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2018
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Defining the mechanisms driving grass community (composition and functional trait) shifts in African savannas

Jason Ernest Donaldson

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg in fulfilment of the requirements for the degree of Doctor of Philosophy

Johannesburg



DECLARATION

I declare that this thesis is my own unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.

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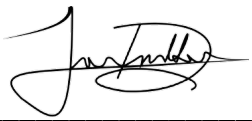

Jason Ernest Donaldson

Date 03.07.2018

ABSTRACT

Traditionally, landscape structure and variability are thought to be largely determined by climatic and edaphic conditions (‘green world’ view). However, it is now accepted that herbivore densities and fire regimes play an important role in shaping vegetation structure due to their role as consumers. In savannas the roles of fire and herbivory have been recognised for a long time but their interactions and feedbacks to vegetation are still being elucidated. Savanna trees in the same environment show evidence for specialisation to either frequently burnt or heavily grazed communities suggesting that alternative system states, representing either a ‘brown’ or ‘black’ world (heavily grazed vs. frequently burnt), can occur in savanna landscapes. When it comes to the grass layer we know that grazers can create and maintain patches of high-quality grazing habitat and exclude fires locally by removing grass biomass and limiting fuel for fires (brown world). Comparatively, large fires disperse grazing animals over broad areas of the landscape as they respond to high quality graze available on burn scars in what has been termed pyric-herbivory. The “thinning” of large mammal herds over wide ranges after a fire decreases concentrated grazing and allows grasses to accumulate biomass and ultimately encourages repeat burning (black world). Thus, both consumers have self-enhancing feedback loops and we would expect grass communities to respond to these: different species with divergent functional traits, either associated with frequent fire or heavy grazing, should be associated with each consumer state. Abiotic conditions, soils and rainfall, influence the strength of these feedbacks and alter the dominance of fire vs. herbivory across environmental gradients. This implies that rainfall variability, and the occurrence of drought, should influence these feedbacks at a particular location. How drought affects the competition between these consumers by shifting the conditions governing feedbacks is not well understood, but is becoming increasingly important in southern Africa where drought events are expected to become more frequent and severe with climate change.

The main aim of this study was to investigate the processes involved in the establishment and break-down of grass-consumer feedbacks and understand how these dictate the balance of fire and grazer driven grass communities in an African savanna. Specifically, I used a landscape-scale experiment setup in the Kruger National Park to test how easily a system switch from fire- to grazer-dominated can be initiated in a landscape, and how the functional traits of the grasses

drive these switches. I then tracked the impacts of a severe two season drought on the established consumer driven feedbacks within the study system and analysed the knock-on implications of these changes in grass community structure and function at broader scales.

The experimental results indicate that altering fire management practices and burning repeated small (<25 ha) fires concentrated grazers. After three seasons (2013-2015) this resulted in a structural shift in grass communities that maintained local grass height in a short-cropped state and excluded fire. Once the dominant consumer pressure shifted there were notable changes in the local grass species composition and novel grass communities had functional traits that favoured repeat grazing (low C : N ratios and high leaf moisture content). Thus, feedbacks between grazers and grass communities established within a relatively short period. This work adds to a growing number of studies that highlight the importance of feedbacks in the establishment of dominant consumer processes within savannas.

Drought altered the forage use patterns of grazers as biomass on grazing-lawns became limited and animals were forced to feed in low-quality tall-grass areas or migrate away from the study site completely. This more intensive grazing in the broader landscape where fire is usually the dominant consumer lead to a convergence in the grass community trait space between lawns and tall-grass areas. This suggests that drought has a homogenising effect on grass community trait space across fire-driven and grazer-driven grass community patches, at least in the short-term. I found that grass-grazer feedbacks did remain at broad scales with lawns re-establishing after the drought, but that these areas were severely restricted in the study system (<4% cover) and only occurred where strong drivers of grazer feedbacks (water availability) repeatedly concentrated grazing. Moreover, drought reduced the basal area of tussock grass, and created large areas of seemingly bare ground in the grazed patches. But grass communities recovered quickly – and within 3 months after the drought broke productivity was at its maximum.

My results highlight the importance of grass-consumer feedbacks in dictating the structure and function of African savannas. Clearly, fire and herbivory need to be considered in conjunction and understanding the state of a given grass community can only be done by assessing the governing grass-consumer relationship. Drought represents a good example of this; changes in the short-term abiotic conditions within a savanna appear to have little impact on savanna function and structure unless it drives changes in the positive feedback loops that govern the

distribution of grazer-driven and fire-driven grass communities within the landscape. Fires remain one of the only major management tools in large protected savannas and my thesis underlines the need to manage them by considering how fire influences grass-grazer dynamics and not simply use fire as a ubiquitous method for improving graze quality in the short-term.

DEDICATION

I dedicate this thesis to my parents, John and Diane Donaldson

Thank you for going to all my parent-teacher meetings.

AKNOWLEDGEMENTS

The running expenses of this project were received from USAID/NAS program “Partnerships for Enhanced Engagement in Research” (sub-grant 2000004946, Cycle 3) and the Andrew Mellon Foundation which allowed me to carry out this field intensive study. I received personal funding form the National Research Foundation Freestanding, Innovation and Scarce Skills Development Fund. I would like to thank and acknowledge all these funders for making this thesis possible.

I have dreamt of living in a tent in the savanna since I began my school career. I owe both of my supervisors a huge debt of gratitude for making this dream a reality. Thank you, Sally Archibald and Catherine Parr, for your substantial contribution not only to my thesis but also to my life experiences.

I would not have managed to complete the fieldwork for this study without the help of my two great friends Happy Mangena and Khensani Mkonto. Thank you both for entertaining me endlessly while we watched grass grow during a drought. I am grateful to South African National Parks for allowing me to carry out research within the Kruger National Park and Working on Fire for applying all experimental burns. I must make special mention of Navashni Govender, Tercia Strydom, Agnes Mukondeleli, Robert Bryden, Samantha Mabuza, and Chenay Simms, your advice, patience and support over the past three years has made my time in Satara highly enjoyable.

I am grateful to all contributing authors on the four respective papers appearing in this thesis, as well as Laurence Kruger and Gareth Hempson for their consistent mentorship and support.

Thank you to the many friends who visited me in Satara and pitched in to help with fieldwork and special thanks to Ronald Walter, Byron, Warwick, Anastasia, Zoë and Elia Donaldson for ensuring that my life never got too serious. My partner in crime Megan Gomes has been the Portuguese rock that has made completing this work so rewarding and enjoyable. Meeting you has been the peak of an incredible few years and the value of your love and support cannot be overstated. Finally, I must thank the two biggest influences on my life, John and Diane Donaldson, the way you approach life is an inspiration to me. I thank you for teaching me to

question the world and for your constant support, but most of all I thank you for having the energy and patience to let me do things my own way.

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Chapter 1 | Introduction

Background literature review, study rationale, aims and objectives, thesis overview

1 | General Introduction and Literature Review

Globally savanna ecosystems support large herds of both domestic and wild herbivores and represent essential food, cultural, and financial resources to people living within them (Mc Pherson, 1997; Tainton, 1999; Shackleton *et al.*, 2002). Savannas in Africa are heavily utilized by pastoralists and commercial rangeland managers, but currently large areas remain relatively untransformed, and thus carry with them a high biodiversity value and house some of the most iconic conservation areas globally. The long-term future of these ecosystems is of global relevance and as a result has been the focus of numerous studies attempting to improve our understanding of systems managed both for livestock and biodiversity in different areas of the world (Oliva *et al.*, 1998a; Fensham, Holman and Cox, 1999; Tainton, 1999; Jones, 2000; Fuhlendorf and Engle, 2001; Knapp *et al.*, 2012). Traditionally, savanna landscape structure and variability were thought to be largely determined by climatic and edaphic conditions ('green world' view) (see Polis, 2007). However, it is now accepted that herbivore densities and fire regimes play an equally, or arguably more, important role than climate or edaphic factors in shaping savanna vegetation structure due to their role as consumers (Bond, 2005). Both grasses and woody plants show evidence for specialisation to either frequently burnt or heavily grazed communities (Archibald and Bond, 2003; Hempson *et al.*, 2015; Simpson *et al.*, 2016). This suggests that alternative system states, representing either a 'brown' or 'black' world (heavily grazed vs. frequently burnt), can occur in savanna landscapes depending on the mix of fire and herbivory (Bond, 2005) with the structure of savanna vegetation driven by the feedbacks between vegetation and consumer (Bond and Keeley, 2005; Archibald and Hempson, 2016). Considering the commercial and conservation value of African savannas, developing an in-depth knowledge of the feedbacks driving their structure and function is imperative for the development of ecological theory on savanna systems and ecosystem management.

1.1 Abiotic extents of fire and grazers in African savannas

Archibald and Hempson (2016) showed that Bond's (2005) fire-controlled 'black-world' and herbivore-controlled 'brown-world' savannas filter out along abiotic gradients, with black-world savannas dominant at high rainfalls (>1000 mm) and brown-world savannas at low rainfalls (<400mm). This separation is dictated by the 'food' requirements of the two consumers and the resultant impact that they have on vegetation under certain climatic and edaphic conditions

(Archibald *et al.*, 2013; Hempson, Archibald and Bond, 2015). Fire requires large quantities of well-connected biomass that is sufficiently cured to allow for spread (Archibald *et al.*, 2009). The impacts of fire on vegetation is thus limited in savannas with lower rainfall where biomass build-up is too slow and too disconnected to allow fire to be a major role player in vegetation structure (Archibald *et al.*, 2009). By contrast, at higher rainfalls fire is afforded enough fuel to burn frequently and at high enough temperatures to substantially alter tree-cover. Thus, fire becomes the dominant role-player in the structuring of savanna communities at high rainfalls, until precipitation becomes so high that fuel is too wet to carry fire and canopies become closed (Sankaran *et al.*, 2005; Staver *et al.*, 2009).

Unlike fire, most mammalian grazers require quality of forage over quantity and are not as reliant on the connectivity of fuel resources and the availability of fuel in space but rather require availability of forage through time (Owen-Smith and Novellie, 1982; Gordan and Illius, 1996). Thus, mammal grazer numbers will be limited at low rainfall but still influence vegetation structure as productivity within these areas is extremely low. While grazer numbers will not be limited by food quantity at high rainfalls, the quality and accessibility of graze becomes restricted and inhibits the build-up of grazer numbers to levels that may influence vegetation structure (Hempson, Archibald and Bond, 2015). Higher soil fertility will mean that grazers can influence vegetation structure at higher rainfalls (East, 1984), but ultimately an upper limit to the impact of grazers on vegetation will exist as access to forage is limited and the herbivore population shifts to browser dominated landscapes (Hempson, Archibald and Bond, 2015).

Despite the shift in dominance between mammalian grazers and fire along rainfall and soil gradients, there are still large portions of Africa's savannas that are not completely predisposed by abiotic conditions to either consumer and support both alternate states (Archibald and Hempson, 2016). These areas are of interest to land managers as they allow for the potential manipulation of consumers to favour specific management targets, but also represent important areas to test our current understanding of trait driven feedbacks and thresholds relating to alternate states.

1.2 Pyric-herbivory and grazer-fire interactions

Fire and herbivory are not mutually exclusive and often act together in savannas with effects on primary production, plant-soil nutrient pools, and the species composition of vegetation (Knapp,

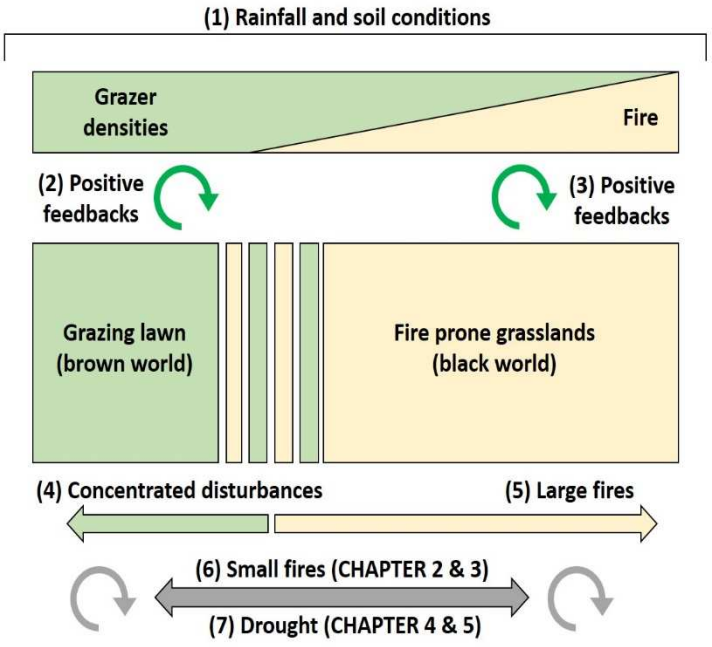
Conrad and Blair, 1998; Van de Vijver, Poot and Prins, 1999). Tall bunch-grasslands (*Themeda triandra* (Forssk.) and *Bothriochloa radicans* (Lehm.) dominated grass communities standing between 40 cm and 120 cm in height) represent fairly low-quality, but high-quantity food reserves that many grazer species only use in the late-dry season or during extreme drought events (Owen-Smith and Novellie, 1982; Macandza, Owen-Smith and Cross, 2004; Yoganand and Owen-Smith, 2014). In normal years these systems are never fully utilised by grazing animals, and fires which burn the unconsumed dead grass biomass are common. After fire, these systems represent a high-quality food resource for a limited amount of time (three-six months – Tomor and Owen-Smith, 2002) before recovering their lost biomass. The majority of grazing species in savanna landscapes benefit from and respond to the highly nutritious regrowth after fire that replaces low nutrient moribund grass (Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2013). Increased grazing on recently burnt patches has been termed 'pyric-herbivory' (Fuhlendorf *et al.*, 2009) and has resulted in a long history of fire manipulation by land users (Trollope, 1982; Collins and Wallace, 1990; Fowler and Konopik, 2007) and documented in a wide suite of wild mammalian grazers (Klop and van Goethem, 2008; Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2016). Increased grazing in the immediate aftermath of burns seldom leads to a long term reduction in grass biomass as grasses quickly recover biomass and stem to leaf ratios make grazing less favourable for selection by herbivores (Tomor and Owen-Smith, 2002). Ultimately, differences in the metabolisms of fire and mammalian grazers means that direct competition for biomass is rare, as grazers are unable to remove enough low-quality biomass to inhibit fire and fires generally increase access to higher quality graze and reduce the need for quantity (Venter, Hawkins and Cramer, 2017).

1.2.1 Consumer separation via feedbacks

The differences in fuel and food requirements of fire and mammalian herbivores means some landscape level separation in their occurrence should be expected even within systems where they are both prevalent. Fire prefers grasses that have high C : N ratios resulting in a build-up of dead material and low leaf moisture to allow curing during the dry season (Simpson *et al.*, 2016). Conversely, grazers require relatively high-quality (low C : N ratio) graze with high leaf moisture content improving digestibility and high biomass density reducing acquisition effort (Owen-Smith and Novellie, 1982). Thus, these two consumers that appear to compete for the

same food source are frequently selecting for different grass communities, whereby, grasses that are flammable are seldom palatable and vice versa (Bond, 2005) (Figure 1.1).

Frequently burnt grasslands favour grass species that grow fast from meristems protected from fire and that are ultimately resource competitive in the period between burn events (Ripley *et al.*, 2015; Simpson *et al.*, 2016). This means that despite grazer numbers increasing on burn scars after a fire to feed on the high nutrient re-growth of grasses, grass tends to "escape" grazing pressure after a fire and reach heights where leaf to shoot and C : N ratios are unfavourable for continued high intensity grazing and the environment favours resource competitive grasses (Archibald and Bond, 2004). Frequently burnt regions tend to become less species diverse and favour species that are high in carbon and avoided by grazers as selective grazing removes



1) Dominance between mammalian grazers and fire shifts along rainfall and soil nutrient gradients (Archibald, 2008; Archibald and Hempson, 2016). Despite this large portions of Africa's savannas are not completely predisposed by abiotic conditions to either consumer and support both herbivore dominated and fire dominated landscapes.
2) Positive feedbacks between mammalian grazers and grass communities promote community dominance by grass species that encourage repeat grazing (Mc Naughton, 1984). This results in the establishment of "brown world" hotspots and grazing lawns that should completely exclude local fires when grass height is kept short (*c.*<5 cm) across 40% of a given area (Turner, Gardner and O'Neill, 2001)
3) Repeated landscape scale large fires favour species that are high in carbon (Simpson et al. 2016) and avoided by grazers. This favours an increase in standing biomass and promotes repeated burning (Archibald *et al.*, 2005). Mammalian grazers occur within these landscapes but their influence on the grass community is limited and does not restrict fire return resulting in a "black world" (Bond, 2005).
4) Localized small-scale disturbances that concentrate grazers such as grazing by white-rhinoceros (Waldrum *et al.*, 2008) can result in the establishment of grazing lawns in fire dominated systems (Cromsigt and Olff, 2008)
5) Large fires disperse grazers over broad areas and encourage ubiquitous grazing over the landscape as grazers feed on fresh, post-fire regrowth. These large fire events can act as magnets that draw grazers off grazing lawns and repeated large fires can result in the loss of grazing lawns (Archibal, Bond and Stock, 2005).
6) If large fires disperse grazers, it is possible that small fires act in the opposite direction and concentrate grazing in similar ways to grazing by white-rhinoceros. In **Chapter 2** of my thesis I assess the impact of small fires on the mammalian grazer community. Specifically I look at whether small fires can concentrate grazing in a broader fire dominated landscape, and test if grazer densities are become high enough to limit local repeated burning. In **Chapter 3** I look at whether a change in the dominant consumer from fire to grazers on small burn patches results in grass community changes that promote positive grazer feedbacks that encourage the long term establishment of grazing lawns.
7) In **Chapter 4** I look at the impact of drought on the productivity of grazing lawns and fire driven grasslands, the response of grazers to these changes, and ultimately the impact on previously established local feedbacks. In **Chapter 5** I explore the impacts of major drought events on the distribution and longevity of grazing lawns and fire driven grass communities at the regional scale.

Figure 1.1. Schematic diagram of the dynamics of fire and grazer driven savanna grass communities including a summary of the chapters in this thesis.

palatable grasses (Anderson *et al.*, 2007). This results in feedbacks that favour the return of fire and repetition of processes that entrench fire as the dominant driver of grassland community structure and function (Archibald *et al.*, 2005). The reduction in graze quality of areas under selective grazing is a well-recognised relationship in commercial livestock systems within African savannas and there is a rich body of literature looking at fire and livestock management techniques to reduce shifts towards low forage quality grass communities (Tainton, 1972, 1999; Trollope, 1982; Ellis and Swift, 1988; Vetter, 2013). Despite this, there is still some debate around the best practice for management of African rangelands, with the periodic burning and resting of pasture via rotational grazing to avoid the removal of palatable species (Tainton, 1999), contrasted with the forced intensive use of grassland to reduce selective grazing and encourage less favourable grasses to be consumed (Augustine and Mc Naughton, 2007; Hawkins, Short and Kirkman, 2017). In systems managed for wildlife neither management practice is practicable responses, and thus at landscape scales it is unlikely that once a grassland develops into a stable fire driven system that it will switch back to one that promotes grazing without some external effort to change the dominant fire regime.

Similar positive feedbacks exist within grazer driven grass communities that exclude fire and promote repeat grazing. Mc Naughton (1984) defined grazing lawns as areas where grasslands experience “a drastic reduction of canopy height and the activation of tillers that lead to a prostrate, dense canopy” and are characterized by a positive consumer-resource relationship where grazing promotes increased productivity and resource availability. Constant removal of leaf material promotes high quality regrowth of leaves that leads to stem to shoot and C : N ratios that favour repeat grazing (Mc Naughton, 1976, 1979; Mc Naughton, Banyikwa and Mc Naughton, 1997; Cromsigt and Olff, 2008). In addition to nutritional advantages related to the use of grazing systems, there is clear evidence of predator detection benefits that result in the continued utilization and maintenance of lawn systems across numerous African savanna systems (Waldram, Bond and Stock, 2008; Anderson *et al.*, 2010; Yoganand and Owen-Smith, 2014). A suite of lawn grass species appear to be completely reliant on this increased relative fitness with their spread and persistence only supported on areas under consistent grazing that limits light competition from other grass species (see Hempson *et al.*, 2015 for review). These grazing intensive systems are clearly inaccessible to fire as biomass quantity is well below that

required to carry fire through a system and require some external change to reduce grazer utilization (Figure 1.1).

The establishment and maintenance of feedbacks within grass communities make it unlikely that fire will suddenly invade grazing lawns or that grazers will remove enough low-quality biomass in a season to limit repeated burning in fire adapted grasslands. Clearly, as with all alternate states, a shift in the dominant consumer from fire to herbivory or vice versa requires some disturbance to the status quo that breaks down the trait related feedbacks maintaining the producer-consumer relationships (Archibald and Hempson, 2016). Thus, whether a landscape is dominated by fire or grazers will depend heavily on the set of conditions that dictate what positive feedbacks are established locally (Figure 1.1). Considering the unique value of both lawn and bunch grass communities to biodiversity (Samways and Kreuzinger, 2001; Warui *et al.*, 2005; Krook, Bond and Hockey, 2007), agriculture (Fynn, 2012), and tourism, there is a need to define what drives shifts between the two communities and when these changes may be expected to occur. Understanding these drivers will be of substantial use to land managers as it will allow for both the manipulation of landscapes to suit specific targets but also enable some predictability in assessing the impacts of major external disturbances such as disease and drought to managed environments. The mechanism of any switch between fire and grazer dominated grass communities is also of substantial interest to ecologists and determining the major drivers of shifts in landscape states has been repeatedly highlighted as an important step in adding to our current understanding of the co-evolutionary relationship between savanna grasses and their consumers (Mc Naughton, 1984; Bond, 2005; Bond and Keeley, 2005; Hempson *et al.*, 2015).

1.3 Shifts between fire and grazer driven systems

In natural systems, the best example of a large-scale disturbance that resulted in switches between grazer and fire driven system states comes from East Africa. The outbreak of the rinderpest virus in the 1970's caused a collapse of migratory wildebeest herds (Prins and van der Jeugd, 1993), and resulted in reduced grazing pressure and increased fire across the Serengeti National Park (Dublin, Sinclair and McGlade, 1990). Recovery of the wildebeest population after eradication of the virus has since led to a decrease in the annual burn area of ~ 30% (Holdo, Holt and Fryxell, 2009). These major changes from a herbivore driven system to a fire dominated system and back with the collapse and recovery of massive migratory herds indicates

the scale over which these changes can operate and has long lasting cascading impacts on the structure and function of the Serengeti system (Holdo, Holt and Fryxell, 2009). This highlights the importance of gaining detailed insights into how and when feedbacks are broken down and the traits involved in changing the consumer landscape. However, the infrequency of events that drive the loss and recovery of over 1 million grazers makes studying changes in grass communities and trait space in any detail difficult. By comparison local scale shifts in the stable state in both directions occur more frequently and are more relevant to land managers in increasingly fragmented landscapes, where both states represent important features for biodiversity.

1.3.1 Grazing lawns and grazers

African grazing lawns have been defined as grassland areas where grazing by large mammalian herbivores has driven a large depletion in the grass sward height to the extent that grass tillers have been activated resulting in the growth of a prostrate, dense canopy (Mc Naughton, 1984). These short stature, dense canopies are seldom associated with fire as they do not maintain sufficient biomass to burn except under extreme conditions. Rather, the high density fresh regrowth provides nutritious forage for mammalian grazers resulting in active selection for grazing lawns by numerous grazing species (Mc Naughton, 1984; Waldram, Bond and Stock, 2008; Anderson *et al.*, 2010; Kleynhans *et al.*, 2010). Moreover, stimulated grazing lawn growth as a result of defoliation has been shown under controlled experimental conditions (Anderson, Dong and Mc Naughton, 2006; Anderson *et al.*, 2013) and repeated grazing by mammalian herbivores seems to be a requirement for the continued existence of grazing in numerous African systems (see Hempson *et al.*, 2015 for review), leading to suggestions of a co-evolutionary history (Mc Naughton, 1984). Thus, grazing lawns represent grassland systems dominated by grazer dynamics with very little direct influence on their functioning by fire. Despite the definition provided by Mc Naughton (1984) there is still scope for interpretation of what exactly constitutes a grazing lawn in African savannas and defining them in the field can require more detailed definitions. Thus, within each chapter of this thesis I will further define grazing lawns in terms relevant to the work presented.

Studies in southern Africa have shown how biological, small-scale disturbances, driven by landscape engineers, that concentrate grazing can generate a matrix of grazing lawn systems

within a broader fire-dominated landscape (Cromsigt and Olff, 2008; Cromsigt and te Beest, 2014). These disturbances appear to be successful in overcoming the low food quality inherent in fire adapted grasses that restricts the invasion of these systems by most mammal grazers and act as catalysts to a novel system state that is then maintained by smaller mesoherbivores. One such example is the termites that engineer the underlying abiotic conditions and improve the nutrient content of grasses to the extent that mammalian grazers actively select these local sites for palatable forage (Cromsigt and Olff, 2008; Davies *et al.*, 2014). A very different savanna species – the white rhino – can also create these improved nutrient patches in and around their middens. Moreover, the large size of white-rhinos allows them to cope with lower quality forage and this in combination with the short height to which they graze make them unique amongst mammalian grazers in their ability to truly compete with fire for the same food source (Waldram, Bond and Stock, 2008). While hippopotamus can play a similar role in the creation and maintenance of short-grass systems, their impact on the broader landscape is restricted by their reliance on permanent deep pools (Lock, 1972). This unique set of life-history traits combined within white-rhinos make their presence in the landscape a clear role-player in the proportional increase of grazer controlled systems in otherwise fire dominated savannas (Waldram, Bond and Stock, 2008; Cromsigt and te Beest, 2014). Thus, any increase in the impact of grazers within fire adapted grass communities under stable climatic conditions requires some interference by ecosystem engineers that enables other grazing mammals to overcome restrictive fire-grass feedbacks.

1.3.2 Fire

Large fires disperse grazers over the landscape and decrease localised herbivory on grazing lawns, thus weakening the positive feedbacks between grazer and grass communities (Archibald *et al.*, 2005). Repeated large fires can drive the homogenisation of the grass layer as grazing lawns within the broader landscape are lost when the feedbacks between grazers and high-nutrient short grass patches are broken down. Shifts in management practice that increase fire sizes or a series of high rainfall years where grass productivity is increased beyond the metabolic requirements of the local grazer population, are likely to drive shifts towards fire dominated landscapes as fire responds faster to increased biomass than herbivore fecundity. A more direct human interference that favours the development of fire driven grass communities and has occurred repeatedly within natural systems on the African continent is the large-scale depletion

of wild mammalian herbivores. The historical depletion of mega-herbivore populations by human hunters (Owen-Smith, 1987, 1989) and land-use change (Williamson and Mbano, 1988; Serneels and Lambin, 2001; Ogutu *et al.*, 2009) has resulted in the majority of current day protected savannas having lower grazer densities when compared to historical levels. The loss of large migratory systems (Harris *et al.*, 2009; Ogutu *et al.*, 2011; Gadd, 2012) and decline of mega-herbivores (Owen-Smith, 1989; Ripple *et al.*, 2015), specifically white rhino (Amin *et al.*, 2006) in numerous savannas managed for wildlife, means that under the current scenario (in areas where abiotic conditions allow for the existence of both grass community states) an over representation of fire-controlled tall-grass communities compared with historical distributions would be expected.

