Precision of duplicate analysis is 0.1‰ for C and 0.2‰ for N (February et al. 2011).

Grass seed biomass was obtained by collecting seeds from 50 sweeps of a 40 cm diameter sweep net in each of four transects through the centre of each plot in January 2014. All seed was weighed and dried at 80° C for 24 hours. One sweep was equivalent to ~0.1256 m^2, which equates to a sampled area of 25.1 m^2 per 707 m^2 plot. This sampling was only done once at the height of the growing season when the majority of the seed would have matured.

2.4 Grasshopper and ant assemblage response

In January 2014 grasshoppers were collected, in the same manner as described above for grass seed, with 50 sweeps of a 40 cm diameter net in each of four transects through the centre of each plot. As the identification of nymphal grasshoppers is problematic, only adult grasshoppers were counted and identified to morphospecies, and where possible species (Gandar 1983, Picker et al. 2004).

Epigaeic ants were sampled using 12 pitfall traps (55 mm diameter) per plot arranged in two transects through the centre of the plot, with six traps spaced ~4 m apart per transect. Each trap contained 30 ml of a 50% water-dipropylene glycol solution. Pitfall traps were open for three days in March 2014. Ants were identified to morphospecies for each genus, species names were assigned where possible, and the number of individuals counted for each (Fisher and Bolton 2016). Army ants (*Aenictus* spp.) and Driver ants (*Dorylus* spp.) were not included in the analysis as these are nomadic with no fixed nesting sites and are therefore not representative of the resident ant assemblage on a plot. Voucher ant specimens are currently held at the Biological Sciences Department, University of Cape Town.

2.5 Ant functional response

Six morphological traits for each ant species were measured to determine the relationship between ant traits, environmental variables, and species abundance. The measured traits were: Weber's length, inter-ocular distance, head width across the eyes, hind femur length, hind tibia length, and mandible length. Traits were measured to the nearest 0.01 mm on seven individuals per species, and 10 individuals for polymorphic species, using an ocular micrometer attached to a Wild M3C stereomicroscope (Wild Heerbrugg, Switzerland). These traits were used to produce four indices that capture variation in feeding and foraging strategies (see Bishop et al. 2016):

1. Weber’s length was measured from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum (Brown 1953). Weber’s length, a measure of body size, can affect the microhabitats in which species may forage, such that larger-bodied ants will favour open habitats whereas smaller species may occupy more closed habitats (Traniello 1987, Weiser and Kaspari 2006, Gibb and Parr 2013).
2. Eye position was calculated by subtracting the inter-ocular distance from the total head width across the eyes**,** divided by Weber’s length to control for body size**.** Eye position relates to habitat complexity, with dorsally positioned eyes favoured in closed habitats (Weiser and Kaspari 2006, Gibb and Parr 2013).
3. Relative leg length is the sum of the hind femur length and the hind tibia length**,** divided by Weber’s length**.** Leg length is affected by habitat complexity: relatively longer legs selected for in open environments (Weiser and Kaspari 2006, Gibb and Parr 2013).
4. Relative mandible length is an expression of the size of the mandible as a proportion of head width and is the length of the mandible from insertion to tip divided by the head width across the eyes. Specialised predators are expected to have relatively longer mandibles (Hölldobler and Wilson 1990, Gronenberg et al. 1997).

2.6 Statistical methods

Student’s t-test was only used to determine if the watered treatments had significantly higher grass biomass than the unwatered treatments (including controls). Simple regression was used to determine the effect of grass biomass on herbaceous and total insect species richness and population size. Simple regression was also used to examine more comprehensively the effect of grass biomass on grasshopper and ant population size, species richness, species diversity, and species evenness. The Shannon Index and Shannon’s equitability was used as the measure of species diversity and evenness respectively.

Nonmetric multidimensional scaling (nMDS) was used to quantify how the herbaceous (species richness and relative abundance), grasshopper (species richness and total abundance), and ant (species richness and total abundance) assemblages differed between experimental treatments, using the metaMDS function in the R package vegan (Oksanen et al. 2017). Relative abundance of herbaceous vegetation was calculated as the total abundance per species divided by the total abundance of all species within the treatment. All analyses of insect assemblage were done for three levels of species assemblage: all-species, common-species only (species accounting for 80% of total grasshopper or ant abundance: 11 grasshopper and 16 ant species), and rare-species only (species accounting for 20% of total abundance: 27 grasshopper and 50 ant species). These different analyses were made to determine if assemblage changes were being driven by the common or rare species. All assemblage data were square-root transformed and Wisconsin double standardised prior to analysis to reduce the weight of very common species. Analysis of similarity (ANOSIM) was used to test for significant differences in community assembly between experimental treatments with the anosim function in vegan (1000 permutations). Ordinations with a 2D stress of 0.20 or greater were corroborated using hierarchical cluster analysis with an average agglomeration method. Full species lists with associated abundances for the herbaceous, grasshopper, and ant assemblages can be found in Appendix 1: Table 1, Table 2, and Table 3.

To examine correlations of assemblages with environmental variables the envfit function in vegan (1000 permutations) was used. This allows for a more objective interpretation of the results of nMDS and generates a measure of fit as well as a significance value. Here, I tested the significance of the relationships between (1) herbaceous assemblages and grass biomass, forb biomass, percentage bare ground, grass seed biomass, and grass foliar C:N ratio, (2) grasshopper assemblages and grass biomass, forb biomass, percentage bare ground, grass foliar C:N ratio, and grass seed biomass, and (3) ant assemblages and grass biomass, percentage bare ground, and grass seed biomass. Variables that were significantly correlated with differences in community assembly between treatments were fitted to the nMDS ordination.

A model-based approach to explore the association between ant total abundance, species traits, and environmental variables was used (Legendre et al. 1997, Brown et al. 2014, Warton et al. 2015). Specifically, generalised linear models (GLMs) were fitted to predict total abundance as a function of species traits and environmental variables using the traitglm function in the package mvabund (Wang et al. 2017). The environmental variables included were: grass biomass, percentage bare ground, and grass seed biomass. Models were run separately on the all, common and rare species assemblages. Assemblage splits for functional trait analysis were conducted in line with the "insurance" hypothesis (Walker 1995, Naeem and Li 1997), whereby common species contribute to ecosystem function or performance and the rare species contribute to ecosystem resilience. The environment-trait interaction is the so called fourth corner and is expressed as a set of coefficients, determined by the traitglm function, that explain how environmental response across species varies as traits vary. The statistical significance of the coefficients were evaluated by calculating the Likelihood-Ratio-Test statistic of the fitted model via resampling (999 resamples) using the anova.traitglm function in mvabund.

To further investigate functional trait responses to nutrient and water addition, the community-weighted mean (CWM) trait values of the four ant indices for each treatment were calculated. CWM trait values and the fourth-corner interaction coefficients are expected to be similar, but CWM traits are useful for visualising trends in trait values between treatments. CWM traits were calculated using the CWM index with the functcomp function in the R package FD (Laliberté et al. 2014). This index calculates the response of individual traits to nutrient and water additions, weighted by individual species abundances, instead of providing an aggregate index based on multi-trait space (Villéger et al. 2008). All statistical analyses were carried out in R version 3.3.3 (R Core Team 2017).

3 | RESULTS

3.1 Herbaceous assemblage response

There was a trend of increasing grass biomass with resource additions such that the control treatment had the lowest grass biomass (261 g.m^{-2}) and the highest grass biomass was observed on the N, P, and water combined treatment (972 g.m^{-2}; Fig. 2.2a). There was also a significant increase in grass biomass on the watered treatments relative to the unwatered treatments (t = 2.93, df = 6, p = 0.03). The percentage cover of bare ground was highest on the control plots (20% and 8.4%), with negligible bare ground on any of the other treatments (0.66% ± 0.41; mean ± standard error). Herbaceous species richness was significantly and negatively related to grass biomass ($y = -0.0171x + 20.121$, $R^2 = 0.59$, p = 0.0005; Fig. 2.2b). The observed decrease in herbaceous species richness was primarily due to the loss of forbs as grass biomass increased on the nutrient and water treatments (Fig. 2.2c). There were 13 and 12 forb species on the control plots but only five and one species on the N, P, and water combined treatment (Fig. 2.2c). Grass species richness, however, varied little between treatments (n = 16, 5.44 ± 0.2; Fig. 2.2c). Grass foliar C:N ratios were lower where N was added (Fig. 2.2d). Nitrogen addition plots had a foliar C:N ratio of 17.49 ± 0.58, while the without nitrogen plots had a C:N foliar ratio of 28.2 ± 1.3. The control plots had a foliar C:N ratio of 26.09 and 25.65.

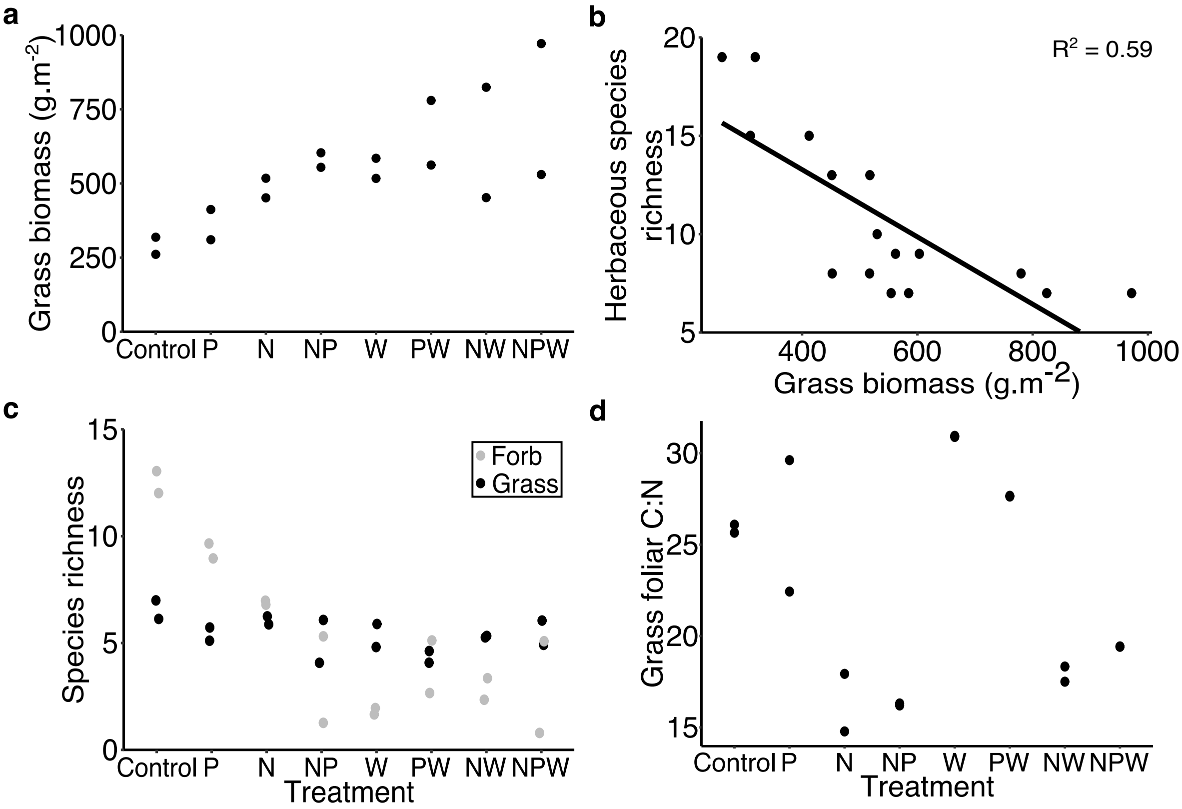

Figure 2.2: Response of (a) grass biomass, (c) forb and grass species richness, and (d) grass foliar C:N ratio to experimental treatments. Plotted data are raw values. Treatment axes correspond to resource additions (N = nitrogen, P = phosphorous, W = water). Simple regression of (b) herbaceous species richness against grass biomass.

There was a significant difference in herbaceous assemblages between treatments (ANOSIM, R = 0.75, p = 0.001; Fig. 2.3). This separation was driven by the significant grouping of watered and unwatered plots along the first nMDS axis (ANOSIM, R = 0.52, p = 0.002). Grass biomass and bare ground showed the strongest correlation with the herbaceous nMDS ordination, with high grass biomass associated with watered plots and increasing bare ground associated with unwatered and control plots (Grass biomass: $r^2 = 0.54$, p = 0.005; Bare ground: $r^2 = 0.53$, p = 0.0005; Fig. 2.3). Grass seed biomass was also correlated with the nMDS ordination ($r^2 = 0.48$, p = 0.02; Fig. 2.3), with the highest seed biomass tending to be on plots where N was combined with either P, water, or both (Appendix 1: Fig. 2). There was no significant association between the grass foliar C:N ratios or the biomass of forbs with herbaceous assemblages in nMDS ordination space. These changes in the herbaceous assemblages were due to changes in the relative abundance of the dominant grasses and the loss of forb species richness as grass biomass increased. Five species of grass accounted for 80% of the herbaceous relative abundance on the control, while four and three species accounted for the same percentage in the unwatered and watered plots respectively (Table 2.1). *D. erianthra* dominated on the control plots representing 50% of the relative abundance. As resources, and in particular water, were added, *U. mosambicensis* and *C. virgata* both increased in relative abundance to dominate the watered plots (Table 2.1).

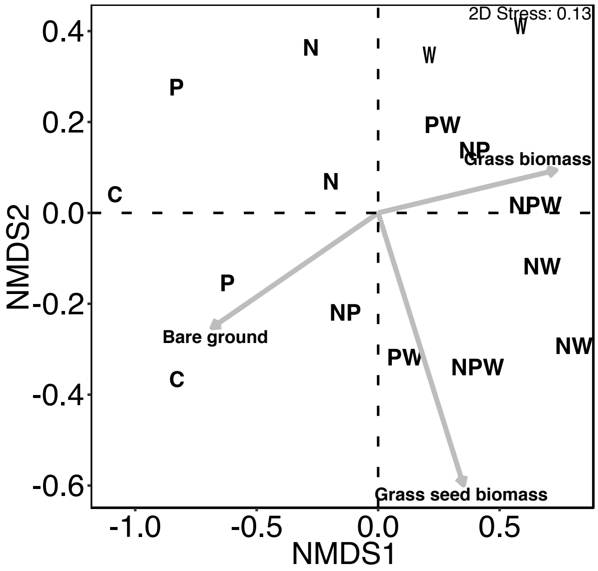

Figure 2.3: Nonmetric multidimensional scaling (nMDS) ordination of herbaceous vegetation with overlaid environmental variables (Bare ground, Grass biomass, and Grass seed biomass) that have significant correlation with the separation of the assemblages. nMDS points correspond to resource additions (C = control, N = nitrogen, P = phosphorous, W = water).

Table 2.1: The relative abundance of herbaceous species that accounted for 80% of the species in the control, unwatered and watered plots. Letters correspond to resource additions (N = nitrogen, P = phosphorous, W = water).

Control plots		Unwatered plots (P, N, NP)		Watered plots (W, PW, NW, NPW)	
Species (Total = 6)	Relative abundance (%)	Species (Total = 4)	Relative abundance (%)	Species (Total = 3)	Relative abundance (%)
Digitaria erianthra	50.38	*Digitaria erianthra*	37.83	*Urochloa mosambicensis*	34.35
Schmidtia pappophoroides	7.91	*Urochloa mosambicensis*	22.36	*Chloris virgata*	30.30
Urochloa mosambicensis	7.54	*Eragrostis rigidior*	12.23	*Dactyloctenium gigantium*	13.89
Eragrostis rigidior	6.48	*Chloris virgata*	7.77		
Tephrosia purpurea	4.36				
Chloris virgata	3.25				

3.2 Grasshopper and ant assemblage response

Simple regressions of combined grasshopper and ant (insect) species richness ($y = -0.01256x + 42.79319$, $R^2 = 0.24$, p = 0.05; Fig. 2.4a) and total abundance ($y = -0.449x + 590.876$, $R^2 = 0.27$, p = 0.04; Fig. 2.4b) were significantly and negatively related to grass biomass. Grasshopper species richness declined as grass biomass increased, although this was not significant. There was also no significant relationship between grasshopper population size and grass biomass or grass foliar C:N ratio. As grass biomass increased, however, the Shannon diversity index for grasshopper assemblages decreased (F = 6.771, df = 14, $R^2 = 0.33$, p = 0.02; Appendix 1: Fig. 3a). Species evenness was, however, not significant. The watered plots were dominated by a single species of grasshopper, *Orthochtha dasycnemis* Gerstaecker. Ant species richness was not affected by grass biomass and varied little between treatments, but ant abundance was significantly and negatively related to grass biomass (F = 5.562, df = 14, $R^2 = 0.28$, p = 0.033; Appendix 1: Fig. 3b). Although ant assemblages tend to be less dominated by a single species when comparing control, unwatered, and watered plots, there was no relationship between Shannon diversity index or species evenness and grass biomass.

The all-species grasshopper assemblage (438 individuals from 38 species) differed significantly between treatments (ANOSIM, R = 0.42, p = 0.015; Fig. 2.4c). Assemblages were separated by the significant grouping of unwatered and watered treatments (ANOSIM, R = 0.55, p = 0.001). The highest abundance for *Zonocerus elegans* Thunberg was on the control plots (n = 11) with fewer on the unwatered plots (n = 6) and none on the watered plots. *Rhachitopis* abundance also tended to be higher on the control (n = 12) and unwatered plots (n = 12) relative to the watered plots (n = 6). *O. dasycnemis* had its highest abundance on watered plots (n = 99) with substantially fewer on the unwatered plots (n = 7) and none on the control plots. There was no significant separation of assemblages when considering either N or P as drivers. The nMDS ordination was significantly correlated with grass biomass ($r^2 = 0.56$, p = 0.004), bare ground ($r^2 = 0.4$, p = 0.02), and forb biomass ($r^2 = 0.39$, p = 0.04; Fig. 2.4c). A higher percentage of bare ground and greater forb biomass was correlated with unwatered plots, whilst increasing grass biomass was correlated with watered plots. Likewise, the common-species assemblage differed significantly between treatments (ANOSIM, R = 0.44, p = 0.009) and treatments were grouped into unwatered and watered plots (ANOSIM, R = 0.5, p = 0.003; Appendix 1: Fig. 4) with significant correlation between the nMDS ordination and grass biomass ($r^2 = 0.4$, p = 0.04), bare ground ($r^2 = 0.45$, p = 0.004), and forb biomass ($r^2 = 0.41$, p = 0.04).

The grasshopper rare-species assemblage did not differ among treatments. The biomass of grass seed and grass foliar C:N ratios were not significantly correlated with any level of grasshopper species assemblage in nMDS ordination space.

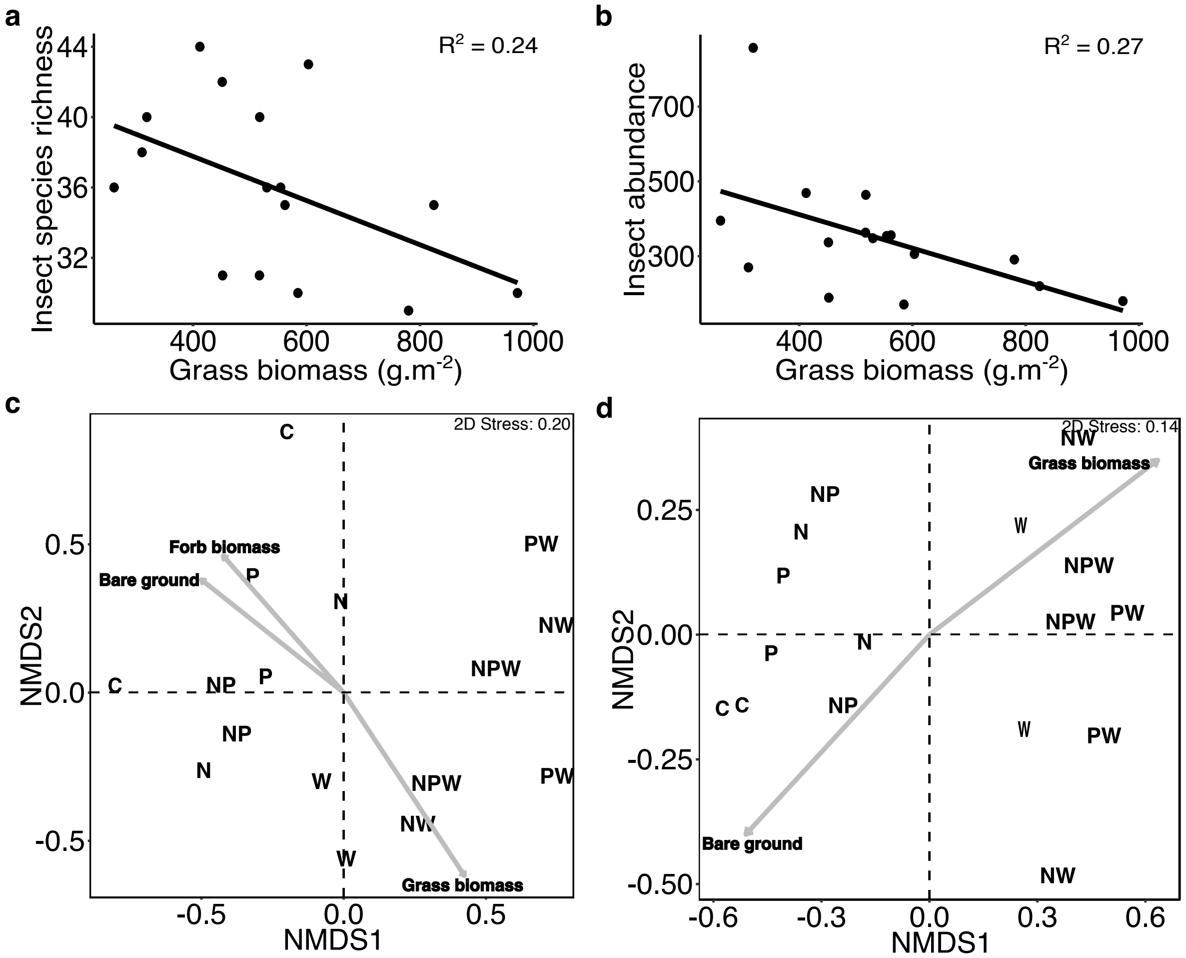

Figure 2.4: Simple regressions of (a) insect (ant and grasshopper) species richness and (b) insect total abundance against grass biomass. Nonmetric multidimensional scaling (nMDS) ordination of (c) grasshopper and (d) ant all-species assemblages with overlaid environmental variables that have significant correlation with the separation of the assemblages. nMDS points correspond to resource additions (C = control, N = nitrogen, P = phosphorous, W = water).

A total of 5132 individuals from 66 ant species was collected. Ant assemblages differed significantly between treatments (ANOSIM, R = 0.52, p = 0.003; Fig. 2.4d). Assemblages were separated by the significant grouping of unwatered and watered treatments along the first nMDS axis (ANOSIM, R = 0.79, p = 0.001). *Monomorium junodi* Forel dominated the low grass biomass plots with a total abundance of 555 on the control plots, declining to 422 on the unwatered plots and 179 on the watered plots. In contrast, *Tetramorium weitzeckeri* Emery, dominated on the high grass biomass plots with a total abundance of 417 on the watered plots, declining substantially to 85 on the unwatered plots with only a single individual on the control plots. There was no significant separation of assemblages when considering either N or P as drivers. The nMDS ordination was significantly correlated with grass biomass ($r^2 = 0.52$, $p = 0.007$) and bare ground ($r^2 = 0.42$, $p = 0.02$; Fig. 2.4d). Likewise, both the common and rare ant assemblages differed between treatments (Common: ANOSIM, $R = 0.44$, $p = 0.02$; Rare: ANOSIM, $R = 0.41$, $p = 0.03$) and were driven by unwatered and watered treatment grouping (Common: ANOSIM, $R = 0.76$, $p = 0.001$; Rare: ANOSIM, $R = 0.69$, $p = 0.001$; Appendix 1: Fig. 5a and 5b). For both common and rare assemblages, the nMDS was significantly correlated with grass biomass (Common: $r^2 = 0.48$, $p = 0.01$; Rare: $r^2 = 0.49$, $p = 0.01$) on watered plots and bare ground (Common: $r^2 = 0.48$, $p = 0.001$; Rare: $r^2 = 0.39$, $p = 0.02$) on unwatered plots. Grass seed biomass had no effect at any level of species assemblage in nMDS ordination space.

3.3 Ant functional response

The fourth corner model for the all-species ant assemblage showed no significant trait environment association despite the significant separation in assemblages between watered and unwatered plots. Using only common species there was a significant association between traits and the environment (residual df = 222, LRT = 35.55, $p = 0.03$), whilst rare species assemblage had no such association. For the common species, we found negative associations in all except two of the trait-environment associations, namely a strong positive Weber's length and grass biomass association and a weak positive eye position and grass biomass association (Fig. 2.5). In other words, Weber's length was greater and eye position more dorsal with nutrient and water additions, and consequently grass biomass increase (Fig. 2.6). There was a strong association between bare ground and relative mandible length (Fig. 2.5), which is also supported by the CWM traits (Fig. 2.6d): the control and P plots with the most bare ground had the smallest relative mandible lengths. The negative association between relative leg length and grass biomass is explained by the one PW plot having the lowest CWM trait value for relative leg length but one of the highest grass biomasses.

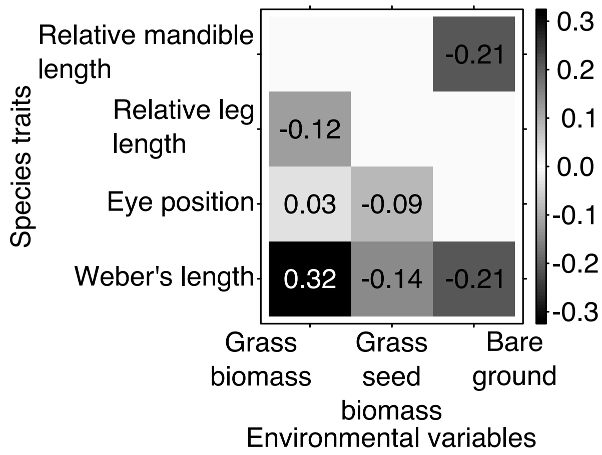

Figure 2.5: Graphical representation of fourth corner interaction coefficients with LASSO penalty for the relationship between species traits and environmental variables for the common-ant species assemblage. Relative tone of colour indicates the strength of association. Values are the fourth corner coefficients.

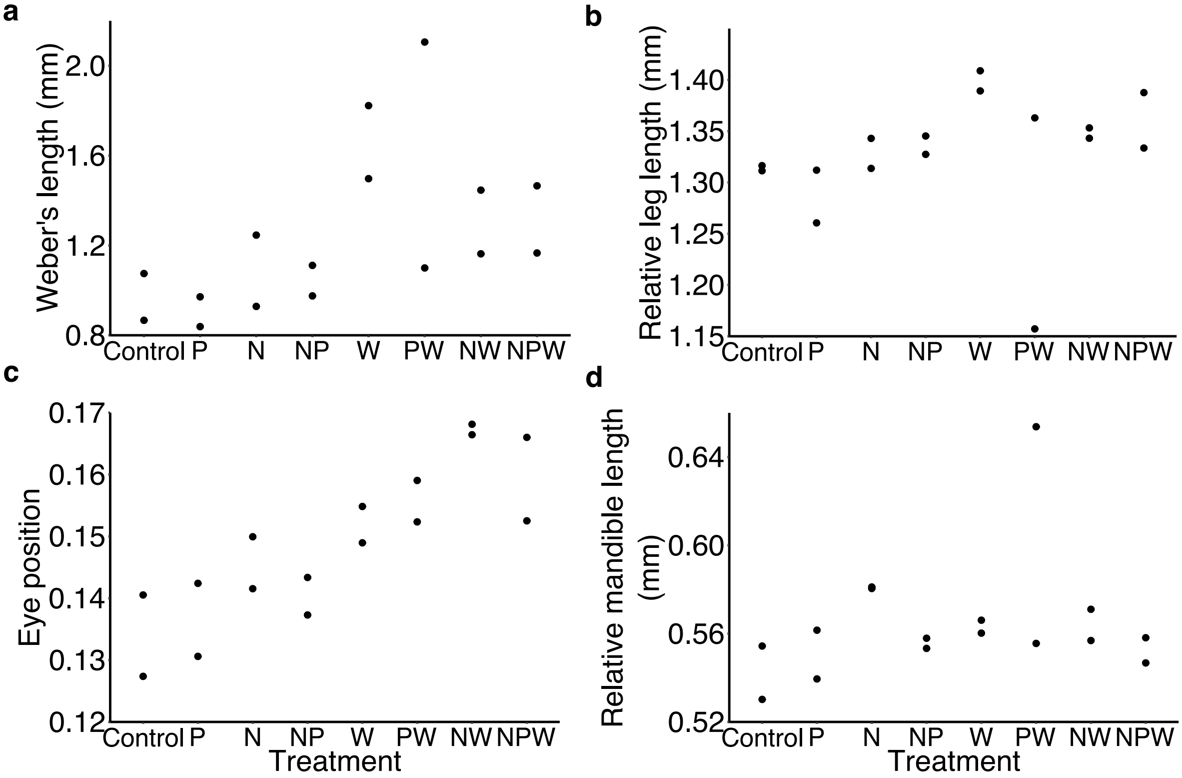

Figure 2.6: Common-ant species assemblage community-weighted mean traits for (a) Weber's length, (b) relative leg length, (c) eye position, and (d) relative mandible length per treatment. Treatment axis corresponds to resource additions (N = nitrogen, P = phosphorous, W = water).

4 | DISCUSSION

The primary objective of this chapter was to simulate the effects of water and nutrient enrichment on savanna herbaceous vegetation that might be generated by GCDs and determine how this may influence the herbaceous (grass and forb), grasshopper, and ant community assembly. My results show that with an increase in both nutrients and water, grass biomass increased with a 60% decrease in herbaceous species richness, supporting the concept of nutrient-induced loss of niches for coexistence (Borer et al. 2014, Grace et al. 2016). Relative to the control plots, there was a substantial increase in grass biomass on the watered plots with a combination of nutrients and water resulting in the highest responses in grass biomass. The combination of increased water availability and higher levels of atmospheric deposition should therefore result in an increase in grass biomass, with cascading implications for insect fauna. My results are contrary to that of Haddad et al. (2000) in that an increase in grass biomass resulted in a decrease in total insect species richness and abundance. Their study did however only manipulate N additions while my study highlights the importance of examining the effect of multiple GCDs on an ecosystem. In particular, my results show the importance of available water for nutrient uptake and increases in grass biomass cascading down to insect assemblages.

Grass biomass was higher on combined N and P plots than on either N or P only plots. These results conservatively extend the findings of Craine et al. (2008) and Fynn and O'Connor (2005) by demonstrating the importance of nutrient enrichment working synergistically with water to increase productivity (Barber 1962, Cramer et al. 2009). My results also show that, resource additions act as a disturbance favouring the pioneer and subclimax grass species *U. mosambicensis* and *C. virgata* (van Oudtshoorn 2012). These competitively superior grasses outcompeted the climax grass species (e.g. *D. erianthra*) and forbs, thereby decreasing species richness. The loss of species richness and especially that of forbs is of special concern, as forbs, and particularly geophytes, rely on a persistence rather than dispersal life strategy and as such, subsequent recolonization may either be very slow or may not be possible at all (Bond and Parr 2010, Zaloumis and Bond 2011).

The nitrogen content and protein-carbohydrate ratios of the leaf are considered to be pivotal in explaining the diets of herbivores such as grasshoppers (Simpson and Raubenheimer 1993, Behmer and Joern 2008, Behmer 2009). While the average foliar C:N ratios of the dominant grass species decrease with N additions, there were no significant effects on the grasshopper assemblages, suggesting that at my study site grasshoppers do not select habitats based on nitrogen availability. There was also no significant correlation between P addition and grasshopper assemblages despite research showing P as being more important than N in explaining grasshopper community assembly or population density (Joern et al. 2012). Rather than available nutrients, my results suggest that vegetation structure and habitat specificity is more important than food related traits in explaining grasshopper patterns of species richness (Prendini et al. 1996, Hendriks et al. 2013, van der Plas and Olff 2014). Grasshopper species richness decreased with increasing grass biomass and assemblages became significantly less diverse, although the evenness of the assemblage was not affected. The dominant cover on the plots, i.e. bare ground or grass, is likely to have played a role in structuring the grasshopper assemblage. As camouflage is a response to the environment, depending on which cover is most abundant or available, grasshoppers can respond accordingly (Pellissier et al. 2011). *Rhachitopis*, a stocky, brown, and clumsy flier, was predominately found on control and unwatered plots, both of which had the highest percentage of bare ground (Picker et al. 2004). In contrast, the preference of *O. dasycnemis* for the high grass biomass plots is not surprising as it is typically associated with thick tall grass areas where it is known to mimic the grass with its elongated body and grass like colouration (Picker et al. 2004). Highlighting the importance of food specialisation in grasshoppers, the predominately forb feeding *Z. elegans* was only found on control and unwatered plots where the greatest species richness and relative abundance of forbs occurred and explains the significant effect of forb biomass on the grasshopper community assembly (Joern 1979, Hendriks et al. 2013).

Differences in ant assemblages with treatment were represented by changes in the total abundance of specific species, such as the decrease in *M. junodi* and increase in *T. weitzeckeri* with an increase in grass biomass. The higher total abundance of ants on control and unwatered plots could be attributed to trapping bias, as catch can be compromised by vegetation complexity (Melbourne 1999). These differences are also likely due to a change in habitat structure and resulting effects on microclimate and food resources (Parr et al. 2012). For example, the dominance of *T. weitzeckeri* on the watered plots and lower abundances on the unwatered plots may be due to it favouring moister, shadier, and dense habitats (Garcia et al. 2010).

These changes do not, however, reflect significantly in the functional traits that were measured using the all species assemblage. There were, however, significant environment trait associations when considering the common-species only. For the common-species there was a positive association between body size (Weber's length) and grass biomass and a negative association between relative mandible length and bare ground. These results do not agree with the hypothesis that smaller ants with shorter legs occupy complex habitats and that larger bodied species occupy open habitats with more bare ground (Farji-Brener et al. 2004, Sarty et al. 2006, Gibb and Parr 2013). My results show that the abundance of one of the largest ants measured, *Megaponera analis* Latreille, increased as grass biomass increased. As *M. analis* is entirely termitophagous, this increase may be linked to changes in food availability. Although no data on termite abundance are available, termite species such as *Hodotermes* are more active in moist soils as they are dependent on soil moisture for their water requirements (Nel and Hewitt 1969).

The lack of a response in the all-species assemblage may be due to rare species mediating the interaction between the environmental variables and the functional traits of the common species. This result is in line with the "insurance" hypothesis (Walker 1995, Naeem and Li 1997), whereby common species contribute to ecosystem function or performance and the rare species contribute to ecosystem resilience. In unfavourable habitats, rare species such as *T. weitzeckeri* on the control plots can be described as "passenger" species (Walker 1992) that maintain themselves in the ecosystem but do not play a role in driving major ecological pathways. In response to changes in vegetation structure, these rare species may ensure ecosystem function is maintained by substituting for the common species. This is highlighted by the change in total abundance of rare species on the control plots becoming common species on the nutrient, and water plots. This would suggest that, based on functional traits, savanna ants are resilient to the impacts of GCDs at the assemblage level.

My results suggest that in African savannas GCDs, such as an increase in rainfall and nitrogen deposition, will result in a loss of biodiversity largely as a result of an increase in primary productivity of grasses. The resulting trophic cascades will directly impact herbivorous insects, and their predator assemblages. Causes of the assemblage change as grass biomass increases are a combination of changes in species richness and total abundances, but differ in importance for herbaceous, grasshopper, and ant assemblages. Herbaceous assemblage change is driven by both species loss and changes in relative abundance, with pioneer and sub climax grass species dominating high grass biomass plots. For grasshoppers, assemblage change is driven by decreases in species richness and change in assemblage membership due to changes in structural complexity and habitat specificity (Prendini et al. 1996). Changes in ant assemblage are driven by changes in the abundances of specific species as the habit changes from a more open system to a relatively closed system. "Passenger" species, however, maintain themselves in the ecosystem and buffer the impacts of GCDs on ant assemblages when considering functional traits.. From a conservation perspective, the increase in grass biomass and consequent loss of savanna-associated diversity are of concern. Grass-dominated communities are fire-prone, and in savannas, fire is a natural driver and a common management tool (Frost et al. 1986, Bond and Archibald 2003, Govender et al. 2006, Archibald et al. 2012). With an increase in grass biomass, fire intensity may increase, with a higher spread rate (Simpson et al. 2016, Wragg et al. 2018). This will pose a challenge for conservation managers as fire intensity in particular has significant effects on savanna vegetation structure (Higgins et al. 2000, Higgins et al. 2007). In the next chapter I explore how herbaceous and insect assemblages at my study site respond to fire.

Chapter 3: **The relationship between top-down and bottom-up controls on savanna plant and insect assemblages**

1 | INTRODUCTION

Trees and grasses are the major plant life forms in savanna, with fire, nutrients, water, and herbivory the most important drivers for determining vegetation structure and community assembly (Frost et al. 1986). The very strong seasonality of the rainfall in savannas means that many of the trees are deciduous while the grasses cure during the dry season (Bond 2008). Once cured, it is this dry grass that provides the fuel for the regular fires that remove plant biomass and determine savanna vegetation structure (Trollope 1984, Stott 2000, Bond and Keeley 2005).

The anthropogenic effect on the interaction between fire and vegetation structure is, however, unclear, but changes in atmospheric properties, global climate, and vegetation distributions may alter fire regimes (Cochrane and Barber 2009, Bowman et al. 2011, Archibald et al. 2018). Understanding the effects of increased N deposition on savanna systems is crucial for effective conservation of these systems. N deposition may result in an increase in grass biomass and a decrease in plant diversity (Fynn and O'Connor 2005, Chapter 2). Any increase in grass biomass will result in an increase in fuel loads with more intense fires (Higgins et al. 2000, Higgins et al. 2007, Simpson et al. 2016, Wragg et al. 2018). Through the volatilisation of nutrients, fire may mitigate the impacts of N deposition. There are, however, two further possible scenarios that may result from fire interacting with N deposition. (1) Fire may reset the system to its original state of high species diversity, particularly of forbs, with low grass biomass (Gandar 1982a, Fynn and O'Connor 2005). In the fire return interval, resource additions may result in high grass biomass and low diversity before the system is again reset by fire to one of high species diversity with low grass biomass (see Hypothesis 1 in Fig. 3.1; Chapter 2). (2) Alternatively, the system is not reset to one of high species diversity with low grass biomass, and continued resource additions during the fire return interval result in a system state of high grass biomass and low species diversity (see Hypothesis 2 in Fig. 3.1).

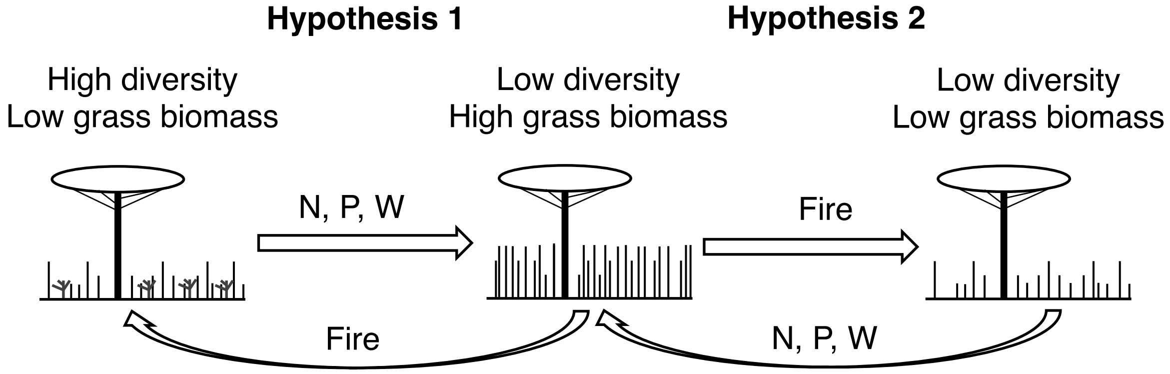

Figure 3.1: Schematic diagram showing two distinct hypothetical herbaceous assemblage responses to fire after nitrogen (N), phosphorous (P), and water (W) additions. Hypothesis 1 – fire resets the system to its original state. Hypothesis 2 – fire maintains the new system state.

As fire is inherent to the system, savanna fauna should be either fire-dependent or fire-adapted. There has, however, been very little research on the effects of fire on savanna fauna and, particularly, on invertebrate fauna (Parr and Chown 2003, Pausas and Parr 2018). What little research there has been is not conclusive, with results showing that after fire, insect populations may decrease, match the control, or become more abundant (Swengel 2001). The literature regarding grasshopper biomass, species richness, and total abundance after fire is likewise contradictory showing a decrease, an increase, or no change, and these results vary with fire frequency (Gandar 1982a, Swengel 2001). Grasshopper community assembly may also change from species favouring long grass and abundant cover before a fire to those favouring bare ground after fire (Gandar 1982a). Fire effects on ants are typically indirect through effects on habitat structure, with habitat openness being a key driver of changes in ant community assembly (Andersen 2019). In savannas, ant assemblages have been shown to be highly resistant and resilient to fire, with the effect of fire depending on whether an area has burned or not or between frequently and infrequently burned areas (Izhaki et al. 2003, Parr et al. 2004, Andersen et al. 2014).

In this chapter I use a taxonomic approach to evaluate the effects of fire at my study site on both grass and insect diversity and biomass. I do this five to eight months after a fire with five hypotheses for both herbaceous and insect responses. (1) As fires open up ecosystems, there will be an increase in the percentage of bare ground with herbaceous biomass decreasing. Resource addition plots, particularly the watered plots, will have higher grass biomass. (2) Fire will decrease grass biomass resulting in an increase in herbaceous diversity (Fig. 3.1), with the least diverse plots before the fire, i.e. the N, P, and water combined plots, having the greatest increase in diversity and amount of assemblage change. (3) Alternatively, on the nutrient addition plots grasses will outcompete other herbaceous species resulting in no change in diversity post-fire (Fig. 3.1.) (4) Fire will change the grasshopper assemblage, relative to the response of the herbaceous assemblage with grasshopper abundance and biomass highest on plots with the highest herbaceous biomass. Hypothesis 2 will result in an increase in forb feeding grasshoppers and a more homogenous assemblage similar to that of the control plots. Hypothesis 3 will result in a maintenance of pre-fire treatment assemblages. (5) Ant assemblages will respond to increased habitat openness by increasing in abundance and species richness. As ants are both resistant and resilient to fire, distinct pre-fire assemblages will be maintained post-fire.

2 | METHODS

2.1 Study site

The study site (see Chapter 2) is located in a semi-arid savanna approximately 10 km north west of the Satara Rest Camp in the central region of Kruger National Park (-24.360676, 31.694549). Rainfall at the nearest weather station at Satara Rest Camp (-24.391700, 31.779700) for the October to April 2014/2015 growing season was 331.7 mm which was well below the 518 mm mean annual precipitation for the previous 30 years (South African National Parks Scientific Services). This reduction in rainfall represented the start of a two year El Niño induced drought.

2.2 Study design

As described in Chapter 2, rainfall and nutrients were manipulated in sixteen 30 m diameter circular plots (707 m^2) spaced ± 10 m apart. The study site was burned in 2009, before the commencement of the experiment, and all of the plots were individually burned in August 2014 (Appendix 2: Fig. 1). The plots were burned five years after they had been originally burned at the start of the experiment. This falls within the three to six year fire return interval for the study site (van Wilgen et al. 2000). The fire was managed and ignited by the SANParks fire ecology team. Fires burned for an average of 389.88 s ± 15. 45 (mean ± standard error) with an average plot rate of spread of 0.79 $m.s^{-1}$ ± 0.003 across the entire plot. Individual plots rather than the entire site was burned to prevent potential damage to study site infrastructure. After the fire, rainfall and nutrient manipulations were continued with N and P additions every second month from October 2014 to February 2015, ending in February 2015. With the below average rainfall for the 2014-2015 wet season, there was very little available groundwater and as a result the water addition treatments only received a combined input of 514.7 mm (331.7 mm precipitation and 183 mm supplementation) instead of the intended combined input of 728 mm but matching the mean annual precipitation. Pre- and post-fire sampling was conducted between January and April in 2014 and 2015 respectively.

2.3 Herbaceous assemblage

The herbaceous community assembly was assessed using five randomly placed 1 m^2 quadrats per plot, both before (April 2014) and after (April 2015) burning at the end of the wet season. The percent bare ground as well as the canopy cover of grass and forb species in each of the five quadrats was visually estimated to the nearest 1% (Mueller-Dombois and Ellenberg 1974). All grass and forb species were separated and clipped at the base in six randomly placed 0.25 x 0.25 m quadrats per plot, with total grass and forb biomass determined after weighing and drying at 80^{o} C for 24 hours.

2.4 Insect assemblage

Grasshoppers were collected using 50 sweeps of a 40 cm diameter sweep net in each of four transects through the centre of each plot at the height of the growing season in January 2014 and 2015. As the identification of nymphal grasshoppers is problematic, only adult grasshoppers were counted and identified to morphospecies, and where possible to species (Gandar 1983, Picker et al. 2004). Grasshopper biomass per plot was determined by wet weighing all adult and nymph grasshoppers caught to the nearest 0.01 g.

Epigaeic ants were sampled using 12 pitfall traps (55 mm diameter) per plot arranged in two transects through the centre of the plot, with six traps spaced ~4 m apart per transect. Each trap contained 30 ml of a 50% water-dipropylene glycol solution. Pitfall traps were open for three days in March 2014 and 2015. Ants were identified to morphospecies for each genus, species names were assigned where possible, and the number of individuals counted for each (Fisher and Bolton 2016). Army ants (*Aenictus* spp.) and Driver ants (*Dorylus* spp.) were not included in the analysis as these are nomadic with no fixed nesting sites and are therefore not representative of the resident ant assemblage on a plot. Voucher ant specimens are currently held at the Biological Sciences Department, University of Cape Town.

2.5 Statistical methods

For the herbaceous assemblage, bare ground, herbaceous biomass, grass biomass, forb biomass, and herbaceous diversity pre- and post-fire were compared using paired t-tests. For the insect assemblage, grasshopper biomass, grasshopper richness, ant richness pre- and post-fire were compared using paired t-tests. All data was assessed for normality and homogeneity. The herbaceous, grass, and grasshopper biomass data were log transformed before analysis. Grasshopper and ant abundance pre- and post-fire, however, was compared using Generalised Linear Models (GLMs). The models were fitted using quasi-Poisson errors, as the response variables are count data and the original fit using Poisson errors indicated over-dispersion as the residual deviance was much greater than the residual degrees of freedom (Crawley 2007, O'Hara and Kotze 2010).

Linear regression was used to test the relationship between pre- and post-fire grass biomass and pre- and post-fire herbaceous diversity. For the herbaceous diversity regression, a slope close to zero would support hypothesis one whilst a slope close to one would support hypothesis two (Fig. 3.1, Appendix 2: Fig. 2). The relationships between post-fire grasshopper abundance and herbaceous biomass, post-fire grasshopper species richness and grasshopper abundance, and post-fire ant species richness and ant abundance were tested using linear regression. All data was assessed for normality and homogeneity. The relationship between post-fire forb species richness and grass biomass and between post-fire ant abundance and bare ground were tested using GLMs and were fitted using Poisson and quasi-Poisson errors respectively. The relationship between post-fire grasshopper biomass and herbaceous biomass was tested using log-log regression.

Grass and forb biomass regrowth was measured by representing the amount of biomass post-fire as a percentage of pre-fire biomass. As bare ground is already measured as a percentage value, the percentage change in bare ground was measured as the amount of bare ground in post-fire subtracted by the amount of bare ground pre-fire. Positive values would then indicate an increase in bare ground.

The effects of treatment and fire, and their interaction, on the multivariate composition of herbaceous, grasshopper, and ant assemblages were evaluated with the semi-parametric Permutational Multivariate Analysis of Variance (PERMANOVA) approach (Anderson 2001). All PERMANOVA tests used 1000 permutations. To aid the interpretation of the PERMANOVA analyses, a constrained ordination termed Canonical Analysis of Principal Coordinates (CAP) was also performed (Anderson and Willis 2003). CAP finds axes that maximise the degree of correlation between a set of predictor (treatment and fire) and response (herbaceous vegetation, grasshopper, and ant assemblages) variables, thereby uncovering patterns that can be masked in unconstrained ordinations. The canonical correlations were tested using 1000 permutations. The similarity percentages (SIMPER) analysis was then used to identify those species contributing at least to 70% of the differences between the pre- and post-fire samples for the herbaceous vegetation, grasshopper, and ant assemblages. SIMPER assesses the dissimilarities between groups and calculates the average contributions of each species to the average overall Bray-Curtis dissimilarity. Full species lists with associated abundances for the herbaceous, grasshopper, and ant assemblages can be found in Appendix 2: Table 1, Table 2, and Table 3.

To determine the amount of assemblage change due to the fire on herbaceous, grasshopper, and ant assemblages, nonmetric multidimensional scaling (nMDS) was performed separately for 2014 and 2015 samples using the metaMDS function in the R package vegan (Oksanen et al. 2017). All assemblage data were square-root transformed and Wisconsin double standardised prior to analysis to reduce the weight of very common species. Procrustes analysis was then used to determine the similarity between the 2014 and 2015 ordinations (Peres-Neto and Jackson 2001). The method estimates the concordance of the ordination solutions by scaling and rotating in order to find an optimal superimposition that maximizes their fit, such that the sum-of-the-squared residuals between corresponding points in both ordinations is minimised. A permutation procedure (PROTEST; permutations = 1000) was then used to test for the statistical significance of the Procrustean fit (Jackson 1995). m_{12} is the PROTEST statistic and smaller values indicate higher concordance between data sets. Procrustes superimposition and the PROTEST is a powerful way to compare multivariate data sets (Peres-Neto and Jackson 2001). The Procrustes superimposition approach generates a residual data matrix that can be used as input for other analytical tools. Here, these residuals indicate the amount of change between corresponding points in both ordinations as a result of the fire. This measure of assemblage change was then used to see if there was a trend of increased herbaceous assemblage change with resource additions. Using linear regression analyses, the residuals were used to test whether grasshopper assemblage change was related to herbaceous assemblage change, change in grass biomass, change in bare ground, or change in forb biomass, and whether ant assemblage change was related to herbaceous assemblage change, change in grass biomass, change in bare ground. All statistical analyses were carried out in R version 3.3.3 (R Core Team 2017).

3 | RESULTS

3.1 Herbaceous assemblage

As predicted, bare ground per plot increased post-fire from an average of 2.35% ± 1.32 (mean ± standard error) to 38.19% ± 3.39 (paired t-test: $t = -12.352$, $df = 15$, $p < 0.0001$). Accordingly, herbaceous biomass decreased from an average of 565.92 $g.m^{-2}$ ± 45.7 per plot to 173.94 $g.m^{-2}$ ± 15.34 (paired t-test: $t = -15.525$, $df = 15$, $p < 0.0001$). Most notably, grass biomass decreased from an average of 540.68 $g.m^{-2}$ ± 47.61 per plot to 168.97 $g.m^{-2}$ ± 16.24 (paired t-test: $t = 15.076$, $df = 15$, $p < 0.0001$). Forb biomass also decreased post-fire (paired t-test: $t = -5.2999$, $df = 15$, $p < 0.0001$). Those plots with either water addition or combined N and P additions tended to have the greatest grass biomass pre- and post-fire (linear regression: estimate = 0.16372, $t = 2.047$, $p = 0.06$; Fig. 3.2a). With post-fire biomass as a percentage of pre-fire grass biomass, though, there was no clear pattern of resource additions promoting regrowth but variation between plots increased when water was added (Fig. 3.2b).

Herbaceous diversity decreased from an average of 11 species ± 1 per plot to 7 species ± 1 per plot (paired t-test: $t = 6.7589$, $df = 15$, $p < 0.0001$). Decreases in both forb and grass species richness accounted for the overall decrease, with plots on average losing two and one species of forb and grass respectively and forb species richness declined as grass biomass increased (GLM: estimate = -0.017778, $z = -5.147$, $p < 0.0001$). Overall, herbaceous diversity post-fire was determined by pre-fire herbaceous diversity (*post-fire herbaceous diversity* = $0.7558x - 1.0322$, where x is herbaceous diversity pre-fire, $R^2 = 0.71$, $p < 0.0001$; Fig. 3.2c).

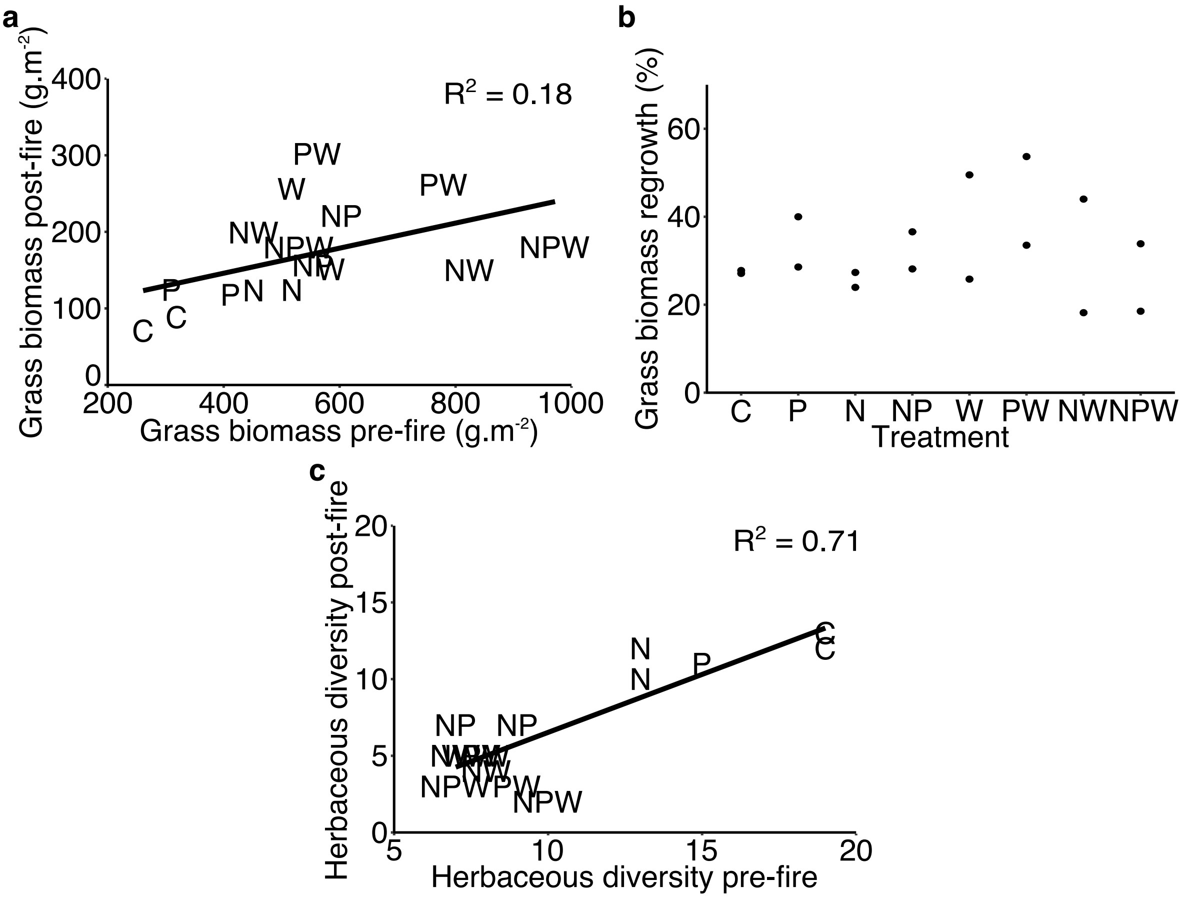

Figure 3.2: (a) Grass biomass post-fire as a function of grass biomass pre-fire, (b) percentage of grass biomass regrowth per treatment post-fire, and (c) herbaceous diversity post-fire as a function of herbaceous diversity pre-fire. Letters correspond to resource additions (C = Control, N = nitrogen, P = phosphorous, and W = water).