In contrast to large fires, it has been suggested that small fires could act to concentrate grazers on specific patches and result in greater grazing intensity per individual plant than larger fires (Archibald and Hempson, 2016). There is indirect evidence of sustained grazing pressure on repeatedly burnt patches within fire-adapted systems (Burkepile *et al.*, 2016) and higher grazing pressure on smaller burn treatments (Sensenig, Demment and Laca, 2010). However, there have been no studies examining whether small repeated burns within fire-adapted grasslands can attract and maintain grazing pressure to the point that grass is maintained in a short, cropped state and ultimately limits repeat burning. Theoretically small fires could act like termite mounds and rhino middens and create patches of grazer-dominated grassland within tall-grass landscapes. Previous work has either failed to account for variation in fire size, initial grass community conditions and ability of grazing to prevent repeat burning (Burkepile *et al.*, 2013) or not explicitly tested the differences of fire size on grazing intensity and longevity of short grass patches (Sensenig, Demment and Laca, 2010). In **Chapter 2 and 3** of my thesis I aim to explore the potential of small fires to increase grazer presence on localised areas in systems that would otherwise be fire-dominated by providing a means for mesoherbivores to heavily utilize patches that are usually devoid of sufficient graze quality. In doing so, I aim to test whether elevated grazing pressure on relatively small burn patches is sufficient to locally remove fire from the system and completely shift the selective pressure acting on grass species. If small patch fires are capable of driving these changes it represents a possible management tool for increasing the between-patch diversity of landscapes (Fuhlendorf and Engle, 2001) and adds to the available

management options while also corroborating current fire-grazer theory (Archibald and Hempson, 2016).

To fully change from one system state to another requires the maintenance of the novel state via feedbacks that do not require the initial disturbance to be repeated. A shift from a fire-controlled state to grazer-controlled state by the application of small-fires can only be successful if the grazer response to small burns is sufficient to drive permanent changes in the grass community that encourage repeated utilization without the need for repeated burning. Globally, grass communities response to increased grazing is non-linear and systems can become both "degraded" (reduced productivity, loss of plant cover and top soil, domination by low graze quality species composition) and discourage repeat grazing or "improve" and change to lawn systems (increased productivity, improved pasture quality, dominance by species resistant to repeated grazing) (Tainton, 1972; Mc Naughton, 1979; O'Connor, 1994; Augustine and Mc Naughton, 2007). Whether grass communities become degraded or improve graze quality in response to grazing is dependent on ecosystem and evolutionary history of the given system (Milchunas, Sala and Lauenroth, 1988). The response of the grass traits within the changing community should show evidence of a negative or positive shift in grassland state with grass communities either improving in graze quality or decreasing markedly (Augustine and Mc Naughton, 2007). I postulate that a complete shift in the dominant consumer should be evident in the functional traits of the local grass community, with a successful change in the governing dynamics of a grass community identifiable by increasing palatability traits and the loss of flammable traits as species that tolerate burning are replaced by those tolerant of grazing. In **Chapter 2** I assess whether grazing on small-repeated fires re-structures grass community composition to be distinct from the surrounding landscape. In doing so I test whether grass communities resulting from the pyric-herbivory associated with small-repeated burns will be dominated by functional traits (low C : N ratios, high leaf moisture content, high biomass density) that encourage repeated grazing and thus continue to attract high numbers of mesoherbivores once burn applications have ceased.

1.4 Drought effects on fire and grazer dynamics

Climate model predictions for savanna regions of Africa suggest an increase in extreme drought events in several key protected areas (Dai, 2013; Trenberth *et al.*, 2014). The effects of shifts in

rainfall patterns, extended dry seasons, and multi-year droughts on both herbivore populations and grass communities has received detailed attention in African focused literature (Homewood and Lewis, 1987; Walker *et al.*, 1987; O'Connor, 1995; Koerner and Collins, 2014). Independent studies across the continent have repeatedly shown decreases in grazer numbers during drought events with mammalian herbivore populations closely linked to rainfall cycles (Walker *et al.*, 1987; Ottichilo *et al.*, 2000; Owen-Smith, Mason and Ogutu, 2005; Ogutu *et al.*, 2008). Moreover, experimental variation of livestock numbers (O'Connor, 1995) and simulated grazing and fire combinations (Koerner and Collins, 2014) in savannas have shown strong differences in grass community responses to drought with and without grazing. In the absence of herbivory grass communities remained largely intact even through severe multi-year drought events, but experienced decreases in both cover and productivity that drove changes in species composition under higher grazing pressure (O'Connor, 1994, 1995; Koerner and Collins, 2014). Die-offs in herbivore populations, local migrations and grazers selecting for different food resources during droughts will change how herbivores impact grass communities. This suggests that increasing drought events will influence the distribution of grazer-driven and fire-driven grass communities within savannas as grazer utilization of the landscape shifts. However, a substantial gap exists in our current understanding of how and when grazing pressure changes during drought events and what the impact is on previously established feedbacks between consumers and grass communities.

Both O'Connor (1994) and Koerner and Collins (2014) tested in or mimicked situations where grazing was largely uniform within the "grazed" treatment. Moreover, in O'Connor's (1994) experiment, grazers were fenced and were not given the option to leave areas that were previously heavily grazed to seek out alternative forage regions, while Koerner and Collins (2014) simulated grazing and did not account for the composition and grazing history of the grass communities on which they assessed drought responses. This does not consider the choices made by grazers within free roaming systems, that select food during the dry season and droughts based on availability rather than quality and are likely to be grazing on very different communities to those they fed on during normal rainfall years (Owen-Smith and Novellie, 1982; Macandza, Owen-Smith and Cross, 2004). Moreover, there have been few studies looking at the changes in the productivity of different grass communities during droughts and how this influences grazer decisions through the season. Grazers in free roaming systems will leave

heavily grazed sites where forage quantity is low during droughts and seek out forage in tall grass areas (Riginos, 2015) or areas where local rain events stimulates productivity (Owen-Smith and Novellie, 1982). Thus, grazer driven grass communities may experience a decrease in offtake during droughts while fire driven communities experience a relative increase. These changes will weaken previously established consumer-grass community feedbacks and potentially shift the proportion of fire and grazer driven grass communities within savanna landscapes. In **Chapter 3** I look at the relative use of grazing- and fire-driven systems by grazers through a major drought event and assess the impacts on established consumer feedbacks and overall changes to species composition and grass trait space. In **Chapter 4** of my thesis I look at the productivity of grazing lawns, tall grass communities, and recently burnt grass areas during a drought and analyse the links between productivity, grazer offtake and resultant functionality of each community during the drought and once rainfall returns. Both chapters aim to identify the underlying changes in the feedbacks between grass communities and their dominant consumers and how droughts alter the fire-grazer balance within the general landscape. In **Chapter 5** of my thesis I look at how drought and fire impact the balance of grazer and fire driven grass communities at the regional scale and attempt to scale-up the processes identified during the previous two chapters.

Chapter 2 | Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns

This chapter has been published in the Journal of Applied Ecology

Donaldson, J. E., Archibald S., Govender, N., Pollard, D., Luhdo, Z. and Parr, C. L. (2017) Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*. 00: 1-11.

AUTHORS' CONTRIBUTIONS

S.A., C.L.P. and N.G. conceived the ideas with all authors designing the methodology; D.P., Z.L. and J.E.D. collected the data; J.E.D. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

1 | Abstract

1) Variation in grass height is beneficial to biodiversity conservation in savanna landscapes. Theory predicts that small fires can promote short-grass areas within savannas. We experimentally assessed the influence of fire season and size on grass height and the resultant response of wild grazer communities and tested three hypotheses: (1) repeated small fires in tall-grass savannas increase short-grass grazer densities in the post-burn environment; (2) increased grazer densities maintain grass height in a short, palatable state and drive feedbacks that exclude fire; and (3) late-dry season burns concentrate grazers more effectively than early dry season burns.

2) We repeatedly applied annual treatments (unburned, early- and late-burns) in 0.25-, 5- and 25-ha plots over a period of three years in a tall-grass savanna system in Kruger National Park, South Africa. Dung counts for grazer density and grass height data were collected along 50-m transects. Grass height was measured in paired 1-m^2 herbivore exclosures on plots before and after applied fires.

3) Dung data indicate that wildebeest occurred most frequently in grass heights below 5 cm. Both impala and wildebeest showed a preference for burn plots regardless of fire size or season and active selection for burn plots by wildebeest increased over time with each repeated burn. Zebra and buffalo favoured burns immediately post-fire, but buffalo did not actively select for burnt areas over longer time periods.

4) By the second year of treatment, herbivory maintained 28% and 91% of the grass height below 10 cm in the early- and late-season burns respectively. In contrast, herbivory on the unburned treatments had no effect on grass height.

5) *Synthesis and applications*. Fires less than 25 ha in size attracted sufficient grazing herbivores to shorten grass height. Repetition of the fire treatments resulted in the active selection of these areas in the longer term by wildebeest, impala and, to a lesser degree, zebra. Grazing pressure was high enough to initiate positive feedbacks and maintain lawns after only two seasons of burning and, depending on the season of burn, reduced grass height to a level that excluded repeat fires. Our study demonstrated that theory on grazer use of the post-fire environment can be implemented practically by applying small repeated burns to promote the formation of short-grass areas within savannas.

Keywords: African savannas, burn area, burning, fire ecology, grass system-state, grazer ecology, grazing, grazing lawns, herbivore

2 | Introduction

Grazers and fire act as competing consumers within savannas, with fires being most prevalent in tall-grass vegetation characterized by low herbivory, and grazers being most abundant in short, heavily grazed grasslands without enough fuel to burn (Staver *et al.*, 2009; Archibald and Hempson, 2016). Both grasses and woody plants show evidence for specialization to either frequently burnt (Ripley *et al.*, 2015) or heavily grazed (Díaz *et al.*, 2007) communities, leading to the realization that alternate system states, representing either a "brown" or "black" world (heavily grazed vs. frequently burnt) can occur in savanna landscapes (Bond, 2005). Despite this, fire and herbivory are not mutually exclusive and often act together in savannas with effects on primary production, plant–soil nutrient pools and the species composition of vegetation (Knapp, Conrad and Blair, 1998; Van de Vijver, Poot and Prins, 1999). Moreover, interactions between fire and grazers in savanna systems have resulted in a long history of fire manipulation by land users for the management of both livestock and wild herbivore populations (Trollope, 1982; Collins and Wallace, 1990; Fowler and Konopik, 2007).

The importance of fire in maintaining grass quality and quantity in rangeland systems is well recognized (Collins and Wallace, 1990). Globally, livestock farmers use fire to improve forage quality by removing moribund, low-nutrient grass biomass. This practice has resulted in a substantial body of literature focusing on managing fires for specific grassland conditions (biomass, height and graze quality) to maximize livestock production (Oliva *et al.*, 1998b; Fensham, Holman and Cox, 1999; Klop and van Goethem, 2008; Sensenig, Demment and Laca, 2010). Until recently, similar studies on wild herbivore populations have been limited (but see Klop and van Goethem, 2008; Fuhlendorf *et al.*, 2009; Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2016); consequently, fire management of wild areas has largely been informed by agricultural research. However, managers in some protected areas in Africa recognized that reliance on agricultural studies was inappropriate in savannas where grazer diversity is high and rejected the implementation of agricultural-based fire management (Biggs and Potgieter, 1999; Van Wilgen and Govender, 2004). Recent work from east and west African savannas has justified their caution, demonstrating that fire size and frequency drives resource partitioning in communities of wild herbivores due to differences in energy requirements related to body size, digestive capabilities and the related stem to leaf, and Nitrogen to Carbon, ratios (Klop and van

Goethem, 2008; Sensenig, Demment and Laca, 2010). In addition, wild ungulate populations vary in their utilization of different grass communities seasonally, with burnt areas, short unburned grazing lawns and tall-grass systems representing valuable resources at different times of the year (Augustine and Derner, 2014; Yoganand and Owen-Smith, 2014). Furthermore, in systems with predators, the increased visibility provided by short-grass patches can reduce predation risk, consequently attracting a range of prey species. Clearly to conserve a diverse suite of herbivores, it is desirable to have a diversity of grass sward heights in the landscape.

The majority of grazing species in savanna landscapes benefits from and responds to the highly nutritious regrowth after fire that replaces low-nutrient moribund grass. However, fires generally occur over large areas and can have homogenizing effects on the landscape, with the post-burn flush dispersing herbivores more evenly and allowing grass to "escape" grazing pressure uniformly (Hobbs *et al.*, 1991; Archibald *et al.*, 2005). This results in feedbacks that promote tall, unpalatable, fire-adapted grass communities (Archibald and Bond, 2004; Archibald *et al.*, 2005), which may support some bulk-feeding herbivores (Trollope, 1995; Estes, Atwood and Estes, 2006), but which reduce the diversity of grazers and grazing habitats overall. In contrast, small-scale disturbances such as mowing and nutrient addition that concentrate grazing within tall-grass savannas have been shown to facilitate the formation of grazing lawn systems (Cromsigt and Olff, 2008). Thus, it is possible that frequent small-scale fires that concentrate grazers on high-quality post-burn graze could also attract and maintain high numbers of grazers and drive a shift in grass communities towards shorter lawn systems that exclude fire. Here, we use an experimental approach to test the influence of fire season, size and return time on grass height and the resultant response of wild grazer communities. In addition to burn size, we predict that burn season will influence herbivore response to the post-fire green flush. Since the high-quality graze environment of the late-dry season burns provides a valuable resource for grazers during a resource poor period of the year, we predict that late-season burns will have a greater "magnet" effect on grazers than early dry season fires (Augustine and Derner, 2014; Yoganand and Owen-Smith, 2014).

We defined grazing lawns as areas where high grazing pressure limits grass height below levels required to carry fire, that is, grazing lawns are formed when positive feedbacks promote their maintenance and restrict fire. Based on this definition, we developed three hypotheses related to the formation of grazing lawns by repeated small-scale burning: (1) small fires (similar in size to

known grazing lawns formed by other grazer-concentrating disturbances) in tall-grass savannas will result in increased short-grass grazer densities in the post-burn environment, with relatively smaller burns demonstrating greater responses; (2) increased grazer densities will maintain grass height in a short, palatable state and drive feedbacks that exclude fire and promote a grazer driven system; and (3) late-dry season burns will concentrate grazers more effectively than early dry season burns and result in a quicker transition to a grazing lawn state.

3 | Methods

3.1 Study site

Kruger National Park (KNP) in South Africa contains the full suite of large African mammals and provides an exception to many African national parks with nearly a century of detailed records on fire history and policy changes (Van Wilgen and Govender, 2004). This makes KNP ideal for studies on the effect of different fire regimes on wild ungulate populations. Management of fires in KNP is currently based on available fuel loads, with management initiating burns when grass biomass is high; fire return times thus vary across the park with rainfall and soil patterns resulting in different grass productivity and biomass accumulation rates (Govender, Trollope and Van Wilgen, 2006). The high fuel loads associated with these burns have resulted in a shift towards larger, higher intensity fires. Variation in the burn regime is generated through changes in season of ignition and intervals between burns. Fire management is focused on increasing heterogeneity at the landscape scale within the KNP (Van Wilgen and Govender, 2004; Govender, Trollope and Van Wilgen, 2006). Because the current KNP burn regime results in large fires, short-grass grazing lawns that support high grazer densities and rely on positive feedbacks associated with frequent grazing should be limited in distribution as animals are drawn off by large, frequent fires in the broader landscape (Archibald *et al.*, 2005). This appears to be the case, with grazing lawns restricted to areas of high white rhinoceros (*Ceratotherium simum* Burch.) densities or areas where small-scale disturbances such as termite mounds, mud wallows and dung middens have resulted in unusually high grazer usage (Cromsigt and te Beest, 2014).

The Satara Land System, one of four major land systems in KNP, is characterized by clayey basalt soils with soil depth not usually deeper than one meter and dominated by the Bonheim, Shortlands, Milkwood, Mayo, Glerosa and Valsrivier Forms (Venter, Scholes and Eckhardt,

2003). The land system is characterized by low relief with 97% of the landscape having a slope of < 2° and supports extensive C4 grass plains in a *Sclerocarya birrea* (A. rich.)–*Acacia nigrescens* (Oliv.) tree savanna (Gertenbach, 1983). Woody cover at our study sites fell consistently below 10% (Table 2.1) and at the beginning of the study period this area was dominated by C4 grasses *Bothriochloa radicans* (Lehm.), *Digitaria eriantha* (Steud.), *Panicum coloratum* (L.), *Urochloa mosambicensis* (Hack.) and *Themeda triandra* (Forssk.) (Knapp *et al.*, 2012), with the high abundance of unpalatable *B. radicans* presenting a concern to land managers. The growing season for grasses occurs during the austral summer (November–April), during which 78% of the mean annual rainfall of 502 mm/year falls with the January on average the hottest month with a mean maximum temperature of 33.7°C (Venter, Scholes and Eckhardt, 2003). Grasses are dormant during the dry, frost-free winters (May–October) with the coldest month of June experiencing a mean minimum temperature of 9.4°C. Prior to this experiment, the area had an average fire return interval of ~ 3 years and a detailed description of fires in the Satara land system during the course of this experiment is given in Appendix A (Figure S2.1).

A complete suite of indigenous herbivores occur in relatively large abundances within the Satara Land System (du Toit, 2003); however, for this study we focus on the four major grazer species (African buffalo [*Syncerus caffer* Sparrman], impala [*Aepyceros melampus* Lichenstein], blue wildebeest [*Connochaetes taurinus* Zimmerman] and plains zebra [*Equus quagga* Boddaert]) due to low dung counts for the remaining species. African elephant (*Loxodonta Africana* Blumenbach) were excluded due to high levels of browse in their diets. Buffalo, impala and wildebeest are all ruminants with studies in KNP showing that 88%, 60% and 90% of their diets are made up of C4 grasses respectively (Codron *et al.*, 2007). Buffalo require large amounts of coarse biomass and tend to occur in grass heights above 20 cm (Macandza, Owen-Smith and Cross, 2004), while wildebeest and impala require high-quality graze and feed more regularly in short-grass areas (<10 cm) (Kleynhans *et al.*, 2010). Zebra digest their food using hind-gut fermentation and feed almost exclusively on C4 grasses (Codron *et al.*, 2007) and ubiquitously across grass heights (Kleynhans *et al.*, 2010).

3.2 Experimental design

To test the influence of fire season and size on grazers and the effect of post-burn herbivory on grass state, we implemented a landscape level experiment between January 2013 and January

2016. We selected three treatment plot sizes: 50 × 50 m (0.25 ha), 220 × 220 m (5 ha), 500 × 500 m (25 ha). These sizes were chosen to represent the three most common short-grass areas in KNP: termite mounds (20–50 m^2—see Davies *et al.*, 2014), naturally occurring sodic site (*c*.250 m^2—see Grant and Scholes, 2006), and large grazing lawn systems (*c*. 500 m^2–1 km^2—see Yoganand and Owen-Smith, 2014). The 0.25-and 5-ha plots were replicated four times for each of the three treatments, with fire either completely excluded (unburned treatment) or with burns applied annually in the early-dry season (April/May, hereafter referred to as early-burns) or late-dry season (September/October, hereafter referred to as late-burns). However, due to space constraints and logistical issues, we were only able to implement three late-burn 25-ha plots. The experimental setup thus had three fire treatments (unburned, early-and late-burns), two fire sizes (0.25 and 5 ha) with four replicate plots and an additional three 25-ha late-burn plots, resulting in a total of 27 treatment plots.

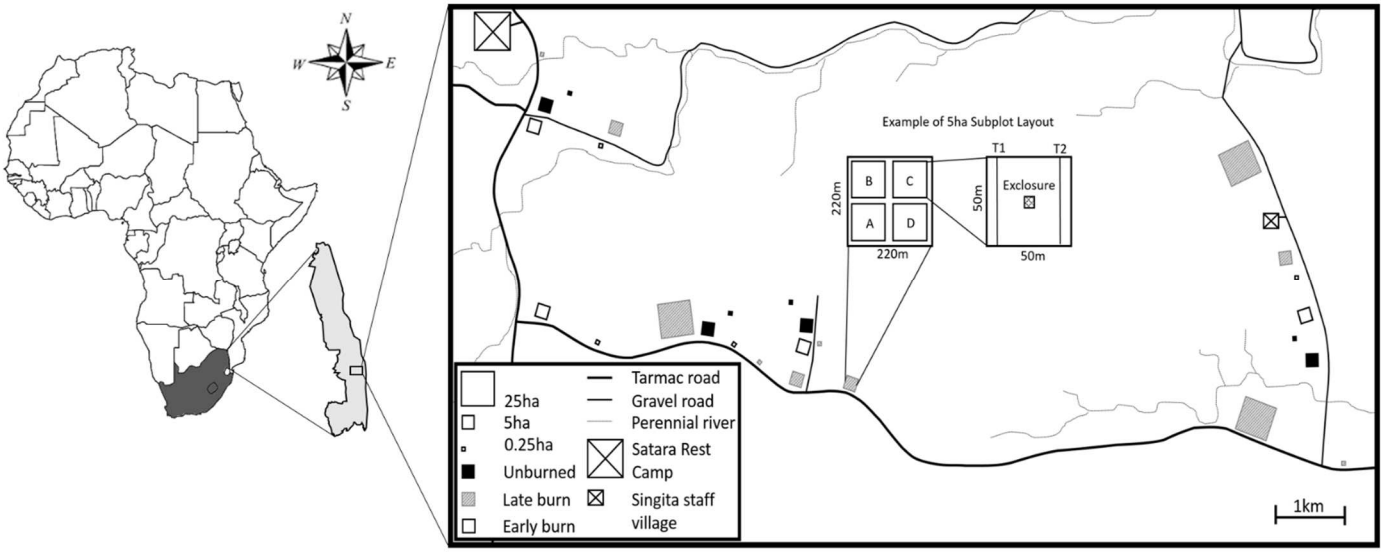


Figure 2.1. Layout of burn treatments in the Satara Land System of Kruger National Park. Late-burn and early-burn plots were burnt in May and October of every year of the study while no fire occurred in the unburned plots or on the remaining landscape. The 5-and 25-ha plots contained four and nine 50 × 50 m sampling subplots, respectively, while 0.25-ha plots were the equivalent of a single subplot. We erected herbivore exclosures (1 m²) in the centre of each subplot to enable us to assess the effect of fire alone, and we sampled two parallel 50-m transects (T1 and T2) placed an equal distance on each side for analysis of combined fire–herbivore effects. All data collection took place along the transect lines and within exclosures of every subplot. Sampling of all subplots occurred every year before and after burn treatments.

Fires were applied every year by experienced teams from "Working on Fire" (http://workingonfire.org) to each of the early-and late-burn treatment plots, resulting in three burn applications per plot by 2016. Plots were selected that had: (1) high grass biomass with grass communities dominated by the fire adapted grasses *B. radicans* and *T. triandra*, (2) similar amounts of woody cover (6 – 10%) and (3) similar distances from permanent water sources (1 -3 km). Sampling effort needed to be higher on the larger plots and required greater sampling effort to represent the variability in grass heights over the larger areas. We, therefore, created a 50 × 50 m subplot sampling design that could be implemented in the 0.25-ha plots and was replicated on the 5-and 25-ha plots four and nine times respectively. We erected 1-m ² herbivore exclosures in the centre of each subplot to enable us to assess the effect of fire alone, and we sampled two parallel 50-m transects placed an equal distance on either side for analysis of combined fire–herbivore effects.

3.3 Data collection

To estimate burn patchiness, we walked the two transect lines of each subplot immediately after burning and recorded burnt/unburned patches every 2 m. A burn patchiness index was calculated using equation:

$$1 - (Burnt\ points/total\ points - (unburnt\ points /total\ points\ x\ number\ of\ unconnected\ burn\ points/total\ points))$$

This gave a value between 0 (all points burnt) and 1 (no points burnt) with weight for the contiguousness of the burn (Table 2.1).

Data on grazer densities and grass biomass were collected using a BACI approach (before-after control-impact) (Smith, 2002). Sampling took place 1 month prior and for 2 months after application of seasonal-burns on both the fire-treated and unburned plots. We sampled early burn plots again in December 2013 when the first major rains of 2013/2014 arrived in order to account for herbivore responses to fresh growth on these plots. Due to logistics, this meant the second month of post-burn sampling for late-burn plots occurred in January 2014. Finally, we sampled all plots again at the end of the rainy season in April when grass biomass was expected to be highest. Thus, the first data collection occurred in April 2013 with early burn and late-burn

treatments applied in May and October 2013, respectively, and repeatedly every year thereafter until 2016.

Table 2.1. Overview of plot characteristics and measurement units for all fire application treatments in 2013. Reported grass heights were measured before the application of fire treatments

Treatment	Size (ha)	Number of plots	Mean distance to water (km)	Woody cover (%)	Mean grass height (cm)	Burn patchiness index
Unburned	0.25	4	1.5 (1.2)	6.8 (3.9)	37.2 (6.7)	NA
	5	4	1.6 (1.2)	7.6 (2.3)	43.2 (3.2)	
Early-burn	0.25	4	1.4 (1.0)	7.6 (1.7)	56.4 (6.3)	0.28 (0.13)
	5	4	1.2 (1.3)	6.1 (3.9)	56.7 (6.3)	0.46 (0.02)
Late-burn	0.25	4	1.8 (1.6)	8.6 (3.8)	37.0 (0.9)	0.08 (0.17)
	5	4	2.7 (1.9)	6.3 (0.7)	40.1 (4.7)	0.01 (0.01)
	25	3	1.3 (1.1)	6.6 (1.6)	37.6 (3.9)	0.01 (0.01)

Vegetative response to fire and grazing was recorded every 5 m along the two transect lines in each subplot. At each point, we measured the grass height of the standing grass biomass. We took the same measurements at five points within the herbivore exclosures to assess grass response in the absence of herbivory.

Grazer presence was measured by recording all dung (species and abundance) including dry dung encountered in 4-m-wide belts along transect lines. Dung transects have been used previously to estimate large herbivore habitat usage in long-term studies within African savannas and perform better than direct observations and other indirect measurements (Cromsigt *et al.*, 2009; Burkepile *et al.*, 2013, 2016), giving relatively reliable measures for comparisons of relative abundance across similar habitats (Marques *et al.*, 2001; Sensenig, Demment and Laca, 2010). Despite this, decomposition rates on different substrates and dung removal rates by dung beetles represent two inherent issues with using dung counts to assess large mammal abundance in savannas. These issues are not easy to mitigate with changes to methodology but were taken

into account when drawing conclusions from our results. Fortunately, in the context of this study both factors would result in an under-representation of the expected response, not a false-positive: the increased bare ground on burnt plots would have increased dung decomposition and removal (Davis *et al.*, 2010), resulting in under-representation of dung counts on burn treatment plots when compared with unburned plots. Finding increased dung on the burn plots is therefore evidence for substantial herbivore utilization. Furthermore, dung beetle activity is higher during the warm wet summers (November–April) than during cold dry winters (May–October) (Davis, 1996) and would have removed more dung during summer post-burn sampling than winter sampling. To eliminate any further bias and ensure that the time period of sampling was equal, we walked and cleared transects of dung 1 month prior to initial data collection. Dung counts were then sampled on a precise monthly (30 day) basis with dung crushed during data collection to avoid recounting. Dung counts per transect were divided by days since previous sampling (30) and the mean dung deposition per week was calculated per species for each plot.

Monthly rainfall data were recorded from the Satara Rest Camp and Singita Lebombo staff village weather stations (Figure 2.1).

3.4 Data analysis

We modelled grazer dung events per week (as a proxy for abundance) using a generalized linear mixed effect model (GLMM) with a Poisson distribution to assess the response of all grazers to early-and late-burns of different sizes (Crawley, 2012). Burn size (0.25, 5 and 25 ha for late-burn), distance to water and month represented fixed effects with plot and subplot acting as nested random effects to control for repeated measures along the transects of each subplot every month.

Following Sensenig, Demment and Laca (2010), we calculated a grazer preference index for species in each treatment plot as the total of dung in a burn treatment plot divided by the sum total of dung in the burned treatment and matched unburned treatment plot. In the case of 5-ha plots, this meant summing the dung across all transects in all subplots prior to calculating the ratio. This gives a value of 0–1 for each early-or late-burn plot, with 0 (total avoidance) and 1 (complete preference for burn treatments). Late-burn 25-ha treatments did not have matched unburned plots and were excluded. We modelled the preference of the four focal grazing species to burn treatments over the three years of the experiment using GLMMs with a binomial

distribution. For each species, the grazer preference index for each plot represented the response variable with fire size (0.25 and 5 ha), distance to water, and treatment (early-burn and late-burn) acting as fixed effects. Plot represented the random effect to control for repeated sampling of plots every year.

To assess what grass height each species of grazer selected throughout the final year of treatment (2015), we binned transect lines by their mean grass height in 5-cm increments from 0 to 40 cm. For each grazer species, we recorded a presence if any dung event occurred along the transect line and an absence if no dung was found. These scores were tallied to give the proportion of presence for a given number of transect lines of a specific grass height class. We ran a Chi-square test to compare observed grazer frequency within the different grass heights to the distribution of sampling effort (Crawley, 2012).

We ran two statistical models on our grass height data. To assess whether our treatments kept grass short throughout the growing season, we assessed grass height in April (end of the growing season) over the 3-year study period using linear mixed models (LMM) with the restricted maximum likelihood method. Burn size (0.25, 5 and 25 ha for late-burn), grazing (presence/absence) and year (2013, 2014, and 2015) represented fixed effects, with plot and subplot acting as nested random effects. For this analysis, we modelled each fire treatment (unburned, early burn and late-burn) separately to enable interpretation of results. We compared the cumulative effect of our fire/grazing treatments on grass height over the 3-year experiment (with April 2015 grass height as the response variable). The fixed effects included treatment (unburned, early burn and late-burn), size (0.25 and 5 ha) and grazing (presence/absence), while plot and subplot were included as nested random effects.

All LMMs and GLMMs were processed using r statistical software (version 3.3.1; R Core Team, 2016) and the lme4 package (Bates *et al.*, 2015). Following the suggestions of Zuur *et al.* (2009) and Bolker *et al.* (2009), we used a top-down approach to model selection with an ANOVA to remove effects that resulted in models that did not differ ($p < 0.05$) significantly from the full model (Table 2.2). We looked for obvious deviations from homoscedasticity and overdispersion in our models by plotting residuals against fitted values and visually assessing plots. To verify normality of the residuals of selected models, we used the Shapiro–Wilks test and assessed histograms and QQ plots visually (Zuur *et al.*, 2009). We ensured that sampling subplots were

not spatially auto-correlated by utilizing the georR package (Ribeiro and Diggle, 2016) to calculate semivariograms for raw data for each year of sampling and using the residuals from all selected models (Zuur *et al.*, 2009). Semivariograms showed that variation in direct measures of grass height and dung counts, as well as residuals, did not increase with increasing distance between plots, indicating no serious autocorrelation issues were present (Figure S2.2 and Table S2.1). Since the GLMM for buffalo burn preference indices showed that residuals were not

Table 2.2. Linear mixed models and generalized linear mixed models used to assess the relationships between herbivore selectivity of plots and the effects of different grazing and fire regimes on grass height. In cases where no fixed effects showed any relationship with the response variable, null models were selected, and more complex models are only shown to indicate effects tested

Selected models	**df**	***F***	***P***
Wildebeest			
Burn preference index ~ Year + (1|plot)	2	13.1	0.001
Impala			
Burn preference index ~ Year + (1|plot)	2	0.9	0.607
Zebra			
Burn preference index ~ Year + (1|plot)	2	3.5	0.17
Buffalo			
Burn preference index ~ Year + (1|plot)	2	0.3	0.843
Unburned			
Grass height ~ Year + (1|plot |subplot)	2	123.4	<0.0001
Early-burn			
Dung density ~ Month + (1|plot |subplot)	4	156.4	<0.0001
Grass height ~ Year * Grazing + (1|plot |subplot)	3	7.8	0.05
Late-burn			
Dung density ~ Month + (1|plot |subplot)	4	156.9	<0.0001
Grass height ~ Year * Size * Grazing + (1|plot |subplot)	12	318.9	<0.0001
All 5ha Treatments in year 2015			
Grass height ~ Grazing + (1|plot |subplot)	2	24.5	<0.0001

normally distributed with clear overdispersion, we used a negative-binomial distribution to improve model performance (Zuur *et al.*, 2009).

4 | Results

4.1 Grazer burnt area and grass height preference

Grazers clearly responded to fire treatments with dung events increasing in abundance on burn plots after fire treatments were applied in 2013 (Figure 2.2). The GLMM confirmed that for both early burn (ES = 1.89, *SE* = 0.56) and late-burn (ES = 4.22, *SE* = 0.24) plots, the months after the fire were strong predictors of grazer densities (Figure S2.3). For the early burn, grazer densities increased immediately after the fire and further increased in December after the first major rains of the 2013–2014 season (Figure 2.2). Similarly, the late-burn treatment GLMM demonstrated that grazers responded strongly to burn treatment in the months after fire application, with the strongest response in the first month post-fire (ES = 2.63, *SE* = 0.11).

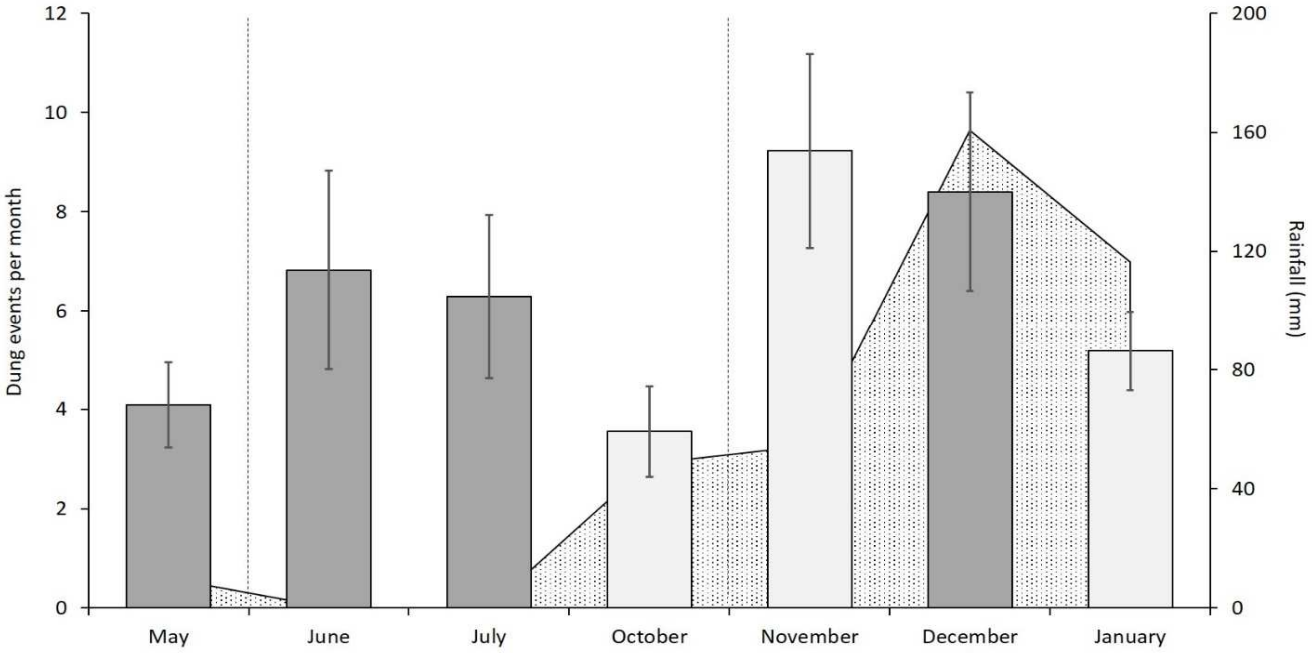


Figure 2.2 Dung deposition per month (mean ± *SE*) and rainfall (hatched) for sample months in 2013 and 2014 when the early- and late-burn fire treatments were initiated. Data was sampled on early-burn (dark grey) for 1 month prior-and 2 months' immediately post-fire and again in December when rainfall returned. Data on late-burn (light grey) plots were sampled 1 month before and one month after burning with a second month of data collected two months later. Dashed lines represent fire application in May and October 2013 for the eight early-burn and 11 late-burn plots respectively.

Densities remained high until January 2014. We found no evidence to suggest that fire size affected these relationships for either early- (ES = 0.14, *SE* = 0.10) or late-burn (ES = −0.02, *SE* = 0.01) treatments, perhaps due to low sample size for dung transects per month.

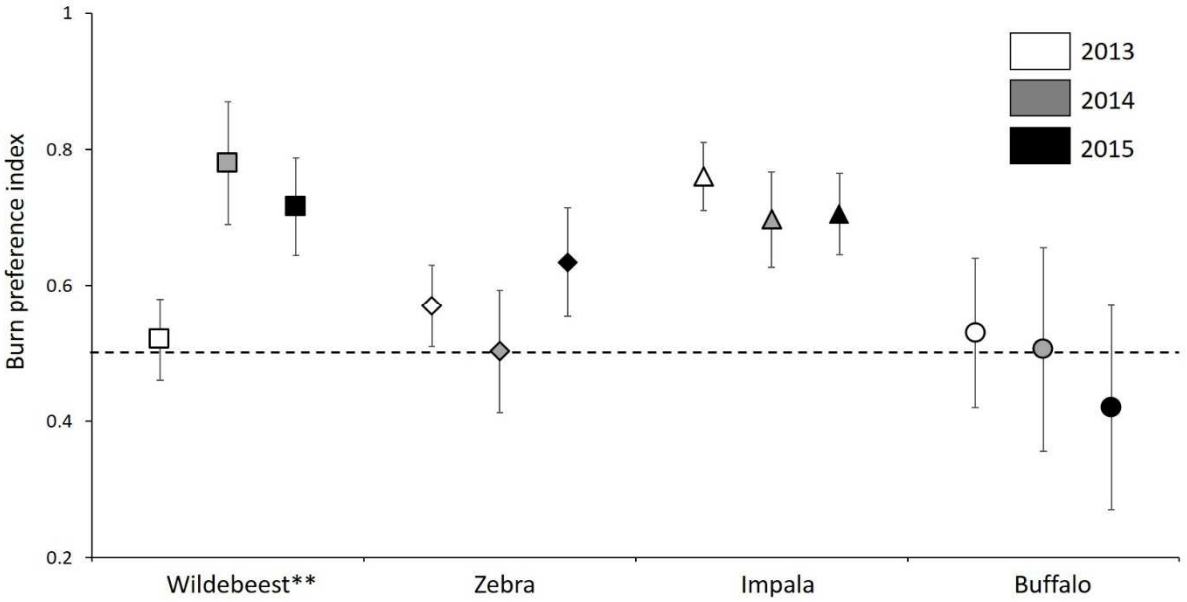


Figure 2.3. Burn preference indexes (0 = absolute avoidance of burnt plots, 1 = complete preference for burnt plots) for three years of fire treatments for grazing herbivores in the Kruger National Park. Data for 2013 is prior to any burn applications with 2014 and 2015 representing the responses of grazers to one and two seasons of burning respectively (**$p < 0.001$).

Wildebeest showed no preference for burn plots prior to treatment in 2013 but switched to actively selecting and staying on both early-and late-burn treatments in the following two years (Figure 2.3—GLMM ES = 0.26, *SE* = 0.09; Figures S2.3 and S2.4). Impala had a constant preference for burnt treatments throughout the study period (ES = −0.05, *SE* = 0.06) but increased in plot utilization year on year (Figures S2.3 and S2.4), In contrast, zebra (ES = 0.06, *SE* = 0.08) and buffalo (ES = −0.11, *SE* = 0.16) showed no significant changes in their preference indices over the study period (Figure 2.3) and other than an initial response to early-burn treatments showed no long-term increases in densities over the study period (Figures S2.4 and S2.5). The burn preference ratios showed no effect of fire size (ES = 0.02, *SE* = 0.02) or fire season (ES = −0.03, *SE* = 0.09). Wildebeest ($\chi2 = 139.9$, $p < 0.001$) and impala ($\chi2 = 38.84$, $p <$

0.001) were also found unexpectedly often in grass heights below 10 cm across the study sites in 2015 and were found rarely in grasses above 25 cm. Zebra occurred uniformly across all grazing height classes between 0 and 40 cm. Buffalo occurred more frequently in grass heights above 15 cm ($\chi 2 = 35.76$, $p < 0.05$) than expected and were seldom found in short-grass areas below 5 cm. Thus, although all grazers clearly responded to the fire treatments in the short-term, only wildebeest appear to have been driving the longer-term grass height differences between plots.

4.2 Grass system response to fire and herbivory

Grass height at the end of the season decreased on all plots over the course of the study (Figure 2.4) due to lower rainfall and moribund grass on unburned plots in the 2014–2015 season (ES = −13.6, *SE* = 0.59). We did not find any evidence that grass height on unburned plots was affected by grazing (ES = −3.60, *SE* = 0.89) or size (ES = 2.00, *SE* = 0.78). Likewise, the grass on burn-only treatments (exclosures) regrew to pre-fire levels by the end of the season (early-burn ES = −3.50, *SE* = 1.41; late-burn ES = 7.85, *SE* = 2.95), while grass height decreased dramatically as a result of lower rainfall and fire treatments by 2015 in early-(ES = −21.56, *SE* = 8.37) but not late-burn plots (ES = −1.45, *SE* = 3.00). This resulted in grass within exclosures (all treatments) being ~ 30 cm by 2015. The attractive effect of fires on grazers, however, resulted in an even greater decrease in grass height by 2015 for both early-burn (ES = −28.73, *SE* = 8.44) and late-burn (ES = −22.36, *SE* = 3.06) treatments (Figure 2.4). Consequently, after three years, the burned–grazed plots were the only ones with grass <20 cm on average, with large proportions of the grass <5 cm on late-burn plots (Table 2.3). Repeated attempts to ignite plots in 2015 failed in a quarter of the early-burn and all late-burn treatments (Table 2.3).

Table 2.3. Overview of plot characteristics for all fire application treatments in 2015

Treatment	Number of plots	Mean proportion of grass height below 10 cm	Mean proportion of grass height below 5 cm	Number of plots where repeat ignition failed	Bare ground (%)
Unburned	8	0.08 (0.04)	0.06 (0.02)	NA	11.4 (1.2)
Early-burn	8	0.28 (0.04)	0.11 (0.03)	2	34.1 (1.3)
Late-burn	11	0.91 (0.03)	0.80 (0.04)	11	36.6 (1.5)

There was no evidence that the size of fire affected grass height for early-burn treatments (ES = −1.55, *SE* = 1.30). However, the LMM for late-burn treatments indicated that there was some effect of fire size on the time it took for grazers to maintain grass in a cropped state. Herbivory on the smallest burns (0.25 ha) resulted in the maintenance of a relatively short-grass state (<25 cm) after the first season of treatment (ES = −15.28, *SE* = 9.22), while a similar response was only seen in the second year of treatment for the two larger burns (5 ha ES = −14.60, *SE* = 11.13; 25 ha ES = −16.84, *SE* = 10.67). Grass height was also kept <5 cm on average by herbivores on the smallest fires, while grass height was maintained <15 cm on both 5-and 25-ha plots by the final year of the study.

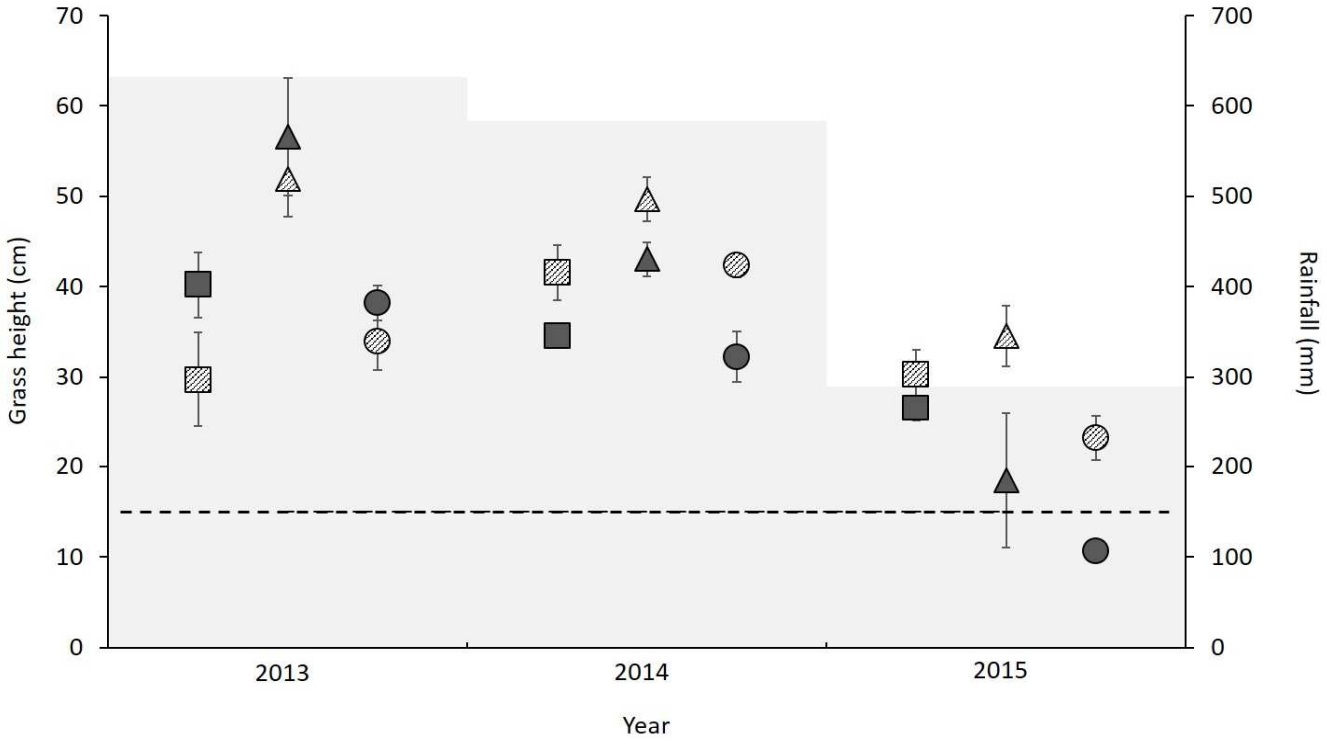


Figure 2.4. Grass height (mean ± *SE*) and total annual rainfall (light grey) on unburned (squares), early-burn (triangles) and late-burn (circles) plots for three years of fire treatment implementation. Grass height decreased in 2015 due to rainfall regardless of treatment. Fire treatment alone (light grey and hatched) had no effect on grass height, but the coupling of herbivory and fire treatment (dark grey) decreased grass height on early-burn and late-burn plots after two years of treatment. The dashed line represents the upper limit of grass height (15 cm) that wildebeest actively select.

5 | Discussion

Our study demonstrates that it is possible to engineer landscapes by applying ecological theory to achieve particular goals. Small fires (<25 ha) attracted all the grazing herbivores studied in large enough numbers to initially shorten grass height, particularly during the wet season. This immediate herbivore response after the first burns was not sufficient to maintain grass communities in a short lawn state over the growing season. However, repeated applications of fire treatments over the following two years resulted in short-grass specialists (wildebeest) actively selecting for burnt patches over the entire growing season. Ultimately, the high densities of impala, wildebeest and to a lesser extent zebra on burnt plots (see Figures S2.3 and S2.4) maintained lawns after the second season of burning and, depending on the season of burn, reduced grass height to a level that excluded repeat fires (Figure 2.5). Theory predicts that at least 40% of a landscape needs to be non-flammable (*c.* <5 cm) to restrict fire spread (Turner, Gardner and O'Neill, 2001). This was achieved on all our late-burn plots by the end of three years, but only 25% of the early-burn plots—with the expected response of switching off fire being evident during our 2015 burns (Table 2.3). Moreover, grass height <10 cm is preferred by wildebeest and >90% of the late-burn and 25% of early-burn grass cover was in this state by the end of 2015 (Table 2.3).

Four of the 32 extant large grazing mammals in Africa are short-grass specialists (see Table S2.1), these species (like wildebeest) often make up a large proportion of herbivore biomass across their range (Hempson *et al.*, 2015). Moreover, the greater visibility on short-grass areas means that many other large herbivores gain additional benefits, including improved predator detection and avoidance and show a preference for utilizing short-grass areas (Anderson *et al.*, 2010; Kleynhans *et al.*, 2010; Burkepile *et al.*, 2013). Short-grass specialists are common in lower rainfall savannas, which make up 50% of sub-Saharan Africa (Hempson *et al.*, 2015). In these areas, including the globally recognized Masai Mara, Serengeti, Etosha, Gorongoza, Chobe and KNP, management to promote and maintain short-grass habitat should be integral to conservation management. Our results suggest that small fires used with specific management outcomes have the potential to engineer savanna grass communities into a short-grass state and diversify grass structure in a similar way to that of white rhinos and termitaria (Cromsigt and Olff, 2008; Waldram, Bond and Stock, 2008; Cromsigt and te Beest, 2014). Initiation and maintenance of short-grass areas will be easier in drier regions (Waldram, Bond and Stock,

2008), but the use of repeated burning in the absence of other lawn drivers could be important in wetter regions and may represent a valuable tool where mega-herbivores are low in density or locally extinct in areas both within Africa and globally (Fuhlendorf *et al.*, 2009).

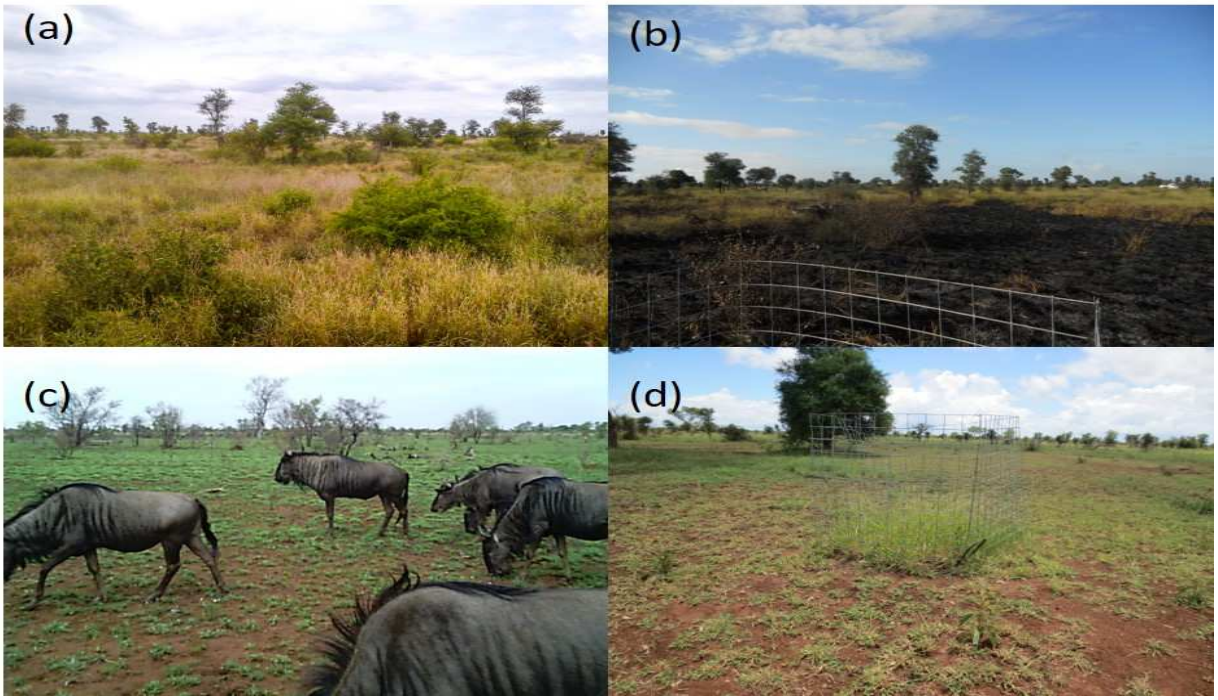


Figure 2.5. Sequence of photos depicting changes in vegetation in response to experimental treatments in the 5-ha late-burn plots in Kruger National Park. From top left: (a) grass structure pre-burn (April 2013); (b) burnt area immediately post-burn (October 2013); (c) wildebeest grazing response to post-burn green flush (November 2014); (d) differences in grass height within and outside of an exclosure after two seasons of burn treatments (April 2015).

5.1 Grazer, burnt area and grass height preference

The active selection of our smallest burn treatments by all herbivores post-burn and by wildebeest over the period of the study supports our first hypothesis. This is a good indication of the importance of short-grass systems as resources for grazers during the breeding season and likely represents a lack of these areas in the general landscape. Furthermore, the long-term use and active selection for burnt plots by wildebeest, as well as the greater presence of both wildebeest and impala in short-grass areas, in contrast to buffalo, supports recent work by Burkepile *et al.* (2016) showing herbivore suite responses on long-term burn plots. Our findings

align with work suggesting that grass height heterogeneity is an important factor in large-grazer resource partitioning in savannas (Kleynhans *et al.*, 2010; Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2016). Although analyzing demographics is beyond the scope of this study, the strong selection bias of wildebeest for short-grass areas, and avoidance of tall-grass areas, suggests that wildebeest populations already impacted by the loss of natural migratory routes, heavy predation and culling may be further impacted by loss of habitat resulting from large scale fires in KNP (Yoganand and Owen-Smith, 2014).

5.2 Grass system response to fire and herbivory

After only two seasons of burning, the fire–grazer effect initiated a new grass structural type in a previously tall-grass system and strongly supported our second hypothesis. Lower rainfall in 2015 and resultant reduction in grass productivity played a role in facilitating the switch to a short-grass state. However, the strong influence of herbivory, coupled with fire, on grass height leaves us confidence that this state would have been reached in subsequent seasons if rainfall had continued at levels seen in 2013 and 2014.