The PERMANOVA analysis for the herbaceous assemblage showed that there were significant differences between treatments (F = 9.5018, p = 0.001) and pre- and post-fire samples (F = 21.606, p = 0.001). The interaction between these two factors was also significant (F = 4.1053, p = 0.001). The first two positive eigenvalues from the constrained CAP analysis accounted for 71% of the variation in the herbaceous assemblage. The CAP analysis showed that the treatments are separated by the first CAP axis but more explicitly so for the post-fire sample where there is no overlap between unwatered and watered treatments, whilst pre- and post-fire samples are separated along both the first and second CAP axes but with overlap between the unwatered treatments compared to no overlap between the watered samples (F = 7.7903, p = 0.001; Fig. 3.3a). Ultimately, there was a change in the mean dissimilarity of plots among the unwatered and watered treatments and there was a decrease in the mean dissimilarity of plots within the watered treatments. The result, the watered treatments were more distinct from the unwatered treatments post-fire (i.e. divergence) but the watered treatments had less assemblage variation than they did pre-fire (i.e. convergence). These differing unwatered and watered treatment assemblage responses post-fire were enough to account for the significant interaction between treatments and pre- and post-fire samples. The PROTEST result concurred with the PERMANOVA and CAP analyses by showing that the herbaceous assemblage differed moderately post-fire ($m_{12} = 0.43$, $p = 0.001$; Fig. 3.3b). Despite the assemblage differences pre- and post-fire, there was an equivalent amount of assemblage change across treatments with only control and N and P combined plots having a greater assemblage change than the other treatments (Fig. 3.3b).

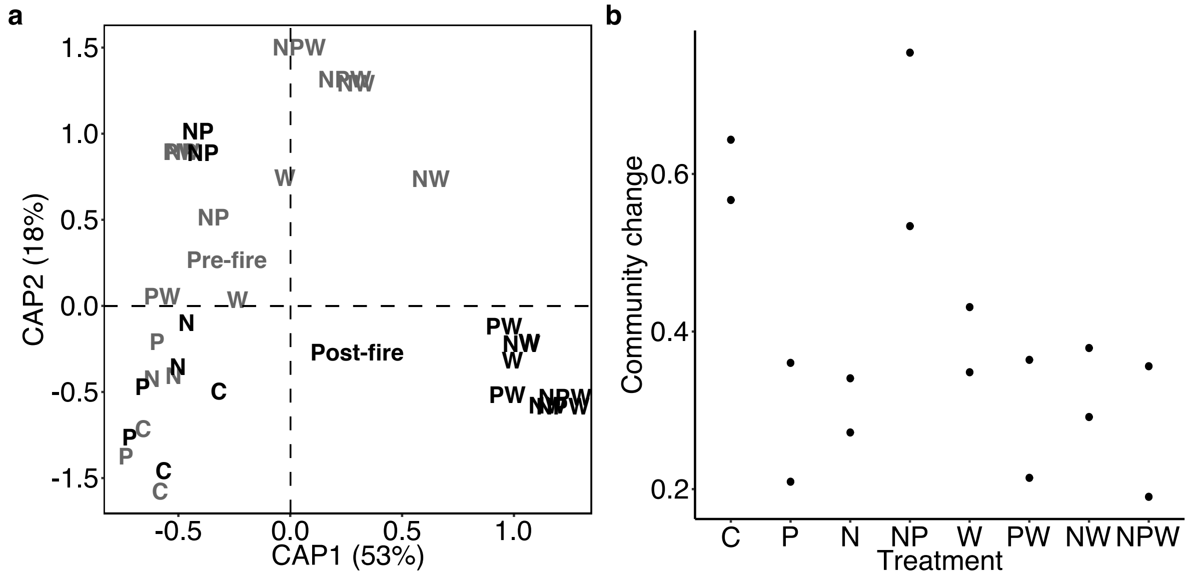

Figure 3.3: (a) Constrained canonical analysis of principal coordinates ordination of the herbaceous assemblage pre- and post-fire. Points in grey represent treatments in 2014 whilst points in black represent treatments in 2015. Pre- and post-fire sample centroids shown. Percentage values indicate the percentage of variation explained by the axis. (b) Amount of assemblage change as a result of the fire represented by the Procrustean superimposition residuals. Letters correspond to resource additions (C = Control, N = nitrogen, P = phosphorous, and W = water).

The SIMPER results show that four grass species were the most influential in separating between pre- and post-fire samples, resulting in 77% of the cumulative change (Table 3.1).

Dactyloctenium gigantium B. S. Fisher and Schweick increased in average abundance from 7.55% to 30.09% post-fire, particularly on watered plots, and accounted for 25% of the total assemblage change. This increase is the likely explanation for the divergence between watered and unwatered treatments and the convergence among the watered treatments. *Digitaria erianthra* Steud, *Urochloa mosambicensis* (Hack) Dandy, and *Chloris virgata* Sw all decreased in abundance post-fire, and combined accounted for 52% of the total assemblage change.

Table 3.1: Similarity percentage (SIMPER) results for the herbaceous vegetation assemblages pre- versus post-fire. Average abundance per plot of species pre- and post-fire and the percentage of the species contribution to assemblage differences shown.

Species	Average abundance pre-fire	Average abundance post-fire	Cumulative sum (%)
Dactyloctenium gigantium	7.55	30.09	24.55
Digitaria erianthra	24.49	6.21	44.32
Urochloa mosambicensis	26.30	10.44	62.73
Chloris virgata	18.38	3.53	77.11

3.2 Insect assemblage

Grasshopper biomass, abundance, and species richness decreased post-fire (Biomass, paired t-test: t = 4.5658, df = 15, p = 0.0004; Abundance, GLM: estimate = -1.2302, t = -4.105, p = 0.0003; Species richness: paired t-test: t = 4.8636, df = 15, p = 0.0002). Grasshopper biomass decreased by roughly 50% from an average of 22.45 g ± 2.74 to 10.81 g ± 1.47 per plot and average abundance per plot decreased from 28 individuals ± 5 to 8 individuals ± 1, but post-fire grasshopper biomass and abundance were positively related to post-fire herbaceous biomass and tended to be highest on the watered treatments (Biomass, log-log regression: estimate = 0.8736, t = 2.921, p = 0.01; Abundance, linear regression: estimate = 0.05128, t = 2.933, p = 0.0109). Furthermore, species richness decreased by two thirds from an average of 9 species ± 1 to 3 species ± 1 per plot and was positively associated with grasshopper abundance (linear regression: estimate = 0.33077, t = 4.862, p = 0.0003).

The PERMANOVA analysis for the grasshopper assemblage showed that there were significant differences between treatments (F = 1.8228, p = 0.001) and pre- and post-fire samples (F = 11.2329, p = 0.001). The interaction between these two factors was also significant (F = 1.5791, p = 0.02). The first two positive eigenvalues from the constrained CAP analysis accounted for 37% of the variation in the grasshopper assemblage (Fig. 3.4a). The CAP analysis showed that the pre- and post-fire samples are separated by the first CAP axis which accounted for 23% of the variation ($F = 2.3364$, $p = 0.001$). As a whole, the grasshopper assemblage diverged post-fire as the mean dissimilarity between plots increased when compared to the pre-fire assemblage. Differences in grasshopper abundance and species richness between the treatments are the likely cause for the divergence, those plots in the top right quadrat have low abundance and species richness compared to those in the bottom right quadrat that have a higher abundance and species richness (Fig. 3.4a). The PROTEST result concurred with the PERMANOVA and CAP analyses by showing that the grasshopper assemblage differed substantially post-fire ($m_{12} = 0.65$, $p = 0.004$). The amount of assemblage change, however, was not predicted by any of the measured variables and there was no clear trend between treatments (Fig. 3.4c). The amount of herbaceous assemblage change nor the change in grass biomass, forb biomass, or bare ground explained the amount of grasshopper assemblage change.

The SIMPER results show that eight species were the most influential in driving assemblage change between pre- and post-fire samples and were responsible for 71% of the cumulative grasshopper assemblage change. The decrease in average abundance of *Orthoctha dasycnemis* Gerstaecker from 6.63 to 0.56 individuals per plot post-fire, particularly on the watered plots, accounted for 20.5% of the assemblage change. *Zonocerus elegans* Thunberg was the only species from the eight that increased in average abundance from 1.06 to 2.19 individuals per plot post-fire and accounted for 9% of the assemblage change. The one *Rhachitopis* species identified as part of the eight also decreased in abundance post-fire but only accounted for 3% of the assemblage change.

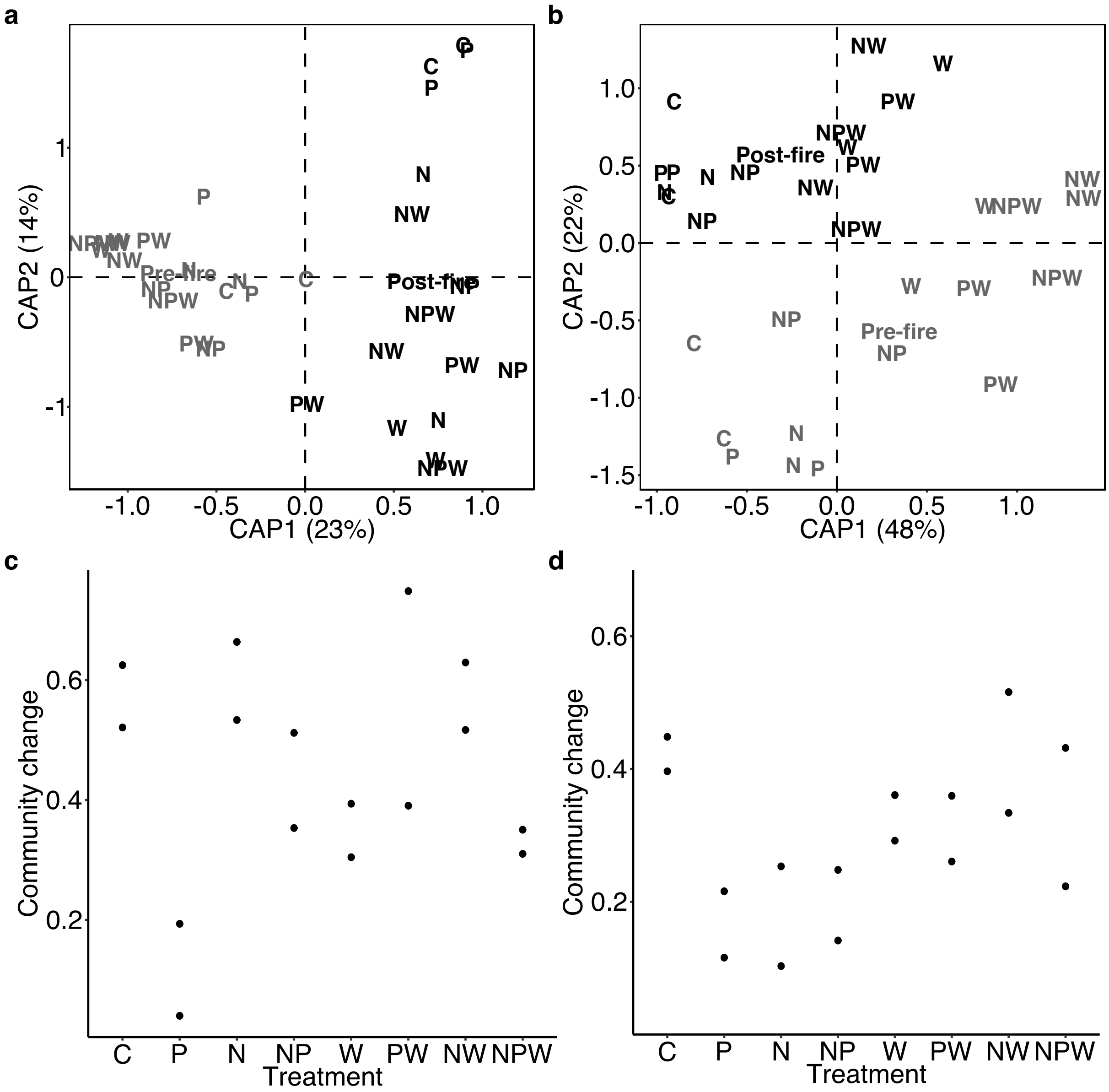

Figure 3.4: Constrained canonical analysis of principal coordinates ordination of (a) grasshopper and (b) ant assemblages pre- and post-fire. Points in grey represent treatments in 2014 whilst points in black represent treatments in 2015. Pre- and post-fire sample centroids shown. Percentage values indicate the percentage of variation explained by the axis. Amount of assemblage change as a result of the fire represented by the Procrustean superimposition residuals for the (c) grasshopper and (d) ant assemblages. Letters correspond to resource additions (C = Control, N = nitrogen, P = phosphorous, and W = water).

Ant abundance increased but species richness decreased post-fire (Abundance, GLM: estimate = 0.5623, t = 2.898, p = 0.007; Richness, paired t-test: t = 2.5877, df = 15, p = 0.02). Ant abundance increased by 75% from an average of 321 ± 38 individuals to 563 ± 78 individuals per plot and tended to be highest on plots with the most bare ground post-fire (GLM: estimate = 0.018289, t = 1.932, p = 0.0738). Ant species richness decreased from an average of 27 ± 1 species to 25 ± 1 species per plot and tended towards being positively associated with ant abundance (linear regression: estimate = 0.005439, t = 2.126, p = 0.0518).

The PERMANOVA analysis for the ant assemblage showed that there were significant differences between treatments (F = 2.4298, p = 0.001) and pre- and post-fire samples (F = 6.5429, p = 0.001), but no interaction between these two factors. The first two positive eigenvalues from the constrained CAP analysis accounted for 70% of the variation in the ant assemblage (Fig. 3.4b). The CAP analysis showed that the treatments are largely separated by the first CAP axis into unwatered and watered treatments with pre- and post-fire samples largely separated by the second CAP axis (F = 2.7684, p = 0.001). The ant assemblage converged post-fire as the mean dissimilarity between plots decreased when compared to the pre-fire assemblage. Despite the convergence, distinct unwatered and watered assemblages were maintained post-fire. The SIMPER results show that 11 species were the most influential in driving the difference between pre- and post-fire assemblages, with eight species increasing and three species decreasing in average abundance (Table 3.2). *Tetramorium setuliferum* Emery, *Messor,* and *Ocymyrmex* abundance increases were important drivers of ant assemblage change and accounted for roughly 30% of ant assemblage change post-fire, with increases of up to 52 times the average abundance pre-fire. These increase were across all plots but more so on unwatered than watered treatments.

The PROTEST result concurred with the PERMANOVA and CAP analyses by showing that the ant assemblage differed moderately post-fire (m_{12} = 0.49, p = 0.001). The amount of assemblage change tended to be greater on watered treatments, with the control plots being a notable exception (Fig. 3.4d). The amount of herbaceous assemblage change nor the change in grass biomass or bare ground, however, explained the amount of ant assemblage change.

Table 3.2: Similarity percentage (SIMPER) results for the ant assemblages pre- versus post-fire. Average abundance per plot of species pre- and post-fire and the percentage of the species contribution to assemblage differences shown.

Species	Average abundance pre-fire	Average abundance post-fire	Cumulative sum (%)
Monomorium junodi	72.25	69.94	11.02
Tetramorium setuliferum	1.625	84.88	22.02
Messor MOT-ZA01	19.06	74.88	32.11
Tetramorium weitzeckeri	31.44	42.38	39.86
Ocymyrmex MOT-ZA01	3.38	47.44	47.29
Trichomyrmex emeryi	20.38	48.75	54.27
Tetramorium sericeiventre	18.5	49.94	60.68
Monomorium MOT-ZA03	1.13	37.19	64.38
Tetramorium MOT-ZA03	15.13	1.38	67.13
Pheidole MOT-ZA05	12.44	8.13	69.45
Pheidole MOT-ZA04	6.56	8.88	71.72

4 | DISCUSSION

The results for Chapter 2 showed that with an increase in N and water there was an increase in grass biomass. Several studies have shown that an increase in grass biomass may result in an increase in fuel loads resulting in an increase in fire frequency and intensity (Higgins et al. 2000, Higgins et al. 2007, Simpson et al. 2016, Wragg et al. 2018). The primary objective of this chapter was to evaluate the effects of fire on savanna herbaceous biomass and diversity and associated insect diversity at my study site after five years of resource additions. The herbaceous assemblage was hypothesised to respond in one of two ways. The first of these is that fire will reset the system by increasing herbaceous diversity with a concomitant decrease in grass biomass. Alternatively, fire will drive the system to a state of low herbaceous diversity and low biomass before continued resource additions result in a state of low herbaceous diversity and high biomass. I found that the resource additions had changed the system to a new state supporting the alternate hypothesis, as five to eight months after fire bare ground had increased and both herbaceous biomass and species diversity had decreased. Furthermore, my results showed that grasshopper biomass, abundance, and species richness were interdependent and decreased as herbaceous biomass decreased. Ant abundance, however, increased post-fire and tended to be related to increasing bare ground, but ant species richness decreased.

The herbaceous, grasshopper, and ant assemblages were significantly different after the fire, with the herbaceous assemblage showing patterns of divergence between watered and unwatered treatments but convergence within the watered treatments. The grasshopper assemblage diverged post-fire, whilst the ant assemblage converged. Diverging assemblages are problematic as the variable assemblage response makes it difficult or impossible to predict, whereas converging assemblages suggest predictability of response to disturbance (Fraterrigo and Rusak 2008, Murphy et al. 2012, Avolio et al. 2015).

4.1 Herbaceous assemblage

My results show that regardless of treatment fire increased habitat openness by increasing the percentage of bare ground and decreasing grass biomass. The water and nutrient treatments did, however, have the highest grass biomass. With no increase in herbaceous diversity post-fire despite the changes in habitat openness, my results suggest that the nutrient additions changed the system to a new state. In particular, the forb assemblage did not recover as expected. In savanna systems, the forb assemblage may recover within five months after fire and can obtain a higher biomass than the grass assemblage (Gandar 1982a). The post-fire response may have been as a result of the lower than average rainfall as many forbs are annuals that can be negatively affected by drought independent of their abundance pre disturbance (Tilman and El Haddi 1992). In savannas, however, grass biomass responds directly to rainfall variability but the preceding rainfall season can buffer drought effects (Sala et al. 2012, Staver et al. 2017, Staver et al. 2019). Furthermore, grass biomass will increase proportional to rainfall for the first four to five years after fire (Govender et al. 2006). The watered plots received the mean annual rainfall amount in 2015 due to the water additions. The percentage of grass regrowth, however, was no greater on watered versus unwatered treatments suggesting that the herbaceous response is despite the onset of drought and may not be as a result of the onset of drought. The positive relationship between pre- and post-fire herbaceous diversity would, however, suggest that herbaceous diversity post-fire is still being controlled by resource-induced loss of ecological niches with grasses outcompeting forbs. The influence of resources is also demonstrated by the trend of increasing grass biomass with resource additions, particularly when water additions are combined with nutrients.

Herbaceous community assembly of watered treatments diverged from the unwatered treatments post-fire, but changes within treatments showed that the unwatered treatments remained similar to their pre-fire equivalents whilst the post-fire watered treatments were distinct from their pre-fire equivalents and became more similar across plots (i.e. converged). Despite these differing responses to the fire, this did not equate to a difference in the amount of assemblage change between treatments. The convergence of the watered treatments and the difference between pre- and post-fire herbaceous assemblages was primarily driven by an increase in *D. gigantium*, a pioneer or subclimax grass species that favours disturbed areas especially when water is readily available after disturbance (van Oudtshoorn 2012). The increase in *D. gigantium*, particularly on the watered plots, is therefore understandable given the post-fire conditions. It is possible that without the reduced rainfall post-fire *D. gigantium* would have increased more on the unwatered plots too, thus making the post-fire treatments more similar than they are represented here.

4.2 Insect assemblage

The grasshopper assemblage was significantly different between watered and unwatered plots post-fire. Grasshopper biomass, abundance, and species richness were all lower post-fire and as suggested by Siemann et al. (1996) interdependent. Grasshopper abundance and biomass post-fire were positively related to post-fire herbaceous biomass and were highest on watered treatments (Haddad et al. 2000). This relationship is a good example of grasshopper foraging decision making (Behmer 2009). The onset of drought may have impacted the grasshopper results generally as grasshopper abundance and diversity has been shown to decrease as drought stress increases, they have drought-resistant egg pods and are well adapted to skipping drought years as the initial diapause is prolonged (Matthée 1951, Ingrisch 1986, Lenhart et al. 2015).

The results of the SIMPER analysis show that seven of the eight species driving the assemblage change between pre- and post-fire samples decreased their average abundance per plot. The only species to increase in abundance was *Z. elegans*, which is unexpected as it is a forb feeding specialist and forb species richness and biomass was lower across all treatments post-fire (Picker et al. 2004). The decrease in *Rhachitopis* abundance was also unexpected as it is a stocky, brown, and clumsy flier that prefers bare ground, as such, it was a prime candidate to dominate the post-fire environment (Gandar 1982a). The decrease in *O. dasycnemis*, particularly on the watered plots, was to be expected though as it is typically associated with thick tall grass areas where it is known to mimic the grass with its elongated body and grass like colouration (Picker et al. 2004).

It was intriguing to find no connection between the amount of grasshopper assemblage change and any variable associated with the herbaceous assemblage or indeed bare ground, despite the links between grasshopper abundance, biomass, and species richness and herbaceous biomass. This variable assemblage response with no clear predictor only serves to increase the difficulty of making an accurate prediction of grasshopper responses to future global change in the savanna.

The effect of fire on ant abundance and species richness was unexpected. In line with the prediction that the ant assemblage will respond to the increased habitat openness post-fire (Andersen 2019), ant abundance increased and was highest on plots with the barest ground. This increase in habitat openness, however, may have contributed to the unexpected decline in species richness as the loss of vegetation likely reduced or eliminated microhabitats (Andersen 1991). Ant abundance and species richness, however, were still correlated such that greater abundance resulted in greater species richness. Ultimately, the greater driver of ant assemblage change was the increase in abundance and this supports the notion that ant assemblages are both resistant and resilient to fire as they can avoid direct mortality by taking refuge underground (Andersen and Yen 1985, Izhaki et al. 2003, Parr et al. 2004, Andersen et al. 2014).

In contrast to the herbaceous and grasshopper assemblages, the ant assemblage across all treatments converged post-fire. The difference between pre- and post-fire assemblages and convergence of the post-fire assemblage was primarily driven by increases in *T. setuliferum*, *Messor,* and *Ocymyrmex*. These species are comparatively large ants that may have benefitted from the increased habitat openness (Farji-Brener et al. 2004, Gibb and Parr 2013). *T. setuliferum* and *Messor* are seed harvesting species that increased uniformly across all treatments, despite decreased grass seed biomass after the fire (Appendix 2: Fig. 3). The increased activity of these species is likely due to fire increasing the rate and distance of seed dispersal by ants as a result of the simplification of the foraging landscape (Parr et al. 2007).

Despite the amount of ant assemblage change post-fire tending towards a predictable response of resource additions thus supporting the theory that convergent assemblages post disturbance allow for accurate predictions (Fraterrigo and Rusak 2008, Murphy et al. 2012, Avolio et al.

2015), the amount of assemblage change was not explained by the amount of herbaceous assemblage change, change in grass biomass, nor the change in bare ground.

4.3 Conclusion

My results demonstrate the complex relationship between nutrients, fire and insect diversity that potentially may result from increased nitrogen deposition, as is occurring at my study site (Mphepya et al. 2006, Conradie et al. 2016). Resource additions have shifted the vegetation to a new state where fire does not reset the system. My results showed that both the herbaceous and grasshopper assemblage response to fire is unpredictable, whilst the ant assemblage demonstrate a level of predictability. My results demonstrate decreases in both herbaceous and insect species richness that would contribute significantly to declines in biodiversity. Managers should develop monitoring stations to ascertain the extent to which such declines in species richness are already evident. Furthermore, this new low diversity system state will likely be perpetuated by continued resource additions. A low diversity ecosystem may be further threatened by a changing fire regime as future disturbances could lead to abrupt and irreversible changes in ecosystem state (Rietkerk et al. 2004, Ives and Carpenter 2007, Barnosky et al. 2012, Hooper et al. 2012, MacDougall et al. 2013).

Chapter 4: Drought effects on termite mound grass and insect assemblages

1 | INTRODUCTION

Large termitaria are common features of African, Australasian, and South American savannas. In the construction of these mounds, termites concentrate large quantities of organic and inorganic material (Turner 2019). As a result, the soils on these mounds have different physical and chemical properties to matrix soils (Sileshi et al. 2010, Jouquet et al. 2011). The soils on termite mounds have increased nutrient availability (Jouquet et al. 2005, Gosling et al. 2012) and moisture content (Steinke and Nel 1989, Erpenbach et al. 2013), and studies have suggested that this affords mounds better fire protection (Joseph et al. 2013, van der Plas et al. 2013). These properties are responsible for distinctive plant assemblages on mounds (e.g. Davies et al. 2014b). Consequently, with better quality grass, mounds are hotspots for grazing (Levick et al. 2010b, Davies et al. 2016).

Bonachela et al. (2015) theorised that the higher soil moisture on mounds may increase vegetation resistance to drought providing islands of refugia for revegetation of the surrounding matrix after drought .Termites have been shown to increase their abundance and activity during drought; thereby maintaining local soil moisture and soil nutrient flows resulting in higher seedling survival rates and accelerated litter decomposition (Ashton et al. 2019). Under climate change, droughts in the tropics and subtropics are likely to become more frequent and severe, especially as these are associated with El Niño events, which are predicted to increase in frequency (Fauchereau et al. 2003, Dai 2013, Cai et al. 2014). These more frequent droughts could cause shifts in plant community assembly and ecosystem functioning (Breshears et al. 2005).

Despite the suggestion of improved conditions during drought for mound vegetation (Bonachela et al. 2015), there is very little empirical evidence to show how mound vegetation assemblages may respond to drought. While grass productivity responds directly to both rainfall amount and variability, there is also a buffering effect of the previous season's rainfall (Govender et al. 2006, Sala et al. 2012, Wilcox et al. 2017). In drought years, the net effect is that grass productivity may be relatively unaffected if the previous year had average or above average rainfall (Frank 2007, Hoover et al. 2014, Byrne et al. 2017). As a result of this buffering effect and the high moisture and nutrient content on mounds, grass productivity on mounds may remain unchanged during a drought.

Alternatively, the relatively higher productivity on mounds during drought could result in an increase in grazing on mounds by mammal herbivores resulting ultimately in lower grass biomass on mounds relative to the surrounding matrix (Levick et al. 2010b, Davies et al. 2016). That improved grass quality and quantity on mounds may mean they are herbivory hotspots was not considered by Bonachela et al. (2015) in their study, nor do they make a distinction between vegetation types (e.g. woody plant or herbaceous). There are, however, distinct grass assemblages on mounds relative to the surrounding matrix, with the mound grasses having higher nutrient concentrations and lower species richness than matrix grasses (Davies et al. 2014b, Muvengwi et al. 2019). Furthermore, during a non-drought wet season there can be no difference in grass biomass on mounds relative to the surrounding matrix (Davies et al. 2014b).

Ecologists have often overlooked the movement of mammalian grazers and their impact on vegetation structure during drought, despite the knowledge that grazers move out of areas where drought is severe to less affected areas (Campbell 1999, Augustine and McNaughton 2006, Butt et al. 2009). During the severe 2014-2016 drought in Kruger National Park (KNP), the rainfall in the southwest region of the park was just on average (Staver et al. 2019), relative to the rest of the southern region where some areas had as much as a 60% reduction in rainfall (South African National Parks Scientific Services). In response to the drought, bulk grazers, such as buffalo, moved towards these drought refugia in the south west (Abraham et al. 2019, Staver et al. 2019). The result was a homogeneous reduction in grass biomass across KNP despite non-uniform rainfall reduction across the park (Staver et al. 2019).