The more complete switch to short-grass state on late-burn plots when compared to early-burns does not seem to be the result of higher grazing densities, as there was no difference in the response of herbivores to either treatment. This observation disputes our third hypothesis. It is possible that dung transect data were not detailed enough to provide a complete picture of the differences in herbivore use. Herbivores present but not feeding (i.e. resting or being vigilant) on plots and variation in dung deposition rates at different times of the year may have created too much noise in the data to allow us to identify subtle variations in plot usage. This makes it difficult to decipher the cause of the greater response of grass height to grazing on late-burn plots compared with early-burn plots. While our data limit definitive conclusions, we know that the higher fuel moisture during the early-burn season resulted in tall-grass clumps within early-burns (note the large standard error of early-burn means in Figure 2.3). These unburned clumps would have been avoided by herbivores and remained uneaten, and may also have acted to discourage consistent feeding due to increased predation risk and increased vigilance (Fortin *et al.*, 2004) potentially reducing effects on the grass layer (Fortin *et al.*, 2004). Thus, while dung deposition is similar on early-vs. late-burn plots, direct grazing effects would be greater on late-burns.

Despite similar dung densities on the smallest and largest late-burn plots grass was shorter on the smallest plots. Wildebeest rest in sites where predator avoidance can be maximized (Owen-Smith and Traill, 2017), which would be greater on larger burn patches. Thus, similar dung densities on larger plots may reflect lower grazing intensity and explain the difference in grass heights.

5.3 Implications for ecosystem properties and management

The switch of the treatment plots to a short-grass state with greater bare ground (Table 2.3) increased structural and functional diversity of the landscape. Concentrated grazing and soil compaction by herbivores can shift grass community composition towards species more tolerant of water stress and heavy grazing (Cromsigt and Olff, 2008; Veldhuis *et al.*, 2014). These potential changes will likely have cascading effects on other communities (Krook, Bond and Hockey, 2007). Grazing lawn systems have been shown to support suites of grasshoppers (Samways and Kreuzinger, 2001), birds (Krook, Bond and Hockey, 2007) and spiders (Warui *et al.*, 2005) unique from tall-grass systems. In addition, ants respond rapidly to changes in bare ground (Parr *et al.*, 2004) and may have already responded to the structural changes experienced on the plots. However, it is also possible that there are negative effects of the treatments. Increased bare ground in plots may result in increased run-off and loss of top soil (Thornes, 1985), and subsequent switches to poor quality grass species (Oliva *et al.*, 1998b; Fensham, Holman and Cox, 1999). This is of concern on poor quality soils and in low rainfall areas. However, the response shown by short-grass specialists to small fires in this study was still apparent (Burkepile *et al.*, 2016) in a nearby long-term burning experiment with similar fire treatments (7-ha blocks burned at various frequencies/seasons since 1955), indicating that this grass structural type can persist in the landscape and continue to create favourable habitat even 60+ years since initial treatments.

The practicality of implementing small burns over large areas in a national park also needs to be addressed. It appears that there is some flexibility in the size of fire needed to achieve the grazing lawn state: all our size treatments were equally effective at attracting grazing herds (i.e. none of our fires were large enough to result in the dispersal of grazers, nor small enough to not be noticed within the broader landscape). However, application of our experiment was labour intensive and required skilled teams to operate over several days and keeping all other fires out

of the surrounding landscape is not feasible across large landscapes. The danger of fires spreading during the late-dry season means that it would be difficult, in practice, for managers to carry out the same small fire application repeatedly over large areas. However, early-season burns tend to be smaller, and frequently burn out naturally if not actively re-ignited. Use of small early-season burns also align with current shifts in KNP fire management towards the use of earlier season fires in response to the increase in the number of large hot wildfires during the late-dry season that negatively affect tall trees in the park. Despite the more limited change on early-season treatments, we believe this is the most realistic option to implement over broader areas in savannas across Africa. A greater number of repeated treatments is also likely to achieve the same result as late-burns given a longer period, especially if the occasional runaway fire results in temporary dispersal of grazers.

Variation in grass community structure and diversity of grass height is now widely accepted as necessary in the conservation of savanna landscapes (Owen-Smith, 2004). With the white rhinoceros, the main driver of large-scale short lawn creation, under threat in most natural systems, it is likely to become increasingly necessary for conservation managers to look at novel ways of manipulating the grass layer over wide areas. Here, we have experimentally shown that small-scale fires have the capacity to concentrate grazers in sufficient densities to maintain grass in a short-grass lawn state. Our findings indicate that theory on spatial patterns of grazer use of the post-fire environment developed by Archibald *et al.* (2005) can be practically implemented to promote short-grass areas within the landscape.

Chapter 3 | Feedbacks between grazers, grass and fire create alternate savanna states

This chapter has been prepared for submission to The American Naturalist

1 | Abstract

The ability of grazers to create and maintain patches of high-quality grazing habitat is well recognised. These patches are initially only distinguished through structure, and therefore require continuous grazing to remain attractive to grazers. More permanent “grazing lawn” habitat, which remains attractive during brief periods of rest from grazing, can only occur through feedbacks between grazing and species composition (or grazing and nutrient cycling). Small fires have been shown to promote this process, by encouraging concentrated intense feeding in one spot, and large fires have been shown to hinder this process, by dispersing grazing animals in the landscape and relieving heavily-grazed patches. Considering that climatic limitations underlie the relationship between grazers and fire as consumers in savannas we should expect that a sudden change in climate will influence the balance between them in the short term. The effect of droughts on fire and grazing in free roaming savanna systems is not well studied, but theoretically drought should act to promote or hinder feedbacks between consumers and grass communities – both by decoupling grazers from grazing lawns where forage is absent or by dispersing animals into generally ungrazed fire-controlled habitats and limiting the chance of repeat burning. Here we use a landscape-scale experiment to test how easily a system switch from fire- to grazer-dominated can be initiated in a landscape, and how the functional traits of the grasses drive these switches. We then track the impacts of a severe two season drought on the consumer driven feedbacks within the study system. Specifically, we hypothesise that:

1) Small fires will focus grazing activity and consequently cause a shift in grass composition.

2) Grass communities resulting from the pyric-herbivory associated with small-repeated burns will be dominated by functional traits that encourage repeated grazing (low C : N ratios, high leaf moisture content, high biomass density) and thus continue to attract high numbers of mesoherbivores once it is no longer possible to burn.

3) Drought events should force grazers to feed in low-quality fire-adapted grasslands and result in convergence of grass community composition between patches.

We burnt small repeated fires in the Kruger National Park in South Africa and monitored the response of grazers and changes in the grass community composition and functional trait space over a five-year period with the final two seasons of sampling occurring during a major drought event. Our results indicate that species composition and grass traits shift in response to increased

grazing driven by small fires. The C : N ratios and leaf moisture content of grass communities shifted in response to higher grazing and resulted in a higher quality forage on burn treatment plots. However, this response was lost during the drought when grazers fed more intensively on the broader landscape and trait space across the treatment plots converged. Our results add to a growing number of studies that highlight the importance of feedbacks in the establishment of dominant consumer processes within savannas. They indicate that it is possible to change the driving consumer within African savannas with directed management that alters plant traits driving the dominant feedback processes.

Keywords: African savanna, alternate state, burning, consumers, fire, grass functional trait, grazing lawns

2 | Introduction

Large swathes of African savanna vegetation are structured by feedbacks between grass and its two dominant consumers, fire and mammalian herbivory (Bond, 2005; Archibald and Hempson, 2016). Both these consumers drive the structuring of grass communities by altering the local resource environment and changing the competitive space within which grasses persist. However, the “metabolic” requirements of these two perturbations and the physical and temporal differences in how they consume grass biomass means that the life history traits of grass communities exert some control on which consumer is dominant within a given landscape. Evidence for divergence in the structure and function (Hempson *et al.*, 2015) of grass communities under the control of fire vs. herbivory and the feedbacks that maintain consumer dominance has led to suggestions that fire-controlled and herbivore-controlled grasslands represent alternate states (Venter, Hawkins and Cramer, 2017). Archibald and Hempson (2016) showed that Bond's (2005) fire-controlled ‘black-world’ and herbivore-controlled ‘brown-world’ savannas filter out along abiotic gradients with black-world savannas dominant at high rainfalls (>1000 mm) and brown-world savannas at low rainfalls (<400 mm). However, there are still large portions of Africa’s savannas that are not completely predisposed by abiotic conditions to either consumer and consumption in these systems is either dominated by herbivory or fire, lending support to the idea of alternate states (Archibald and Hempson, 2016). These areas are of interest to land managers as they allow for the potential manipulation of consumers to favour specific management targets, but also represent important areas to test our current understanding of trait driven feedbacks and thresholds relating to alternate states.

The differences in fuel and food requirements of fire and mammalian herbivores means some landscape level spatial separation in their occurrence should be expected as feedbacks entrench the role of the dominant consumer. Fire can only take large, dry bites and requires a threshold amount of cured biomass before it is able to spread (Archibald *et al.*, 2009). Grasses that have high C : N ratios resulting in a build-up of dead material, low leaf moisture to allow curing during the dry season, and low bulk density to encourage burn intensity represent the ideal habitat for fires (Simpson *et al.*, 2016). Conversely, grazers require relatively high-quality (low C : N ratio) forage with high leaf moisture content improving digestibility and high biomass density reducing acquisition effort (Owen-Smith and Novellie, 1982). Thus, although these two

consumers compete for the same food source, they frequently favour divergent traits in grass communities with grasses that are flammable seldom palatable and vice versa (Bond, 2005).

2.1 Switching the dominant consumer – fire to grazer

Due to differences in food requirements, 'black world' savannas that burn frequently represent a barrier to grazer communities as a combination of low food quality and poor visibility in tall grass makes fire prone bunch grasslands suboptimal habitat for grazers (Owen-Smith and Novellie, 1982; Yoganand and Owen-Smith, 2014). Grazers therefore spend less time in tall bunch grasslands, leaving large amounts of standing biomass, and encouraging repeat burning. This entrenches fire as the dominant consumer and stabilize fire prone grass communities temporally. Despite this, the ability of grazers to create and maintain short grass grazing-lawn patches that represent high quality grazing habitat within tall-grass fire prone savannas has been recognized in numerous African systems (Mc Naughton, 1984; Waldram, Bond and Stock, 2008; Cromsigt and te Beest, 2014). To overcome the feedbacks that maintain savannas in a fire-dominated state requires some external disruption that encourages herbivores to crop tall grasses short (Hempson *et al.*, 2015). These disruptions have been occur in the form of small-disturbances (<20 m^2), such as the formation of termite mounds that concentrate grazers and increase local grazing offtake (Davies *et al.*, 2014), seasonal increases in localized grazing pressure resulting from large mammal migrations (Mc Naughton, 1985) or as a result of grazing by white rhino that are unique among African grazers in their ability to crop tall grass into short grass states (Waldram, Bond and Stock, 2008). At this stage of grazing lawn formation heavily grazed patches are only defined from the surrounding tall grass landscape by differences in grass structure and no permanent change has been effected, with fire likely to return if patches do not attract grazers over a number of seasons (Hempson *et al.*, 2015). The longer term formation of permanent lawns that consistently attract high grazing can only occur if grass communities change in response to elevated grazing (Mazancourt and Loreau, 2000), trampling (Veldhuis *et al.*, 2014) or nutrient cycling (Cromsigt and Olff, 2008) and patches maintain their attractiveness to grazers from season to season. In these cases, fire will be excluded due to low standing biomass and ultimately a switch to a novel herbivore-driven state will have occurred as feedbacks between grass communities and grazers maintain the dominant processes.

2.2 Grazing impacts on grass community composition and function

Global meta-analyses of grass community response to grazing indicate that species richness decreases but that grazing selects for different species, resulting in higher beta-diversity overall in systems with heavily grazed patches (Milchunas, Sala and Lauenroth, 1988). There is also an increase in species evenness associated with grazing (Eby *et al.*, 2014). However, species compositional shifts in the form of richness and evenness scores are not useful for predicting the functional responses of systems to changes from fire to grazer dominated savannas. At the functional level the plant traits associated with heavily grazed grass communities are not resolved (Díaz *et al.*, 2007) and there is no clarity on whether grazing increases or decreases palatability overall across different grazing ecosystems globally. Likewise, although we expect grazing tolerance traits to decrease flammability (low-statured), this has never explicitly been tested. Here we attempt to address these gaps by assessing changes in the genotypic trait space of grass communities at the local scale when there is a switch in the dominant consumer from fire to grazing.

2.3 Fire and drought impacts on grazing systems

Grazing mammals and their respective densities change following burns (Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2016; **Chapter 2**) in what has been termed 'pyric-herbivory' (Fuhlendorf, 2005). Large landscape-scale fires disperse grazers over the broad areas as they feed on the fresh regrowth of bunch grasslands and this decreases localised herbivory on grazing lawns (Archibald *et al.*, 2005). Thus, repeated large fires drive homogenisation of the grass layer at larger scales as grazing lawns in the broader landscape are lost when the feedbacks between grazers and high-nutrient short grass patches are broken down (Archibald, 2008). In contrast, there is evidence that small fires (<500 m^2) draw high numbers of animals onto patches and result in greater grazing intensity per individual plant than larger fires (Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2016; **Chapter 2**). The higher grazing pressure maintains grass in a cropped state for longer periods of time with feedbacks that attract constant elevated unselective grazing (Sensenig, Demment and Laca, 2010; Donaldson *et al.*, 2017). **Chapter 2** showed that elevated grazing in small burnt patches can remove fire from the system locally and completely shift the selective pressure acting on grass species from fire to herbivory. Here we take this concept further and test whether the structural changes observed in **Chapter 2** result in shifts in

grass community functional trait space that enhance feedbacks with grazers and result in permanent grazing lawn establishment.

Global climate models predict that southern Africa is set to experience drought events with increasing frequency (Ratnam *et al.*, 2014). Developing an understanding of the influence that drought has on the interactions between fire and grazing is thus of increasing importance in African savannas. Drought effects on wild grazer systems and the balance between fire and grazer dominated grass communities at the landscape scale has received little attention due to the difficulties of studying drought effects on productivity at scales that are relevant to free roaming grazers. This is problematic as the feedbacks being assessed here play out within the backdrop of repeated but erratic drought events (Ekblom *et al.*, 2012). Considering that climatic limitations underlie the relationship between grazers and fire as consumers in savannas (Archibald and Hempson, 2016) we should expect that a sudden change in climate will influence the balance between them in the short term. Drought should increase the relative pressure of the grazing population on grass communities as less productivity is available for an initially similar metabolic demand. In better studied rangeland systems high grazing pressure during droughts impact grass basal cover and changes community composition over several seasons (O'Connor, 1995). Moreover, during drought events grazers move into lower quality forage areas to feed on less-optimal food sources (Owen-Smith and Novellie, 1982; Macandza, Owen-Smith and Cross, 2004). The combination of these two processes could result in the decoupling of grass communities from their dominant consumers. Grazers are forced to feed in sub-optimal fire-prone grasslands and off grazing lawns with the increased grazing pressure in fire adapted grass communities driving a reduction in standing biomass, basal cover and a shift in species composition towards grass communities that hinder fire return periods. Thus, it could be expected that extended droughts result in high, but unselective grazing over broad areas and potentially homogenise grass communities. In this study we look to test how drought events impact established fire herbivory feedbacks.

The idea that savanna rangelands operate within this framework and exist as multiple states between woodlands and grasslands depending on the dynamics of relevant fire and herbivore regimes has been a fundamental concept in rangeland management (Westoby, Walker and Noy-Meir, 1989; Briske, Fuhlendorf and Smeins, 2005). To change from one state to another requires the maintenance of the novel state via feedbacks that do not require the initial disturbance to be

repeated (Westoby, Walker and Noy-Meir, 1989). We postulate that a shift in the dominant consumer should be evident in the functional traits of the local grass community. Thus, a general shift from low to high palatability that corresponds with consistent high grazer presence in the absence of fire should be indicative of the establishment of feedbacks and the successful switch to a grazing adapted state. Here we use a landscape-scale experiment to test how easily a system switch from fire- to grazer-dominated can be initiated in a landscape, and how the functional traits of the grasses drive these switches. We then track the impacts of a severe two season drought on the consumer driven feedbacks within the study system. Specifically, we hypothesise that:

1) Small fires will focus grazing activity and consequently cause a shift in grass composition.

2) Grass communities resulting from the pyric-herbivory associated with small-repeated burns will be dominated by functional traits that encourage repeated grazing (low C : N ratios, high leaf moisture content, high biomass density) and thus continue to attract high numbers of mesoherbivores once it is no longer possible to burn.

3) In contrast, drought events should force grazers to feed in low-quality fire-adapted grasslands and result in convergence of grass community composition between patches.

3 | Methods

The Kruger National Park (KNP) is a 2 million ha protected area in South Africa containing the full suite of native mega-herbivores including white rhinoceros (Venter, Scholes and Eckhardt, 2003). Moreover, the reserve has a well-established fire management plan and detailed records of changes in fire policy (Govender, Trollope and Van Wilgen, 2006), making it ideal for studies on pyric-herbivory. The Satara Land System, one of four major land systems in KNP, is characterized by clayey basalt soils with soil depth not usually deeper than one meter and dominated by the Bonheim, Shortlands, Milkwood, Mayo, Glerosa and Valsrivier Forms (Venter, Scholes and Eckhardt, 2003). The land system is characterized by low relief with 97% of the landscape having a slope of < 2° and supports extensive C4 grass plains in a *Sclerocarya birrea* (A. rich.)–*Acacia nigrescens* (Oliv.) tree savanna (Gertenbach, 1983). Woody cover at our study sites fell consistently below 10% (Table 2.1) and at the beginning of the study period this area was dominated by C4 grasses *Bothriochloa radicans* (Lehm.), *Digitaria eriantha* (Steud.), *Panicum coloratum* (L.), *Urochloa mosambicensis* (Hack.) and *Themeda triandra* (Forssk.)

(Knapp *et al.*, 2012), with the high abundance of unpalatable *B. radicans* presenting a concern to land managers. The growing season for grasses occurs during the austral summer (November–April), during which 78% of the mean annual rainfall of 502 mm/year falls with the January on average the hottest month with a mean maximum temperature of 33.7°C (Venter, Scholes and Eckhardt, 2003). However, summer rainfall in Satara was well below the long-term average during both the 2014/2015 (288 mm) and 2015/2016 (138 mm) season when much of southern Africa experienced the most extreme drought of the past 20 years (Figure 3.1b). Grasses are dormant during the dry, frost-free winters (May–October) with the coldest month of June experiencing a mean minimum temperature of 9.4°C. Prior to this experiment, the area had an average fire return interval of ~ 3 years and a detailed description of fires in the Satara land system during the course of this experiment is given in Appendix A (Figure S2.1).

3.1 Experimental design

To test the influence of small-repeated fires on grazers and the effect of post-burn herbivory on grass species composition we implemented a landscape-level experiment between January 2013 and May 2017. We selected three treatment plot sizes: 50 x 50 m (0.25 ha), 220 x 220 m (5 ha), 500 x 500 m (25 ha). These sizes were chosen to represent the sizes of the three most common short-grazed areas in KNP: a termite mound (*c.* 20-50 m^2 – see Davies *et al.*, 2014), a sodic site (*c.* 250 m^2- See Grant and Scholes, 2006) and a large grazing lawn system (*c.* 500 m^2-1 km^2-see Yoganand and Owen-Smith, 2014). The 0.25 and 5 ha plots were replicated four times for each of the three treatments, with fire either completely excluded (no-burn treatment) or with burns applied annually in the early-dry season (April/May, hereafter referred to as early-burns) or late-dry season (September/October, hereafter referred to as late-burns). However, due to space constraints and logistical issues we were only able to implement three late-burn 25 ha plots. The experimental setup thus had three fire treatments (no-burn, early-, and late-season burns), two fire sizes (0.25 ha and 5 ha) with four replicate plots and an additional three 25 ha late-burn plots resulting in a total of 27 treatment plots (Figure 3.1a).

Fires were applied every year by experienced teams from 'Working on Fire' (http://workingonfire.org) to each of the early- and late-burn treatment plots resulting in three burn applications per plot by the end of burn treatments in 2015, after which attempted ignitions on all plots failed due to low grass biomass. To reduce the possibility of external fires (non-

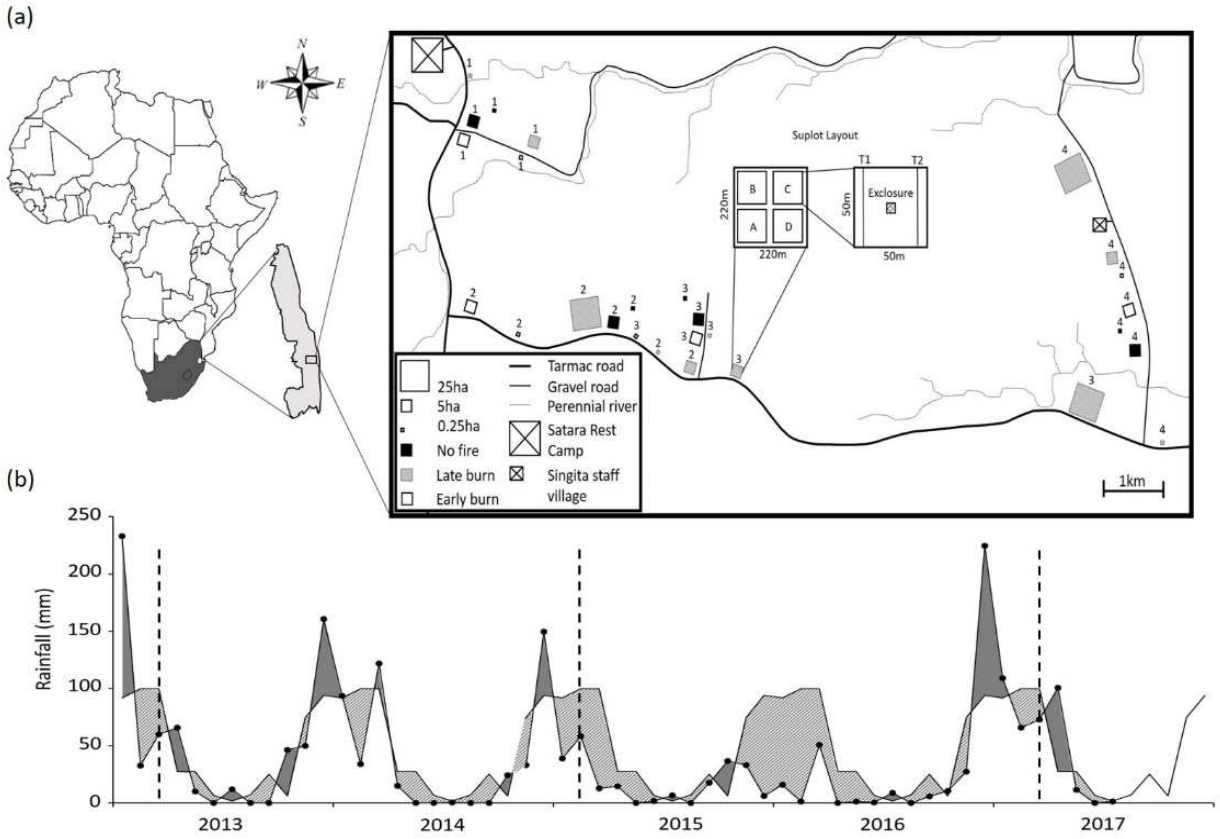


Figure 3.1. (a) Layout of burn treatments and (b) deviation from long-term (1980 – 2017) precipitation in the Satara Land System of Kruger National Park. Late-burn and early-burn plots were burnt in May and October of 2013, 2014 and 2015 after which fires failed on all fire treatment plots. Fires occurred once at the end of October 2015 on the no-burn plots labelled 2 and 3 due to a runaway lightning ignition. The 5 and 25 ha plots contained four and nine 50 x 50 m sampling subplots respectively while 0.25 ha plots were the equivalent of a single subplot. We erected herbivore exclosures (1 m^2) in the centre of each subplot to enable us to assess the effect of fire alone, and we sampled two parallel 50 m transects (T1 and T2) placed an equal distance on each side for analysis of combined fire-herbivore effects. All data collection took place along the transect lines and within exclosures of every subplot. Sampling of all species composition data occurred in April at the end of every second rainfall season

experimental) influencing our study, KNP managers extinguished any unplanned fires within the area of the experiment. Despite these efforts a lightning fire burnt through two of the no-burn plots in October of 2015. Initially the burn plots were selected to have: (1) high grass biomass with grass communities dominated by *B. radicans* and *T. triandra* in their climax states, (2) similar amounts of woody cover, and (3) similar abiotic conditions. The 5 and 25 ha plots contained four, and nine, 50 x 50 m sampling subplots respectively, which meant the sampling unit remained the same across all size-treatments, but the sampling effort increased for the large fire sizes. We marked a fixed-plot (1 m^2) for repeat sampling in the centre of each subplot by hammering in metal droppers and marked two parallel 50 m transects placed an equal distance on either side for analysis of grazer presence within the area (Figure 3.1a). All data collection took place along the transect lines and fixed plots of every subplot during sampling months.

3.2 Environmental variables

We did a full texture analysis for percentage sand by taking samples to a depth of 20 cm in the centre of each fixed-plot of every subplot. Monthly rainfall data was recorded from the Satara Rest Camp and Singita Lebombo staff village weather stations for the entire duration of the study (Figure 3.1a). To estimate the success of burn treatments, we walked the two transect lines of each subplot immediately after burning and recorded burnt/unburned every two metres and calculated the percentage of each subplot burnt. Burn percentage scores and soil percentage scores were then averaged for 5 ha and 25 ha plots. **Chapter 2** had shown that grazer (wildebeest, zebra and impala) use of late-burn and early-burn treatments was higher than on no-burn treatments. To assess whether this higher grazer presence was also associated with increased grazing pressure, we placed a 30 cm diameter disc every 2 m long a transect line and determined for each placement whether there was any bitten grass under the disc. We collected this data at the end of the wet and dry seasons to allow estimates of the proportion of the plot that had been bitten. In addition, we recorded all dung (species and abundance) including dry dung encountered in 4-m-wide belts along transect lines to estimate grazer use for each subplot. Dung transects have been used previously to estimate large herbivore habitat usage in long-term studies within African savannas and perform better than direct observations and other indirect measurements (Cromsigt *et al.*, 2009; Burkepile *et al.*, 2013, 2016), giving relatively reliable measures for comparisons of relative abundance across similar habitats (Marques *et al.*, 2001; Sensenig, Demment and Laca, 2010). To eliminate any bias between plots and ensure that the

period between sampling was equal, we walked and cleared transects of dung one month prior to initial data collection. Dung counts were then sampled on a precise monthly (30 day) basis with dung crushed during data collection to avoid recounting. Dung was sampled within all subplots on all treatments one month prior and two months after burns were applied for the first two years (2013/2014) of treatments resulting in three months of data collection for each plot within a given year. From 2015 onwards, data was collected for every month of the year. All grazing species' dung was summed between burn events to calculate an annual "graze pressure" score for each plot.