While there may be some understanding as to how mammals may respond, the effects of drought on plant and insect herbivore interactions are poorly understood (Huberty and Denno 2004). There are distinct mound and matrix grasshopper and ant assemblages, with mounds having higher abundances and more species of both grasshoppers and ants (Leitner et al. in revision). Earlier work on grasshoppers suggests that abundance and species richness increase during drought (White 1984, Mattson and Haack 1987, Franzke and Reinhold 2011), but a more recent study suggests decreases in both as a result of lower grass biomass despite stable grass macronutrient content during drought (Lenhart et al. 2015). Grasshoppers, though, have drought-resistant egg pods and are well adapted to skipping drought years as the initial diapause is prolonged resulting in a decrease in grasshopper numbers during drought (Matthée 1951, Ingrisch 1986). The higher plant nutrient concentration on termite mounds may, however, buffer drought effects, as vegetation with a higher nutrient concentration can support larger insect population sizes (Strauss 1987, Haddad et al. 2000, Behmer 2009). Although, with the potential for increased mammalian herbivory on mounds, invertebrate abundance, and consequently diversity, may decrease as grazing impacts insects by making persistence and recolonization of insects on plants difficult (Kruess and Tscharntke 2002, Pöyry et al. 2006, van Klink et al. 2015).

Ant responses to climate change and drought are relatively unknown but could be very different from other insects, as ant colonies are comparatively sessile and once nests are established, movement tends to be local (Banschbach and Herbers 1999, McGlynn et al. 2004, Underwood and Fisher 2006). Recently, Gibb et al. (2019) showed that in a desert environment the activity and species richness of ants is determined by rainfall amount, and in particular dominant ant activity declining as rainfall declined. It is possible, however, that ant abundance could increase during drought years, caused by changes in habitat structure to a more open system as grass biomass decreases (Andersen 2019).

In this chapter I report a study where I took advantage of the recent 2-year drought in southern Africa to observe the effect of drought on termite mound grass and associated insect assemblages. I compared grass cover and standing biomass with insect abundance, species richness, and community assemblages both on and off *Macrotermes* mounds on two different vegetation types that also differed in drought severity. The aims of this study were to: (1) determine the grass and associated insect assemblage drought responses both on and off termite mounds and (2) investigate whether the drought induced patterns on grass and insects are similar to those caused by mammal grazer movement towards non-droughted refugia.

I expected that at the high drought severity site: (1) There would be an overall decrease in grass cover and biomass, but higher cover and biomass on mounds than in the savanna matrix, hence, greater resistance to drought on mounds (Bonachela et al. 2015). (2) Alternatively, preferential grazing on mounds might result in mounds having less grass cover and biomass than the savanna matrix. (3) Grasshopper abundance should decrease (Lenhart et al. 2015), but higher abundance may be expected on mounds due to increased grass nutrient concentrations (Behmer 2009, Davies et al. 2014b, Leitner et al. in revision). (4) Ant abundance will increase as habitat structure decreases, resulting in mound and savanna matrix community assemblages becoming more similar (Andersen 2019). Mounds are expected to have greater ant abundance and species richness than the savanna matrix (Leitner et al. in revision).

At the low drought severity site, I expected that: (5) large mammalian grazer movement would result in a more pronounced difference between mound and savanna matrix grass cover and biomass, with the savanna matrix having more biomass and cover than the mounds. (6) The competitive effect of large herbivores on herbivorous insects would result in a decrease in grasshopper abundance on mounds relative to the savanna matrix (Kruess and Tscharntke 2002, Pöyry et al. 2006, van Klink et al. 2015). (7) Ant abundance would increase on mounds as habitat complexity decreases due to increased herbivory, resulting in mound and savanna matrix community assemblages becoming more distinct.

2 | METHODS

2.1 Study site description and design

The study took place at two sites in the southern region of KNP. The first of these was approximately 4.5 km south east of Pretoriuskop Rest Camp (-25.207050, 31.281683) and the second 12 km south west of Skukuza Rest Camp (-25.045417, 31.509533). Mean annual rainfall at Pretoriuskop is 707 mm and at Skukuza 588 mm (South African National Parks Scientific Services). Pretoriuskop has a comparatively nutrient-poor vegetation classified as Pretoriuskop Sour Bushveld, and is dominated by *Terminalia sericea* Burch ex DC and *Dichrostachys cinerea* (L.) Wight & Arn (Rutherford et al. 2006). Dominant grasses on mounds are *Cynodon dactylon* (L.) Pers and *Panicum maximum* Jacq, whilst dominant grasses in the matrix are *Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss, *Loudetia simplex* (Nees) C.E.Hubb, *Pogonarthria squarrosa* (Roem. & Schult.) Pilg, and *Schizachyrium sanguineum* (Retz.) Alston (Davies et al. 2014b). Skukuza has a relatively nutrient-rich vegetation that falls within the Granite Lowveld, with dominant woody species *Senegalia nigrescens* Oliv and *Combretum apiculatum* Sond (Rutherford et al. 2006). The dominant grasses on mounds are *P. maximum* and *Urochloa mosambicensis* (Hack.) Dandy, whilst *P. maximum*, *P. squarrosa*, *Digitaria eriantha* Steud, and *Brachiaria nigropedata* (Ficalho & Hiern) Stapf dominate the matrix (Davies et al. 2014b). Both sites occur in an undulating landscape with distinct uplands and bottomlands on a granite and gneiss substrate where *Macrotermes* mounds are associated with crests and upper sections of hillslopes (Venter et al. 2003, Levick et al. 2010a, Davies et al. 2014a). Herbivore biomass is greater at Skukuza (1568 kg.km^{-2}) than at Pretoriuskop (838 kg.km^{-2}). During the 2014-2016 drought, however, Skukuza experienced a more severe drought than Pretoriuskop (Appendix 3: Fig. 1) resulting in a grazer movement from Skukuza towards Pretoriuskop (Abraham et al. 2019, Staver et al. 2019).

The dominant *Macrotermes* species at both study sites were *M. flaciger* Gerstäker and *M. natalensis* Haviland (Davies et al. 2014a). At both study sites, areas of *Macrotermes* mound densities ≥ ~1 mound.ha^{-1} were selected (Davies et al. 2014b). Ten termite mounds spaced at least 50 m apart and often over 100 m apart were sampled at each of the study sites before (January 2012) and during (February 2016) the drought of 2014-2016. As both active and inactive mounds are vegetated at the study site, there was no attempt to discriminate between these two classes.

The pre-drought (2012) grass and insect data used as a comparison was collected by Andrew Davies and Monica Leitner (Davies et al. 2014b, Leitner et al. in revision). For consistency, the termite mounds I sampled and the grass and insect sampling methods I used in 2016 were the same as those used by by Davies and Leitner.

2.2 Grass cover and biomass sampling

In January 2012 and February 2016, sixteen 1 m^2 quadrats were randomly placed at six locations on the upper sections and 10 locations on the lower sections of each mound (Davies et al. 2014). Sampling was stratified by aspect, with eight quadrats on the north and eight on the south side of each mound. For each termite mound, a paired matrix plot situated 30 m from the edge of the mound, and at least 30 m away from neighbouring mounds, was also sampled. An arbitrary direction for the location of each matrix plot was chosen each time. For each matrix plot, 16, 1 m^2 quadrats were placed in a 4 x 4 grid formation with 1 m spacing between each quadrat. For each quadrat, both on and off mounds, the percentage canopy cover of all the grass was visually estimated after which a disc pasture meter was used to determine standing grass biomass. The disc pasture meter has been calibrated for this vegetation type and biomass was calculated using the following formula (Trollope 1990):

$$\left(\sqrt{x} \times 2260\right) - 3019 = \text{kg.ha}^{-1}$$

where x is the disc height reading in cm obtained from the disc pasture meter. The Trollope (1990) formula was used in 2016 in order to be consistent with the 2012 measurements. In 2012, all grasses were identified to species, but this was not possible in 2016 as there was not enough biomass and few inflorescences in order to do this.

2.3 Insect sampling

All 10 termite mounds at each site were sampled for grasshoppers in January 2012 and February 2016. Ant sampling also occurred at all 10 mounds in both years at Pretoriuskop, but in 2016 only six mounds were sampled for ants at Skukuza. Grasshoppers were collected using a 40 cm diameter sweep net, with 24 sweeps performed on each termite mound in both 2012 and 2016 with a further 24 sweeps 20 m away, around the periphery of the mound, in 2012 and on the paired matrix plot in 2016. All life stages of grasshoppers were used for abundance scores with only adults used for community assemblage analyses because of uncertainty in identification of nymphs.

Epigaeic ants were sampled using pitfall traps containing a 50% water-dipropylene glycol solution. In 2012, six evenly spaced traps were placed on the upper sections of each mound and six around the base with a further six traps equally spaced 20 m away around the periphery of the mound. The traps were left open for five days. In 2016, five evenly spaced traps were placed on the upper sections of the mound and five around the base with a further 10 traps on the paired matrix plot. The matrix plot traps were arranged in a 5 x 2 block with 2 m between each trap in a string of five and a 4 m gap separating the two strings. The traps were left open for three days. Ants were identified to morphospecies for each genus, species names were assigned where possible, and the number of individuals counted for each species. Army ants (*Aenictus* spp.) and Driver ants (*Dorylus* spp.) were not included in the analysis as these are nomadic with no fixed nesting sites and are therefore not representative of the resident ant assemblage. Voucher ant specimens are currently held at the Biological Sciences Department, University of Cape Town and the Zoology and Entomology Department, University of Pretoria. Due to challenging field conditions, there were no voucher grasshopper specimens for neither 2012 nor 2016.

2.4 Data analysis

The effects of differing drought severity on mound and matrix grass and associated grasshopper and ant assemblages were examined at the Skukuza (high drought severity) and Pretoriuskop (low drought severity) sites. Analyses were conducted for each location separately because they differed in drought severity. To determine and confirm the severity of the El Niño induced drought of 2014-2016 at both Pretoriuskop and Skukuza, the standardised precipitation index (SPI) was calculated for the wet season from 1985/86 to 2015/16 for both. SPI is a climatic proxy used to quantify and monitor drought and is represented as the number of standard deviations that observed precipitation deviates from the average.

Grass cover at Skukuza was compared using the Aligned Rank Transform (ART) for nonparametric factorial Analysis of Variance (Wobbrock et al. 2011, Kay and Wobbrock 2019), and at Pretoriuskop grass cover was compared using two-way Analysis of Variance (ANOVA) after data were assessed for normality and homogeneity of variance. A log transformation was applied to the Pretoriuskop grass cover data before analysis. Standing grass biomass at Skukuza was compared using two-way ANOVA after data were log transformed, and at Pretoriuskop standing grass biomass was compared using ART.

Grass biomass resistance to the severe drought at Skukuza was calculated as the difference in biomass between 2012 and 2016. Mound and matrix grass biomass resistance was compared using two-way Analysis of Covariance, after data were assessed for normality and homogeneity of variance. Grass biomass resistance was the response variable and treatment (mound and matrix) and grass species richness in 2012 were the explanatory variables. Grass species richness was included as a variable because species richness pre-disturbance can increase primary productivity resistance and resilience (Tilman and Downing 1994), and at Skukuza grass species richness was lower on mounds than off mounds (Davies et al. 2014b). This means that the savanna matrix grass assemblages may be more resistant to drought than the mound grass assemblages as a function of their increased species richness.

Grasshopper and ant abundance (number of individuals) at Skukuza and ant abundance at Pretoriuskop were compared using Generalised Linear Models (GLMs). The models were fitted using quasi-Poisson errors because the response variables were overdispersed count data (Crawley 2007, O'Hara and Kotze 2010). Grasshopper abundance at Pretoriuskop and ant species richness at Skukuza and Pretoriuskop were compared using two-way ANOVA. Treatment (mound and matrix) and year (2012 and 2016), and their interaction, were the response variables for all grass and insect models. Model simplification, for all grass and insect models, was performed using backward step selection, with the highest-order non-significant interaction removed until the minimal adequate model was determined. For all grass and insect models, 2012 was used as the baseline for the contrast.

At both Skukuza and Pretoriuskop, the effect of treatment (mound vs matrix) during the drought (2016) on the composition of the grasshopper assemblage was evaluated with semi-parametric Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson

2001), using 1000 permutations. As 2012 and 2016 grasshopper community assembly data could not be collated, the effect of treatment (mound vs matrix) interacting with year (2012 and 2016) could not be analysed. The effect of treatment (mound and matrix) interacting with year (2012 and 2016) on the composition of the ant assemblage at Skukuza and Pretoriuskop were evaluated with PERMANOVA. To aid the interpretation of the ant PERMANOVA, Canonical Analysis of Principal Coordinates (CAP) ordination was also performed (Anderson and Willis 2003). CAP finds axes that maximise the degree of correlation between a set of predictor (treatment and year) and response (ant assemblage) variables, thereby uncovering patterns that can be masked in unconstrained ordinations. The canonical correlations were tested using 1000 permutations. The similarity percentages (SIMPER) analysis was then performed to identify ant species contributing at least 70% of the difference between the predictor variables for the ant assemblage. SIMPER assesses the dissimilarities between groups and calculates the average contributions of each species to the average overall Bray-Curtis dissimilarity.

To determine if ant assemblages on mounds changed more than matrix assemblages during the drought at Skukuza, nonmetric multidimensional scaling was performed separately for 2012 and 2016 samples. All assemblage data were square-root transformed and Wisconsin double standardised prior to analysis to reduce the weight of very common species. Procrustes analysis was then used to determine the similarity between the 2012 and 2016 ordinations (Peres-Neto and Jackson 2001). This method estimates the concordance of the ordination solutions by scaling and rotating in order to find an optimal superimposition that maximizes their fit, such that the sum-of-the-squared residuals between corresponding points in both ordinations is minimised. A permutation procedure (PROTEST; permutations = 1000) was then used to test for the statistical significance of the Procrustean fit (Jackson 1995). The Procrustes superimposition approach generates a residual data matrix that can be used as input for other analytical tools. Here, these residuals indicate the amount of change between corresponding points in both ordinations as a result of the drought. This measure of assemblage change on and off mounds was then compared using Student’s t-test, after data were assessed for normality and homogeneity of variance. All statistical analyses and data visualisation were carried out in R version 3.3.3 (R Core Team 2017), using the packages “ARTool”, “emmeans”, “ggplot2”, “HH”, and “vegan”.

3 | RESULTS

The SPI showed that the 2011/12 sampling at both sites occurred during a wetter-than-average wet season (Fig. 4.1). The SPI results confirmed that the drought was more severe at Skukuza (Fig. 4.1b) than at Pretoriuskop (Fig. 4.1a), with the 2015/16 Skukuza wet season being the driest since 1985/86 (Appendix 3: Fig. 4.1b).

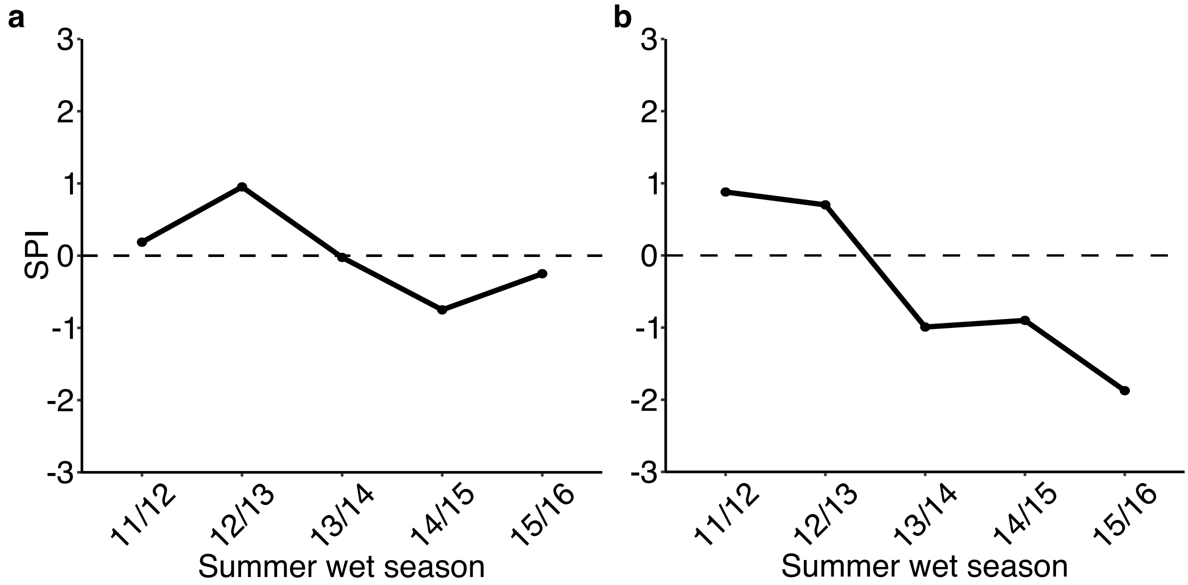

Figure 4.1: Wet season standardised precipitation index (SPI) for (a) Pretoriuskop and (b) Skukuza from 2011/12 to 2015/16. SPI calculated using precipitation data for Pretoriuskop and Skukuza from 1985/86 to 2015/16. Negative values indicate drier-than-average conditions and positive values indicate wetter-than-average conditions, with the dashed line indicating average conditions.

3.1 Effects at Skukuza

At Skukuza, overall grass cover differed between years and was greater in 2012 than in 2016 (two-way ART, $F = 56.16$, $p < 0.001$; Fig. 4.2a), but it did not differ between treatments (mound and matrix). The interaction between these two factors was not significant, indicating that the effect of treatment was similar across years. Standing grass biomass also differed overall between years and was greater in 2012 than in 2016 (two-way ANOVA, $F = 103.95$, $p < 0.001$; Fig. 4.2b), but not between treatments. The interaction between these two factors was not considered because the most parsimonious model after step selection excluded this term. Grass biomass resistance to the drought at Skukuza did not differ on or off mounds, nor as a function of grass species richness, measured in 2012. Furthermore, the interaction between treatment (mound and matrix) and grass species richness was not a significant predictor of biomass resistance to drought.

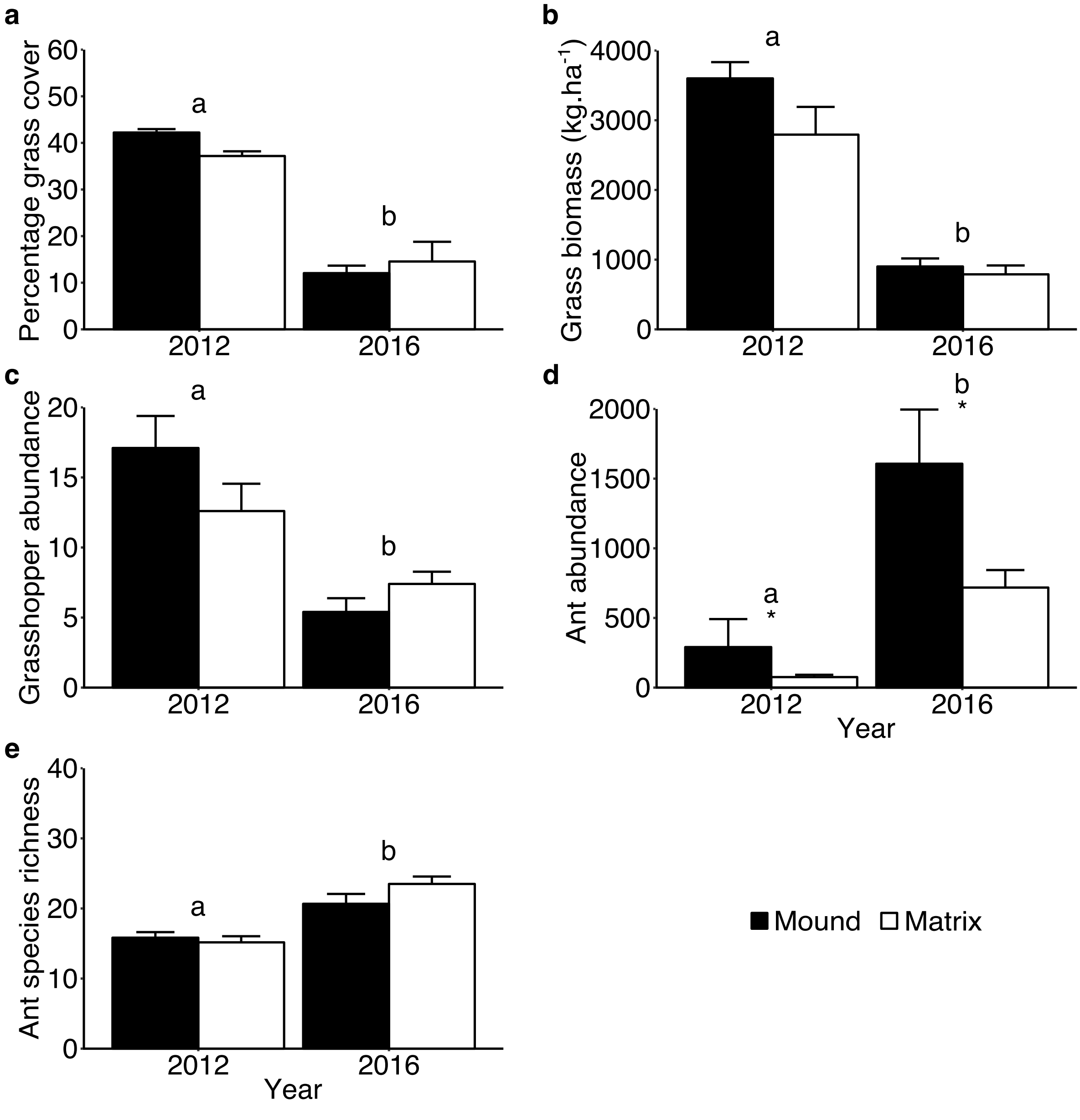

Figure 4.2: Mean of mounds and matrix plots ± standard error for grass (a) percentage cover and (b) standing biomass, (c) grasshopper abundance, and (d) ant abundance and (e) ant species richness on and off *Macrotermes* mounds before (2012) and during drought (2016) at Skukuza. Letters indicate significant differences between sampling years, while asterisks denote significant differences between treatments (mound vs savanna matrix).

Grasshopper abundance differed between years with greater abundance in 2012 (GLM, $\beta = -1.15$, $t = -4.96$, $p < 0.001$; Fig. 4.2c), but abundance did not differ between treatments. The interaction between these two factors was not significant. Ant abundance differed between year, with greater abundance in 2016, and treatment, with greater abundance on mounds (GLM: year, $\beta = 1.85$, $t = 4.05$, $p = 0.001$; treatment, $\beta = -0.87$, $t = -2.54$, $p = 0.02$; Fig. 4.2d). There was no interaction between these two factors, which was excluded from the most parsimonious model. Similarly, ant species richness differed between years and was greater in 2016 (two-way ANOVA, $F = 35.72$, $p < 0.001$; Fig. 4.2e), but species richness did not differ between treatments. There was also no interaction between these two factors, which was excluded from the most parsimonious model.

There was no significant difference in grasshopper community assembly between mounds and matrix in 2016. There were, however, differences in the ant assemblage between treatments (PERMANOVA, $F = 4.67$, $p = 0.001$) and years ($F = 9.58$, $p = 0.001$), with the interaction between these two factors also significant ($F = 2.23$, $p = 0.04$). The CAP analysis showed that mounds and matrix plots were separated by the first CAP axis and the 2012 and 2016 samples were separated by the second CAP axis ($F = 5.49$, $p = 0.001$; Fig. 4.3a). The first two positive eigenvalues from the constrained CAP analysis accounted for 90% of the variation. Ultimately, there was a change in assemblage mean for both mound and matrix assemblages but no apparent change in variance among replicates. With the change in assemblage mean, the mound and matrix assemblages were more distinct, difference in ant composition between mound and matrix increased, during the drought than they were pre-drought (i.e. divergence). The SIMPER result shows that eight and five ant species were responsible for at least 70% of the cumulative change in ant community assembly between mounds and matrix plots for 2012 and 2016, respectively (Appendix 3: Table 1). In both years, *Monomorium junodi* Forel contributed roughly half of the 70% cumulative change and dominated the mound assemblages with little to no abundance off mounds. *M. junodi* increased on mounds from ~215 in 2012 to ~915 individuals per mound in 2016. Another notable increaser on mounds was a *Pheidole* spp. (*Pheidole* MOT-ZA03, Appendix 3: Table 1), which increased from an average of ~5 in 2012 to ~280 individuals per mound in 2016 but recorded a mean of <10 individuals per mound in the matrix in both years. Combined, *M. junodi* and the *Pheidole* spp. accounted for 54% of the cumulative change in 2016.

The PROTEST result concurred with the PERMANOVA and CAP analysis, and showed that the mound and matrix ant assemblage differed moderately in response to the drought ($m_{12} =$

0.61, p = 0.02). There was, however, no significant difference in community assembly change on mounds versus matrix plots during the drought (t = 0.55, df = 10, p = 0.6).

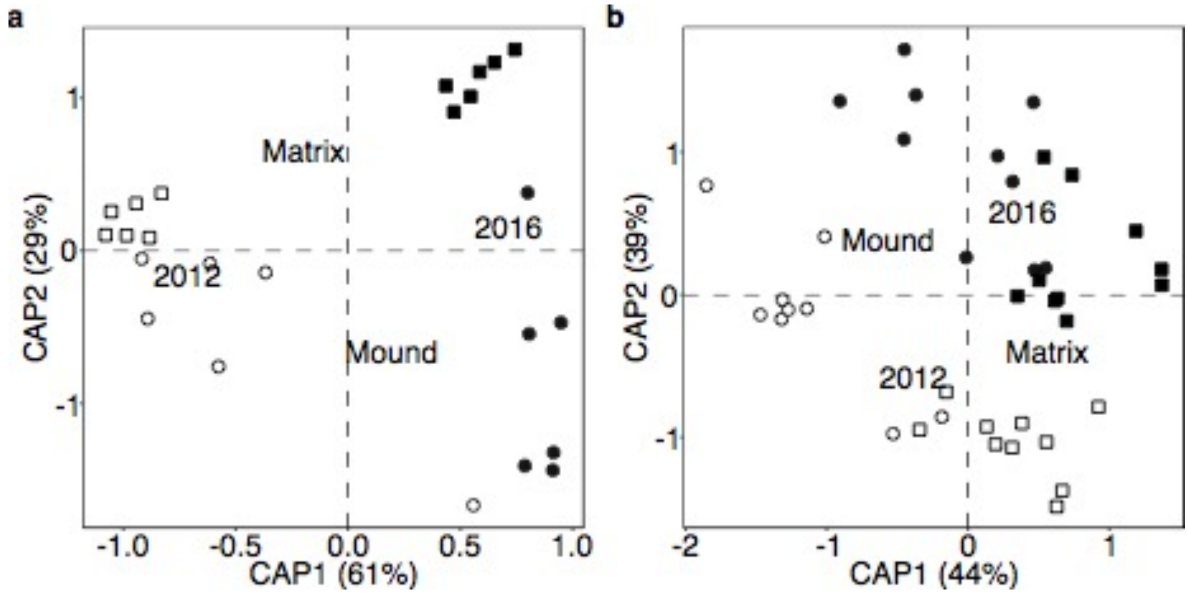

Figure 4.3: Constrained canonical analysis of principal coordinates ordination of the ant assemblage on and off *Macrotermes* mounds in 2012 and 2016 at (a) Skukuza and (b) Pretoriuskop. Mound samples in 2012 are represented as open circles with solid circles representing 2016. Similarly, savanna samples in 2012 are represented as open squares with solid squares representing 2016. Treatment (Matrix and Mound) and year (2012 and 2016) centroids are shown. Percentage values indicate the percentage of variation explained by each axis.

3.2 Effects at Pretoriuskop

At Pretoriuskop, overall grass cover differed between treatments with greater grass cover in the matrix than on mounds (two-way ANOVA, F = 6.14, p = 0.02; Fig. 4.4a), but grass cover did not differ between years (2012 and 2016). The interaction between these two factors was significant (two-way ANOVA, F = 5.48, p = 0.02), as mound and matrix grass cover went from parity in 2012 to significantly more cover in matrix the matrix than mounds in 2016. Overall standing grass biomass differed between years with 2012 having greater biomass than 2016 (two-way ART, F = 19.17, p < 0.001; Fig. 4.4b), but biomass did not differ between treatments. The interaction between these two factors was not significant.

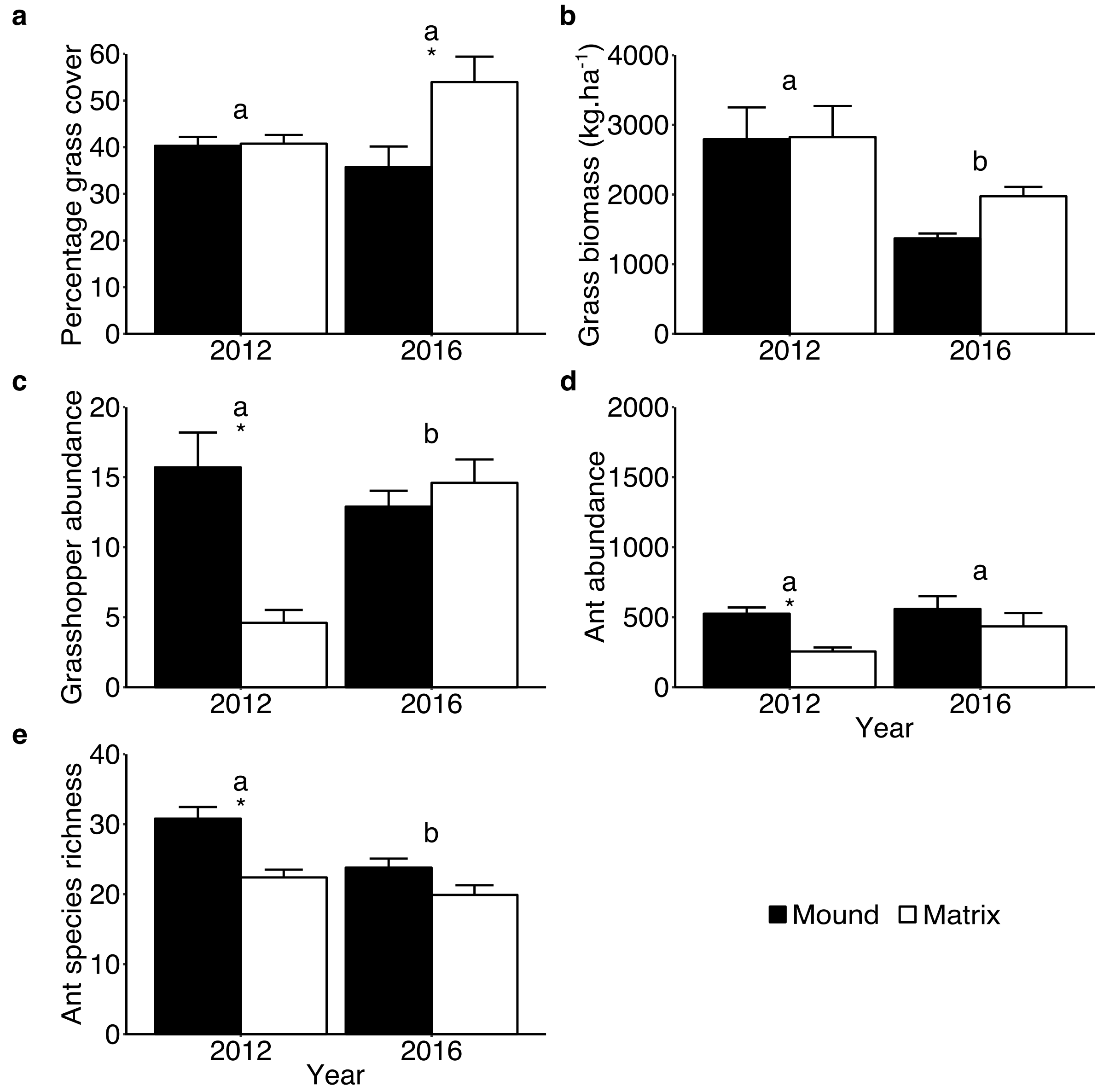

Figure 4.4: Mean of mounds and matrix plots ± standard error for grass (a) percentage cover and (b) standing biomass, (c) grasshopper abundance, and (d) ant abundance and (e) ant species richness on and off *Macrotermes* mounds before (2012) and during drought (2016) at Pretoriuskop. Letters indicate significant differences between sampling years, while asterisks denote significant differences between treatments (mound vs savanna matrix).

Grasshopper abundance differed between treatments and years (two-way ANOVA: treatment, F = 7.95, p = 0.008; year, F = 4.67, p = 0.04), with greater abundance on mounds compared to the matrix and with greater abundance in 2016 than in 2012 (Fig. 4.4c). The interaction between these two factors was significant, with there being significantly more grasshoppers on mounds than the matrix in 2012, but equal abundance on mounds and the matrix in 2016 (two-way

ANOVA, F = 14.75, $p < 0.001$). Ant abundance differed between treatments with greater abundance on mounds than in the matrix (GLM, $\beta = -0.72$, $t = -2.88$, $p = 0.007$), but abundance did not differ between years (Figure 4d). The interaction between these two factors was not significant. Ant species richness differed between treatments and years (two-way ANOVA: treatment, F = 19.14, $p < 0.001$; year, F = 11.42, $p = 0.002$), with greater species richness on mounds than in the matrix and greater in 2012 than in 2016 (Fig. 4.4e). There was no interaction between these two factors, with the interaction excluded from the most parsimonious model.

The mound and matrix grasshopper assemblages differed in 2016 (PERMANOVA, F = 2.46, $p = 0.008$), as did the ant assemblage (PERMANOVA, F = 4.90, $p = 0.001$), which also differed between years (F = 4.79, $p = 0.001$). The interaction between these two factors for the ant assemblage was also significant (F = 2.09, $p = 0.02$). Mound and matrix ant assemblages were separated by the first CAP axis whilst the 2012 and 2016 samples were separated by the second CAP axis (F = 3.92, $p = 0.001$; Fig. 4.3b). The first two positive eigenvalues from the constrained CAP analysis accounted for 83% of the variation. Like the Skukuza ant assemblage results, there was a change in assemblage mean for both mound and matrix assemblages but no apparent change in variance among replicates. Unlike at Skukuza, the change in assemblage mean did not result in the mound and matrix assemblages becoming more distinct. The SIMPER result showed that nine and eight ant species were responsible for at least 70% of the cumulative change in mound and matrix ant community assemblage 2012 and 2016, respectively, and that the Pretoriuskop community assemblage was a far more evenly distributed one compared to Skukuza in both 2012 and 2016 (Appendix 3: Table 2). In both years, three ant species each accounted for an equivalent proportion of cumulative change as *M. junodi* did at Skukuza. Unlike at Skukuza, *M. junodi* mean abundance on mounds was only ~85 individuals per mound for both years at Pretoriuskop; contributing only 16% and 11% to the cumulative change in 2012 and 2016, respectively.

4 | DISCUSSION

4.1 Drought effects at Skukuza

Prior to the drought, at Skukuza, there were no differences between mound and matrix grass cover and biomass (Davies et al. 2014b). According to Bonachela et al. (2015), increased drought resistance benefits to plants on termite mounds should occur when rainfall decreases to between 0.6 and 0.75 $mm.day^{-1}$ from a mean of 1.25 $mm.day^{-1}$. Rainfall at Skukuza was within this range (0.72 mm.day^{-1}), but the predicted drought resistance pattern was not observed. Rather, grass cover and biomass, both on mounds and in the matrix, decreased markedly. This hypothesis may, however, pertain only to woody species that may have better access to deep water in the termitaria than the relatively shallower rooted grasses (Kulmatiski et al. 2010, Kulmatiski and Beard 2013a). The likely mechanism for the observed pattern, however, is more intense foraging by large mammal herbivores both on and off mounds as the drought intensified and grass biomass decreased (Abraham et al. 2019, Staver et al. 2019). As grasses dry out at the end of the wet season, there is an increase in foraging on mound grasses in the dry season which would likely intensify with droughts (Davies et al. 2016).

As predicted, grasshopper abundance decreased as grass biomass decreased with the drought (Haddad et al. 2000, Lenhart et al. 2015). Alternatively, grasshopper abundance may have decreased as a result of the prolonging of the initial diapause (Matthée 1951, Ingrisch 1986). Contrary to my predictions, however, there was no difference in grasshopper abundance between mounds and matrix plots. These results may relate to the relatively smaller grass foliar nutritional gradient between mounds and the matrix at Skukuza (compared with the higher rainfall site, Pretoriuskop). For aboveground herbivorous insects, nutrient concentration is a driver in foraging decision-making, and grass macronutrient content remains constant during drought (Behmer 2009, Lenhart et al. 2015). The weaker nutritional gradient on and off mounds (Davies et al. 2014b), and equal grass biomass between mounds and matrix plots, likely reduced the effect of nutrition-based foraging decisions by grasshoppers. The even use of the habitat during drought by grasshoppers is clearly shown by the lack of difference in mound and matrix grasshopper community assemblages.

In agreement with my predictions, ant abundance and species richness increased in response to the drought. These increases were likely the result of the change in habitat structure to a more open system, favoured by some ant species, as grass cover and biomass decreased (Andersen 2019). Pre-drought patterns of ant abundance and species richness were maintained, however, as termite mounds had far greater ant abundance, but equivalent ant species richness to the savanna matrix. Contrary to my predictions, the increase in ant abundance and richness did not result in mound and matrix assemblages becoming more homogenised, as distinct mound and matrix ant assemblages were maintained during the drought but differed from pre-drought assemblages. The difference from the pre-drought assemblages was caused by *M. junodi* increasing in abundance and driving the assemblage change during the drought coinciding with an increase in species richness.

Despite the potential for *M. junodi* and the *Pheidole* spp. to exert numerical or behavioural dominance and alter the structure of the ant assemblage, this appears not to have happened (Parr 2008). There was ultimately little assemblage change on mounds relative to the matrix when determining how much the assemblages had changed. The lack of a difference suggests that both mound and matrix assemblages responded similarly to the drought, despite the implied stability of mound habitat which I hypothesised would result in a more stable ant assemblage. Overall, the response of mound and matrix savanna ants suggests a remarkable resistance to drought akin to their resistance to fire (Parr et al. 2004, Andersen et al. 2014).

4.2 Drought effects at Pretoriuskop

Large-scale movement of grazers to non-drought refugia, such as Pretoriuskop, not only extended the effects of drought on vegetation, but likely prevented grazer population crashes (Staver et al. 2019). The overall decrease in grass biomass, particularly on mounds, at Pretoriuskop, combined with the lower grass cover on mounds compared with the savanna matrix suggests selective grazing pressure on mound vegetation resulting from the increase in herbivory. Grass biomass on mounds decreased by half, whereas matrix biomass only decreased by a third. There is a pronounced foliar nutrient gradient on versus off mounds that already accounts for selective feeding on mounds at Pretoriuskop (Davies et al. 2014b, Davies et al. 2016). This pattern of increased foraging on mound vegetation likely intensified during the drought, due to the increase in grazer density at Pretoriuskop. Our results not only underscore the importance of rainfall heterogeneity creating refugia thus maintaining mammalian herbivore populations, but also reaffirms the importance of termite mounds as a key resource to grazers, particularly in nutrient poor savannas, such as at Pretoriuskop.

Overall, grasshopper abundance at Pretoriuskop increased and tended to be greater in the matrix than on mounds during the drought. Mound grasshopper abundance in 2016, however, tended to be lower than mound abundance in 2012. In 2012, grasshoppers preferentially selected mound habitats (Leitner et al. in revision), suggesting strong foraging decision-making as grass biomass and cover was equivalent, but grass foliar nutrient concentrations differed on and off mounds (Behmer 2009, Davies et al. 2014b). The increase in grasshopper abundance in 2016 was, however, driven by an increase in grasshoppers in the savanna matrix rather than on mounds. This matrix increase could be explained by an unfavourable reaction to the influx of large mammalian grazers selectively feeding on the nutrient enriched mound vegetation, as intensive grazing makes persistence and recolonization of insects on plants difficult (Kruess and Tscharntke 2002, Pöyry et al. 2006, van Klink et al. 2015). Unlike the drought response at Skukuza, however, the mammalian grazer effect did not homogenise the mound and matrix grasshopper assemblages. The distinct mound and matrix assemblages suggest that a group of grasshoppers moved from the mounds to the matrix. The large mammalian grazers forcing the mound grasshoppers that could not tolerate the increase in grazing to occupy the less favourable matrix habitat, thereby maintaining distinct mound and matrix assemblages.

Although there was a decrease in grass biomass on mounds and in the matrix at Pretoriuskop, total grass cover on mounds was equivalent between 2012 and 2016 whilst matrix grass cover increased from 2012 and 2016. Total ant abundance, however, did not increase with the decrease in grass biomass either on the mounds or in the matrix. This suggests that the decrease in mound and matrix grass biomass was not a substantial enough change in habitat structure to affect ant diversity. Furthermore, distinct mound and matrix ant assemblages were maintained and did not increase in their distinction. Observed changes to the ant assemblage, both mound and matrix, can be ascribed to natural variation over the four-year period between sampling. Overall, my results suggest no positive or negative influence of the influx of large herbivores at Pretoriuskop on the ant assemblages.

4.3 Conclusion

To provide accurate predictions of how savanna ecosystems will respond to increasingly frequent droughts, more comprehensive observational analyses such as those presented here will be critical. In African savannas the role of large mammal herbivores cannot be ignored when assessing the effects of drought on vegetation structure and how these may cascade down to insects. Ultimately, during a drought grasses on termite mounds are no more resistant than grasses in the savanna matrix as these are preferentially grazed by mammal herbivores with cascading, but differing, effects on grasshopper and ant assemblages. Ant abundance and diversity is, however, very closely aligned with the amount of bare ground. At Pretoriuskop where rainfall was high enough to show no significant difference in grass biomass between the mound and matrix there was also no significant difference in the ant assemblages during the drought. At Skukuza, however, where the drought was more severe, there is a significant increase in ant abundance and diversity. These results demonstrate the importance of bare ground in determining ant species assemblages. The reduction in grass biomass both on and off mounds at Skukuza resulted in a decrease in grasshoppers. While this may have been related to diapause it is unlikely because without grass there cannot be any grasshoppers. At Pretoriuskop where the drought was less severe, the increased herbivory on the mounds resulted in a decrease in grasshoppers on the mounds and increase off. These results demonstrate the importance of herbivory in determining both vegetation structure and insect species diversity in African savannas. It would, therefore, be interesting to see how mound and matrix grasses would respond to drought in the absence of mammal herbivores. These results also indicate that the Bonachela et al. (2015) model, at least for grasses, needs refining with a consideration of herbivory as mounds are grazing focal points during drought. Ultimately, the preferential grazing on mounds combined with the influx of large herbivores to drought refugia affects the grasshoppers but not the ants. These findings provide some insights into the potential, and variable effects that increased drought may have on biodiversity in the future.

Chapter 5: **Synthesis**

When discussing the future of African terrestrial biodiversity and ecosystems, Midgley and Bond (2015) suggest that "*climate change impacts on biodiversity in metastable savanna in Africa cannot be credibly considered without including responses of vegetation structure, and therefore habitat, to changing climate, disturbance and CO_2 concentration*." This comment was primarily directed toward bush encroachment, and its impacts on biodiversity and ecosystem services (Eldridge et al. 2011). More recently, however, there has been an increasing understanding of the threat of N deposition and its impacts on tropical and sub-tropical ecosystems (Bobbink et al. 2010). This understanding has, however, largely stemmed from N addition experiments in grass dominated systems outside of Africa (e.g. Grace et al. 2016). While my thesis was inspired by these studies, my focus is not on disturbance and CO_2 concentration but on N deposition, available water, fire, and drought and how these may interact with and cascade down to vegetation structure and insect assemblages.

In my first data chapter (Chapter 2), I looked at the effects of increased available water and nutrients on savanna herbaceous vegetation and the cascading effects that this may have on grasshopper and ant assemblages. The results of this chapter conservatively extend the findings of Fynn et al. (2004) and Craine et al. (2008) by demonstrating the importance of nutrient enrichment working synergistically with water to increase productivity (Barber 1962, Cramer et al. 2009). My results also show that resource additions act as a disturbance favouring competitively superior grasses that outcompeted the climax grass species and forb species, thereby decreasing species richness. While these herbaceous results may agree with earlier studies (Fynn and O'Connor 2005, Grace et al. 2016), my results also show that the increased grass biomass results in a decrease in ant and grasshopper species richness and abundance. In grass dominated ecosystems, grasshoppers are the most abundant invertebrate herbivore and can severely reduce aboveground biomass (Gibson 2009). Furthermore, ants generally have a high diversity and biomass and influence key ecosystem processes like decomposition and seed dispersal in savannas (Parr et al. 2007, Lach et al. 2010, Parr et al. 2016). With the renewed global focus on the insect apocalypse (Cardoso and Leather 2019, Saunders et al. 2019), my results highlight that more studies need to address the link between plants and insects and not primarily focus on plant responses when addressing human-mediated global change. A trait-based view of ecology must also become more prevalent when examining ecosystem change.

My results show that rare ant species mediated the interaction between the changing environment and the ant assemblage.

N deposition is predicted to increase in KNP while global circulation models predict an increase in precipitation intensity while mean annual precipitation will remain unchanged for the region (Easterling et al. 2000, Frich et al. 2002, Conradie et al. 2016, Pohl et al. 2017). It would be interesting to see if this combination results in similar increases in grass biomass with cascading effects on insect assemblages. My results are relevant to predictions for grass dominated systems of east Africa though, as these are to increase in both N deposition and mean annual precipitation (Phoenix et al. 2006, Shongwe et al. 2011). With the increase in available water and nutrients increasing grass biomass, several studies have shown that fire frequency and intensity may also increase (Higgins et al. 2000, Higgins et al. 2007, Simpson et al. 2016, Wragg et al. 2018, Chapter 2). The effect of an anthropogenic induced change to vegetation structure on fire is, however, still unclear (Archibald et al. 2018). Fire is one of the most important drivers determining savanna vegetation structure and composition and is commonly used as a management tool (Frost et al. 1986, Moritz et al. 2014). In my second data chapter (Chapter 3), I looked at the interaction between resource additions and fire with the aim of determining if fire was able to reset the system, and how this may affect grasshoppers and ants.

My results for chapter 3 show that contrary to expectations fire did not reset the system to one of high diversity with low grass biomass (Fynn and O'Connor 2005). Rather, the positive relationship between pre- and post-fire herbaceous diversity suggests that herbaceous diversity post-fire is controlled by resource-induced loss of ecological niches, with competitively superior grasses outcompeting other grasses and forbs. This result suggests that the natural successional patterns have been altered by the resource additions and that the low diversity system state will likely be perpetuated. The continued reduction in forbs is of special concern, as forbs, and particularly geophytes, rely on a persistence rather than dispersal life strategy and my findings suggest that they are not able to persist with an increase in nutrients (Bond and Parr 2010, Zaloumis and Bond 2011). Not only forbs but trees may also decrease in a high grass biomass system where fire intensity and frequency is predicted to increase (Higgins et al. 2000). Fire thus acts synergistically with N deposition to maintain species poor grasslands. Aligned with grass biomass results, grasshopper abundance and biomass post-fire were positively related to post-fire herbaceous biomass and were highest on watered treatments, agreeing with the findings of Haddad et al. (2000). This relationship is a good example of grasshopper foraging decision making as reviewed by Behmer (2009). The increased abundance of ants as a result of the increased habitat openness post-fire, were largely driven by seed harvesting species. This increase in seed harvesting species is likely due to fire increasing the rate and distance of seed dispersal by ants as a result of the simplification of the foraging landscape (Parr et al. 2007), and supporting the notion that ant assemblages are both resistant and resilient to fire (Andersen and Yen 1985, Izhaki et al. 2003, Parr et al. 2004, Andersen et al. 2014).

It is not only understanding how species adjust to disturbance, but also understanding the causes of how the entire assemblage may change that is extremely important for understanding the effects of anthropogenic change on ecosystems (Avolio et al. 2015). The herbaceous, grasshopper, and ant assemblages were all changed by resource additions (Chapter 2). Post fire, I expected the assemblages to either become more similar (converge) or more distinct (diverge). Diverging assemblages are problematic as it makes the assemblage response difficult or impossible to predict, whereas converging assemblages suggest predictability of response to disturbance (Fraterrigo and Rusak 2008, Murphy et al. 2012, Avolio et al. 2015). The herbaceous assemblage diverged as a whole post-fire, but the differences between watered treatments decreased. This highlights the importance of post-fire conditions in determining herbaceous recovery and is in line with the relationship between pre- and post-fire herbaceous diversity. The grasshopper assemblage diverged post-fire with no measured variable explaining the amount or direction of assemblage change. The ant assemblage, however, converged post-fire. This predictable response was likely driven by ant resistance and resilience to fire. The predictable response also demonstrates that ants rather than grasshoppers should be used as bioindicators in fire prone GCD threatened grass dominated systems.

A drought at the end of two years of field sampling meant that I could not evaluate the extent to which my experimental results are also evident in a natural system. I did, however, take advantage of the most severe drought in more than 30 years to compare grass and associated insect assemblages both on and off high nutrient *Macrotermes* mounds (Chapter 4). Ultimately, during a drought grasses on termite mounds are no more resistant than grasses in the savanna matrix and are likely preferentially grazed by mammal herbivores, especially in non-droughted refugia, with cascading effects on grasshopper and ant assemblages. The ability of mammalian herbivores to move extended the effects of the drought to non-droughted refugia, and likely prevented the population crashes associated with a more homogenous drought or drought in smaller reserves and rangelands where animals cannot move (Augustine 2010, Staver et al.

2019). In Africa, the loss of long-distance seasonal migrations and declines of mammal populations are a direct result of anthropogenic pressures and changes in land use (Nelson 2008). An increasing human population is central to this but the expansion of fences is a critical threat resulting in animals being constricted to the boundaries of reserves (Løvschal et al. 2017). These animals will then come up against fences when they try to move out of a drought affected area resulting in high mortality (Williamson and Williamson 1984, Knight 1995). As grazers were able to move within KNP, grass biomass decreased ubiquitously through KNP despite the heterogenous drought (Staver et al. 2019). My results, however, show that grass biomass decreased more on than off mounds, particularly in the non-droughted refugia where there is a greater grass nutritional gradient that likely resulted in greater grazing pressure on mounds (Davies et al. 2014b, Davies et al. 2016). Ultimately, my findings highlight the importance of mounds as a foraging resource during drought and that reserve size is critical in mitigating drought fatality among mammal herbivores.

Termite mounds were theorised to increase vegetation resistance to drought, providing islands of refugia for revegetation of the surrounding matrix after drought (Bonachela et al. 2015). My results indicate that the Bonachela et al. (2015) model, at least for grasses, needs refining with a consideration of herbivory as mounds are grazing focal points during drought and were no more resistant to drought than matrix grasses. It would be interesting to see how mound and matrix grasses would respond to drought in the absence of mammal herbivores and whether their absence would validate the Bonachela et al. (2015) model. Woody plants were not examined and it would be interesting to see if browsing mammals impact woody plants as much as grazers do grasses during drought. Abraham et al. (2019) showed that obligate mammal browsers did not respond to drought but mixed feeders moved towards drought and incorporated more trees and forbs in their diet. This suggests that the Bonachela et al. (2015) model should also include the impact of browsing, as woody plant biomass on mounds may be as equally affected as grass biomass during drought; despite the potential for some deep rooted woody species to have greater access to the water stores in termite mounds (Kulmatiski et al. 2010, Kulmatiski and Beard 2013a).

Savannas are nutrient limited and any increase in N will have major consequences for vegetation structure with cascading effects on insect assemblages, particularly when combined with an increase in available water. KNP is fortunate to have a long history of research that has established baseline data for both plants and animals. My study suggests that conservation managers need to look more broadly at anthropogenic climate and environment change.

Management should also consider implementing a monitoring protocol for N deposition. Since 1989, regular veld condition assessments have been conducted in KNP at more than 500 sites that were chosen to proportionally represent the different landscapes in the park (Trollope et al. 1989). The assessment protocol, however, was simplified to evaluate 18 grass species and use these as indicators. Continuing assessments like these are vital but incorporating forbs into these assessments is critical, as these are indicators for fluctuations in plant species diversity. KNP does have a program for monitoring the diversity of large mammals but there is nothing on insect diversity. Although smaller in scale, baseline data for ants is available for at least three sites in KNP (Parr 2003). As ants respond to increases in grass biomass that correspond with declines in plant species diversity (Chapter 2), ants could be used as bioindicators for plant species diversity in grassy ecosystems. By expanding the veld condition assessments and by monitoring ants, the effects of N deposition and other GCDs on KNP can be determined.

References

Abraham, J. O., G. P. Hempson, and A. C. Staver. 2019. Drought-response strategies of savanna herbivores. Ecology and Evolution **9**: 7047-7056.

Andersen, A. N. 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. Biotropica **23**:575-585.

Andersen, A. N. 2019. Responses of ant communities to disturbance: five principles for understanding the disturbance dynamics of a globally dominant faunal group. Journal of Animal Ecology **88**:350-362.

Andersen, A. N., and W. M. Lonsdale. 1990. Herbivory by insects in Australian tropical savannas: a review. Journal of Biogeography **17**:433-444.

Andersen, A. N., J. A. Ludwig, L. M. Lowe, and D. C. F. Rentz. 2001. Grasshopper biodiversity and bioindicators in Australian tropical savannas: responses to disturbance in Kakadu National Park. Austral Ecology **26**:213-222.

Andersen, A. N., R. R. Ribbons, M. Pettit, and C. L. Parr. 2014. Burning for biodiversity: highly resilient ant communities respond only to strongly contrasting fire regimes in Australia's seasonal tropics. Journal of Applied Ecology **51**:1406-1413.

Andersen, A. N., and A. L. Yen. 1985. Immediate effects of fire on ants in the semi-arid mallee region of north-western Victoria. Australian Journal of Ecology **10**:25-30.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26**:32-46.

Anderson, M. J., and T. J. Willis. 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology **84**:511-525.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Annual Review of Entomology **36**:561-586.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? The American Naturalist **134**:545-561.

Archibald, S., W. J. Bond, W. A. Hoffmann, C. E. R. Lehmann, A. C. Staver, and N. Stevens. 2020. Distribution and determinants of savannas. Pages 1-24 *in* P. F. Scogings and M. Sankaran, editors. Savanna woody plants and large herbivores. John Wiley & Sons Ltd.

Archibald, S., C. E. R. Lehmann, C. M. Belcher, W. J. Bond, R. A. Bradstock, A. L. Daniau, K. G. Dexter, E. J. Forrestel, M. Greve, T. He, S. I. Higgins, W. A. Hoffmann, B. B. Lamont, D. J. McGlinn, G. R. Moncrieff, C. P. Osborne, J. G. Pausas, O. Price, B. S. Ripley, B. M. Rogers, D. W. Schwilk, M. F. Simon, M. R. Turetsky, G. R. V. d. Werf, and A. E. Zanne. 2018. Biological and geophysical feedbacks with fire in the Earth system. Environmental Research Letters **13**:033003.

Archibald, S., A. C. Staver, and S. A. Levin. 2012. Evolution of human-driven fire regimes in Africa. Proceedings of the National Academy of Sciences **109**:847.

Ashton, L. A., H. M. Griffiths, C. L. Parr, T. A. Evans, R. K. Didham, F. Hasan, Y. A. Teh, H. S. Tin, C. S. Vairappan, and P. Eggleton. 2019. Termites mitigate the effects of drought in tropical rainforest. Science **363**:174.

Augustine, D. J. 2010. Response of native ungulates to drought in semi-arid Kenyan rangeland. African Journal of Ecology **48**:1009-1020.

Augustine, D. J., and S. J. McNaughton. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. Ecosystems **9**:1242-1256.

Avolio, M. L., K. J. L. Pierre, G. R. Houseman, S. E. Koerner, E. Grman, F. Isbell, D. S. Johnson, and K. R. Wilcox. 2015. A framework for quantifying the magnitude and variability of community responses to global change drivers. Ecosphere **6**:1-14.

Bai, Y., J. Wu, Q. Xing, Q. Pan, J. Huang, D. Yang, and X. Han. 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology **89**:2140-2153.

Banschbach, V. S., and J. M. Herbers. 1999. Nest movements and population spatial structure of the forest ant *Myrmica punctiventris* (Hymenoptera: Formicidae). Annals of the Entomological Society of America **92**:414-423.

Barber, S. A. 1962. A diffusion and mass-flow concept of soil nutrient availability. Soil Science **93**:39-49.

Barnosky, A. D., E. A. Hadly, J. Bascompte, E. L. Berlow, J. H. Brown, M. Fortelius, W. M. Getz, J. Harte, A. Hastings, P. A. Marquet, N. D. Martinez, A. Mooers, P. Roopnarine, G. Vermeij, J. W. Williams, R. Gillespie, J. Kitzes, C. Marshall, N. Matzke, D. P. Mindell, E. Revilla, and A. B. Smith. 2012. Approaching a state shift in Earth's biosphere. Nature **486**:52.