3.3 Species composition data

To test the effect of the different treatments on species composition we identified and counted individual plants before estimating total bare ground and aerial cover for every species within the 1 m^2 fixed plot. This gave us an abundance and aerial cover score for April of every year after the growing season. Moreover, to look at the effect of grazing and drought on established grass plants we measured the radius of all grass tussocks within the fixed plots during species sampling in 2015 and 2017. This gives information on whether perennial tussocks are increasing or decreasing in size on average (O'Connor, 1995).

3.4 Species trait data

We measured species traits on all the species recorded (Table S3.1) during the study in April of 2017 when grasses had experienced a full season of good rainfall. We designated an unburned grass patch located outside of our treatment plots that had not been burned for the duration of the study as our trait measurement area. We walked 100 m perpendicular to the road from a predetermined GPS point before starting a 50 m transect to select individual plants for trait measurement. The first six plants of a given species encountered within a two-meter-wide belt along the transect line were selected for measurement. If there were not enough plants from a species encountered within the transect line, then another transect line running parallel to the first was setup five metres away and this process was repeated until six specimens were located from all species recorded in the study. Six green, mature leaves from each individual were clipped and weighed before air-drying in paper bags to a constant weight. Dried leaves were ground to a powder and the carbon and nitrogen content ratios measured by mass spectrometry (see Appendix B for detailed description; Cornelissen *et al.*, 2003). We also calculated grass leaf

moisture content (LMC) for all communities over the full period of the study as $(w - d) / d$, where w is the wet mass of leaves and d is the mass after drying to a constant weight (Saura-Mas and Lloret, 2007). Finally, we calculated biomass density of individual plants following the methods of Simpson *et al.* (2016) by clipping entire plants at 5 cm intervals along the entire length of the plant. Each portion of the plant was then dried and weighed, and cumulative weight calculated for every height. The slope of the linear relationships between logged cumulative dry biomass and vertical height was then used as a proxy of biomass density ($g.m^{-3}$).

3.5 Statistical analysis

We modelled the proportion of grazer bites per subplot (as a proxy for graze intensity) using a generalized linear mixed effect model (GLMM) with a binomial distribution to assess the difference in pressure on no-burn, early- and late-burns treatments at the end of the wet- and dry-seasons of 2015 and 2016 (Crawley, 2012). Season and treatment represented fixed effects with plot and subplot acting as nested random effects to control for repeated measures along the transects of each subplot at the end of every season. All GLMMs were processed using R statistical software (version 3.3.1 R Core Team, 2016) and the lme4 package (Bates *et al.*, 2015). Following the suggestions of Zuur *et al.* (2009) and Bolker *et al.* (2009), we used a top-down approach to model selection with an ANOVA to remove effects that resulted in models that did not differ ($p < 0.05$) significantly from the full model. We looked for obvious deviations from homoscedasticity and overdispersion in our models by plotting residuals against fitted values and visually assessing plots. Semivariograms showed that variation in residuals did not increase with increasing distance between plots, indicating no serious autocorrelation issues were present (see Appendix B Figure S3.1 in Supporting Information).

All species composition analyses were carried out using packages vegan (Oksanen *et al.*, 2016) and ade4 (Dray *et al.*, 2014). Species data were transformed using the Hellinger's transformation to reduce the impact of large abundances and rare species (Legendre and Gallagher, 2001; Legendre and Legendre, 2012). We analysed species composition pre-treatment (2013), two years after treatments were initiated before the onset of the drought (2015), and after four years of treatment and two years of drought (2017). We ordinated species composition between treatment plots using redundancy analysis (RDA; Legendre and Legendre, 2012). We assessed environmental data for autocorrelation and removed variables that with a Pearsons *r* score of

greater than 0.6 resulting in tree density, distance to water, percentage sand, cumulative dung, percentage of plot bitten, and cumulative burn percentage representing final environmental variables. We used a two-stepped forward selection approach proposed by Blanchet, Legendre and Borcard (2008) to select the most appropriate model and ran a Monte-Carlo permutation test with 9999 iterations to assess the significance of the model and the marginal effect of each environmental variable at 0.05% significance (Legendre and Legendre, 2012).

We performed an R-mode linked to Q-mode (RLQ) analysis, combined with the fourth corner method (Dray *et al.*, 2014; Charles-Dominique *et al.*, 2015), to test whether the functional traits of the grasses were responding to pyric-herbivory on treatment plots. Combining RLQ and fourth corner analysis allowed us to test for the species traits involved in any observed differences in community composition associated with our applied treatments (Dray *et al.*, 2014). We used the three different fire treatments as our environmental effects (early-burn, late-burn or no-burn). The RLQ analysis is a method designed to study the environmental filters of ecological communities (Dolédec *et al.*, 1996). To achieve this RLQ analysis assesses the combination of functional traits of maximum covariance with a given set of selected environmental variables.

To perform RLQ we first ran three separate analyses for species composition, environmental variables and grass species trait data for the 27 experimental plots to allow us to test the outputs resulting from of the three table RLQ analysis. Firstly, we analysed the species occurrence frequencies on all plots stored within the matrix L by performing principal component analysis (PCA). Environmental plot data stored in the matrix R were then used to ordinate plots according to fire treatments (no-burn, early-burn and late-burn) using principal components analysis with multi-state discrete characters described by Hill and Smith (1976) (Legendre and Legendre, 2012). Traits of grass species were stored in matrix Q and we analysed these using a PCA. We assessed the statistical significance of the co-structure between R and Q by comparing 9999 Monte-Carlo permutations of the rows of R and Q tables with the total inertia in the RLQ analysis (Dolédec *et al.*, 1996). We used a two-step testing procedure (Dray and Legendre, 2008) to assess the significance of the relationship between traits and environmental variables in the fourth corner analysis (habitat filtering). In all the randomization procedures we used 9999 permutations and adjusted *p* values for multiple testing with the false discovery rate (FDR) method (Benjamini and Hochberg, 1995).

Finally, we modelled the area covered by tussocks within fixed-plots using a GLMM with the package lme4 (Bates *et al.*, 2015) using a poisson distribution to assess the difference tussock cover on no-burn, early- and late-burn treatments at the beginning (2015) and end (2017) of the drought (Crawley, 2012). Year and treatment represented fixed effects with plot and subplot acting as nested random effects to control for repeated measures along transects of each subplot at the end of every season. Due to our method of data collection for species traits, any changes observed in trait space from the RLQ analyses would be the result of genotypic responses due to changes in species composition rather than phenotypic responses to grazing.

Table 3.1. Generalized linear mixed models used to assess the relationships between bite pressure and different fire treatments during the dry and wet seasons of 2015 and 2016 and the relationship between grass tussock cover and fire treatment during the drought

Selected models	**df**	***F***	***P***
Proportion plot bitten ~ Rainfall season * Fire treatment + (1|plot|subplot)	11	703.81	<0.001
Total tussock area ~ Year * Treatment + (1|plot|subplot)	5	18 796	<0.001
B. radicans tussock area ~ Year * Treatment + (1|plot|subplot)	5	23 259	<0.001

4 | Results

4.1 Pre-treatment

Prior to any burn treatment the environmental variables explained very little (5.2%) of the variation in species composition within plots with permutation tests indicating the model was weak ($p = 0.189$). None of the tested environmental variables had any significant influence with distance to water the closest to having an effect ($F = 2.03$, $p = 0.06$) across the sampling plots, indicating a balanced selection of the plots used in this study with no obvious pattern that would pre-determine responses to burn treatments appearing in the ordination plot (Figure S3.2).

4.2 Grazer and grass cover responses to treatments

The selected GLMM (Table 3.1) confirmed bite pressure in both the 2015 wet and dry season was higher on early-burn (ES = 1.95, SE = 0.36) and late-burn (ES = 3.47, SE = 0.35) fire treatments than no-burn plots with almost the entire plot experiencing some level of biomass removal on burnt plots (Figure 3.2). Grazing pressure remained high on both the early-burn and late-burn treatment plots throughout the drought (Figure 3.2) and increased substantially on no-burn plots (ES = 1.15, SE = 0.09) in the second season of failed rainfall. The GLMM of tussock cover in fixed-plots showed that prior to the drought in 2015 the early-burn (ES = −0.68, SE = 0.59) and late-burn (ES = −1.39, SE = 0.68) treatments had lower tussock cover than in the no-burn treatments (Figure 3.3). All the treatment plots declined from 2015 tussock cover during the two years of drought with early-burn (ES = −3.27, SE = 0.08) and late-burn (ES = −3.1, SE = 0.09) decreasing to near zero cover in 2017, while the no-burn plot decreased to nearly half of the original measures.

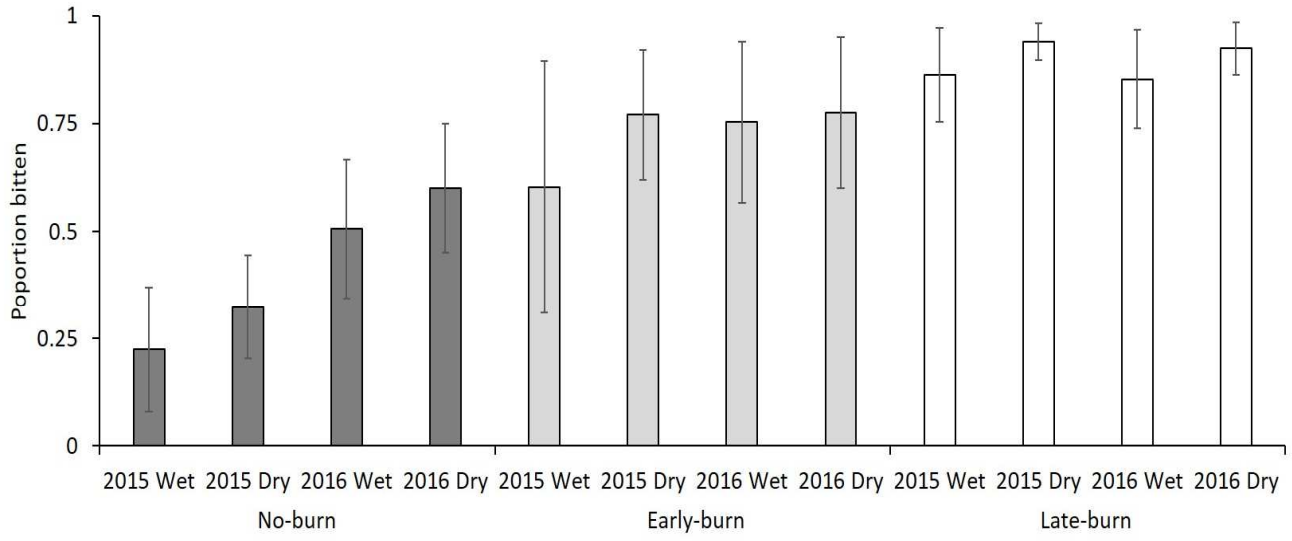


Figure 3.2. Proportion (mean ±SE) of the burn treatment plots bitten at the end of the wet (May) and dry seasons (October) after two-years of fire treatment (2015) and during the most intense season of drought (2016).

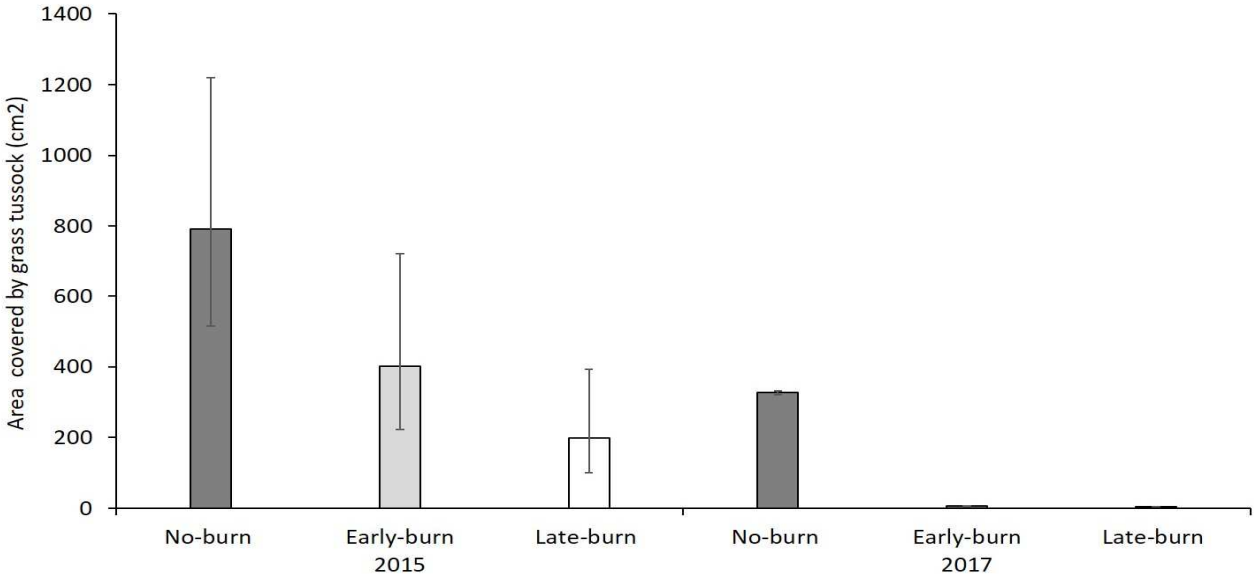


Figure 3.3. Total area (mean ±SE) of fixed plots (1 m^2) covered by established grass tussocks in different treatment plots after two-years of fire treatment (2015) and after two seasons of drought (2017).

4.3 Effect of concentrated pyric-herbivory on species composition (Hypothesis 1) and community trait space (Hypothesis 2)

After two seasons of burn and grazing treatments the RDA indicated that the environmental variables explained 14.7% of the variation in species composition with permutation tests indicating the relationship was significant ($p = 0.013$). Only the grazer dung scores of plots had any significant influence ($p = 0.007$) on the species composition and therefore only the first axis was of any interest (Figure 3.4a), suggesting that grass communities were only responding to grazing pressure.

The first axis of RLQ separated grass communities growing in late-burn treatment plots and experiencing grazing from any of the other treatment combinations (Figure 3.5). The results of the RLQ (Monte-Carlo permutation tests, $p < 0.01$) and fourth corner analyses (Table 3.2) confirmed that grass species which increased under high grazing on the late-burn treatments had lower C : N ratios and higher LMC than those on other treatments, while species on no-burn plots had high C : N ratios and low LMC (Table 3.2). However, the bulk density of species on different treatment plots did not change significantly (Table 3.2). These results represent the traits of ungrazed and unburned plant individuals, and therefore indicate a long-term, more

permanent change in trait distribution across plots, not a phenotypic response based on structure. The second axis of the RLQ, had low eigenvalues (Figure 3.5) and suggested that C : N ratio and LMC were only affected by differences in grazing rather than fire treatment.

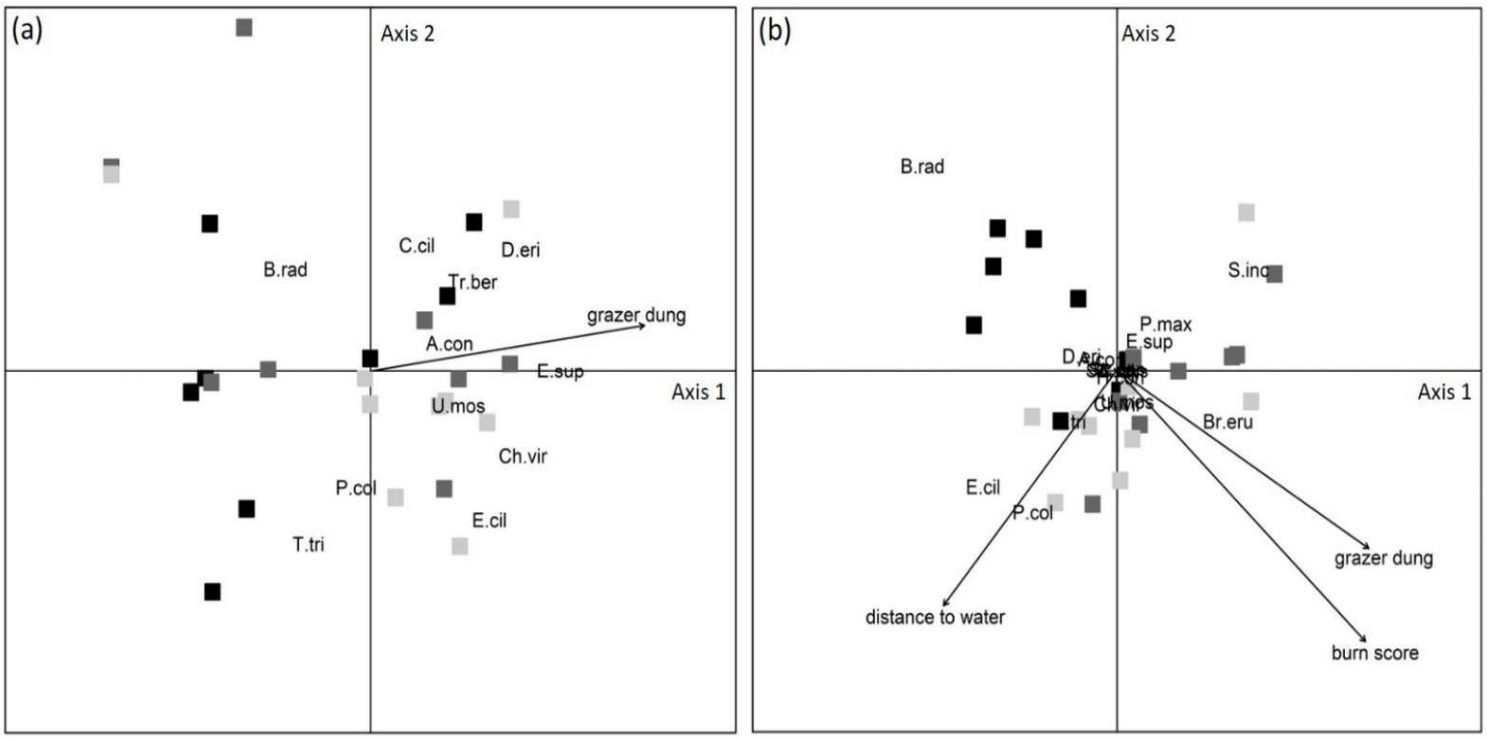


Figure 3.4. Correlation biplots based on RDA ordination of the grass species aerial cover on no-burn (black), early-burn (dark-grey) and late-burn (light-grey) treatment plots for (a) 2015 and (b) 2017 constrained by the environmental variables. Only the environmental factors retained by forward selection ($p < 0.05$) are shown with arrows. A. con = *Aristida congesta congesta* (Roem. & Schult), B. eru = *Brachiaria eruciformis* (Sm.), B. rad = *Bothriochloa radicans* (Lehm.), C. cil = *Cenchrus ciliaris* (L.), Ch. vir = *Chloris virgata* (Sw.), D. eri = *Digitaria eriantha* (Steud.), E. cil = *Eragrostis cilianensis* (All.), E. sup = *Eragrostis superba* (Pehr.), H. con = *Heteropogon contortus* (L.) , P. col = *Panicum coloratum* (L.), P. max = *Panicum maximum* (Jacq.), S. inc = *Setaria incrassata* (Hochst.) , Sc. pap = *Schmidtia pappophoroides* (Steud.), So. ver = *Sorghum versicolor* (Anderss.), T. tri = *Themeda triandra* (Forssk.), Tr. ber = *Tragus berteronianus* (Schult), U. mos = *Urochloa mosambicensis* (Hack).

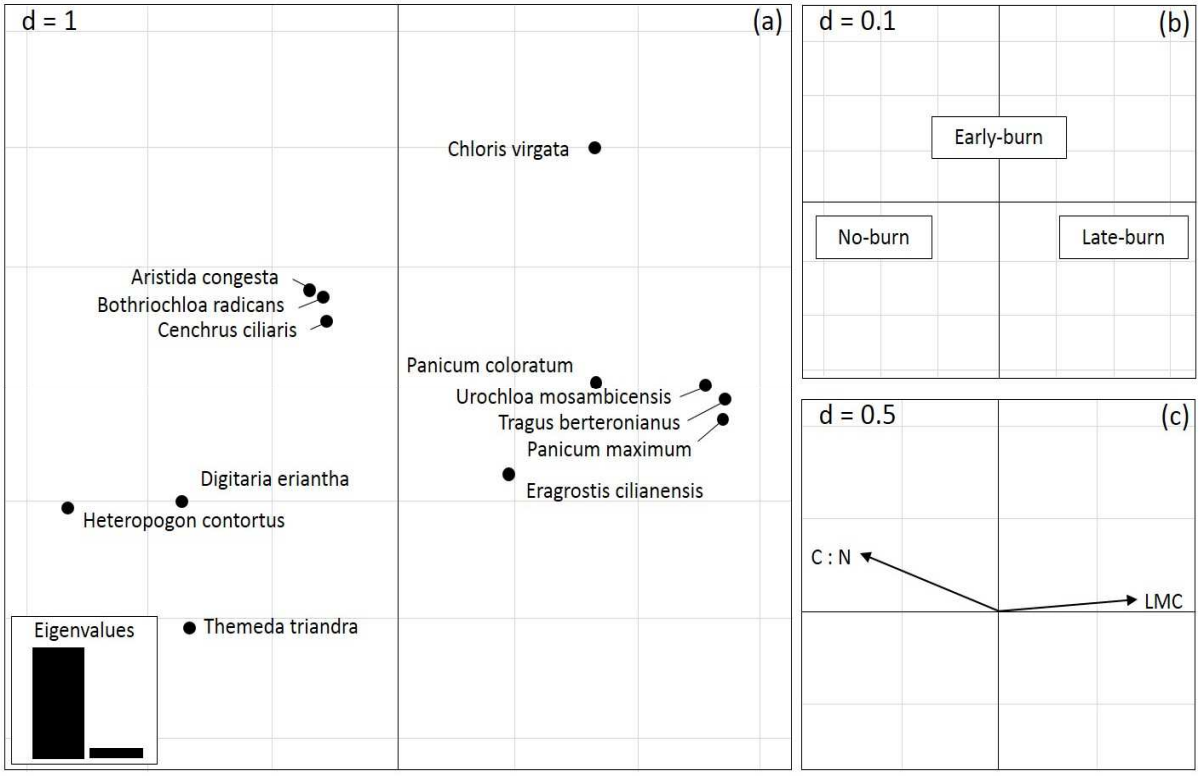


Figure 3.5. Results for 2015 of the first two axes of R-mode linked to Q-mode (RLQ) analysis: the RLQ space maximizes the relationships between traits and environments. The positions of species in the RLQ space are shown in (a), environmental factors in (b) and species traits in (c). The 'd' values give the grid size for scale comparison across the three figures. C : N ratio and leaf moisture content (LMC) are negatively and positively associated with heavily grazed late-burn plots respectively, indicating higher palatability on these plots associated with differences in species composition.

4.4 Effect of pyric-herbivory and drought on species composition and community trait space (Hypothesis 3)

After two seasons of drought the RDA indicated that the environmental variables explained 25.6% of the variation in species composition with permutation tests indicating the relationship was highly significant ($p < 0.001$). The first two axis of ordination explained 81.2% of this relationship and the permutation test indicated that they were the only significant axes (RDA 1 $p < 0.01$, RDA 2 $p = 0.03$) (Figure 3.4b). Among the seven environmental variables tested, three had a significant influence on the species composition: distance to the nearest permanent water

source (p = 0.004), cumulative burn score (p = 0.04) and grazer dung score (p = 0.009; Figure. 3b).

Visually, the first axis of RLQ appears to separate grass communities according to herbivory pressure, with plots that experienced high herbivory distinguished from plots with low herbivory (Figure S3.3). However, the results of the RLQ (Monte-Carlo permutation tests, p = 0.09) and fourth corner analyses (Table 3.2) failed to support this. The changes observed in RDA on species composition did not seem to be directionally driven by commonalities in the traits of the species found in the communities post-drought. As a result, all the RLQ axes explained very little of the variation in trait space (eigenvalues <0.06) which suggests that after a drought the trait space of grass communities across all treatments were similar.

Table 3.2. Relationships between the biological traits and burn treatment plots tested using fourth corner method. C : N ratio decreases in the heavily grazed late-burn plots and leaf moisture content (LMC) increases, indicating an overall increase in palatability on these plots. After the droughts these differences disappear

Year	Environmental	Trait	*r*	*P-value*
2015	No-burn	C : N	0.17	0.034
		LMC	−0.2	0.03
		Bulk density	−0.1	*ns*
	Early-burn	C : N	0.03	*ns*
		LMC	−0.01	*ns*
		Bulk density	0.09	*ns*
	Late-burn	C : N	−0.21	0.027
		LMC	0.2	0.046
		Bulk density	0.01	*ns*
2017	No-burn	C : N	0.17	*ns*
		LMC	−0.21	0.077
		Bulk density	0.14	*ns*
	Early-burn	C : N	-0.2	*ns*
		LMC	0.07	*ns*
		Bulk density	−0.03	*ns*
	Late-burn	C : N	0.03	*ns*
		LMC	0.13	*ns*
		Bulk density	−0.17	*ns*

All *p*-values were adjusted for multiple comparisons with the false discovery rate method. *ns*, non-significant.

5 | Discussion

We found that pyric-herbivory driven by small, annually-repeated burns in the late-dry season can result in a shift in local grass communities towards higher quality graze than is available in the broader landscape. This shift in the trait space of grass communities is evidence of the establishment of positive feedbacks between mesoherbivores and the grass community that should entrench the long-term repeated use of patches by grazing ungulates and maintain short-grazed patches in the broader landscape (Cromsigt and Olff, 2008). The continued use of burn treatment plots several seasons after fire treatments were stopped supports this conclusion and suggests that small fires can be an effective tool for shifting savannas prone to burning towards grazing-driven states. This result is a novel addition to our understanding of the complex interactions between fire and grazers in savanna systems as it highlights for the first time a link between fire size and its implications for grazer responses and changes in the functionality of grass communities.

Short-grass grazing lawn systems have been identified in savannas throughout Africa (see Hempson *et al.*, 2015 for review). The exact benefits grazing lawns provide to the herbivores that concentrate on them has not been definitively identified within every system that they occur. However, it is clear they provide a pivotal wet season resource to the largest migratory herds on the continent (Mc Naughton, 1985), and have been observed as key resources for resident herbivores across variable savanna systems (Mc Naughton, Banyikwa and Mc Naughton, 1997; Traill, 2004; Verweij *et al.*, 2006; Kleynhans *et al.*, 2010; Yoganand and Owen-Smith, 2014). Apart from large ungulate lawn-specialists that rely heavily on the presence of lawns for success, there is a wealth of evidence showing the co-evolution between grazing lawns and bird (Krook, Bond and Hockey, 2007) and invertebrate communities (Prendini *et al.*, 1996; Samways and Kreuzinger, 2001; Warui *et al.*, 2005). Thus, grazing-lawns and the feedbacks that maintain them represent an important component of savanna biodiversity and a failure to incorporate them in the management of wildlife systems would be a clear oversight. The historical removal of mega-herbivore populations (particularly white rhino; Owen-Smith, 1989), and the increased use of large, hot fires to control bush encroachment (Trollope, 1982) and use of savannas for livestock grazing (Tainton, 1999) would all have promoted the loss of grazing-driven grass communities as fire-adapted grass communities were promoted both within wildlife reserves and pastoral rangelands. Considering that under current circumstances white rhino populations are unlikely to

recover to historical densities in wildlife reserves across the majority of its natural range, a manipulation of the fire regime may represent one of the few tools available to managers to generate herbivore feedbacks that promote the formation of lawn systems in areas where white rhinos are absent and migration of other ungulates are limited.