Behmer, S. T. 2009. Insect herbivore nutrient regulation. Annual Review of Entomology **54**:165-187.

Behmer, S. T., and A. Joern. 2008. Coexisting generalist herbivores occupy unique nutritional feeding niches. Proceedings of the National Academy of Sciences **105**:1977.

Binkley, D., and P. Högberg. 1997. Does atmospheric deposition of nitrogen threaten Swedish forests? Forest Ecology and Management **92**:119-152.

Binkley, D., and P. Högberg. 2016. Tamm Review: Revisiting the influence of nitrogen deposition on Swedish forests. Forest Ecology and Management **368**:222-239.

Bishop, T. R., M. P. Robertson, H. Gibb, B. J. van Rensburg, B. Braschler, S. L. Chown, S. H. Foord, T. C. Munyai, I. Okey, P. G. Tshivhandekano, V. Werenkraut, and C. L. Parr. 2016. Ant assemblages have darker and larger members in cold environments. Global Ecology and Biogeography **25**:1489-1499.

Bobbink, R., K. Hicks, J. Galloway, T. Spranger, R. Alkemade, M. Ashmore, M. Bustamante, S. Cinderby, E. Davidson, F. Dentener, B. Emmett, J. W. Erisman, M. Fenn, F. Gilliam, A. Nordin, L. Pardo, and W. De Vries. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications **20**:30-59.

Bonachela, J. A., R. M. Pringle, E. Sheffer, T. C. Coverdale, J. A. Guyton, K. K. Caylor, S. A. Levin, and C. E. Tarnita. 2015. Termite mounds can increase the robustness of dryland ecosystems to climatic change. Science **347**:651.

Bond, W. J. 2008. What limits trees in C_4 grasslands and savannas? Annual Review of Ecology, Evolution, and Systematics **39**:641-659.

Bond, W. J., and S. Archibald. 2003. Confronting complexity: fire policy choices in South African savanna parks. International Journal of Wildland Fire **12**:381-389.

Bond, W. J., and J. E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution **20**:387-394.

Bond, W. J., and G. F. Midgley. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology **6**:865-869.

Bond, W. J., and C. L. Parr. 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. Biological Conservation **143**:2395-2404.

Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, P. B. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, L. Biederman, D. Blumenthal, C. S. Brown, L. A. Brudvig, Y. M. Buckley, M. Cadotte, C. Chu, E. E. Cleland, M. J. Crawley, P. Daleo, E. I. Damschen, K. F. Davies, N. M. DeCrappeo, G. Du, J. Firn, Y. Hautier, R. W. Heckman, A. Hector, J. HilleRisLambers, O. Iribarne, J. A. Klein, J. M. H. Knops, K. J. La Pierre, A. D. B. Leakey, W. Li, A. S. MacDougall, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, B. Mortensen, L. R. O'Halloran, J. L. Orrock, J. Pascual, S. M. Prober, D. A. Pyke, A. C. Risch, M. Schuetz, M. D. Smith, C.

J. Stevens, L. L. Sullivan, R. J. Williams, P. D. Wragg, J. P. Wright, and L. H. Yang. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. Nature **508**:517-520.

Bowman, D. M. J. S., J. Balch, P. Artaxo, W. J. Bond, M. A. Cochrane, C. M. D'Antonio, R. DeFries, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, M. Mack, M. A. Moritz, S. Pyne, C. I. Roos, A. C. Scott, N. S. Sodhi, and T. W. Swetnam. 2011. The human dimension of fire regimes on Earth. Journal of Biogeography **38**:2223-2236.

Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, J. H. Kastens, M. L. Floyd, J. Belnap, J. J. Anderson, O. B. Myers, and C. W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences of the United States of America **102**:15144.

Brock, C. E., J. H. Brock, and M. C. Grant. 1992. Effects of bird predation on grasshopper densities in an Arizona grassland. Ecology **73**:1706-1717.

Brown, A. M., D. I. Warton, N. R. Andrew, M. Binns, G. Cassis, and H. Gibb. 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. Methods in Ecology and Evolution **5**:344-352.

Brown, W. L. 1953. Revisionary studies in the ant tribe Dacetini. The American Midland Naturalist **50**:1-137.

Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: >50 years of data suggests CO_2 as a driver. Global Change Biology **18**:675-684.

Butt, B., A. Shortridge, and A. M. G. A. WinklerPrins. 2009. Pastoral herd management, drought coping strategies, and cattle mobility in southern Kenya. Annals of the Association of American Geographers **99**:309-334.

Byrne, K. M., P. B. Adler, and W. K. Lauenroth. 2017. Contrasting effects of precipitation manipulations in two Great Plains plant communities. Journal of vegetation science **28**:238-249.

Cai, W., S. Borlace, M. Lengaigne, P. van Rensch, M. Collins, G. Vecchi, A. Timmermann, A. Santoso, M. J. McPhaden, L. Wu, M. H. England, G. Wang, E. Guilyardi, and F.-F. Jin. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. Nature Climate Change **4**:111.

Campbell, D. J. 1999. Response to drought among farmers and herders in Southern Kajiado District, Kenya: a comparison of 1972-1976 and 1994-1995. Human Ecology **27**:377-416.

Cardoso, P., and S. R. Leather. 2019. Predicting a global insect apocalypse. Insect Conservation and Diversity **12**:263-267.

Cochrane, M. A., and C. P. Barber. 2009. Climate change, human land use and future fires in the Amazon. Global Change Biology **15**:601-612.

Cole, M. M. 1963. Vegetation and geomorphology in Northern Rhodesia: an aspect of the distribution of the savanna of Central Africa. Geographical Journal 129: 290–305.

Conradie, E. H., P. G. Van Zyl, J. J. Pienaar, J. P. Beukes, C. Galy-Lacaux, A. D. Venter, and G. V. Mkhatshwa. 2016. The chemical composition and fluxes of atmospheric wet deposition at four sites in South Africa. Atmospheric Environment **146**:113-131.

Craine, J. M., C. Morrow, and W. D. Stock. 2008. Nutrient concentration ratios and co-limitation in South African grasslands. New Phytologist **179**:829-836.

Cramer, M. D., H.-J. Hawkins, and G. A. Verboom. 2009. The importance of nutritional regulation of plant water flux. Oecologia **161**:15-24.

Crawley, M. J. 2007. The R Book. John Wiley & Sons.

Dai, A. 2013. Increasing drought under global warming in observations and models. Nature Climate Change **3**:52-58.

Dangerfield, J. M., T. S. Mccarthy, and W. N. Ellery. 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. Journal of Tropical Ecology **14**:507-520.

Davies, A. B., S. R. Levick, G. P. Asner, M. P. Robertson, B. J. van Rensburg, and C. L. Parr. 2014a. Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. Ecography **37**:852-862.

Davies, A. B., S. R. Levick, M. P. Robertson, B. J. van Rensburg, G. P. Asner, and C. L. Parr. 2016. Termite mounds differ in their importance for herbivores across savanna types, seasons and spatial scales. Oikos **125**:726-734.

Davies, A. B., M. P. Robertson, S. R. Levick, G. P. Asner, B. J. van Rensburg, and C. L. Parr. 2014b. Variable effects of termite mounds on African savanna grass communities across a rainfall gradient. Journal of Vegetation Science **25**:1405-1416.

Diamond, J. M. 1975. Assembly of species communities. Pages 342-444 *in* M. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard Univ. Press, Cambridge, MA.

Driver, A., K. Maze, A. T. Lombard, J. Nel, M. Rouget, J. K. Turpie, R. M. Cowling, P. Desmet, P. Goodman, J. Harris, Z. Jonas, B. Reyers, K. Sink, and T. Strauss. 2004. South African National Spatial Biodiversity Assessment 2004: Summary Report. Pretoria: South African National Biodiversity Institute.

Dumbrell, A. J., M. Nelson, T. Helgason, C. Dytham, and A. H. Fitter. 2009. Relative roles of niche and neutral processes in structuring a soil microbial community. The Isme Journal **4**:337.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology Letters **5**:558-567.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science **289**:2068.

Edwards, E. J., C. P. Osborne, C. A. E. Strömberg, and S. A. Smith. 2010. The origins of C_4 grasslands: integrating evolutionary and ecosystem science. Science **328**:587.

Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters **14**:709-722.

Erpenbach, A., M. Bernhardt-Römermann, R. Wittig, A. Thiombiano, and K. Hahn. 2013. The influence of termite-induced heterogeneity on savanna vegetation along a climatic gradient in West Africa. Journal of Tropical Ecology **29**:11-23.

Farji-Brener, A. G., G. Barrantes, and A. Ruggiero. 2004. Environmental rugosity, body size and access to food: a test of the size-grain hypothesis in tropical litter ants. Oikos **104**:165-171.

Fauchereau, N., S. Trzaska, M. Rouault, and Y. Richard. 2003. Rainfall variability and changes in southern Africa during the 20th century in the global warming context. Natural Hazards **29**:139-154.

February, E. C., N. Allsopp, T. Shabane, and D. Hattas. 2011. Coexistence of a C_4 grass and a leaf succulent shrub in an arid ecosystem. The relationship between rooting depth, water and nitrogen. Plant and Soil **349**:253-260.

February, E. C., S. I. Higgins, W. J. Bond, and L. Swemmer. 2013. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. Ecology **94**:1155-1164.

February, E. C., C. Wigley-Coetsee, G. D. Cook, J. Ratnam, and B. J. Wigley. 2020. Physiological traits of savanna woody species. Pages 309-329 *in* P. F. Scogings and M. Sankaran, editors. Savanna woody plants and large herbivores. John Wiley & Sons Ltd.

Fisher, B. L., and B. Bolton. 2016. Ants of Africa and Madagascar: a guide to the genera. University of California Press.

Frank, D. A. 2007. Drought effects on above- and belowground production of a grazed temperate grassland ecosystem. Oecologia **152**:131-139.

Franzke, A., and K. Reinhold. 2011. Stressing food plants by altering water availability affects grasshopper performance. Ecosphere **2**:1-13.

Fraterrigo, J. M., and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. Ecology Letters **11**:756-770.

Frich, P., L. V. Alexander, P. Della-Marta, B. Gleason, M. Haylock, A. M. G. K. Tank, and T. Peterson. 2002. Observed coherent changes in climatic extremes during the second half of the twentieth century. Climate Research **19**:193-212.

Frost, P., J.-C. Menaut, B. H. Walker, E. Medina, and T. Solbrigo. 1986. Responses of savannas to stress and disturbance. Biology International Special Issue 10 International Union of Biological Sciences, Paris, France.

Fynn, R. W. S., C. D. Morris, and T. J. Edwards. 2004. Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. Applied Vegetation Science **7**:1-10.

Fynn, R. W. S., and T. G. O'Connor. 2005. Determinants of community organization of a South African mesic grassland. Journal of Vegetation Science **16**:93-102.

Gandar, M. V. 1982a. Description of a fire and its effects in the Nylsvley Nature Reserve: a synthesis report. 0798826088, South African National Scientific Programmes Report No. 63, Pretoria.

Gandar, M. V. 1982b. The dynamics and trophic ecology of grasshoppers (Acridoidea) in a South African savanna. Oecologia **54**:370-378.

Gandar, M. V. 1983. Ecological notes and annotated checklist of the grasshoppers (Orthoptera: Acridoidea) of the savanna ecosystem project study area, Nylsvley. 0798828374, South African National Scientific Programmes Report No. 74, Pretoria.

Garcia, F. H., G. Fischer, and M. K. Peters. 2010. Taxonomy of the *Tetramorium weitzeckeri* species group (Hymenoptera: Formicidae) in the Afrotropical zoogeographical region. Zootaxa **2704**:1-90.

Gertenbach, W. P. D. 1983. Landscapes of the Kruger National Park. Koedoe **26**:113.

Gibb, H., B. F. Grossman, C. R. Dickman, O. Decker, and G. M. Wardle. 2019. Long-term responses of desert ant assemblages to climate. Journal of Animal Ecology **88**:1549-1563.

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

Gibson, D. J. 2009. Grasses and grassland ecology. Oxford University Press Inc., New York, NY.

Gosling, C. M., J. P. G. M. Cromsigt, N. Mpanza, and H. Olff. 2012. Effects of erosion from mounds of different termite genera on distinct functional grassland types in an African savannah. Ecosystems **15**:128-139.

Govender, N., W. S. W. Trollope, and B. W. V. Wilgen. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. Journal of Applied Ecology **43**:748-758.

Grace, J. B., T. M. Anderson, E. W. Seabloom, E. T. Borer, P. B. Adler, W. S. Harpole, Y. Hautier, H. Hillebrand, E. M. Lind, M. Pärtel, J. D. Bakker, Y. M. Buckley, M. J. Crawley, E. I. Damschen, K. F. Davies, P. A. Fay, J. Firn, D. S. Gruner, A. Hector, J.

M. H. Knops, A. S. MacDougall, B. A. Melbourne, J. W. Morgan, J. L. Orrock, S. M. Prober, and M. D. Smith. 2016. Integrative modelling reveals mechanisms linking productivity and plant species richness. Nature **529**:390-393.

Grant, C. C., and M. C. Scholes. 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. Biological Conservation **130**:426-437.

Greaver, T. L., C. M. Clark, J. E. Compton, D. Vallano, A. F. Talhelm, C. P. Weaver, L. E. Band, J. S. Baron, E. A. Davidson, C. L. Tague, E. Felker-Quinn, J. A. Lynch, J. D. Herrick, L. Liu, C. L. Goodale, K. J. Novak, and R. A. Haeuber. 2016. Key ecological responses to nitrogen are altered by climate change. Nature Climate Change **6**:836-843.

Gronenberg, W., J. Paul, S. Just, and B. Hölldobler. 1997. Mandible muscle fibers in ants: fast or powerful? Cell and Tissue Research **289**:347-361.

Haddad, N. M., J. Haarstad, and D. Tilman. 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia **124**:73-84.

Hempson, G. P., S. Archibald, and A. C. Staver. 2020. Fire and browsers in savannas. Pages 439-468 *in* P. F. Scogings and M. Sankaran, editors. Savanna woody plants and large herbivores. John Wiley & Sons Ltd.

Hendriks, R. J. J., L. G. Carvalheiro, R. M. J. C. Kleukers, and J. C. Biesmeijer. 2013. Temporal-spatial dynamics in orthoptera in relation to nutrient availability and plant species richness. PLoS ONE **8**:e71736.

Higgins, S. I., W. J. Bond, E. C. February, A. Bronn, D. I. W. Euston-Brown, B. Enslin, N. Govender, L. Rademan, S. O'Regan, A. L. F. Potgieter, S. Scheiter, R. Sowry, L. Trollope, and W. S. W. Trollope. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. Ecology **88**:1119-1125.

Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. Journal of Ecology **88**:213-229.

Higgins, S. I., M. D. Delgado-Cartay, E. C. February, and H. J. Combrink. 2011. Is there a temporal niche separation in the leaf phenology of savanna trees and grasses? Journal of Biogeography **38**:2165-2175.

Higgins, S. I., M. Keretetse, and E. C. February. 2015. Feedback of trees on nitrogen mineralization to restrict the advance of trees in C_4 savannahs. Biology Letters **11**.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O/'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature **486**:105-108.

Hoover, D. L., A. K. Knapp, and M. D. Smith. 2014. Resistance and resilience of a grassland ecosystem to climate extremes. Ecology **95**:2646-2656.

Huberty, A. F., and R. F. Denno. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology **85**:1383-1398.

Ingrisch, S. 1986. The plurennial life cycles of the European Tettigoniidae (Insecta: Orthoptera). 3. The effect of drought and the variable duration of the initial diapause. Oecologia **70**:624-630.

Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. Science **317**:58.

Izhaki, I., D. J. Levey, and W. R. Silva. 2003. Effects of prescribed fire on an ant community in Florida pine savanna. Ecological Entomology **28**:439-448.

Jackson, D. A. 1995. PROTEST: A procrustean randomization test of community environment concordance. Écoscience **2**:297-303.

Jamieson, M. A., A. M. Trowbridge, K. F. Raffa, and R. L. Lindroth. 2012. Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. Plant Physiology **160**:1719.

Joern, A. 1979. Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. Oecologia **38**:325-347.

Joern, A. 1992. Variable impact of avian predation on grasshopper assemblies in sandhills grassland. Oikos **64**:458–463.

Joern, A., T. Provin, and S. T. Behmer. 2012. Not just the usual suspects: insect herbivore populations and communities are associated with multiple plant nutrients. Ecology **93**:1002-1015.

Joseph, G. S., C. L. Seymour, G. S. Cumming, Z. Mahlangu, and D. H. M. Cumming. 2013. Escaping the flames: large termitaria as refugia from fire in miombo woodland. Landscape Ecology **28**:1505-1516.

Jouquet, P., V. Tavernier, L. Abbadie, and M. Lepage. 2005. Nests of subterranean fungus-growing termites (Isoptera, Macrotermitinae) as nutrient patches for grasses in savannah ecosystems. African Journal of Ecology **43**:191-196.

Jouquet, P., S. Traoré, C. Choosai, C. Hartmann, and D. Bignell. 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. European Journal of Soil Biology **47**:215-222.

Kay, M., and J. O. Wobbrock. 2019. ARTool: aligned rank transform for nonparametric factorial ANOVAs. R package version 0.10.6. http://doi.org/10.5281/zenodo.594511.

Keeley, J. E., and P. W. Rundel. 2005. Fire and the Miocene expansion of C_4 grasslands. Ecology Letters **8**: 683–690.

Knapp, A. K., D. L. Hoover, J. M. Blair, G. Buis, D. E. Burkepile, A. Chamberlain, S. L. Collins, R. W. S. Fynn, K. P. Kirkman, M. D. Smith, D. Blake, N. Govender, P. O'Neal, T. Schreck, and A. Zinn. 2012. A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing. Journal of Plant Ecology **5**:357-365.

Knight, M. H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. African Journal of Ecology **33**:377-394.

Korb, J., and K. E. Linsenmair. 2001. The causes of spatial patterning of mounds of a fungus-cultivating termite: results from nearest-neighbour analysis and ecological studies. Oecologia **127**:324-333.

Kruess, A., and T. Tscharntke. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. Biological Conservation **106**:293-302.

Kulmatiski, A., and K. H. Beard. 2013a. Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. Oecologia **171**:25-37.

Kulmatiski, A., and K. H. Beard. 2013b. Woody plant encroachment facilitated by increased precipitation intensity. Nature Climate Change **3**:833-837.

Kulmatiski, A., K. H. Beard, R. J. T. Verweij, and E. C. February. 2010. A depth-controlled tracer technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savanna. New Phytologist **188**:199-209.

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

Laliberté, E., P. Legendre, and B. Shipley. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Langenheder, S., and A. J. Székely. 2011. Species sorting and neutral processes are both important during the initial assembly of bacterial communities. The Isme Journal **5**:1086.

Leakey, A. D. B., E. A. Ainsworth, C. J. Bernacchi, A. Rogers, S. P. Long, and D. R. Ort. 2009. Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. Journal of Experimental Botany **60**:2859-2876.

Legendre, P., R. Galzin, and M. L. Harmelin-Vivien. 1997. Relating behavior to habitat: solutions to the fourth-corner problem. Ecology **78**:547-562.

Lehmann, C. E. R., T. M. Anderson, M. Sankaran, S. I. Higgins, S. Archibald, W. A. Hoffmann, N. P. Hanan, R. J. Williams, R. J. Fensham, J. Felfili, L. B. Hutley, J. Ratnam, J. San Jose, R. Montes, D. Franklin, J. Russell-Smith, C. M. Ryan, G. Durigan, P. Hiernaux, R. Haidar, D. M. J. S. Bowman, and W. J. Bond. 2014. Savanna vegetation-fire-climate relationships differ among continents. Science **343**:548-552.

Lehmann, C. E. R., S. A. Archibald, W. A. Hoffmann, and W. J. Bond. 2011. Deciphering the distribution of the savanna biome. New Phytologist **191**:197-209.

Lenhart, P. A., M. D. Eubanks, and S. T. Behmer. 2015. Water stress in grasslands: dynamic responses of plants and insect herbivores. Oikos **124**:381-390.

Levick, S. R., G. P. Asner, O. A. Chadwick, L. M. Khomo, K. H. Rogers, A. S. Hartshorn, T. Kennedy-Bowdoin, and D. E. Knapp. 2010a. Regional insight into savanna hydrogeomorphology from termite mounds. Nature Communications **1**:65.

Levick, S. R., G. P. Asner, T. Kennedy-Bowdoin, and D. E. Knapp. 2010b. The spatial extent of termite influences on herbivore browsing in an African savanna. Biological Conservation **143**:2462-2467.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science **294**:804-808.

Lourens, A. S. M., T. M. Butler, J. P. Beukes, P. G. van Zyl, S. Beirle, T. K. Wagner, K.-P. Heue, J. J. Pienaar, G. D. Fourie, and M. G. Lawrence. 2012. Re-evaluating the NO_2 hotspot over the South African Highveld. South African Journal of Science **108**:83-91.

Løvschal, M., P. K. Bøcher, J. Pilgaard, I. Amoke, A. Odingo, A. Thuo, and J.-C. Svenning. 2017. Fencing bodes a rapid collapse of the unique Greater Mara ecosystem. Scientific Reports **7**:41450.

MacDougall, A. S., K. S. McCann, G. Gellner, and R. Turkington. 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. Nature **494**:86.

Matimati, I., G. A. Verboom, and M. D. Cramer. 2014. Nitrogen regulation of transpiration controls mass-flow acquisition of nutrients. Journal of Experimental Botany **65**:159-168.

Matthée, J. J. 1951. The structure and physiology of the egg of *Locustana pardalina* (Walk.). Pretoria.

Mattson, W. J., and R. A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. BioScience **37**:110-118.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution **21**:178-185.

McGlynn, T. P., R. A. Carr, J. H. Carson, and J. Buma. 2004. Frequent nest relocation in the ant *Aphaenogaster araneoides*: resources, competition, and natural enemies. Oikos **106**:611-621.

Melbourne, B. A. 1999. Bias in the effect of habitat structure on pitfall traps: An experimental evaluation. Australian Journal of Ecology **24**:228-239.

Midgley, G. F., and W. J. Bond. 2015. Future of African terrestrial biodiversity and ecosystems under anthropogenic climate change. Nature Climate Change **5**:823-829.

Mobæk, R., A. K. Narmo, and S. R. Moe. 2005. Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda. Journal of Zoology **267**:97-102.

Moncrieff, G. R., S. Scheiter, L. Langan, A. Trabucco, and S. I. Higgins. 2016. The future distribution of the savannah biome: model-based and biogeographic contingency. Philosophical Transactions of the Royal Society B: Biological Sciences **371**:20150311.

Moritz, M. A., E. Batllori, R. A. Bradstock, A. M. Gill, J. Handmer, P. F. Hessburg, J. Leonard, S. McCaffrey, D. C. Odion, T. Schoennagel, and A. D. Syphard. 2014. Learning to coexist with wildfire. Nature **515**:58.

Mphepya, J. N., C. Galy-Lacaux, J. P. Lacaux, G. Held, and J. J. Pienaar. 2006. Precipitation chemistry and wet deposition in Kruger National Park, South Africa. Journal of Atmospheric Chemistry **53**:169-183.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. Wiley.

Murphy, G. E. P., T. N. Romanuk, J. G. Associate Editor: Kevin, and L. B. Editor: Judith. 2012. A meta-analysis of community response predictability to anthropogenic disturbances. The American Naturalist **180**:316-327.

Muvengwi, J., F. Parrini, E. T. F. Witkowski, and A. B. Davies. 2019. Are termite mounds always grazing hotspots? Grazing variability with mound size, season and geology in an African savanna. Ecosystems **22**:125-136.

Nackley, L. L., A. G. West, A. L. Skowno, and W. J. Bond. 2017. The nebulous ecology of native invasions. Trends in Ecology & Evolution **32**:814-824.

Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature **390**:507.

Nel, J. J. C., and P. H. Hewitt. 1969. A study of the food eaten by a field population of the Harvester termite, *Hodotermes mossambicus* (Hagen) and its relation to population density. Journal of the Entomological Society of Southern Africa **32**:123-131.

Nelson, F. 2008. Are large mammal declines in Africa inevitable? African Journal of Ecology **46**:3-4.

O'Connor, T. G., L. M. Haines, and H. A. Snyman. 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. Journal of Ecology **89**:850-860.

O'Connor, T. G., J. R. Puttick, and M. T. Hoffman. 2014. Bush encroachment in southern Africa: changes and causes. African Journal of Range & Forage Science **31**:67-88.

O'Hara, R. B., and D. J. Kotze. 2010. Do not log-transform count data. Methods in Ecology and Evolution **1**:118-122.

Ofiţeru, I. D., M. Lunn, T. P. Curtis, G. F. Wells, C. S. Criddle, C. A. Francis, and W. T. Sloan. 2010. Combined niche and neutral effects in a microbial wastewater treatment community. Proceedings of the National Academy of Sciences **107**:15345.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2017. vegan: community ecology package. R package version 2.4-3. https://CRAN.R-project.org/package=vegan.

Oksanen, L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos **94**:27-38.

Osborne, C.P., and D. J. Beerling. 2006. Review. Nature's green revolution: the remarkable evolutionary rise of C_4 plants. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences **361**: 173–194.

Parr, C. L. 2003. Ant assemblages in a Southern African savanna: local processes and conservation implications. University of Pretoria.

Parr, C. L. 2008. Dominant ants can control assemblage species richness in a South African savanna. Journal of Animal Ecology **77**:1191-1198.

Parr, C. L., A. N. Andersen, C. Chastagnol, and C. Duffaud. 2007. Savanna fires increase rates and distances of seed dispersal by ants. Oecologia **151**:33-41.

Parr, C. L., and S. L. Chown. 2003. Burning issues for conservation: a critique of faunal fire research in Southern Africa. Austral Ecology **28**:384-395.

Parr, C. L., P. Eggleton, A. B. Davies, T. A. Evans, and S. Holdsworth. 2016. Suppression of savanna ants alters invertebrate composition and influences key ecosystem processes. Ecology **97**:1611-1617.

Parr, C. L., E. F. Gray, and W. J. Bond. 2012. Cascading biodiversity and functional consequences of a global change–induced biome switch. Diversity and Distributions **18**:493-503.

Parr, C. L., H. G. Robertson, H. C. Biggs, and S. L. Chown. 2004. Response of African savanna ants to long-term fire regimes. Journal of Applied Ecology **41**:630-642.

Pausas, J. G., and C. L. Parr. 2018. Towards an understanding of the evolutionary role of fire in animals. Evolutionary Ecology **32**:113-125.

Pellissier, L., J. Wassef, J. Bilat, G. Brazzola, P. Buri, C. Colliard, B. Fournier, J. Hausser, G. Yannic, and N. Perrin. 2011. Adaptive colour polymorphism of *Acrida ungarica* H. (Orthoptera: Acrididae) in a spatially heterogeneous environment. Acta Oecologica **37**:93-98.

Peres-Neto, P. R., and D. A. Jackson. 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. Oecologia **129**:169-178.

Phoenix, G. K., B. A. Emmett, A. J. Britton, S. J. M. Caporn, N. B. Dise, R. Helliwell, L. Jones, J. R. Leake, I. D. Leith, L. J. Sheppard, A. Sowerby, M. G. Pilkington, E. C. Rowe, M. R. Ashmore, and S. A. Power. 2012. Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. Global Change Biology **18**:1197-1215.

Phoenix, G. K., W. K. Hicks, S. Cinderby, J. C. I. Kuylenstierna, W. D. Stock, F. J. Dentener, K. E. Giller, A. T. Austin, R. D. B. Lefroy, B. S. Gimeno, M. R. Ashmore, and P. Ineson. 2006. Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. Global Change Biology **12**:470-476.

Picker, M. D., C. Griffiths, and A. Weaving. 2004. Field guide to insects of South Africa. Struik Publishers, Cape Town.

Pohl, B., C. Macron, and P.-A. Monerie. 2017. Fewer rainy days and more extreme rainfall by the end of the century in Southern Africa. **7**:46466.

Polley, H. W., H. S. Mayeux, H. B. Johnson, and C. R. Tischler. 1997. Viewpoint: atmospheric CO_2, soil water, and shrub/grass ratios on rangelands. Journal of Range Management **50**:278-284.