5.1 Grass community response to pyric-herbivory

Pyric-herbivory pressure was high on both early-burn and late-burn plots in 2015 and had been high for the previous two years (**Chapter 2**). Intense grazing both directly and indirectly impacts individual grass tussocks by removing foliage and changing soil and light properties (Veldhuis *et al.*, 2014), which affects the competitive ability of individual plants (Van der Wal *et al.*, 2000; Anderson, Dong and Mc Naughton, 2006; Anderson *et al.*, 2013; Veldhuis *et al.*, 2014). However, these changes in the competitive space take time to result in composition changes. A previous study looking at the response of grass community composition to the onset of increased grazing indicated that in a higher productivity system it took grazing lawn species up to four years to become dominant (Cromsigt and Olff, 2008). In this study, we were only able to observe the grazing increase for two growing seasons before the onset of the drought. Despite this, we found lower cover of established grass tussocks on burnt plots and a negative relationship between the two-dominant fire-adapted grass species (*B. radicans* and *T. triandra*) and grazer dung (Figure 3.3a) suggesting a strong negative response of fire adapted grasses to increased grazing. It is important to note that both species have a positive response to burning alone and under burn conditions (landscape-scale burns) that do not concentrate grazing pressure these species are generally found to be dominant features of the grass communities within Kruger National Park (Trollope, Potgieter and Zambatis, 1989). Ultimately, this led to an observable shift in the community trait space with lower C : N ratios and higher leaf moisture content species such as *U. mosambicensis* and *T. berteronianus* being favoured on late-burn plots.

The lower grazing pressure on early-burns meant that the same trend was not observable within the two-year period of this study. This makes it difficult to draw conclusions on the effectiveness of small early-burns in generating grazer driven feedbacks that would result in the creation and maintenance of lawns within a broader fire adapted system. However, the response of late-burn treatment plots supports both of our initial hypotheses and supports the theoretical idea that

small-repeated fires can be used to drive pyric-herbivory and result in the establishment of positive grazer feedbacks and ultimately switch the dominant consumer.

Clear directional differences in plant community structure in the form of phenotypic differences in bulk-density did not arise. We recognise that this is potentially a result of our trait selection and identifying traits that respond consistently to consumers is notoriously difficult (Díaz *et al.*, 2007). We selected bulk density as it incorporates elements of the architectural makeup of grasses while also retaining measures of biomass and height – traits highlighted in past literature as traits that respond divergently when burnt regularly as appose to grazed intensively (Briske, 1995; Anderson *et al.*, 2013; Hempson *et al.*, 2015; Simpson *et al.*, 2016). Rather than critique the trait selected, we suggest the lack of an obvious response is due to the presence of facultative species in this study. *Panicum coloratum* occurred evenly across plots, while *U. mosambicensis* was prominent in heavily grazed plots in 2015. These species are recognized for the plasticity in their growth form and are known to grow prostrate during the initial establishment phase of grazing lawns (Cromsigt and Olff, 2008; Cromsigt and te Beest, 2014; Hempson *et al.*, 2015), but can also grow tall and compete for light in frequently burnt areas that experience moderate levels of grazing (van Oudtshoorn, 1999; Archibald and Bond, 2004; Koerner *et al.*, 2014). The presence of these species on our plots is an obvious result of the short time since lawn establishment and presence of low densities of grazers in tall-grass communities. However, the existence of life-strategies that straddle the boundary between fire- and grazer-controlled communities are clear evidence that in African savannas switches between the two alternate states do occur. Indeed, on continental Africa prior to fences grass communities in frequently burnt systems would seldom, if ever, occur in the complete absence of large mammal grazing. Similarly, grazing lawns systems would likely be at risk of burning when herbivore populations fluctuate (Holdo *et al.*, 2009).

5.2 Drought effects and landscape homogenisation of grass traits

Global climate models predict that southern Africa is set to experience drought events with increasing frequency (Ratnam *et al.*, 2014). Developing an understanding of the influence that drought has on the interactions between fire and grazing is thus of increasing importance in African savannas. O'Connor (1995) found that the intensity of pastoral grazing played an important role in the way that South African grasslands responded to drought events, with grass

communities largely unaffected in the absence of grazing during droughts but tussock size declining in the presence of drought/grazing combinations where intolerant species became locally extinct. We found similar patterns in this wild ungulate system in 2017: heavily-grazed bunt plots almost completely lost their established tussock cover while the no-burn plots retained tussock cover throughout the drought. Moreover, species composition responded to both burn history and grazing history with *B. radicans* found most commonly in plots where grazing pressure was lowest (no-burn plots). This aligns with previous findings that species palatable to livestock were reduced in lightly grazed treatments, while unpalatable species were relatively unaffected (O'Connor, 1995). Despite the strong changes in species composition under higher grazing there was no clear difference in the trait space of the three treatments in 2017.

The loss of a directional shift in the traits selected for burn treatment plots compared with no-burn plots after the drought is the result of an increase in *Aristida congesta congesta* (Roem. and Schult) an short lived perennial species observed across all treatments (Figure 3.4b). During the second year of drought, graze pressure on no-burn plots doubled from the first year in both dry and wet seasons and coincided with an overall decrease in tussock cover. The reduced tussock cover, although still higher than burn-treatment plots, was seemingly sufficient to enable the invasion of annual and seed-recruiting species (O'Connor, 1994, 1995). Thus, the drought drove a convergence in the functional trait space of species across all treatments despite differences in grass species composition remaining apparent. Assessing the consequence of this drought for the development of positive feedbacks on the grazing patches we initiated in this landscape requires further years of data: possibly the drought has increased the rate at which species compositional differences are occurring on the late- and early-season plots due to the increased grazing pressure. Alternatively, the drought might have "re-set" the landscape, in the same way that large fires do, and broken the positive feedbacks which were developing on the grazed patches. Nevertheless, our results clearly indicate that in systems where grazers are forced to source poor quality forage during drought events, the short-term homogenisation of grass traits at broad scales is likely to occur as grazing pressure becomes ubiquitous within the landscape.

5.3 Conclusion

The divergent selective pressure and physiological requirements of fire vs. herbivory means that the consumer dominating within a given landscape has observable consequences on the structure

and functioning of African savannas (Bond, 2005). Our results add to a growing number of studies that highlight the importance of feedbacks in the establishment of dominant consumer processes within savannas (Mc Naughton, Banyikwa and Mc Naughton, 1997; Archibald *et al.*, 2005; Archibald, 2008; Cromsigt and Olff, 2008; Archibald and Hempson, 2016). The "desirable" balance of grazing vs. fire dominated savannas (i.e. "brown-world" and "black-world") within a given landscape is a purely subjective decision, however this work underlines the importance of recognising these feedbacks when managing landscapes using fire. Across African savannas, fire represents a key tool for land managers looking to control bush encroachment (Roques, O'Connor and Watkinson, 2001), manage graze for livestock and reduce tick loads (Tainton, 1999; Butz, 2009), and to open landscapes and manipulate the movement of wild herds for tourism (Eriksen, 2007), in many of these situations the effects of fire-driven feedbacks on the formation and destruction of grazing systems within the local area have been ignored. Our results suggest that in landscapes managed for biodiversity this represents an oversight in the use of fire, particularly in cases where the natural establishment pathway of grazing systems via white rhinos and migratory herds are no longer in existence.

The interaction between these consumers, and the feedback pathways that establish, act on an underlying abiotic map (Archibald and Hempson, 2016). Drought events alter this abiotic map in the short-term, which will have repercussions on grazing pressure per unit forage, and therefore on the feedbacks established in the period between drought events. This study suggests that drought has a homogenising effect on grass community trait space across fire-driven and grazer-driven grass community patches, although differences in species composition remain. Temporal stability of heterogeneity at landscape scales is increasingly being linked to the stability of between patch variation at local scales (Wang and Loreau, 2014; McGranahan *et al.*, 2016). Thus, the homogenisation of local patches during drought events (even if it increases the diversity within local patches) may result in the loss of heterogeneity at larger scales. Ultimately, the predicted increase in drought events that destabilise the feedbacks between grazers, fire and their respective grass communities at the patch scale could make management for heterogeneity in savanna parks increasingly difficult. Thus, our results underline the need to manage savanna landscapes by considering the feedbacks that are maintaining the structure and function of grass communities in their current state and not simply use fire as a ubiquitous method for improving graze quality in the short-term.

Chapter 4 | The role of drought in the seasonal selectivity of grass communities by African savanna grazers and the repercussions for system productivity.

This chapter has been prepared for submission to Journal of Ecology

1 | Abstract

1) Drought events fundamentally alter spatio-temporal patterns of forage availability and therefore herbivore usage patterns. The recovery after drought and the long-term response of ecosystems are not easy to predict because prior history of grazing and fire are known to impact both forage availability during the drought and the sensitivity of the ecosystem to drought. Here we addressed three questions focusing on grazer movements and grass productivity during a major drought event in Kruger National Park: (1) when do grazers use lawn grass, bunch grass and burnt-bunch grass communities during and after drought events? (2) How does the timing of grazer use of these communities relate to grass productivity? (3) How does grazing intensity and timing influence the recovery of grass communities once rainfall returns?

2) We monitored grazer utilization of three different grass communities (lawn, bunch and burned-bunch) by looking at dung deposition and bite proportions at a landscape scale through the 2014-2016 drought in Kruger National Park. We also set up an experiment to monitor primary productivity of these communities through the drought and continued once rainfall returned.

3) Lawns and bunch grasslands experienced different grazing regimes during droughts events with grazer numbers initially highest on grazing lawn communities with dung events per month more abundant on lawns (mean = 45.0, SE = 12.16) during the 2015 dormant-season compared with burned (mean = 5.8, SE = 1.02) and bunch grass communities (mean = 19.8, SE = 5.88). This pattern continued into the following 2015/2016 growing season, but herbivores left the study area completely when rains failed for the second season. Both lawns and bunch grasslands were productive (>150 $g.m^{-2}$ per month) after the first good month of rainfall in the 2016/2017 rainfall season. However, the most severe impact on lawn productivity was the reduction of grazing pressure after droughts when grazers did not return to feed on the same lawn patches they had frequented pre-drought resulting in grasses self-shading and senescing.

4) We show that the patterns of herbivore usage during and after the drought are contingent on i) the extent of the drought, ii) the pre-existing patterns of grazing habitat in the landscape, and that iii) this has knock-on impacts on patterns of productivity after the drought. This limits the value of detailed experimental work on drought and productivity in savanna ecosystems, which assumed uniform grazing during and after drought events. Rather, it seems that savanna system

functioning immediately after droughts is the result of grazers decisions related to where and when they feed during droughts.

Keywords: African savannas, drought, fire ecology, grazer ecology, grazing, grazing lawns, productivity

2 | Introduction

Predictive climate models suggest that the effects and frequency of El Niño Southern Oscillation (ENSO) events will increase in southern Africa with the continued increase of atmospheric CO_2 (Gizaw and Gan, 2017). The onset of ENSO in southern Africa is associated with drought events across the eastern regions of the country (Ratnam *et al.*, 2014). These areas are dominated by the savanna and grassland biomes (Mucina and Rutherford, 2006) and support most of southern Africa's domestic and wild ungulate populations. Thus, any projected increases in the frequency and severity of drought events associated with ENSO will have far reaching implications for commercial agriculture and conservation efforts within southern African states (Stige *et al.*, 2006). Savannas with wild ungulate populations are often managed with hard boundaries in southern Africa with limited options for ungulate migration and as a result management decisions of individual reserves made during drought events have lasting impacts on grass communities and herbivore populations (Walker *et al.*, 1987). It seems pertinent to develop an understanding of the functioning of different grass communities and what resources they represent to free roaming wild grazers both during and immediately after drought events.

Free ranging ungulate populations in African savannas vary their utilisation of different grass communities throughout the year with selectivity dependant on their seasonal requirements (Owen-Smith and Novellie, 1982; Walker *et al.*, 1987; Macandza, Owen-Smith and Cross, 2004; Holdo, Holt and Fryxell, 2009; Yoganand and Owen-Smith, 2014). Bunch-grasslands and grazing lawns represent spatially and temporally distinct resources throughout the year. Bunch-grasslands represent low-quality, but high-quantity food reserves and are characterised by species that grow vertically from long living tussocks that build up moribund material (Simpson *et al.*, 2016). In normal years these systems are never fully utilised by grazing animals due to the poor quality of old growth grasses and high risk of predation in low visibility environments (Anderson *et al.*, 2010; Yoganand and Owen-Smith, 2014). This means that sufficient dead grass biomass is left unconsumed and fires are common (Bond and Keeley, 2005). After fire, these systems represent a high quality food resource and grazers increase their utilization of bunch grass areas for a limited amount of time (three-six months –Tomor and Owen-Smith, 2002; Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2016). Grazer use of bunch grass areas also increases in the late-dry season and during drought events when moribund material is often the only available high quantity resource (Walker *et al.*, 1987; Illius and O'Connor, 2000;

Macandza, Owen-Smith and Cross, 2004). By contrast, it has been suggested that grazing lawns co-evolved with certain ungulate grazers and require constant high grazing pressure during the growing season to maintain a competitive advantage over light-competitive bunch grass species (Mc Naughton, 1984). Lawn communities generally consist of prostate growing species that capture space through stoloniferous or rhizomatous growth and generally have higher nutrient content than bunch grasses (see Hempson *et al.*, 2015 for review). Lawns are preferred and selected for by several grazer species (Kleynhans *et al.*, 2010) during the wet season when fresh growth is readily available (Bonnet *et al.*, 2010) and represent an important resource to breeding animals (Holdo, Holt and Fryxell, 2009; Owen-Smith and Ogutu, 2013). This high quality wet-season resource becomes almost completely absent during the dry season and in drought years when productivity declines sharply. During this period grazing lawns experience a decrease in grazer presence with the ability to detect predators the only value of lawns for local grazers (Yoganand and Owen-Smith, 2014; Riginos, 2015).

Lawn grass communities are often considered far less productive than bunch grass communities due to their low standing biomass (Tainton, 1999). Experiments on community level productivity in African savannas have focused on the effects of fire and grazing on tall grass communities (Fay *et al.*, 2003; Knapp *et al.*, 2012) or grazing lawns (Mc Naughton, 1985; Bonnet *et al.*, 2010) separately with comparative experiments in east Africa indicating higher productivity on grazing lawns occurring on abandoned cattle bomas (Augustine, McNaughton and Frank, 2003; Augustine and Mcnaughton, 2006). Global food web models suggest grass communities made up of grazing-tolerant species can remain equally productive to grass communities where grazers are removed (Chase *et al.*, 2000), with some evidence that under certain conditions heavy grazing can even increase the NPP of grasslands (Mc Naughton, 1979). In addition, although tall-grass areas are valued as “reserve forage”, there is very limited understanding of the comparative productivity and thus herbivore available resources of these two communities in African savannas during and immediately after drought events. Yahdjian and Sala (2006) found that post-drought productivity of South American grasslands was largely the result of vegetation structure with lower productivity in grasslands with lower basal cover. These two communities are by definition structurally different due to dissimilarities in grazing pressure and the differences are only compounded during drought conditions (O’Connor, 1995). Thus, we would

expect differences both in their productivity during drought events and the productivity lag time immediately after drought events.

Van der Plas *et al.* (2013) carried out drought experiments on individual plants from lawn and bunch grass communities and showed they had distinct methods for coping with drought conditions. They suggested that lawn grass species are potentially better suited than bunch grass species to recolonise areas once a drought has broken (van der Plas *et al.*, 2013) with O'Connor (1991) showing that species can rapidly recolonise bare ground after drought dieback if they are capable of rhizomatous or stoloniferous growth compared with those that need to reseed. Pulsed grass productivity linked to large rainfall events in grazing lawns in South Africa support the idea that grazing lawns are well suited to quickly respond to water availability (Bonnet *et al.*, 2010). Here we experimentally test the feedbacks between grass community productivity and their use by free-roaming ungulate grazers during and after a major ENSO related drought event.

Lawn grass communities are known to provide high quality wet-season forage with productivity that closely matches rainfall events and are adapted to constant heavy grazing during periods of growth (Bonnet *et al.*, 2010). During the dry season, dormant lawn grasses offer little in the way of forage to grazers and we would therefore expect that they will experience low grazer impacts during drought periods. This coupled with high seedling recruitment on bare ground and adaptations that allow the fast re-colonisation of bare ground (van der Plas *et al.*, 2013) should result in the fast recovery of lawn areas when rain returns and thus represent an important resource to drought-weary herbivores during this period. In contrast, bunch grasses only experience intensive grazing after fire events and during drought events. The lack of adaptations to persistent heavy grazing in bunch grass communities and reliance on water to compensate for lost foliage (Anderson *et al.*, 2013) should mean they experience a greater disturbance to productivity during drought events because of increased herbivore pressure with communities requiring a longer period to recover once rainfall returns. This reduced functioning of bunch grass communities during and after a drought should only be exacerbated by pre-drought burning that would increase herbivore pressure during a vulnerable period for individual plants. Based on these predictions we aimed to address three questions: (1) when do grazers use lawn grass, bunch grass and burnt-bunch grass communities during and after drought events? (2) How does the timing of grazer use of these communities relate to grass productivity? (3) How does grazing

intensity and timing of grazing influence the recovery of grass communities once rainfall returns after a drought?

3 | Methods

3.1 Study site

Kruger National Park (KNP) in South Africa contains the full suite of large African mammals and occupies ~ 19 485 km^2. Animals are free to move throughout the park and into numerous adjacent private reserves, and the Limpopo National Park in Mozambique where shared fences have been removed to increase natural movement. Fences that limit movement out of these protected areas do exist at their extremes with the most notable being the western boundary fence, which when erected stopped the historical western migration (Whyte and Joubert, 1988). The Satara Land System, one of four major land systems in KNP, is characterized by clayey basalt soils (Venter, Scholes and Eckhardt, 2003), supporting extensive C_4 grass plains in a *Sclerocarya birrea-Acacia nigrescens* tree savanna (Gertenbach, 1983). This area is currently dominated by bunch grass C_4 species *Bothriochloa radicans* (Lehm.), *Digitaria eriantha* (Steud.), *Panicum coloratum* (L.), *Urochloa mosambicensis* (Hack.) and *Themeda triandra* (Forssk.) (Knapp *et al.*, 2012) that burn on average every 3 - 4 years and a detailed description of fires in the Satara land system during the course of this experiment is given in Appendix A (see Figure S2.1).. Interspersed within these bunch grass communities are the heavily grazed short-grass lawn patches that make up a very small proportion (<2%) of the broader landscape (Cromsigt and te Beest, 2014) with grass species including *Urochloa mosambicensis, Tragus berteronianus* (Schult), *Eragrostis cilianensis* (All.), *Chloris virgata* (Sw.), and *Brachiaria eruciformis* (Sm.).

A complete suite of indigenous herbivores occur in relatively large abundances within the Satara Land System (du Toit, 2003); however, for this study we focus on the four major grazer species (African buffalo [*Syncerus caffer* Sparrman], impala [*Aepyceros melampus* Lichenstein], blue wildebeest [*Connochaetes taurinus* Zimmerman] and plains zebra [*Equus quagga* Boddaert]) due to low dung counts for the remaining species. Zebras are non-ruminant grazers with their diet consisting of 92% C_4 grasses (Codron *et al.*, 2007). Buffalo, impala and wildebeest are all ruminants with studies in KNP showing that 88, 60 and 90% of their diets are made up of C_4 grasses, respectively (Codron *et al.*, 2007).

3.2 Rainfall

The growing season for grasses occurs during the austral summer (November–April), during which 78% of the mean annual rainfall of 502 mm/year falls with the January on average the hottest month with a mean maximum temperature of 33.7°C (Venter, Scholes and Eckhardt, 2003). Grasses are dormant during the dry, frost-free winters (May–October) with the coldest month of June experiencing a mean minimum temperature of 9.4°C. The last major drought event in the area occurred during the early 1990's after which rainfall has been consistently high up until the 2014 – 2015 season when rainfall was well below the long-term mean, with rains failing again over the 2015 – 2016 season before recovering with above average rainfall in 2016 – 2017 (Figure 4.1). Satara had the most severe proportional decrease in rainfall over these two seasons within the Kruger National Park (Izak Smit personal communication) and represented a rare opportunity to assess the effects of drought on a well-studied grazing system.

Monthly rainfall data were recorded from the Satara Rest Camp and Singita Lebombo staff village weather stations.

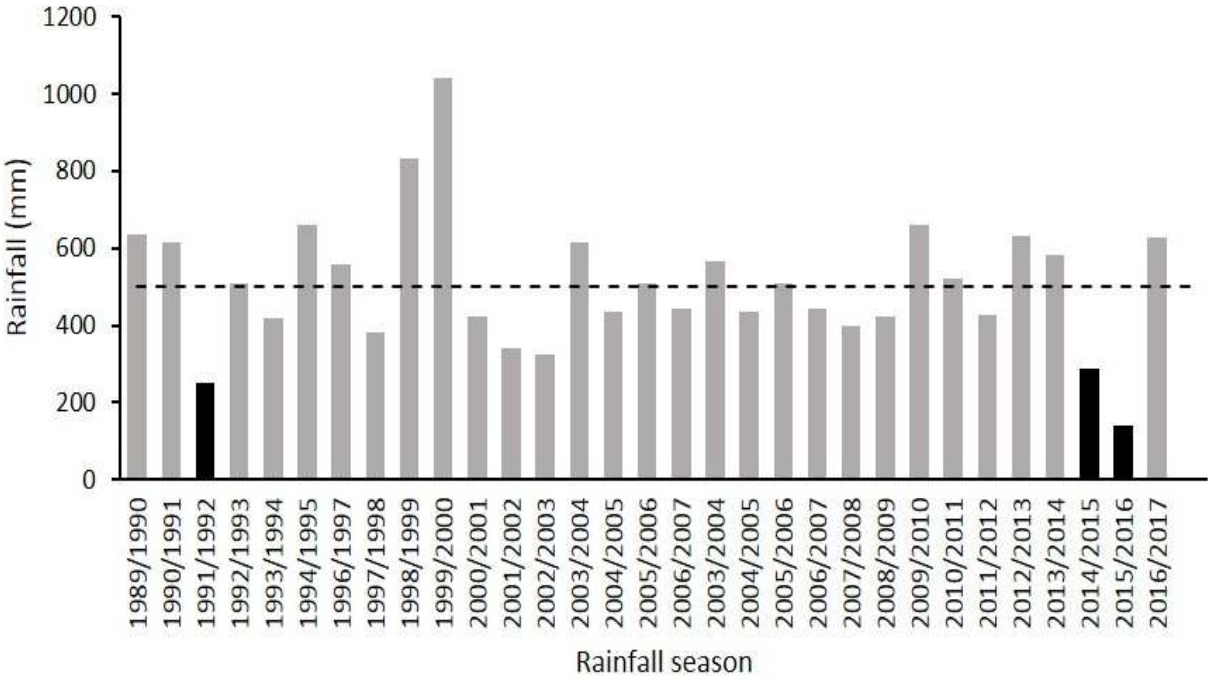


Figure 4.1. Wet season rainfall from the South African National Parks' Satara weather station over the past 17 years. The 2014-2016 and 1991 drought years (black shading) falling over 200 mm below the 502 mm long term average (hatched line).

3.3 Grass productivity

We estimated monthly grass and forb productivity, end of season standing biomass and biomass removal by grazers over the two growing seasons (2015/2016 and 2016/2017) on matched lawn, bunch and burned grass plots located in the field. Five lawn grass patches were located that were surrounded by bunch grass communities and within 50 m of an area that had been burned by Kruger National Park management in October of 2015. Methods from Mc Naughton, Milchunas and Frank (1996) with improvements made by Knapp *et al.* (2012) for estimating annual net primary productivity (ANPP) in grazed communities were adjusted to suit an assessment of monthly net primary productivity (MNPP) in different grass communities. We erected a single 1 m^2 permanent exclosure (PE) and four smaller 50 x 50 cm mobile exclosures (ME) with paired "exposed" plots (PPs) on each of the five grazing lawns and their respective matched bunch and burned patches resulting in 15 PEs, 60 MEs and 60 PPs. Mobile exclosures were initially placed at the four cardinal points of the respective PEs but were moved 1 m in a clockwise direction during sampling when all the above ground biomass within a 25 x 25 cm quadrat was harvested both in the MEs and the PPs. Sampling occurred at monthly time intervals to avoid over harvesting resulting in productivity overestimates (Knapp *et al.*, 2012) and we included both positive and negative differences between ME's and matched grazed plots when calculating relative grass productivity (Sala *et al.*, 1988; Biondini, Patton and Nyren, 1998; Knapp *et al.*, 2012). The harvested biomass was split into forbs and grasses with grass material split further into dead and live (green) material before being weighed once when wet and again after being oven dried at 60°C to a constant weight. Monthly net primary productivity in $g.m^{-2}$ was estimated as the sum of the differences between biomass from PPs at the beginning of a time interval (i.e. beginning of a sampling month) and the biomass in the MEs at the end of a time interval (i.e. end of a sampling month). Positive values for a month indicate continued productivity, while negative net productivity values suggest grass growth has stopped and the grass is curing. To account for the accumulation of previous growth in tall grass communities only differences in the dry weight of live material was summed (Briggs and Knapp, 1995). Sampling of MEs and PPs occurred over all months of the growing season and only stopped once grasses had cured during the dry season at which point grass biomass was collected from the PEs by harvesting four 25 x 25 cm quadrats from the four corners of the exclosures. This material was then sorted and dried to estimate ANPP in the absence of grazing (Knapp *et al.*, 2012).

Aside from the growth response of the grass communities to drought and grazing we also looked at the death of individual tussocks on the three communities by counting and measuring the diameter of live and dead grass tussocks within 25 x 25 cm quadrats in MEs, PPs and four in each PE at the end of the growing season in May 2017.

3.4 Grazer utilization

We addressed the question of temporal use of lawn, bunch and burned grass communities during and after drought events by assessing herbivore presence on the three different communities from the onset of the growing season in 2015/2016 to the end of the growing season in 2016/2017. Data on grazer presence and utilization was collected via dung counts and bite prevalence on 5 ha plots. For each of the three grass communities (lawn, bunch and burned) we selected three replicate plots within a 70 km^2 area of the Satara landscape. We defined lawns as areas where >80% grass was below 5 cm and dominated by *U. mosambicensis* and *T. berteronianus*. Bunch grass areas were selected where grass height was over 30 cm and dominated by *T. triandra* and *B. radicans* with fires excluded for three years. Finally, burned grass communities represented bunch grass communities that were burned either in management or lightning fires at the end of the dry season in October 2015. Plots were selected that had similar amounts of woody cover (6 – 8%), and that were between 1 and 3 km from permanent water.

Sampling took place in four 50 x 50 m subplots within each larger 5 ha plot. Within each subplot we sampled two parallel 50 m transects 25 m apart. Grazing pressure was recorded once at the end of the growing season (May) and once at the end of the dormant season (October) by observing bite presence or absence on the grass tussock closest to each 2-m point along the 50 m transects. This gave a cumulative measure of grazing pressure per season. Grazer presence was measured by recording all dung (species and abundance) including dry dung encountered in 4-m-wide belts along transect lines. Dung sampling was done on a strict monthly basis for the entirety of the study with only two months in 2016 (February and May) excluded from the dataset when time constraints meant dung was not accurately identified to species level but was crushed in these months as in all usual sampling months to avoid recounting. Dung transects have been used previously to estimate large herbivore habitat usage in long term studies within African savannas and have repeatedly been shown to perform better than both direct observations and other

indirect measurements (Cromsigt *et al.*, 2009; Burkepile *et al.*, 2013, 2016; Hema *et al.*, 2017), giving relatively reliable measures for comparisons of relative abundance across similar habitats (Marques *et al.*, 2001; Sensenig, Demment and Laca, 2010). Despite this, decomposition rates on different substrates and dung removal rates by dung beetles represent two inherent issues with using dung counts to assess large mammal abundance in savannas.

3.5 Data analysis

We ran statistical models on dry grass-biomass data to assess how grass productivity changed through the growing season in different communities. We assessed grass biomass accumulation using a linear mixed model (LMM) with the restricted maximum likelihood method. Grass community, month and forb biomass represented fixed effects, with patch acting as the random effect. A separate LMM was run to look at differences in tussock cover in the three grass communities, with grass community the only fixed effect and patch the random effect.

We modelled grazer dung events per month for all four grazer species (wildebeest, zebra, impala, and buffalo) combined (as a proxy for grazer abundance) using a generalized linear mixed effect model (GLMM) with a Poisson distribution to assess the changes in the density of grazers during four different seasons over the two-year study period on all three grass community types (Crawley, 2012). Dormant (June, July, August and September) and growing (December, January, February and March) season, distance to water, and grass community (lawn, bunch and burned) represented fixed effects with plot and subplot acting as nested random effects to control for repeated measures along transects of each subplot every month. To get a more detailed assessment of the specific species responses we ran GLMMs with Poisson distributions for monthly dung events of each species on the three different treatments (lawn, bunch and burned) resulting in a total of 12 models (Table 4.1) model, species dung density represented the response variable with month representing the fixed effect and plot and subplot the nested random effects.

To understand how grazer presence impacted grazing pressure we modelled the bite intensity for all grass communities using GLMMs with binomial distributions. Bite intensity represented the response variables and year, distance to water, and grass community (lawn, bunch and burned) acted as fixed effects. Plot and subplot represented the nested random effects to control for repeated sampling each season for bite intensity (Table 4.1).

Table 4.1. Linear mixed models and generalized linear mixed models used to assess the relationships between herbivore utilization of grass communities. In cases where no fixed effects showed any relationship to the response variable, null models were selected, and more complex models are only shown to indicate effects tested

Selected models	df	*F*	*P*
Grazer utilization			
Dung density ~ Season * Grass community (1|plot |subplot)	8	171.3	<0.0001
Lawn treatment wildebeest dung ~ Month (1|plot | subplot)	20	1518.8	<0.0001
Bunch treatment	20	50.92	<0.0001
Burn treatment	20	709.15	<0.0001
Lawn treatment zebra dung ~ Month (1|plot | subplot)	20	274.8	<0.0001
Bunch treatment	20	36.19	<0.001
Burn treatment	20	143.2	<0.0001
Lawn treatment impala dung ~ Month (1|plot | subplot)	20	552.3	<0.0001
Bunch treatment	20	73.14	<0.0001
Burn treatment	20	201.75	<0.0001
Lawn treatment buffalo dung ~ Month (1|plot | subplot)	20	144.87	<0.0001
Bunch treatment	20	24.81	<0.0001
Burn treatment	*NA*		
Bites per subplot ~ Season * Grass community (1|plot |subplot)	10	917.9	<0.0001
Grass productivity			
Dry grass growth ~ Month * Treatment (1|Site)	12	102.5	<0.0001
Tussock area ~ Treatment (1|Site)	1	4.1	= 0.043

All LMMs and GLMMs were processed using R statistical software (Version 3.3.1.; R Core Team, 2016) and the lme4 package (Bates *et al.*, 2015). Following the suggestions of Zuur *et al.* (2009) and Bolker *et al.* (2009), we used a top-down approach to model selection with an ANOVA to remove effects that resulted in models that did not differ ($p < 0.05$) significantly from the full model. We looked for obvious deviations from homoscedasticity and overdispersion in our models by plotting residuals against fitted values and visually assessing

plots. To verify normality of the residuals of selected models, we used the Shapiro-Wilks test and assessed histograms and QQ-plots visually (Zuur *et al.*, 2009). We ensured that sampling points were not spatially auto-correlated by utilizing the georR package (Ribeiro and Diggle, 2016) to calculate semivariograms for raw data and using the residuals from all selected models (Zuur *et al.*, 2009). Semivariograms showed that variation in direct measures of grass biomass, dung counts and bites, did not increase with increasing distance between plots, indicating no serious autocorrelation issues were present (see Appendix C Figure S4.1 in Supporting Information).

4 | Results

4.1 Established grass tussock cover

Established grass tussocks were absent from lawn patches and after the drought the LMM showed that tussock cover in 1 m^2 plots was lower on burnt (mean = 891 cm^2, SE = 437.9) when compared to bunch grass (mean = 2699 cm^2, SE = 571.8) communities (Table 4.2).

Table 4.2. Overview of grass characteristics and structural differences between grass communities (mean with standard error in brackets). Area covered by grass tussocks was sampled within 1 m^2 sampling plots on the three different grass communities in February of

Community	Total tussock cover (cm^2)	Live tussock cover (cm^2)	Dead tussock cover (cm^2)
Lawn	0 (0)	0 (0)	0 (0)
Bunch	2699 (571.8)	1589 (537.8)	1110 (362.3)
Burned	891 (437.9)	106 (63.7)	784 (456.2)

4.2 Grass productivity

During the 2015/2016 growing season there was only a single rainfall event occurring in late March large enough to stimulate growth in the three grass communities with productivity extremely restricted over the entire season (Figure 4.2). Primary production in this single growth month was low across all communities (<50 $g.m^{-2}$) with bunch grass plots showing almost no growth response to rainfall (mean = 4.25 $g.m^{-2}$, SE = 2.51) while burned communities had the

greatest growth (mean = 46.42 g.m^{-2}, SE = 6.67). Rains arriving late in December 2016 meant low productivity continued until early 2017 when the LMM confirmed a substantial increase in grass growth across all grass communities (ES = 171.23 g.m^{-2}, SE = 98.08). Productivity did not differ between grass communities during January and February. However, by March the continued low grazing pressure on the experiment resulted in the initially highly productive lawn grasses senescing resulting in a decrease in productivity (ES = −273.78 g.m^{-2}, SE = 169.92). Similarly, burnt bunch grasslands were unable to maintain early-season growth and productivity decreased (ES = −214.20 g.m^{-2}, SE = 117.73) in March. In contrast, bunch grasses continued to grow vertically and maintained productivity while rainfall persisted (mean = 46.42 g.m^{-2}, SE = 6.67). All communities stopped growing and began to cure by May when rainfall dropped to 11.5 mm. Forb biomass had little impact on LMM performance (F = 0.18, p = 0.67) and was dropped as a fixed effect from the final selected model.

4.3 Grazer utilization

Grazer numbers were initially highest on grazing lawn communities with dung events per month more abundant on lawns (mean = 45.01, SE = 12.16) during the 2015 dormant-season compared with burned (mean = 5.76, SE = 1.02) and bunch grass communities (mean = 19.75, SE = 5.88). This pattern continued into the 2015/2016 growing season (Figure 4.2), but herbivores responded strongly when rains failed for the second year in a row (Figure 4.2). Herbivore utilization of lawn communities dropped in the 2016/2017 dormant season (ES = −41.67, SE = 6.8) and dung events per month became very rare (mean = 7.24, SE = 1.24) in the 2016 dormant season and the 2016/2017 growing season (Figure 4.2). The LMM confirmed that although grazer dung events were low in burnt areas during the 2016 dormant season (mean = 5.76, SE = 1.02), herbivores moved briefly into burned grass communities in the 2015/2016 growing season (ES = 3.57, SE = 1.21), but left again in the 2016 dry season (ES = −3.09, SE = 0.87) and dung remained low the following rain season (Figure 4.2). In contrast to the other two grass communities, bunch grass communities did not experience the same fluctuations in grazer use over the four seasons of data collection, and instead dung events displayed only minor declines season on season (Figure 4.2) and had the highest grazer dung abundance (mean = 10.52, SE = 1.90) in the 2016/2017 dormant season during the second year of drought (Figure 4.2). The decline in dung events on all grass community types during the 2016 dormant season declined further (ES = −2.68, SE = 0.57) during the 2016/2017 growing season even with the return of rainfall (Figure 4.2).

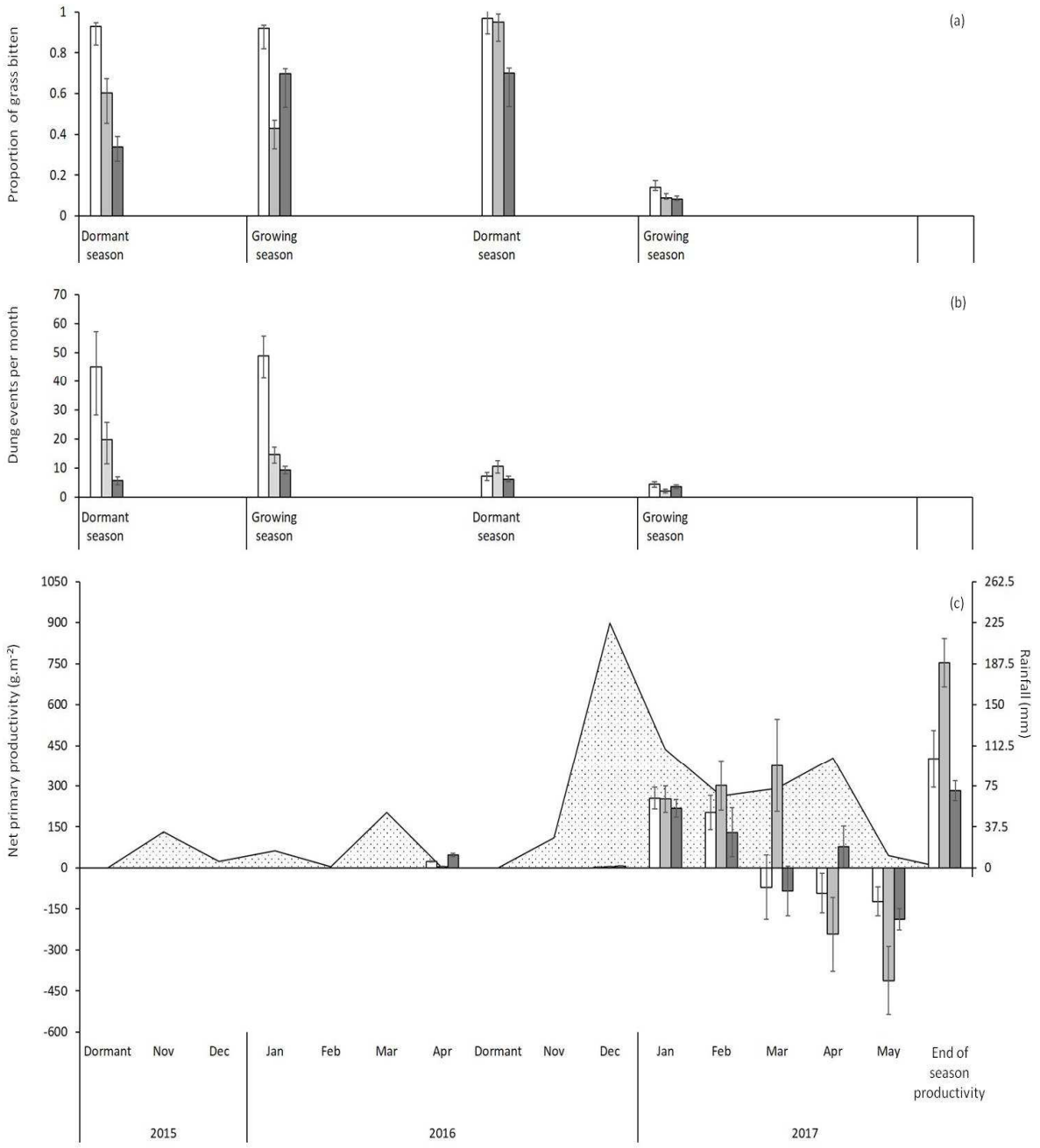


Figure 4.2. Proportional available grass bitten (mean ± SE) (a), dung deposition (mean ± SE) (b), and monthly net primary production (mean ± SE) found in the three grass communities (lawn, bunch and burned) over the entire study period. Dormant season data represents data collected in June, July and August and growing season data was collected in December, January and February. Data was sampled on lawn (white), bunch (light grey) and burned bunch grass communities (dark grey) with fires burnt in the 2015 late-dry season. Rainfall (hatched) was collected at the Satara Rest Camp weather station. Positive net primary production values for a month indicate continued productivity, while negative values suggest grass growth has stopped and the grass is curing.

The patterns in grazer utilization through the seasons were largely driven by wildebeest, impala and zebra that accounted for 53% and 28% and 12% of the total grazing dung events recorded respectively, with buffalo (6%) accounting for far less of the overall trends in grass community use during this study (Figure S4.2). It is therefore unsurprising that the GLMMs for individual species dung counts showed similar trends for wildebeest, impala and zebra to those observed in the full grazer model with severe declines on grazing lawns in June 2016 dung events (wildebeest ES = -18.22, SE = 2.12; impala ES = −7.32, SE = 1.39) after rains failed for the second year running (Figure S4.2). Buffalo dung was completely absent from burned areas throughout the study and differed from the other species by increasing slightly in abundance when rainfall returned in 2017 on both lawns (ES = 1.43, SE = 0.74) and bunch (ES = 1.43, SE = 0.91) grasslands from being completely absent in the preceding months (Appendix C). Finally, all species responded to the single good rainfall event in March 2016 by increasing their utilization of lawns (wildebeest ES = 6.35, SE = 1.92; impala ES = 8.18, SE = 1.20; zebra ES = 0.77, SE = 0.36; buffalo ES = 2.26, SE = 1.24) and burned (wildebeest ES = 7.02, SE = 3.70; impala ES = 3.11, SE = 1.18; zebra ES = 2.07, SE = 1.53) grass communities in April that year, although buffalo dung remained absent on burned plots.

The high grazer numbers on grazing lawn communities translated into lawns experiencing the highest bite pressure throughout the study except for the 2016 dormant season (Figure 4.2). During the 2016 dormant season bites per transect decreased on lawns (ES = −0.56, SE = 0.034) but remained high on burned grass areas after increasing during the 2015/2016 wet season (mean = 0.08, SE = 0.02) immediately after fires had burnt (Figure 4.2). Bunch grass areas (mean = 0.43, SE = 0.05) experienced consistent grazing pressure throughout the entire study excluding the 2017 growing season (ES = −0.34, SE = 0.06) when grazer pressure decreased across all communities (ES = −0.57, SE = 0.05).

5 | Discussion

Current understanding dictates that having large areas of bunch grasslands in rangeland savannas provides reserve forage for local grazers during the dormant season (Owen-Smith and Novellie, 1982). Our work does not dispute that bunch grasslands provide resources to grazers during droughts but highlights the importance of short grass patches to all study species. Wildebeest in particular were found in high densities on lawn systems when compared with bunch grasslands

in the 2015 dormant season and continued to frequent lawns during the 2015/2016 growing season even when rainfall and productivity was severely limited. This is not a unique finding within this system, Yoganand and Owen-Smith (2014) found that wildebeest in the western Kruger National Park rarely use bunch grasslands in average rainfall years with both high predation risk and low forage quality making bunch grasslands an unattractive resource even when alternative food resources are limited. But what is novel for the Kruger National Park that we have shown, is that this trend extends even one season into a severe drought when available graze on lawns is almost completely depleted and the perceived benefits of remaining on lawns by grazers is unlikely to be a nutritional decision.

5.1 Grazers and grass communities

Continued use of lawn systems by grazers during droughts aligns with work done by Augustine and Mcnaughton (2004) that found similar patterns during a local drought in east Africa where impala in a Kenyan rangeland fed in bunch grasslands during the day but remained on grazing lawns at night to avoid predation. This pattern of use resulted in an overall high utilisation of short grass areas throughout the drought. In the KNP system, Owen-Smith and Traill (2017) looked at wildebeest movements and showed that predator avoidance was the overriding control of their habitat selection even during the late-dormant season. They found that during the late-dormant season wildebeest remained on lawns at night and restricted their use of lawn edges where tall bunch grasslands concealed lions, with animals only moving into high risk bunch grasslands in the day time. The patterns of grazer use in this study were largely driven by wildebeest and impala and both these species are likely to be using lawns for predator avoidance even during drought. We found increased grazing intensity (bites per transect) during the second season of drought in bunch grasslands, but dung counts remained high on lawns, which suggests grazers were using protected lawns at night (high dung counts) and moving into the bunch grass areas in the day time to feed (high bite intensity). Thus, lawn grass communities represent an important resource to smaller herbivores beyond pure forage value and previous suggestions that low standing biomass on lawns makes them an unwanted feature of managed wildlife landscapes appear misplaced.

Macandza, Owen-Smith and Cross (2004) showed that buffalo shift their diet during the dormant season in Kruger National Park to feed on lower quality reserve bunch grass communities. Our

study area had very low buffalo presence throughout the observed period and it would be beyond the scope of this work to draw conclusions about buffalo responses to drought conditions. However, as bulk feeders, buffalo may be expected to react earlier than smaller grazers to changes in forage quantity (Owen-Smith and Novellie, 1982; Macandza, Owen-Smith and Cross, 2004) and may have already left the study area in Satara before the 2015 dormant season and not returned when rains failed in the 2015/2016 growing season. This idea is supported by the highest values for buffalo being recorded on lawns and bunch grasslands in May 2017 once rainfall and productivity were the highest they had been throughout the study period.

Aside from buffalo, most grazing species were able to withstand the first season of drought, but by the second failed rainfall season herds largely left the study area in Satara. Satara experienced the most extreme drought conditions within KNP and although standing biomass was still available in bunch grasslands, the low quality and less severe drought conditions in other areas of the park (Izak Smit personal communication) will have drawn many animals away. Our finding that animals moved away from Satara, and did not die in high numbers has been corroborated by other work showing animal numbers decreasing in Satara and increasing elsewhere in the KNP (Thobile Dlamini personal communication; Izak Smit personal communication). Local patterns of animal movements to regions where drought conditions are less severe is not unexpected and has been recorded in several species in other African savanna systems (Georgiadis, Hack and Turpin, 2003; Augustine, 2010).Whether the localised nature of the severe drought in Satara is unique to the 2015/2016 drought, or common in most droughts is not yet known. However, climatological research shows that past drought severity in southern Africa shows high spatial variability (Richard *et al.*, 2001). The large size of KNP improves the chance that it encompasses some variation in drought severity and animals are more likely to have access to areas with greater forage quality during droughts in KNP than in smaller fenced reserves where the impact of drought on grass communities has been shown to be far more severe than what we have found in our study system (Boone, 2007).

5.2 Grazers and grass productivity

Our study highlights a fundamental flaw in using agricultural systems or artificial clippings to understand drought responses of grass communities in systems with free roaming herbivores. This is clear from the substantial decline in grazer numbers across our study sites in the 2016

dormant season and the large variation in grazer presence and grazing intensity on the three different grass communities over time. In fenced, commercial grazing systems the grazing pressure is determined artificially and not dictated by the preference of grazers for different resources in the landscape as large scale movement to completely new resource pools is normally impossible (O'Connor, 1995). Although studies have looked at grass productivity under simulated grazing (clipping) throughout a drought on burnt and unburnt bunch grass communities (Koerner and Collins, 2014), our work shows clearly that this fails to account for actual grazer decisions on where and when to feed during drought events with clear repercussions for community productivity.

The most notable relationship between grass productivity and grazer use occurred after the major rainfall event in March 2016. Grazer numbers and grazing intensity increased on both lawns and burned areas as grazers responded to the fresh growth available in the middle of a drought year. The same trend was not true of bunch grasslands that did not respond to the rainfall event and produced little new foliage with no observed increase in herbivore utilization of these communities. The result was an intense grazing pressure on burned and lawn grass areas during a period of growth, in comparison to bunch grasses that experienced low grazing pressure throughout the entire study and their highest grazing pressure was during a period of dormancy. In the absence of grazing pressure, African savanna bunch grasses are largely unaffected by drought and recover productivity and maintain ground cover when rainfall returns (O'Connor, 1994, 1995; Koerner and Collins, 2014). This was observed in bunch grass communities that had high tussock cover and were the most productive grass community when rainfall returned, compared with adjacent burnt patches that experienced high grazing and had substantially lower tussock cover and the lowest productivity after the drought. Considering that recently burnt grasslands usually have higher productivity than unburnt grasslands (Koerner and Collins, 2014) it is clear grazer preference and selectivity of burnt areas in free roaming systems will dictate the spatial pattern of grass recovery once rainfall returns.

The apparent co-evolution of grazers and grazing lawn grasses (Mc Naughton, 1979) results in a complicated feedback system during droughts. Grazing lawn grasses have repeatedly been shown to cope well with dry conditions (Anderson *et al.*, 2013; van der Plas *et al.*, 2013; Veldhuis *et al.*, 2014), respond quickly to brief rainfall events (Bonnet *et al.*, 2010) and cope with defoliation stress (Anderson *et al.*, 2013). The increased productivity on lawns in response to rainfall in

2016 clearly attracted grazers, and the ability of lawn grasses to persist with high grazing pressure meant that productivity the following season when rainfall returned to average levels was high on lawns and matched those of bunch grasses for the first three months of the growing season. However, the fact that lawns are a very limited resource during droughts and the dormant season (Bonnet *et al.*, 2010) means grazers eventually have to move away from areas with large areas of lawn cover during major droughts, and thus the grazing pressure on lawns when rainfall returns will at least initially be low. In this study, grazers did not return in large numbers for the entire 2017 rainfall season and the low graze pressure coincided with grazing lawn productivity declining in March despite good rainfall until April that year. This finding aligns with work done in East Africa that found when grazers that left grazing lawns during droughts were prevented from returning lawns became unproductive due to self-shading while grazing lawns where grazers could return maintained pre-drought productivity (Augustine and Mcnaughton, 2006). Ultimately, this break down in feedbacks after the return of rainfall in 2017 resulted in an absence of rainfall productivity pulses and lack of grazer driven productivity facilitation on lawns that has been observed in other studies (Mc Naughton, 1979; Bonnet *et al.*, 2010). The lack of grazing pressure on a lawn system for an entire growing season indicates a decoupling of grazer-grazing lawn dynamics and if burnt in a large fire that spreads grazing out the following dry-season this may represent a pathway for the breakdown of grazing lawn systems more generally.

5.3 Conclusion

The exact response of grazers to drought events and the impact of their forage selection on a given savanna system will be dependent on the unique set of conditions created by the drought event, grazing history and grazer guild. This limits the value of detailed experimental work on drought and productivity in savanna ecosystems, which assumed uniform grazing during and after drought events. Here we have shown that lawns and bunch grasslands experience different grazing regimes during droughts but that both appear to be robust systems and recover to high levels of productivity shortly after droughts break. Perhaps surprisingly it appears that the most severe impact on lawn productivity is the loss of grazing pressure after droughts if grazers do not return to feed in the same areas they frequented pre-drought. In terms of bunch grasslands, area burned prior to, or during drought events is likely to be the most defining driver of post-drought ecosystem function. Fire events inevitably interact with grazers and shift feeding patterns, either

attracting grazers during short rainfall events during drought or rendering entire areas devoid of forage for the duration of the drought. The former severely reduces the productivity of local areas after droughts have broken while the latter may act to remove established grazer/grass feedbacks in broad areas of the landscape. This finding is pertinent as fires remain one of the few major management tools in large protected savannas but needs to be understood in conjunction with herbivory rather than as an independent driver to fully identify the effect of drought on savanna grass structure and function.

Chapter 5 | Grazing lawns in a burning landscape: A case study of the effects of drought on grazer- and fire-controlled alternate savanna states

This chapter has been prepared for submission to Ecography

1 | Abstract

Fire and grazers in African savannas establish self-promoting positive feedbacks with grass communities that negatively impact the other consumer. Thus, at some level fire and grazers are not only competing for grass quantity but also competing to maintain feedbacks within grass communities. How drought affects the competition between these consumers by shifting the conditions governing feedbacks is not well understood but is becoming increasingly important in southern Africa where drought events may become more frequent and severe with climate change. Drought changes the resource landscape by reducing the productivity of the system during the wet season and forcing grazers to feed in low quality grass communities that usually burn, this could potentially reduce biomass and restrict fire in the landscape. Alternatively, drought could result in grazer die-off and the decoupling of grazers from grazing-lawn areas where food becomes limited and potentially results in grazing-lawns growing tall and burning when droughts end. In this study, for an area of Kruger National Park, South Africa, we developed high resolution (30 m^2) maps of fire and grazer-adapted grass communities for five years, including two seasons of severe drought. Using these maps we tested whether drought either: (1) acts in a similar capacity to large fires and results in the breakdown of grazing lawns – grazer relationships and the consequent loss of established grazing lawns at the landscape scale, or (2) results in tall grass communities experiencing higher than normal grazing intensity during droughts and consequently larger areas of the landscape experiencing repeat grazing after drought, increasing the proportion of established short-grass communities.

We found that grazing lawns covered < 4% of the landscape prior to drought but were largely resistant to drought and grazing lawns identified pre-drought were still present post-drought. Tall-grass (>15 cm) areas usually associated with fire were strongly impacted by drought and areas that burnt had probabilities of 0.54 and 0.93 of remaining short (<15 cm) for the following year in the first and second season of drought respectively. This resulted in a large reduction in tall-grass cover from a high of ~ 780 km^2 pre-drought to a low of ~ 151 km^2 during the drought. Despite these changes grass recovered quickly after the drought and tall-grass communities were once again the dominant landscape cover (53%). The long-term effects of drought on consumer-grass feedbacks thus seem relatively minor and, contrary to predictions, established feedbacks appear to give the system resilience to drought events. However, if dry spells represent a more

permanent, chronic change to lower rainfall conditions, pyric-herbivory could drive an accelerated change to a grazer dominated state.