Pöyry, J., M. Luoto, J. Paukkunen, J. Pykälä, K. Raatikainen, and M. Kuussaari. 2006. Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. Oikos **115**:401-412.

Prendini, L., L-J. Theron, K. van der Merwe, and N. Owen-Smith. 1996. Abundance and guild structure of grasshoppers (Orthoptera: Acridoidea) in communally grazed and protected savanna. African Zoology **31**:120-130.

Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics **11**:41-65.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. Global Biogeochemical Cycles **13**: 997–1027.

Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science **305**:1926.

Rutherford, M. C., L. Mucina, M. C. Lötter, G. J. Bredenkamp, J. H. L. Smit, C. R. Scott-Shaw, D. B. Hoare, P. S. Goodman, H. Bezuidenhout, L. Scott, F. Ellis, L. W. Powrie, F. Siebert, T. H. Mostert, B. J. Henning, C. E. Venter, K. G. T. Camp, S. J. Siebert, W. S. Matthews, J. E. Burrows, L. Dobson, N. van Rooyen, E. Schmidt, P. J. D. Winter, P. J. du Preez, R. A. Ward, S. Williamson, and P. J. H. Hurter. 2006. Savanna biome. Pages 439-539 *in* L. Mucina and M. C. Rutherford, editors. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Sala, O. E., L. A. Gherardi, L. Reichmann, E. Jobbágy, and D. Peters. 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. Philosophical Transactions of the Royal Society B: Biological Sciences **367**:3135-3144.

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

Sarmiento, G. 1984. The ecology of neotropical savannas. Harvard University Press, Harvard.

Sarty, M., K. L. Abbott, and P. J. Lester. 2006. Habitat complexity facilitates coexistence in a tropical ant community. Oecologia **149**:465-473.

Saunders, M. E., J. K. Janes, and J. C. O'Hanlon. 2019. Moving on from the insect apocalypse narrative: engaging with evidence-based insect conservation. BioScience **70**:80-89.

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics **28**:517-544.

Scholes, R. J., and B. H. Walker. 2004. An African savanna: synthesis of the Nylsvley study. Cambridge University Press.

Shongwe, M. E., G. J. v. Oldenborgh, B. v. d. Hurk, and M. v. Aalst. 2011. Projected changes in mean and extreme precipitation in Africa under global warming. Part II: East Africa. Journal of Climate **24**:3718-3733.

Siemann, E., D. Tilman, and J. Haarstad. 1996. Insect species diversity, abundance and body size relationships. Nature **380**:704-706.

Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. The American Naturalist **152**:738-750.

Sileshi, G. W., M. Arshad, S. Konaté, and P. O. Nkunika. 2010. Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. Journal of vegetation science **21**:923-937.

Simpson, K. J., B. S. Ripley, P. A. Christin, C. M. Belcher, C. E. R. Lehmann, G. H. Thomas, and C. P. Osborne. 2016. Determinants of flammability in savanna grass species. Journal of Ecology **104**:138-148.

Simpson, S. J., and D. Raubenheimer. 1993. A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. Philosophical Transactions: Biological Sciences **342**:381-402.

Sinclair, A. R. E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. Journal of Animal Ecology **44**:497-520.

Skowno, A. L., C. J. Poole, D. C. Raimondo, K. J. Sink, H. Van Deventer, L. Van Niekerk, L. R. Harris, L. B. Smith- Adao, K. A. Tolley, T. A. Zengeya, W. B. Foden, G. F. Midgley, and A. Driver. 2019. National Biodiversity Assessment 2018: the status of South Africa's ecosystems and biodiversity. Synthesis Report. South African National

Biodiversity Institute, an entity of the Department of Environment, Forestry and Fisheries, Pretoria.:1-214.

Smit, I. P. J., G. P. Asner, N. Govender, N. R. Vaughn, and B. W. Wilgen. 2016. An examination of the potential efficacy of high-intensity fires for reversing woody encroachment in savannas. Journal of Applied Ecology **53**:1623-1633.

Staver, A. C., W. J. Bond, W. D. Stock, S. J. van Rensburg, and M. S. Waldram. 2009. Browsing and fire interact to suppress tree density in an African savanna. Ecological Applications **19**:1909-1919.

Staver, A. C., J. Botha, and L. Hedin. 2017. Soils and fire jointly determine vegetation structure in an African savanna. New Phytologist **216**:1151-1160.

Staver, A. C., C. Wigley-Coetsee, and J. Botha. 2019. Grazer movements exacerbate grass declines during drought in an African savanna. Journal of Ecology **107**:1482-1491.

Steinke, T. D., and L. O. Nel. 1989. Some effects of termitaria on veld in the eastern Cape. Journal of the Grassland Society of Southern Africa **6**:152-155.

Stott, P. 2000. Combustion in tropical biomass fires: a critical review. Progress in Physical Geography: Earth and Environment **24**:355-377.

Strauss, S. Y. 1987. Direct and indirect effects of host-plant fertilization on an insect community. Ecology **68**:1670-1678.

Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodiversity & Conservation **10**:1141-1169.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature **427**:145-148.

Thuiller, W., S. Lavergne, C. Roquet, I. Boulangeat, B. Lafourcade, and M. B. Araujo. 2011. Consequences of climate change on the tree of life in Europe. Nature **470**:531-534.

Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. Nature **367**:363-365.

Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in Grasslands. Oecologia **89**:257-264.

Traniello, J. F. A. 1987. Comparative foraging ecology of north temperate ants: the role of worker size and cooperative foraging in prey selection. Insectes Sociaux **34**:118-130.

Trollope, W. S. W. 1984. Fire in savanna. Pages 149-175 *in* P. d. V. Booysen and N. M. Tainton, editors. Ecological effects of fire in South African ecosystems. Springer Berlin Heidelberg, Berlin, Heidelberg.

Trollope, W. S. W. 1990. Development of a technique for assessing veld condition in the Kruger National Park using key grass species. Journal of the Grassland Society of Southern Africa **7**:46-51.

Trollope, W. S. W., A. L. F. Potgieter, and N. Zambatis. 1989. Assessing veld condition in the Kruger National Park using key grass species. 1989 **32**:27.

Turner, J. S. 2019. Termites as mediators of the water economy of arid savanna ecosystems. Pages 401-414 *in* P. D'Odorico, A. Porporato, and C. Wilkinson Runyan, editors. Dryland ecohydrology. Springer International Publishing, Cham.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters **11**:1351-1363.

Underwood, E. C., and B. L. Fisher. 2006. The role of ants in conservation monitoring: if, when, and how. Biological Conservation **132**:166-182.

van der Plas, F., R. Howison, J. Reinders, W. Fokkema, and H. Olff. 2013. Functional traits of trees on and off termite mounds: understanding the origin of biotically-driven heterogeneity in savannas. Journal of vegetation science **24**:227-238.

van der Plas, F., and H. Olff. 2014. Mesoherbivores affect grasshopper communities in a megaherbivore-dominated South African savannah. Oecologia **175**:639-649.

van Klink, R., F. van der Plas, C. van Noordwijk, M. F. WallisDeVries, and H. Olff. 2015. Effects of large herbivores on grassland arthropod diversity. Biological reviews **90**:347-366.

van Oudtshoorn, F. 2012. Guide to grasses of Southern Africa. Briza Publications, Pretoria.

van Wilgen, B. W., H. C. Biggs, S. P. O'Regan, and N. Mare. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. South African Journal of Science 96:167-178.

van Wilgen, B. W., N. Boshoff, I. P. J. Smit, S. Solano-Fernandez, and L. van der Walt. 2016. A bibliometric analysis to illustrate the role of an embedded research capability in South African National Parks. Scientometrics **107**:185-212.

van Wilgen, N. J., and M. Herbst. 2017. Taking stock of parks in a changing world: The SANParks Global Environmental Change Assessment. SANParks, Cape Town.

Venter, F. J., R. J. Scholes, and H. C. Eckhardt. 2003. The abiotic template and its associated vegetation pattern. Pages 83-129 *in* J. T. du Toit, K. H. Rogers, and H. C. Biggs, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, DC.

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology **89**:2290-2301.

Walker, B. H. 1992. Biodiversity and ecological redundancy. Conservation Biology **6**:18-23.

Walker, B. H. 1995. Conserving biological diversity through ecosystem resilience. Conservation Biology **9**:747-752.

Walker, B. H., R. H. Emslie, R. N. Owen-Smith, and R. J. Scholes. 1987. To cull or not to cull: lessons from a southern African drought. Journal of Applied Ecology **24**:381-401.

Wang, Y., U. Naumann, S. T. Wright, D. Eddelbuettel, and D. I. Warton. 2017. Statistical methods for analysing multivariate abundance data. R package version 3.12. https://CRAN.R-project.org/package=mvabund.

Warton, D. I., S. D. Foster, G. De'ath, J. Stoklosa, and P. K. Dunstan. 2015. Model-based thinking for community ecology. Plant Ecology **216**:669-682.

Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos **74**:159-164.

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

Weltzin, J. F., and M. B. Coughenour. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. Journal of Vegetation Science **1**:325-334.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia **63**:90-105.

Wigley, B. J., W. J. Bond, and M. T. Hoffman. 2010. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? Global Change Biology **16**:964-976.

Wilcox, K. R., Z. Shi, L. A. Gherardi, N. P. Lemoine, S. E. Koerner, D. L. Hoover, E. Bork, K. M. Byrne, J. Cahill, S. L. Collins, S. Evans, A. K. Gilgen, P. Holub, L. Jiang, A. K. Knapp, D. LeCain, J. Liang, P. Garcia-Palacios, J. Peñuelas, W. T. Pockman, M. D. Smith, S. Sun, S. R. White, L. Yahdjian, K. Zhu, and Y. Luo. 2017. Asymmetric responses of primary productivity to precipitation extremes: a synthesis of grassland precipitation manipulation experiments. Global Change Biology **23**:4376-4385.

Williamson, D., and J. Williamson. 1984. Botswana's fences and the depletion of Kalahari wildlife. Oryx **18**:218-222.

Wilson, E. O., and B. Hölldobler. 2005. The rise of the ants: a phylogenetic and ecological explanation. Proceedings of the National Academy of Sciences **102**:7411-7414.

Wobbrock, J. O., L. Findlater, D. Gergle, and J. J. Higgins. 2011. The aligned rank transform for nonparametric factorial analyses using only anova procedures. Pages 143-146 Proceedings of the SIGCHI Conference on Human Factors in Computing Systems. ACM, Vancouver, BC, Canada.

Wragg, P. D., T. Mielke, and D. Tilman. 2018. Forbs, grasses, and grassland fire behaviour. Journal of Ecology **106**:1983-2001.

Zaloumis, N. P., and W. J. Bond. 2011. Grassland restoration after afforestation: no direction home? Austral Ecology **36**:357-366.

Appendix 1

Figures

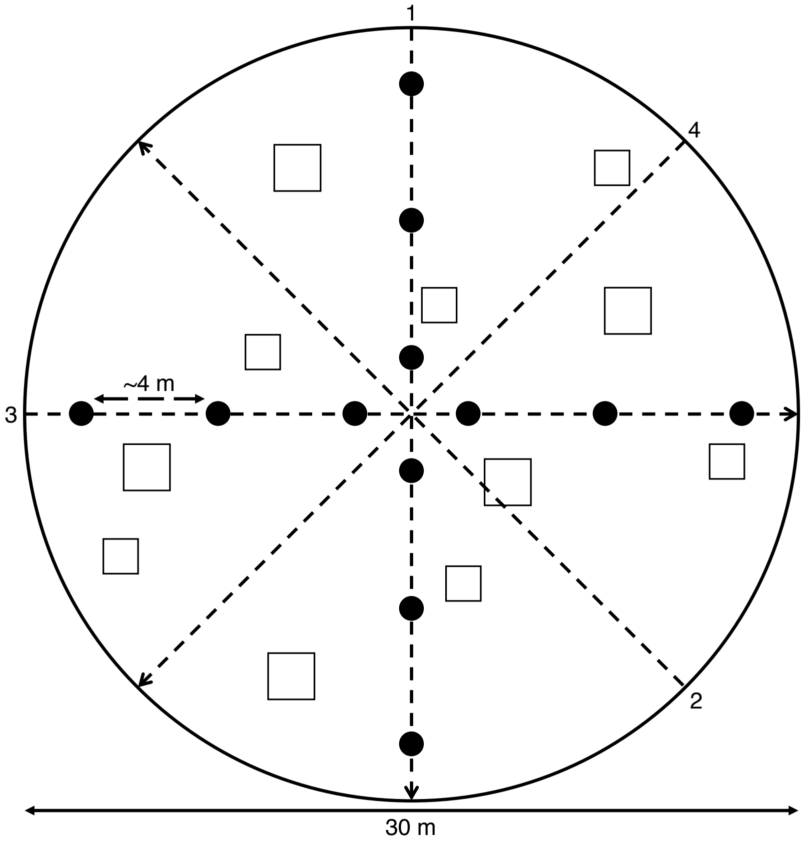

Figure 1: Schematic representation of an experimental plot, shown as partitioned for measurement of grass and forb species richness and percent cover (five 1 m^2 subplots, large squares), grass and forb biomass (six 0.0625 cm^2 subplots, small squares), grass seed biomass and grasshoppers (four sweep-net transects, dashed arrows), and ants (twelve pitfall traps, circles) (not to scale).

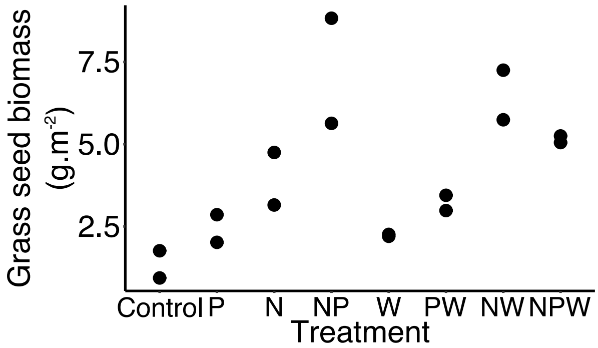

Figure 2: Response of grass seed biomass to experimental treatments. Plotted data are raw values. Treatment axis corresponds to resource additions (N = nitrogen, P = phosphorous, W = water).

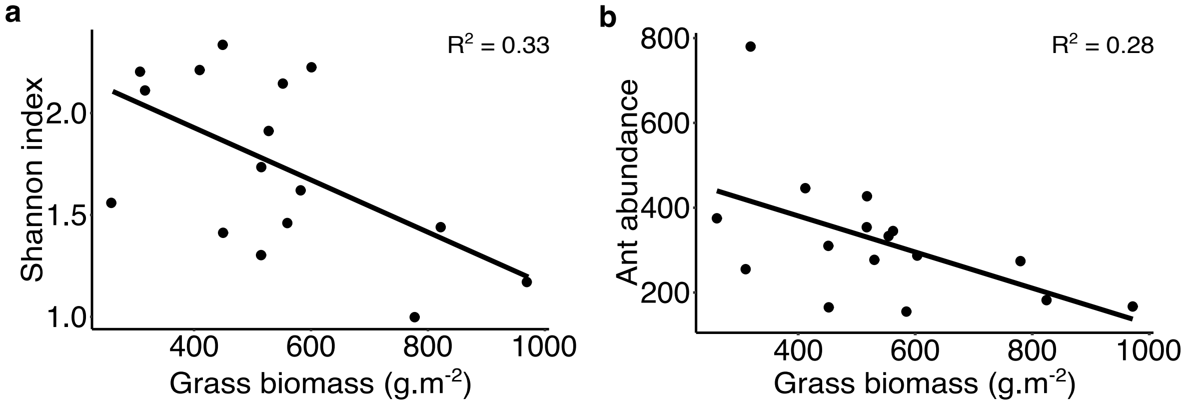

Figure 3: Simple regressions of (a) grasshopper Shannon index ($y = -0.001282x + 2.441356$, $R^2 = 0.33$, $p = 0.02$) and (b) ant total abundance ($y = -0.42584x + 550.993$, $R^2 = 0.28$, $p = 0.03$) against grass biomass.

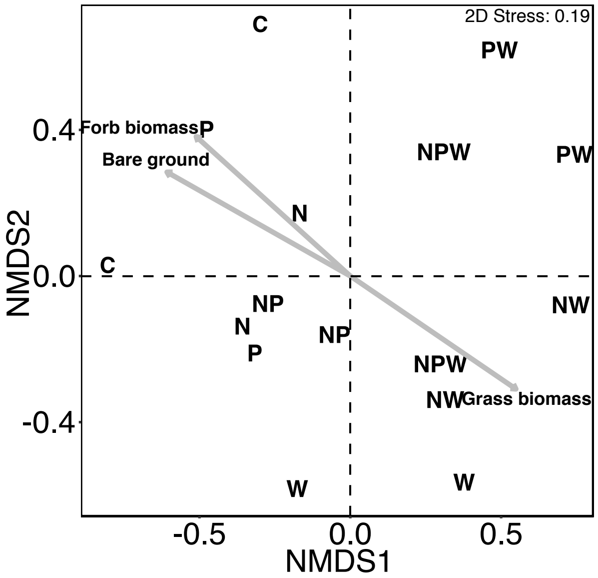

Figure 4: Nonmetric multidimensional scaling (nMDS) ordination of grasshopper common-species with overlaid environmental variables that have significant correlation with the separation of the assemblages. The nMDS ordination of grasshopper common-species was significantly correlated with increasing forb biomass ($r^2 = 0.41$, $p = 0.04$) and bare ground ($r^2 = 0.45$, $p = 0.004$) on control and unwatered plots and increasing grass biomass ($r^2 = 0.40$, $p = 0.04$) on watered plots. nMDS points correspond to resource additions (C = control, N = nitrogen, P = phosphorous, W = water).

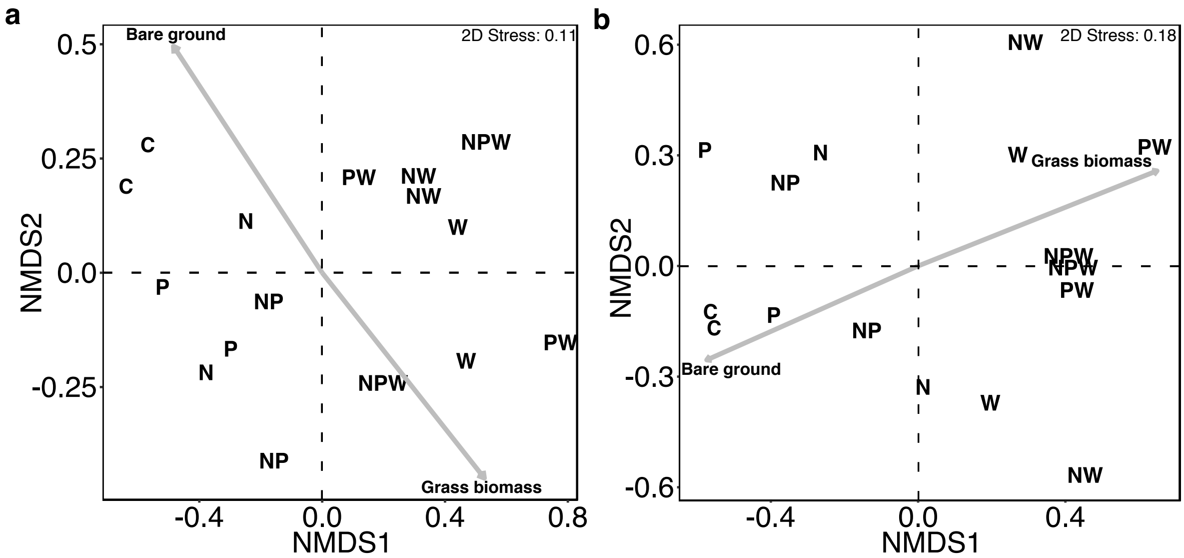

Figure 5: Nonmetric multidimensional scaling (nMDS) ordination of ant (a) common-species and (b) rare-species with overlaid environmental variables that have significant correlation with the separation of the assemblages. Both the nMDS ordinations of ant common and rare species were significantly correlated with increasing grass biomass on watered plots (Common-species: $r^2 = 0.48$, $p = 0.01$; Rare-species: $r^2 = 0.49$, $p = 0.01$), and increasing bare ground on control and unwatered plots (Common-species: $r^2 = 0.48$, $p = 0.001$; Rare-species: $r^2 = 0.39$, $p = 0.02$). nMDS points correspond to resource additions (C = control, N = nitrogen, P = phosphorous, W = water).

Tables

Table 1: Herbaceous species and their relative abundance with respect to control, unwatered, and watered plots. Relative abundance was calculated as the abundance per species divided by the abundance of all species within the plots. Species that were exclusive to the control, unwatered, or watered plots are denoted with a †. Letters correspond to resource additions (N = nitrogen, P = phosphorous, W = water).

Control plots		Unwatered plots (P, N, NP)		Watered plots (W, PW, NW, NPW)	
Species (Total = 26)	Relative abundance (%)	Species (Total = 25)	Relative abundance (%)	Species (Total = 20)	Relative abundance (%)
Digitaria eriantha	50.38	*Digitaria eriantha*	37.83	*Urochloa mosambicensis*	34.35
Schmidtia pappophoroides	7.91	*Urochloa mosambicensis*	22.36	*Chloris virgata*	30.30
Urochloa mosambicensis	7.54	*Eragrostis rigidior*	12.23	*Dactyloctenium gigantium*	13.89
Eragrostis rigidior	6.48	*Chloris virgata*	7.77	*Digitaria eriantha*	10.49
Tephrosia purpurea	4.36	*Panicum maximum*	7.09	*Eragrostis rigidior*	6.37
Chloris virgata	3.25	*Commelina africana*	3.15	*Panicum maximum*	1.75
Kyphocarpa angustifolia	2.91	*Dactyloctenium gigantium*	1.63	*Sida cordifolia*	0.67
Sida cordifolia	2.60	*Sida cordifolia*	1.34	*Cucumis zeyheri*†	0.57
Commelina africana	2.39	*Schmidtia pappophoroides*	1.01	Unidentified†	0.53
Waltheria indica	2.28	*Aristida bipartitia*†	0.89	*Crotolaria virgulata*	0.36
Ipomoea plebeia	2.14	*Tephrosia purpurea*	0.85	*Commelina benghalensis*	0.19
Commelina benghalensis	1.66	*Albutilon pervenica*	0.78	*Waltheria indica*	0.13
Evolvulus alsinoides	1.25	*Commelina benghalensis*	0.61	*Albutilon pervenica*	0.10
Corchorus asplendifolius	0.88	*Hibiscus micranthus*	0.58	*Ipomoea plebeia*	0.08
Tephrosia semiglabra†	0.63	*Talinum caffrum*	0.36	*Phyllanthus maderaspatensis*	0.08
Phyllanthus maderaspatensis	0.52	*Leucas sexdentata*†	0.35	*Solanum panduriforme*†	0.04
Heliotropum steudneri	0.51	*Ipomoea plebeia*	0.29	*Ipomoea magnusiana*†	0.03

Table 1 continued

Control plots		Unwatered plots (P, N, NP)		Watered plots (W, PW, NW, NPW)	
Species (Total = 26)	Relative abundance (%)	Species (Total = 25)	Relative abundance (%)	Species (Total = 20)	Relative abundance (%)
Hibiscus micranthus	0.51	*Rhuellia cordata*	0.26	*Rhuellia cordata*	0.03
Pogonathria squarosa†	0.38	*Kyphocarpa angustifolia*	0.25	*Hibiscus micranthus*	0.02
Talinum caffrum	0.33	*Heliotropum steudneri*	0.13	*Sida dregei*†	0.02
Phyllanthus nummulariifolius†	0.31	*Corchorus asplendifolius*	0.09		
Panicum maximum	0.31	*Evolvulus alsinoides*	0.06		
Melhania accuminata†	0.13	*Tragus berteronianus*†	0.03		
Portulaca quadrifida†	0.13	*Chaemechrista absus*†	0.03		
Indigastrum costatum†	0.10	*Cyperus rupestris*†	0.03		
Rhuellia cordata	0.10				

Table 2: The total abundance of grasshopper species in the control, unwatered and watered plots. Species that were exclusive to the control, unwatered, or watered plots are denoted with a †. Letters correspond to resource additions (N = nitrogen, P = phosphorous, W = water).

Control plots		Unwatered plots (P, N, NP)		Watered plots (W, PW, NW, NPW)	
Species (Total = 19)	Total abundance (n = 97)	Species (Total = 27)	Total abundance (n = 142)	Species (Total = 19)	Total abundance (n = 199)
Conocephalus caudalis	27	Orthoptera MOT-ZA01	37	*Orthoctha dasycnemis*	99
Orthoptera MOT-ZA01	13	Orthoptera MOT-ZA07	19	*Acrotylus* MOT-ZA01†	14
Rhachitopis MOT-ZA01	12	*Conocephalus caudalis*	11	Orthoptera MOT-ZA01	11
Zonocerus elegans	11	Orthoptera MOT-ZA20	10	*Conocephalus caudalis*	10
Orthoptera MOT-ZA02†	9	Orthoptera MOT-ZA15	9	Orthoptera MOT-ZA10	10
Phaneroptera MOT-ZA01	5	*Orthoctha dasycnemis*	7	Orthoptera MOT-ZA07	8
Brachytypus rotundifrons	4	*Rhachitopis* MOT-ZA04	7	Orthoptera MOT-ZA20	6
Orthoptera MOT-ZA07	4	*Zonocerus elegans*	6	Orthoptera MOT-ZA22†	6
Orthoptera MOT-ZA04†	2	*Phaneroptera* MOT-ZA01	5	*Rhachitopis* MOT-ZA04	6
Orthoptera MOT-ZA03	1	Orthoptera MOT-ZA21	4	*Phaneroptera* MOT-ZA01	5
Orthoptera MOT-ZA05†	1	Orthoptera MOT-ZA12†	3	Orthoptera MOT-ZA16	5
Orthoptera MOT-ZA06†	1	*Rhachitopis* MOT-ZA01	2	Orthoptera MOT-ZA21	5
Orthoptera MOT-ZA08†	1	*Brachytypus rotundifrons*	2	Orthoptera MOT-ZA11†	4
Orthoptera MOT-ZA13	1	Orthoptera MOT-ZA13	2	Orthoptera MOT-ZA15	3
Orthoptera MOT-ZA14	1	Orthoptera MOT-ZA14	2	Orthoptera MOT-ZA09†	2
Orthoptera MOT-ZA15	1	*Rhachitopis* MOT-ZA03†	2	*Truxalis* MOT-ZA01	2
Phaneroptera MOT-ZA02	1	*Orthoptera* MOT-ZA17†	2	Orthoptera MOT-ZA18†	1
Orthoctha MOT-ZA01	1	*Tylopsis* MOT-ZA01†	2	Orthoptera MOT-ZA19	1
Orthoptera MOT-ZA20	1	*Orthoctha* MOT-ZA01	2	*Orthoctha* MOT-ZA02†	1
		Orthoptera MOT-ZA03	1		
		Truxalis MOT-ZA01	1		

Table 2 continued

Control plots		Unwatered plots (P, N, NP)		Watered plots (W, PW, NW, NPW)	
Species (Total = 19)	Total abundance (n = 97)	Species (Total = 27)	Total abundance (n = 142)	Species (Total = 19)	Total abundance (n = 199)
		Orthoptera MOT-ZA10	1		
		Rhachitopis MOT-ZA02†	1		
		Orthoptera MOT-ZA16	1		
		Phaneroptera MOT-ZA02	1		
		Orthoptera MOT-ZA19	1		
		Orthoctha MOT-ZA03†	1		

Table 3: The total abundance of ant species in the control, unwatered and watered plots. Species that were exclusive to the control, unwatered, or watered plots are denoted with a †. Letters correspond to resource additions (N = nitrogen, P = phosphorous, W = water).

Control plots		Unwatered plots (N, P, NP)		Watered plots (W, NW, PW, NPW)	
Species (Total = 33)	Total abundance (n = 1155)	Species (Total = 53)	Total abundance (n = 2058)	Species (Total = 56)	Total abundance (n = 1919)
Monomorium junodi	555	*Monomorium junodi*	422	*Tetramorium weitzeckeri*	417
Tetramorium baufra	79	*Trichomyrmex emeryi*	199	*Tetramorium* MOT-ZA03	229
Pheidole MOT-ZA05	69	*Tetramorium sericeiventre*	168	*Messor* MOT-ZA01	185
Trichomyrmex emeryi	64	*Monomorium* MOT-ZA04	150	*Monomorium junodi*	179
Tetramorium sericeiventre	57	*Pheidole* MOT-ZA05	120	*Megaponera analis*	95
Pheidole MOT-ZA03	56	*Pheidole* MOT-ZA03	101	*Pheidole* MOT-ZA09	76
Tapinolepis MOT-ZA01	39	*Messor* MOT-ZA01	85	*Tetramorium sericeiventre*	71
Ocymyrmex MOT-ZA01	37	*Tetramorium weitzeckeri*	85	*Trichomyrmex emeryi*	63
Messor MOT-ZA01	35	*Pheidole* MOT-ZA04	85	*Camponotus maculatus*	60
Tetramorium MOT-ZA04	33	*Tetramorium* MOT-ZA04	68	*Tetramorium setigerum*	60
Monomorium damarense	22	*Monomorium damarense*	60	*Bothroponera* MOT-ZA02	45
Monomorium MOT-ZA01	14	*Tetramorium* MOT-ZA07	59	*Lepisiota* MOT-ZA02†	33
Pheidole MOT-ZA08	10	*Carebara* MOT-ZA01	56	*Pheidole* MOT-ZA03	32
Camponotus MOT-ZA01	9	*Megaponera analis*	55	*Monomorium albopilosum*†	27
Monomorium MOT-ZA02	9	*Tetramorium* MOT-ZA05	39	*Tetramorium* MOT-ZA07	27
Camponotus MOT-ZA03	8	*Bothroponera crassa*	36	*Bothroponera crassa*	23
Pheidole MOT-ZA07	7	*Tetramorium baufra*	25	*Pheidole* MOT-ZA08	23
Tapinoma MOT-ZA01	7	*Tapinolepis* MOT-ZA01	22	*Pheidole* MOT-ZA07	21
Lepisiota MOT-ZA03	7	*Pheidole* MOT-ZA08	22	*Pheidole* MOT-ZA04	20
Carebara MOT-ZA01	6	*Tetramorium setuliferum*	20	*Myrmicaria* MOT-ZA01	17
Camponotus maculatus	6	*Pheidole* MOT-ZA07	16	*Cardiocondyla* MOT-ZA02	15

Table 3 continued

Control plots		Unwatered plots (N, P, NP)		Watered plots (W, NW, PW, NPW)	
Species (Total = 33)	Total abundance (n = 1155)	Species (Total = 53)	Total abundance (n = 2058)	Species (Total = 56)	Total abundance (n = 1919)
Ophthalmopone berthoudi	6	*Tapinoma* MOT-ZA01	15	*Monomorium* MOT-ZA03	15
Monomorium MOT-ZA04	5	*Tetramorium fridigum*	15	*Lepisiota* MOT-ZA01	13
Bothroponera crassa	3	*Camponotus maculatus*	13	*Brachyponera sennaarensis*	12
Camponotus MOT-ZA05	3	*Tetramorium* MOT-ZA03	13	*Carebara* MOT-ZA01	12
Monomorium MOT-ZA03	2	*Tetramorium setigerum*	12	*Ocymyrmex* MOT-ZA01	12
Tetramorium weitzeckeri	1	*Lepisiota* MOT-ZA03	9	*Pheidole* MOT-ZA06	12
Tetramorium MOT-ZA02	1	*Ophthalmopone berthoudi*	9	*Camponotus* MOT-ZA03	11
Pheidole MOT-ZA02	1	*Camponotus* MOT-ZA03	7	*Monomorium* MOT-ZA02	11
Meranoplus glaber	1	*Brachyponera sennaarensis*	7	*Pheidole* MOT-ZA05	10
Tetramorium MOT-ZA01	1	*Camponotus* MOT-ZA01	6	*Monomorium* MOT-ZA04	9
Anochetus MOT-ZA01†	1	*Tetramorium* MOT-ZA02	6	*Camponotus* MOT-ZA01	8
Crematogastor MOT-ZA01†	1	*Myrmicaria* MOT-ZA01	6	*Tetramorium* MOT-ZA05	7
		Ocymyrmex MOT-ZA01	5	*Crematogastor* MOT-ZA02	6
		Monomorium MOT-ZA01	5	*Tapinolepis* MOT-ZA01	6
		Pheidole MOT-ZA02	4	*Tetramorium notiale*	6
		Bothroponera MOT-ZA02	4	*Tetramorium setuliferum*	6
		Crematogastor MOT-ZA02	4	*Leptogenys* MOT-ZA01	5
		Lepisiota MOT-ZA01	3	*Strumigenys* MOT-ZA01†	5
		Pheidole MOT-ZA09	3	*Mesoponera ambigua*†	4
		Solenopsis MOT-ZA02†	3	*Cardiocondyla emeryi*†	3
		Meranoplus magretti	2	*Cardiocondyla* MOT-ZA01	3
		Pheidole MOT-ZA01	2	*Monomorium damarense*	3
		Pheidole MOT-ZA06	2	*Monomorium* MOT-ZA01	3

Table 3 continued

Control plots		Unwatered plots (N, P, NP)		Watered plots (W, NW, PW, NPW)	
Species (Total = 33)	Total abundance (n = 1155)	Species (Total = 53)	Total abundance (n = 2058)	Species (Total = 56)	Total abundance (n = 1919)
		Solenopsis MOT-ZA01[†]	2	*Tetramorium fridigum*	3
		Monomorium MOT-ZA03	1	*Calyptomyrmex* MOT-ZA01[†]	2
		Meranoplus glaber	1	*Camponotus* MOT-ZA05	2
		Tetramorium MOT-ZA01	1	*Carebara* MOT-ZA02[†]	2
		Cardiocondyla MOT-ZA01	1	*Tetramorium decem*[†]	2
		Cardiocondyla MOT-ZA02	1	*Tetramorium* MOT-ZA04	2
		Leptogenys MOT-ZA01	1	*Leptogenys* MOT-ZA02[†]	1
		Tetramorium MOT-ZA12	1	*Meranoplus magretti*	1
		Tetramorium notiale	1	*Pheidole* MOT-ZA01	1
				Tapinoma MOT-ZA01	1
				Tetramorium MOT-ZA02	1
				Tetramorium MOT-ZA12	1

Appendix 2

Figures

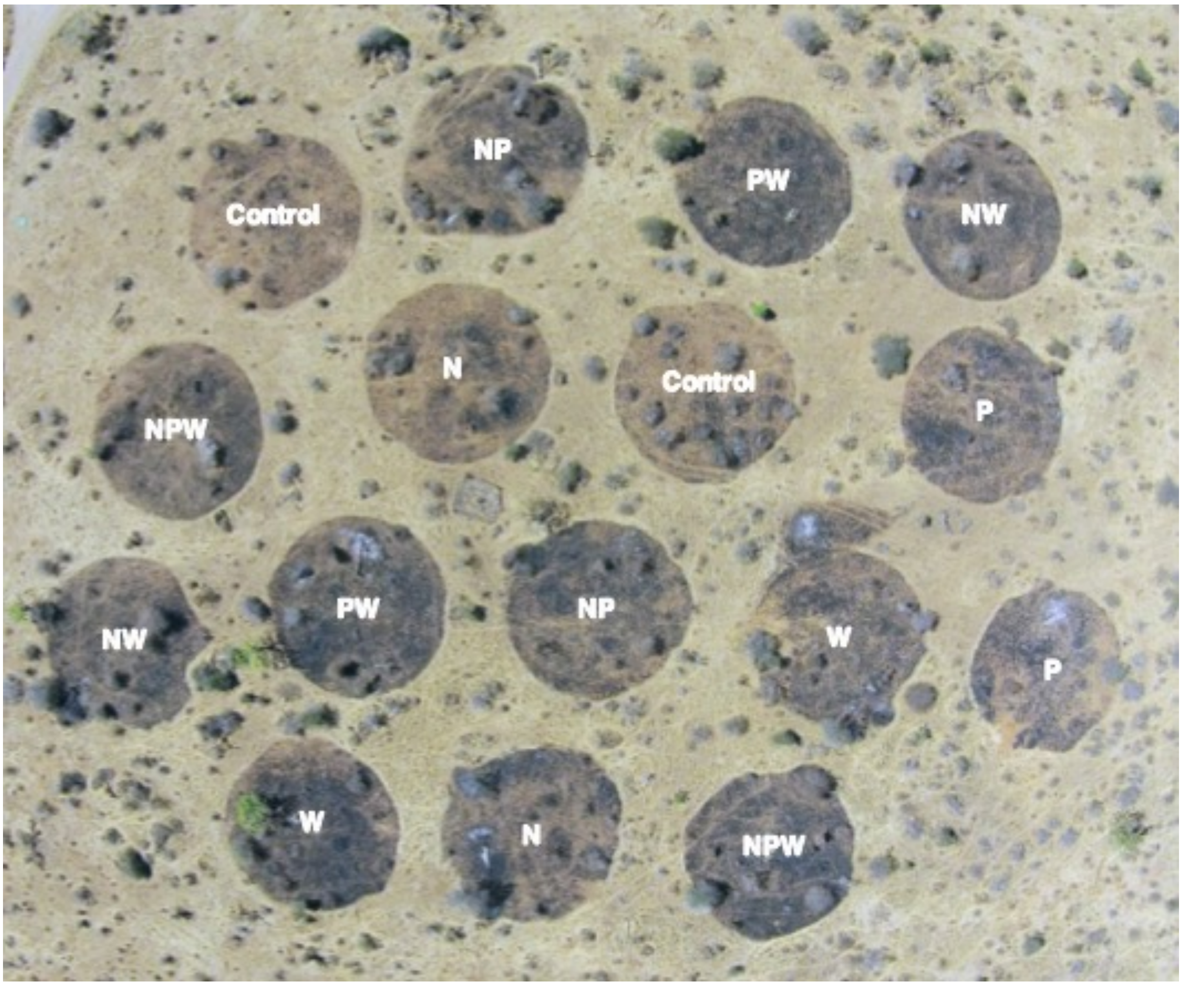

Figure 1: Study site after fire in August 2014. Letters correspond to resource additions (N = nitrogen, P = phosphorous, W = water). Photo: Navashni Govender.

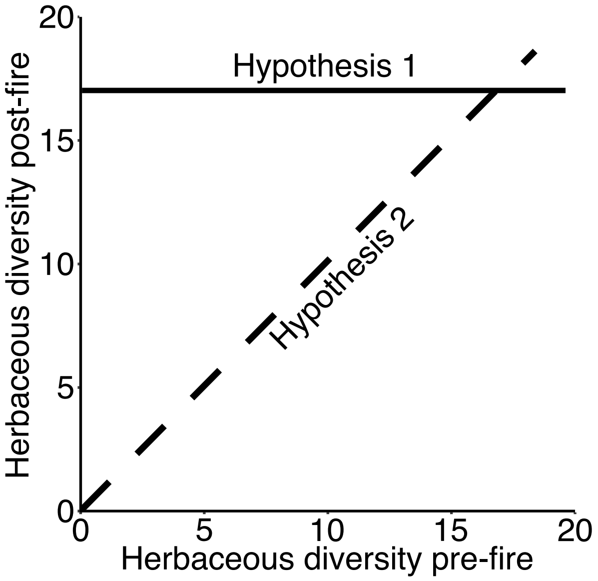

Figure 2: Hypothetical relationships between pre- and post-fire herbaceous diversity with regression slope close to zero supporting hypothesis one and a regression slope close to one supporting hypothesis two.

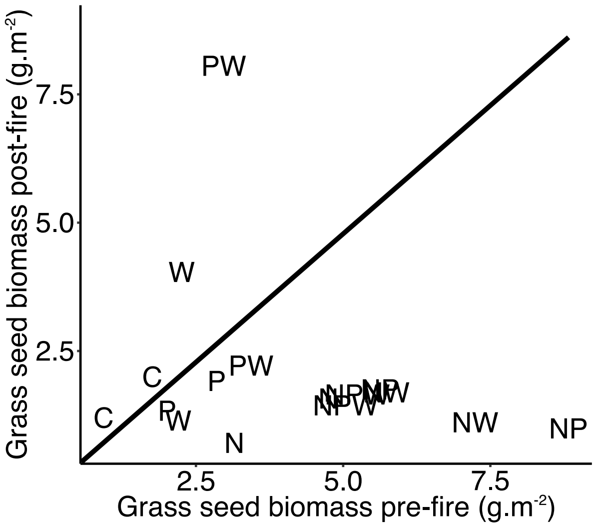

Figure 3: Grass seed biomass post-fire vs pre-fire. Plotted line is the 1:1 ratio. Grass seed biomass decreased as a result of the fire (paired t-test: t = -3.2249, df = 15, p = 0.006). Points correspond to resource additions (C = control, N = nitrogen, P = phosphorous, and W = water). Grass seed biomass was obtained by collecting seeds from 50 sweeps of a 40 cm diameter sweep net in each of four transects through the centre of each plot in January 2014 and 2015. All seed was weighed and dried at 80 ºC for 24 hours. One sweep was equivalent to ~0.1256 m^2, which equates to a sampled area of 25.1 m^2 per plot.

Tables

Table 1: Herbaceous species and their relative abundance post-fire with respect to control, unwatered, and watered plots. Relative abundance was calculated as the abundance per species divided by the abundance of all species within the plots. Species that were exclusive to the control, unwatered, or watered plots are denoted with a †. Letters correspond to resource additions (N = nitrogen, P = phosphorous, W = water).

Control plots		Unwatered plots (P, N, NP)		Watered plots (W, PW, NW, NPW)	
Species (Total = 17)	Relative abundance (%)	Species (Total = 20)	Relative abundance (%)	Species (Total = 8)	Relative abundance (%)
Commelina benghalensis	26.10	*Urochloa mosambicensis*	40.65	*Dactyloctenium gigantium*	83.24
Eragrostis rigidior	23.33	*Digitaria erianthra*	25.11	*Chloris virgata*	9.16
Digitaria erianthra	15.47	*Eragrostis rigidior*	15.24	*Urochloa mosambicensis*	4.56
Urochloa mosambicensis	10.85	*Commelina africana*	3.33	*Eragrostis rigidior*	1.38
Tragus berteronianus	6.70	*Commelina benghalensis*	3.21	*Digitaria erianthra*	0.81
Commelina africana	4.85	*Dactyloctenium gigantium*	2.84	*Zaleya pentantra*†	0.71
Leucas sexdentata	2.77	*Tragus berteronianus*	1.67	*Cucumis anguria*†	0.07
Chloris virgata	1.85	*Gisekia africana*†	1.54	Unidentified†	0.07
Indigofera vicioides	1.39	*Tribulus terrestris*†	1.48		
Limeum sulcatum†	1.39	*Chloris virgata*	0.93		
Dactyloctenium gigantium	1.39	*Ipomea sinensis*†	0.74		
Ipomea obscura†	1.15	*Leucas sexdentata*	0.74		
Ornithogalum seineri	1.15	*Portulaca quadrifida*	0.62		
Portulaca quadrifida	0.46	*Indigofera vicioides*	0.43		
Waltheria indica	0.46	*Laggera diccurrens*†	0.37		
Kyllinga alba†	0.46	*Ornithogalum seineri*	0.31		
Sida cordifolia	0.23	*Aristida bipartitia*	0.31		

Table 1 continued

Control plots		Unwatered plots (P, N, NP)		Watered plots (W, PW, NW, NPW)	
Species (Total = 17)	Relative abundance (%)	Species (Total = 20)	Relative abundance (%)	Species (Total = 8)	Relative abundance (%)
		Hibiscus physciloides†	0.19		
		Sida cordifolia	0.19		
		Waltheria indica	0.12		

Table 2: Grasshopper abundance post-fire split by species and the control, unwatered and watered plots. Species that were exclusive to the control, unwatered, or watered plots are denoted with a †. Letters correspond to resource additions (N = nitrogen, P = phosphorous, W = water).

Control plots		Unwaterd plots (P, N, NP)		Watered plots (W, PW, NW, NPW)	
Species (Total = 2)	Abundance (n = 7)	Species (Total = 7)	Abundance (n = 142)	Species (Total = 18)	Abundance (n = 199)
Zonocerus elegans	6	*Zonocerus elegans*	23	*Conocephalus caudalis*	37
Orthoctha dasycnemis	1	*Conocephalus caudalis*	10	*Orthoctha dasycnemis*	8
		Orthoptera MOT-ZA25	3	Orthoptera MOT-ZA24†	8
		Orthoptera MOT-ZA01†	1	*Zonocerus elegans*	6
		Orthoptera MOT-ZA27†	1	Orthoptera MOT-ZA25	4
		Tylopsis MOT-ZA01	1	*Truxalis* MOT-ZA01†	2
		Orthoptera MOT-ZA20†	1	Orthoptera MOT-ZA15†	2
				Ruspolia MOT-ZA01†	2
				Rhachitopis MOT-ZA04†	2
				Tetrigidae MOT-ZA01†	2
				Phaneroptera MOT-ZA01†	1
				Acrotylus MOT-ZA01†	1
				Orthoptera MOT-ZA23†	1
				Orthoptera MOT-ZA26†	1
				Orthoptera MOT-ZA28†	1
				Tylopsis MOT-ZA01	1
				Orthoptera MOT-ZA18†	1
				Orthoctha MOT-ZA02†	1

Table 3: Ant abundance post-fire split by species and the control, unwatered and watered plots. Species that were exclusive to the control, unwatered, or watered plots are denoted with a †. Letters correspond to resource additions (N = nitrogen, P = phosphorous, W = water).

Control plots		Unwatered plots (N, P, NP)		Watered plots (W, NW, PW, NPW)	
Species (Total = 31)	Abundance (n = 998)	Species (Total = 44)	Abundance (n = 4828)	Species (Total = 49)	Abundance (n = 3179)
Tetramorium setuliferum	231	*Tetramorium setuliferum*	893	*Tetramorium weitzeckeri*	619
Ocymyrmex MOT-ZA01	114	*Monomorium junodi*	623	*Messor* MOT-ZA01	532
Tetramorium sericeiventre	111	*Monomorium* MOT-ZA03	581	*Monomorium junodi*	435
Messor MOT-ZA01	102	*Messor* MOT-ZA01	564	*Trichomyrmex emeryi*	281
Trichomyrmex emeryi	100	*Tetramorium sericeiventre*	477	*Tetramorium setuliferum*	234
Monomorium junodi	61	*Ocymyrmex* MOT-ZA01	423	*Ocymyrmex* MOT-ZA01	222
Tetramorium baufra	49	*Trichomyrmex emeryi*	399	*Tetramorium* sericeiventre	211
Pheidole MOT-ZA05	48	*Pheidole* MOT-ZA04	99	*Myrmicaria* MOT-ZA01	98
Tapinolepis MOT-ZA01	32	*Monomorium damarense*	91	*Brachyponera sennaarensis*	65
Pheidole MOT-ZA04	25	*Brachyponera sennaarensis*	83	*Monomorium damarense*	47
Monomorium MOT-ZA04	15	*Tapinolepis* MOT-ZA01	79	*Megaponera analis*†	45
Myrmicaria MOT-ZA01	14	*Monomorium* MOT-ZA04	73	*Pheidole* MOT-ZA05	43
Pheidole MOT-ZA07	13	*Tetramorium weitzeckeri*	59	*Tetramorium setigerum*	33
Ophthalmopone berthoudi	11	*Pheidole* MOT-ZA03	50	*Bothroponera crassa*	28
Tetramorium MOT-ZA04	10	*Tetramorium baufra*	40	*Ophthalmopone berthoudi*	28
Bothroponera crassa	9	*Pheidole* MOT-ZA05	39	*Tetramorium* MOT-ZA03†	22
Meranoplus magretti	9	*Tetramorium* MOT-ZA02	26	*Monomorium* MOT-ZA04	21
Pheidole MOT-ZA03	8	*Tetramorium* MOT-ZA07	25	*Pheidole* MOT-ZA03	19
Camponotus MOT-ZA07†	6	*Camponotus* MOT-ZA01	24	*Pheidole* MOT-ZA04	18
Crematogastor MOT-ZA02	5	*Pheidole* MOT-ZA07	22	*Pheidole* MOT-ZA08	18
Monomorium damarense	5	*Tetramorium* MOT-ZA04	17	*Camponotus* MOT-ZA01	16
Pheidole MOT-ZA08	5	*Ophthalmopone berthoudi*	15	*Monomorium* MOT-ZA03	13

Table 3 continued

Control plots		Unwatered plots (N, P, NP)		Watered plots (W, NW, PW, NPW)	
Species (Total = 31)	Abundance (n = 998)	Species (Total = 44)	Abundance (n = 4828)	Species (Total = 49)	Abundance (n = 3179)
Camponotus MOT-ZA03	4	*Camponotus* MOT-ZA03	14	*Pheidole* MOT-ZA06	13
Camponotus maculatus	2	*Pheidole* MOT-ZA09	14	*Pheidole* MOT-ZA09	11
Euponera sharpi	2	*Bothroponera crassa*	13	*Tapinolepis* MOT-ZA01	10
Tetramorium MOT-ZA07	2	*Pheidole* MOT-ZA06	12	*Tetramorium* MOT-ZA07	10
Camponotus MOT-ZA05	1	*Meranoplus magretti*	10	*Camponotus maculatus*	9
Monomorium MOT-ZA03	1	*Tetramorium* MOT-ZA01	9	*Camponotus* MOT-ZA03	9
Tapinoma MOT-ZA01	1	*Crematogastor* MOT-ZA02	8	*Tetramorium decem*[†]	6
Tetramorium MOT-ZA01	1	*Pheidole* MOT-ZA08	7	*Tetramorium* MOT-ZA04	6
Tetramorium MOT-ZA02	1	*Tapinoma* MOT-ZA01	7	*Carebara* MOT-ZA01[†]	5
		Pheidole MOT-ZA02	6	*Leptogenys* MOT-ZA01[†]	5
		Mesoponera ambigua[†]	5	*Pheidole* MOT-ZA07	5
		Myrmicaria MOT-ZA01	5	*Crematogastor* MOT-ZA02	4
		Lepisiota MOT-ZA03[†]	3	*Lepisiota* MOT-ZA02[†]	4
		Monomorium MOT-ZA01[†]	3	*Strumigenys* MOT-ZA01[†]	4
		Euponera sharpi	2	*Tetramorium* MOT-ZA01	4
		Tetramorium fridigum	2	*Tetramorium* MOT-ZA02	4
		Camponotus maculatus	1	*Camponotus* MOT-ZA05	3
		Camponotus MOT-ZA05	1	*Lepisiota* MOT-ZA01	3
		Lepisiota MOT-ZA01	1	*Leptogenys* MOT-ZA02[†]	3
		Meranoplus glaber[†]	1	*Tetramorium baufra*	3
		Solenopsis MOT-ZA01[†]	1	*Tetramorium fridigum*	3
		Tetramorium setigerum	1	*Tetramorium notiale*[†]	2
				Bothroponera MOT-ZA02[†]	1
				Monomorium MOT-ZA02[†]	1

Table 3 continued

Control plots		Unwatered plots (N, P, NP)		Watered plots (W, NW, PW, NPW)	
Species (Total = 31)	Abundance (n = 998)	Species (Total = 44)	Abundance (n = 4828)	Species (Total = 49)	Abundance (n = 3179)
				Odontomachus troglodytes†	1
				Pheidole MOT-ZA02	1
				Tapinoma MOT-ZA02†	1

Appendix 3

Figures

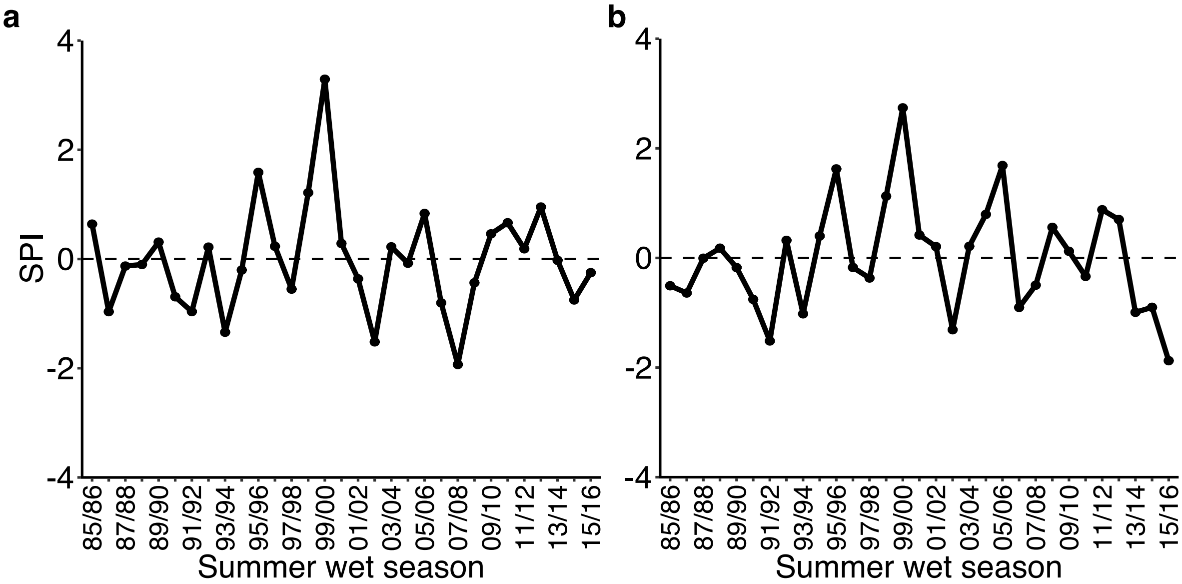

Figure 1: Wet season standardised precipitation index (SPI) for (a) Pretoriuskop and (b) Skukuza from 1985/86 to 2015/16. SPI calculated using precipitation data from Pretoriuskop and Skukuza from 1985/86 to 2015/16. Negative values indicate drier-than-average conditions and positive values indicate wetter-than-average conditions, with the dashed line indicating average conditions.

Tables

Table 1: Similarity percentage (SIMPER) results for the Skukuza ant assemblage on the mounds versus at the savanna plots for (a) 2012 and (b) 2016. Average abundance per mound and savanna plot and the percentage of the species contribution to assemblage differences shown.

Species	Average abundance mounds	Average abundance savanna plots	Cumulative (%)
(a) 2012			
Monomorium junodi	214.17	0.34	34
Monomorium MOT-ZA04	11.83	21.67	43
Pheidole MOT-ZA07	9	2.33	49
Ocymyrmex MOT-ZA01	9	4.83	56
Pheidole MOT-ZA03	5.33	0.17	61
Monomorium damarense	8.33	3.67	65
Tapinoma MOT-ZA01	0.5	5.17	69
Pheidole MOT-ZA02	2.33	3.67	72
(b) 2016			
Monomorium junodi	916.83	0	39
Pheidole MOT-ZA03	279.5	9.17	54
Pheidole MOT-ZA14	79	57.17	63
Anoplolepis custodiens	1.17	146.17	69
Tapinoma MOT-ZA01	6.83	74.83	74

Table 2: Similarity percentage (SIMPER) results for the Pretoriuskop ant assemblage on the mounds versus at the savanna plots for (a) 2012 and (b) 2016. Average abundance per mound and savanna plot and the percentage of the species contribution to assemblage differences shown.

Species	Average abundance mounds	Average abundance savanna plots	Cumulative (%)
(a) 2012			
Monomorium junodi	85	0	16
Crematogaster MOT-ZA04	84.7	15.3	29
Monomorium MOT-ZA04	79.1	76.4	39
Pheidole MOT-ZA11	39.4	3.5	47
Pheidole MOT-ZA08	31.2	5.1	53
Anoplolepis custodiens	23.3	5.4	58
Pheidole MOT-ZA07	26.4	8.1	62
Monomorium albopilosum	24.6	27	66
Tapinoma MOT-ZA01	15.4	25.4	70
(b) 2016			
Anoplolepis custodiens	111.9	105.9	18
Monomorium MOT-ZA04	95.9	91	30
Monomorium junodi	84.3	1	41
Pheidole MOT-ZA03	72.9	5.6	51
Crematogaster MOT-ZA03	2.7	43.8	57
Tetramorium baufra	13.2	39.5	63
Crematogaster MOT-ZA04	12.9	29.3	67
Tapinoma MOT-ZA01	20.1	22.1	70