Keywords: African savannas, drought, fire ecology, grazer ecology, grazing, grazing lawns

2 | Introduction

Our understanding of how wild herbivore populations interact with fire to shape savanna systems has developed significantly since Bond's (2005) call to investigate further the interplay between herbivore controlled "brown-world" savannas and fire dominated "black-world" savannas. Literature focusing on the effects of fire size, season and frequency on wild grazers has begun to untangle the feedbacks between grass communities and these two consumers that govern vegetation structure and function in African savannas (Archibald and Bond, 2004; Archibald *et al.*, 2005; Archibald and Hempson, 2016; **Chapter 1**; **Chapter 2**). Development of the theory of grazer response to fire in the form of pyric-herbivory has shown how changes in fire regimes and burning practices can change not only the structure (**Chapter 2**) but also the functioning of savanna systems (Burkepile *et al.*, 2016; **Chapter 3**). However, Africa is not only a continent of fire and grazers, it is also a continent that is forecast to be heavily affected by changes in climate (Collier, Conway and Venables, 2008): southern Africa is expected to experience more frequent and severe droughts associated with strengthening El Niño Southern Oscillation (ENSO) effects with elevated CO_2 (Gizaw and Gan, 2017). Developing an understanding of how feedbacks between grazers and fire may be influenced by droughts in southern Africa is thus of increasing importance.

The active use of fire for specific management outcomes within grasslands and savannas is a global phenomenon and fire has been manipulated by humans for at least the past ~ 60 kyr (Archibald, Staver and Levin, 2012). As a result, the repercussions of different fire management approaches on the structure and function of savanna ecosystems have been studied on every continent where savannas are found (Trollope, 1982; Williams *et al.*, 1999; Peterson and Reich, 2001; Hoffmann *et al.*, 2009) and there is a rich body of literature looking at fire effects on trees and grasses. This solid theory on the effect of fire on tree-grass dynamics has paved the way for the incorporation of fire into global vegetation models (Thonicke *et al.*, 2001). In the context of African savannas, good theory on fire management for commercial livestock systems exist and has been successfully implemented for rangeland management (Trollope, 1982). In contrast, research looking at the influence of fire on wild grazers and particularly mega-herbivores have only recently shed light on the complexities of fire-grazer interactions within wildlife systems (Archibald, 2008; Sensenig, Demment and Laca, 2010; Allred *et al.*, 2011; Burkepile *et al.*, 2016; **Chapter 2 and 3**). One major caveat in current literature is a lack of studies looking at the

impact of drought events on the known feedbacks between fire and grazers in free roaming landscapes.

The direct impact of fire on free roaming grazers is limited to the loss of animals that are killed during burns, which in the case of large herbivores is generally low as their mobility allows them to escape flames. Rather, the major effects of fire on communities of grazers is via indirect influences through the shared resource of grass (Archibald and Hempson, 2016). At its most simple this relationship is competitive, if fire burns and grasses are unable to "green up" or regrow before the dry season then a key resource is lost to herbivores at a critical period of the season (Macandza, Owen-Smith and Cross, 2004). However, if burnt grasses are able to regrow then fire facilitates grazing in the short-term by improving the availability of high quality forage; indeed wild grazers have repeatedly been found to increase their utilization of burn scars immediately after fire (Klop and van Goethem, 2008; Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2013; **Chapter 2**) and burn scars play an important role in the structuring of grazer communities in African savannas (Klop and van Goethem, 2008; Sensenig, Demment and Laca, 2010; Burkepile *et al.*, 2013).

Despite the short-term benefits of fire to grazers, the long-term implications of burns on the quality of graze tends to be negative due to feedbacks between grass communities and fire. Burning favours light competitive, high carbon, fast growing grasses that regrow quickly after fire (Ripley *et al.*, 2015; Simpson *et al.*, 2016) and continued burning can result in a decrease in the landscape level quality of forage as a result of grass community changes (Anderson *et al.*, 2007). This trend is exacerbated in the absence of grazing when defoliation by grazers no longer limits light competitive grass species and they dominate community composition (Eby *et al.*, 2014). Large fires that disperse grazers over broad areas and reduce concentrated grazing thus drive landscapes towards grass community states that are limiting to grazing by small-bodied ruminants and favour repeat burning (Archibald and Bond, 2004; Archibald *et al.*, 2005). This contrasts with small fires that concentrate grazing for longer periods and can shift the grass community composition towards grasses with higher graze quality that encourages repeat grazing (Burkepile *et al.*, 2013; **Chapter 2**). Similarly, localised disturbances such as repeat grazing by white rhino (Waldram, Bond and Stock, 2008; Cromsigt and te Beest, 2014), rhino-middens (Cromsigt and Olff, 2008) and the formation of termite mounds (Davies *et al.*, 2014) can drive the concentration of grazers and lead to feedbacks promoting repeat grazing. This

intense grazing can theoretically exclude fire in the broader landscape (Archibald, 2008). Thus, at some level fire and grazers are not only competing purely for grass quantity but also competing to maintain feedbacks within grass communities that favour their dominance of the system. How drought affects the competition between these consumers by shifting the conditions governing feedbacks is not well understood. Here we examine how the structure of grass communities' changes through a major drought event and link our findings to developed grazer-fire theory.

Drought changes the resource landscape upon which fire and grazing interact by reducing the productivity of the system during the wet season and limiting the availability of high protein fresh grass growth. Changes to productivity and resource availability can result in disruptions to previously established feedback loops (**Chapter 4**). During droughts herbivores are often forced to move away from areas where grazing habitat is usually high quality as productivity slows and available quantity of grass is limited (Owen-Smith and Novelie 1982; Riginos 2015; Owen-Smith and Traill 2017). This has been observed to drive an increase in the utilization of tall-grass fire-prone areas (Riginos 2015; Owen-Smith and Traill 2017). This, in turn, can affect feedbacks between grazers and grazing-lawns with potential repercussions for their long-term stability within a landscape (**Chapter 4**). Thus, it has been suggested that droughts can act in similar ways to large fires and disperse grazers over broad areas, which result in the loss of grazing lawns in the broader landscape and the promotion of repeat large fires (**Chapter 4**).

An alternative scenario is that grazers feeding in tall bunch-grass systems increase herbivore pressure on these resource competitive grasses to levels that result in the die-off of grasses and drive localized extinctions of sensitive species (O'Connor 1995; **Chapter 3**) and reduce productivity over large areas. Heavily grazed systems and grazing pressure on fire adapted grasslands during droughts reduces basal cover (**Chapter 4**) and shifts species composition from tufted perennial species to annual species and prostrate growing perennials resulting in a decrease of productivity in African savannas (O'Connor 1995, Koerner and Collins 2014). It is possible that drought-induced grazing in tall grass communities will shift them towards a low productivity state after drought and limit the extent and frequency of fires in the landscape when rainfall does return. In the latter scenario it could be expected that grazing-driven grass communities become established over larger areas as fire becomes more limited.

In this study, for an area of Kruger National Park, South Africa, we developed high resolution (30 m^2) maps of fire and grazer-adapted grass communities for five years, including two seasons of severe drought. Using these maps we were able to test whether drought either (1) acts in a similar capacity to large fires and results in the breakdown of grazing lawn – grazer relationships and the consequent loss of established grazing lawns at the landscape scale, or (2) results in tall grass communities experiencing higher than normal grazing intensity during droughts and consequently larger areas of the landscape experiencing repeat grazing after drought, increasing the proportion of established short-grass communities.

3 | Methods

3.1 Study area

Kruger National Park (KNP) in South Africa contains the full suite of large African mammals and occupies ~ 19 485 km^2. We focused our study on the south-eastern corner of KNP (*c.* 1340 km^2) in an area of clayey high nutrient basalt derived soils (Venter, Scholes and Eckhardt, 2003) in a continuous vegetation type defined as *Sclerocarya birrea* (A. rich.)–*Acacia nigrescens* (Oliv.) tree savanna (Gertenbach, 1983). This contiguous region of the park has low tree and high grass cover and afforded the best opportunity to identify grass communities from satellite imagery over a large section of the park (Figure 5.1). The extensive C_4 grass plains can be separated into two grass communities; (1) fire adapted bunch grasslands dominated by *Bothriochloa radicans* (Lehm.), *Digitaria eriantha* (Steud.), *Panicum coloratum* (L.), and *Themeda triandra* (Forssk.) (Knapp *et al.*, 2012) that burn on average every 3 - 4 years and (2) heavily grazed short-grass grazing lawns with grass species including *Urochloa mosambicensis* (Hack.), *Tragus berteronianus* (Schult), *Eragrostis cilianensis* (All.), *Chloris virgate* (Sw.), and *Brachiaria eruciformis* (Sm.) (Cromsigt and te Beest, 2014). Animals are free to move throughout the park and into numerous adjacent private reserves, and the Limpopo National Park in Mozambique where shared fences have been removed to increase natural movement. Fences that limit movement out of these protected areas do exist at their extremes with the most notable being the western boundary fence, which when erected ended the historical western migration (Whyte and Joubert, 1988).

Management of fires in KNP is currently based on available fuel loads, with managers initiating burns when grass biomass is considered high; fire return times thus vary across the park with

rainfall and soil patterns resulting in different grass productivity and biomass accumulation rates (Govender, Trollope and Van Wilgen, 2006).

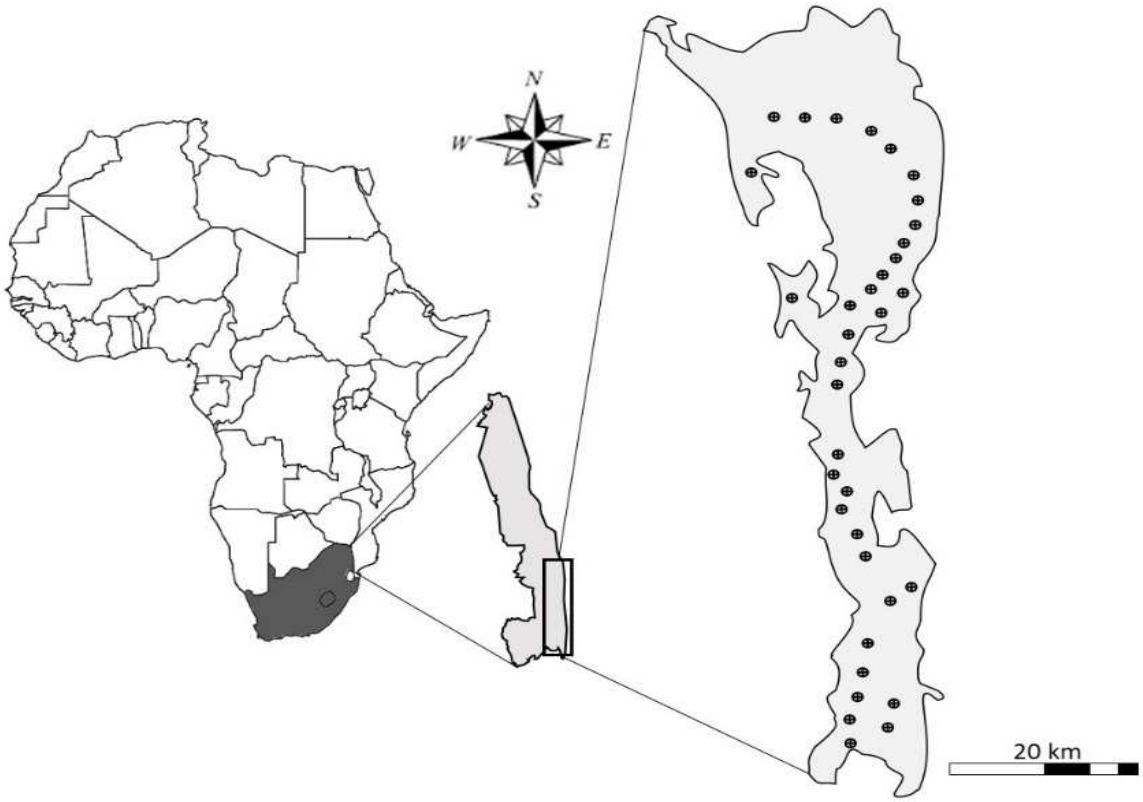


Figure 5.1. Position of 750 m transect lines used to collect ground truth data for classification of grass communities in the *Sclerocarya birrea-Acacia nigrescens* tree savanna region of Kruger National Park as defined by Gertenbach (1983). This land system is approximately1400 km^2 and cover 7% of Kruger National Park. Sampling of 35 transect

3.2 Rainfall

The 20 year mean annual rainfall for this area of KNP is 502 mm.year^{-1} with the majority (78%) of rainfall falling in the austral summer (November-April) and grasses becoming dormant during dry winter months (Venter, Scholes and Eckhardt, 2003). The last major drought event in KNP occurred during the early 1990s after which rainfall has been consistently high up until the 2014 – 2015 season when rainfall was 58% of the long-term mean, with only 28% of the long term average rainfall falling during the 2015 – 2016 season before recovering with above average rainfall in 2016 – 2017 (Figure 5.2).

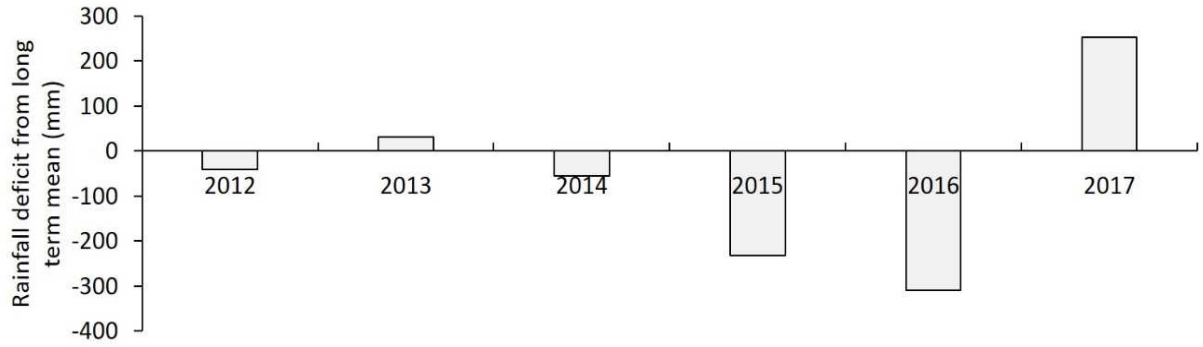


Figure 5.2. Deviation from the long-term (1980 – 2017) precipitation of the south-eastern area of Kruger National Park for the wet seasons of the five focal years of this study. Rainfall data was accessed from the South African National Parks' Satara, Crocodile Bridge, N'wanetsi, Tshokwane, and Lower Sabie weather stations.

3.3 Satellite vegetation data

We used cloudless georeferenced Landsat-8 images (path 168, band 77) from the U.S. Geological Survey for March (end of the wet season) for five years (2013-2017). Previous studies have shown that at this point in the season a combination of a higher green reflectance at the end of the wet season and greater exposure of soil makes grazing lawns (short grass) appear distinct from bunch grasslands (tall grass) in South African savannas (Archibald *et al.*, 2005). Images were cropped to the outline of the *Sclerocarya birrea-Acacia nigrescens* tree savanna as defined by Gertenbach (1983) which covers an area of ~ 1400 km^2 (~7% of KNP). Prior to any analyses we excluded areas where tree cover was greater than 40% using tree cover products developed by Bucini and Hanan (2007).

3.4 Field data

To collect information on grass communities we walked 35 transects distributed across the study area during March of 2017 (Figure 5.1a). Due to the logistics of working in KNP where movement is restricted due to current rhino management protocols, transects were restricted to areas where major road networks were available and spaced at set distances of 5 km apart (Figure 5.1a). Transects started 200 m from roads and ran perpendicular to the nearest road to avoid confounding effects of road verges. We followed the methods of Cromsigt and te Beest (2014) and walked 750 m transects. Along each transect we measured standing grass height every 2 m using a disc pasture meter (DPM) calibrated for KNP (Zambatis *et al.*, 2006). We then

estimated percentage grass cover under the DPM disc and recorded ground cover. We defined bare ground as 2 m segments of transects where grass cover was below 30%. Short-grass and tall-grass segments were defined where grass height was below and above 15 cm respectively. We defined grazing lawns as areas where grass height was maintained below 5 cm and dominated by the grass species *U. mosambicensis*, *T. berteronianus, E. cilianensis, C. virgata,* and *B. eruciformis* commonly associated with grazing lawns in the KNP (Cromsigt and te Beest, 2014).

Data on grass height for all other years (2013 – 2016) were sourced from long term grass measurements that matched the resolution of data collected in 2017 collected for the experimental fire project described in **Chapter 2**. These data are from fixed 50 m transects along which grass height has been measured using a DPM and grass cover estimated under the DPM disc every 2m during March of every year since 2013. This work gave us a total of 78 Landsat scale ground truth points for each year.

3.5 Classification

We performed a supervised *c*lassification in ENVI 5.4 (*Exelis Visual Information Solutions, Boulder, Colorado*) using 70% of our ground-truth points to define spectral signatures. Following a priori successful classification of grazing lawns and bunch grasslands in another South African savanna (Archibald *et al.*, 2005), cells were classified using the maximum likelihood decision rule with prior probabilities (McIver and Friedl, 2002). We performed a comprehensive test of the output map using the remaining 30% of the ground truth points (Congalton, 2001). The classification of spectral signatures defined for 2017 were then used to create similar maps for the previous four years (2013 – 2016) and tested using ground truth data collected in those years (78 test points). Analyses of initial maps showed poor results for defining differences between lawns and short grass (<15 cm) vegetation as both had high green reflectance and bare ground. We therefore did not separate these two vegetation classes and grouped them under a single short-grass classification. This resulted in maps of south-eastern KNP for each of the five years classified into short-grass (<15 cm), tall-grass (>15 cm), bare ground or undefined (*c.* 10%) where rocky cover or low shrub cover was not recognised as any of the defined fields.

For each year we defined the length of time that any short grass cell had existed as the number of consecutive years that a cell had remained short. This meant that from 2014 we could define lawns as two-year-lawns or lawns present longer than three years and we used this to calculate the proportion of the landscape that was covered by different lawn age groups for each year.

It is possible that areas where grass was kept short for longer than one season were the result of low productivity during the 2016 - 2017 rainfall season and not purely the result of grazers removing biomass. However, previous studies in this region of KNP have shown repeatedly that grass biomass on burned areas responds quickly in the absence of grazing and recovers to previous levels even after long-term simulated drought events (Knapp *et al.*, 2012; Koerner and Collins, 2014). Moreover, grass biomass accumulation in the 2016/2017 wet season was vigorous even on lawns that were completely bare in the March 2016 with grass height well above 20 cm in areas free of herbivory when the growing season concluded (**Chapter 4**). We therefore made the assumption that grass which remained short (<15 cm) after a full season of rainfall would primarily be the result of grazers consuming biomass and cropping grass height rather than limited productivity in the growing season.

3.6 Environmental data

We assembled spatially explicit datasets for environmental factors that have previously been associated with grazing lawn formation or identified as major drivers of vegetation dynamics in savannas. We selected long term (20 year) mean annual rainfall, rainfall of the previous growing season, distance to closest permanent water source, long term fire frequency (20 years), area burnt the previous dry season, percentage sand in top 50 cm of the soil layer, and landscape slope as potential drivers of vegetation dynamics.

Rainfall is a key driver of grassland productivity (Knapp and Smith, 2001) and has been shown to impact the distribution of grazing and fire systems at the continental (Archibald and Hempson, 2016) and landscape scale (Archibald, 2008). Long-term patterns are important for identifying established vegetation structure, while rainfall during the previous growing season is useful for identifying short-term changes as it impacts the immediate distribution of landscape productivity with implications for local herbivore movements (Mc Naughton, 1985). Following the methods of Smit *et al*. (2013) we used monthly records of rainfall from six South African National Parks (SANParks) weather stations in the study region over the past 20 years and interpolated them

using thin plate smoothing splines (Hutchinson, 1998) to get spatially explicit layers at 500 m^2 resolution.

The distance from perennial rivers is an important factor in both fire and herbivore dynamics within KNP (Smit *et al.*, 2013). We generated maps of distance from perennial rivers at 500 m^2 resolution to match those for rainfall.

Fire was a key focus of this study and we wanted to assess the long-term impact of fire on established grass communities and how it interacted in the short-term during the 2015-2016 drought. We accessed burn scar maps for KNP over the past 20 years from SANParks at a resolution of 500 m^2 and calculated the median burn frequency. Separately, we designated cells as burnt/not-burnt for each focal year of this study (2013-2016).

The proportional makeup of clay and sand in the soil surface influences the formation of grazing lawns under heavy grazing with clayey soils more frequently associated with grazing lawns than sandy soils (Hempson *et al.*, 2015). We accessed 250 m^2 resolution maps of percentage soil content within the top 50 cm of the soil layer from 250mSoilGrids (Hengl *et al.*, 2017). These areas were then aggregated to match the 500 m^2 of other environmental layers.

Landscape slope is important for both the spread of fire (Smit, 2011) and landscape utilization by mammalian grazers (Anderson *et al.*, 2010). We calculated the slope of 30 m^2 cells as the difference in altitude and distance between cell centres using the Shuttle Radar Topography Mission (SRTM) spatial elevation data layer (Farr *et al.*, 2007). These elevation models are provided at 30 m^2 resolution and we therefore aggregated maps to the same resolution (500 m^2) as all other environmental layers.

3.7 Data analysis

To limit the effects of auto-correlation we created a 5km grid over the study area and used the intersections of each grid line as a sampling point resulting in 262 data points. Using this data, we assessed the impact of burns from the previous dry season, percentage sand content, prior wet season rainfall, and distance to water on major vegetation changes each year (2013-2017). Specifically, we used generalized linear models (GLMs) with binomial distributions (Crawley 2012) to test the effects of these variables on the probability that grazing lawns remained grazing lawns or tall-grass communities remained tall between years. This resulted in three GLMs for

changes in lawns between years and four for changes in tall grass communities (Table 5.1). All GLMs were processed using the stats package in R statistical software (version 3.3.1 R Core Team, 2016).

To try and develop a clear understanding of the long term environmental drivers of temporally stable lawns we defined long-term lawns as those present in 2017 that had remained stable for the duration of the study (5 years). We then grew a classification tree in package rpart (Therneau and Atkinson, 2018) with mean annual rainfall, proportion sand content, mean fire return time and mean slope angle representing environmental predictors of grazing lawn presence and absence and tested its ability to predict lawn presence and absence in a set of 100 test data points.

Table 5.1. Generalized linear models used to assess the relationships between grass community changes and environmental drivers. In cases where no fixed effects showed any relationship to the response variable, null models were selected, and more complex models are only shown to indicate effects tested

Selected model	DF	χ^2	*P*
Lawn change 2014 – 2016 ~ previous years rainfall + distance to water + sand content %	3	0.45	0.79
Lawn change 2015 – 2016 ~.	3	5.19	0.16
Lawn change 2016 – 2017 ~.	3	3.02	0.39
Tall to short grass 2013 - 2014 ~ previous years rainfall	1	5.56	0.02
Tall to short grass 2014 - 2015 ~ burnt previous season	1	22.72	<0.0001
Tall to short grass 2015 - 2016 ~ burnt previous season	1	13.63	<0.001
Tall to short grass 2016 - 2017 ~ previous years rainfall + distance to water + burnt previous season	3	0.69	0.41

4 | Results

4.1 Classification performance

Supervised classification of grass communities for the year 2017 indicated strong matches with test data with the overall accuracy 86.36% (Table 5.2). This accuracy level is high for classification of grass communities (Congalton, 2001; Archibald *et al.*, 2005), which is likely

due to the simple differentiation of tall-grass and short-grass that meant exposed ground and green reflectance were strong differentiating features.

Table 5.2. Error matrix for classification of grass communities in the south-eastern region of Kruger National Park

Actual grass community	Predicted grass community				
	Tall-grass	Short-grass	Bareground	Undefined	Sum
Tall-grass	33	3	0	2	35
Short-grass	0	30	1	4	35
Bareground	0	0	13	2	11
Sum	33	33	10	9	88

Note: Overall accuracy for the classification was 86.36%

The accuracy for other years was reasonable (2013 = 77%, 2014 = 81%, 2015 = 78%) except in the second year of drought (2016) when accuracy dropped to (72.5%). The complete absence of good rainfall by March meant the spectral signatures of green grasses calibrated for 2017 could not be used to clearly identify dry grass during 2016 and thus some areas remained undefined (Figure 5.3).

4.2 Grazing lawns and drought

Classification tree analysis failed to identify any of the selected environmental variables as major predictors of grazing lawn presence. The classification tree that was defined performed poorly when predicting test data with an accuracy score of only 34%. Similarly, GLMs of lawn change failed to provide evidence of any relationships between lawn change over 2014-2015, 2015-2016 or 2016-2017 and the previous seasons rainfall, distance to perennial rivers or sand content (Table 5.1.).

There were clear changes in landscape lawn cover at the onset of the drought. During 2014 two-year-lawns covered 7.8% (Figure 5.4) of the landscape with the largest contiguous area kept short for two consecutive seasons ~ 0.74 km^2 (Table 5.3). At the onset of the drought (2015) this increased and two-year-lawns expanded to cover the largest area (113.8 km^2) recorded during the entire study (Figure 5.4.). Moreover, contiguous two-year- and three-year-lawns reached their maximum sizes of the study (Table 5.3) indicating that low rainfall conditions enabled grazers to keep larger areas short through the 2014-2015 rainfall season and driving an expansion of

established grazing lawns. Despite this, total lawn cover was still only 10.9% of the landscape and 95% of three-year-lawns were smaller than 5400 m^2 (Table 5.3) highlighting the dominance of the landscape by tall-grass communities. At the peak of the drought (2016) all lawn cover decreased substantially to the lowest recorded landscape cover (5.5%) as 59% of lawns changed to bare-ground (Figure 5.3). Ultimately, lawns recovered over the 2016-2017 rainfall season and grazers maintained two-year-lawn cover in the landscape at 7.8% of the landscape, almost the exact same area as pre-drought conditions and contiguous lawn size of individual lawns was notably similar to 2014 (Table 5.3).

Table 5.3. Overview of total grazing lawn cover and area of individual grazing lawns over the four years where grazing lawns were identifiable in the south-eastern basalt soils of the Kruger National Park (*c.* 1340 km^2)

	Lawns older than 2 years			Lawns older than 3 years		
Year	Total landscape cover (km^2)	95th percentile lawn size (km^2)	Largest lawn (km^2)	Total landscape cover (km^2)	95th percentile lawn size (km^2)	Largest lawn (km^2)
2014	90.7	0.0063	0.74	NA	NA	NA
2015	113.8	0.0081	1.2	53.7	0.0054	0.31
2016	54.3	0.0054	0.31	2.1	0.0027	0.01
2017	88.6	0.0063	0.61	44.3	0.0027	0.2

4.3 Tall grass communities and drought

Tall grass was the dominant vegetation type across the landscape during normal rainfall years covering over 51% and 66% of the landscape in 2013 and 2014 respectively (Figure 5.3 and 5.4). Thus, prior to the drought the majority of tall grass communities present in 2013 remained tall into the 2014 season. The GLM for change from tall-grass to short-grass from 2013 to 2014 indicated that only rainfall influenced the probability that this change occurred (ES = −0.51, SE = 0.19). The probability of tall-grass changing to short-grass at the mean rainfall for 2013 of 506 mm was 0.11 with this probability decreasing to 0.03 at the highest recorded rainfall of 687 mm and increasing to 0.19 at the lowest recorded rainfall (414 mm).

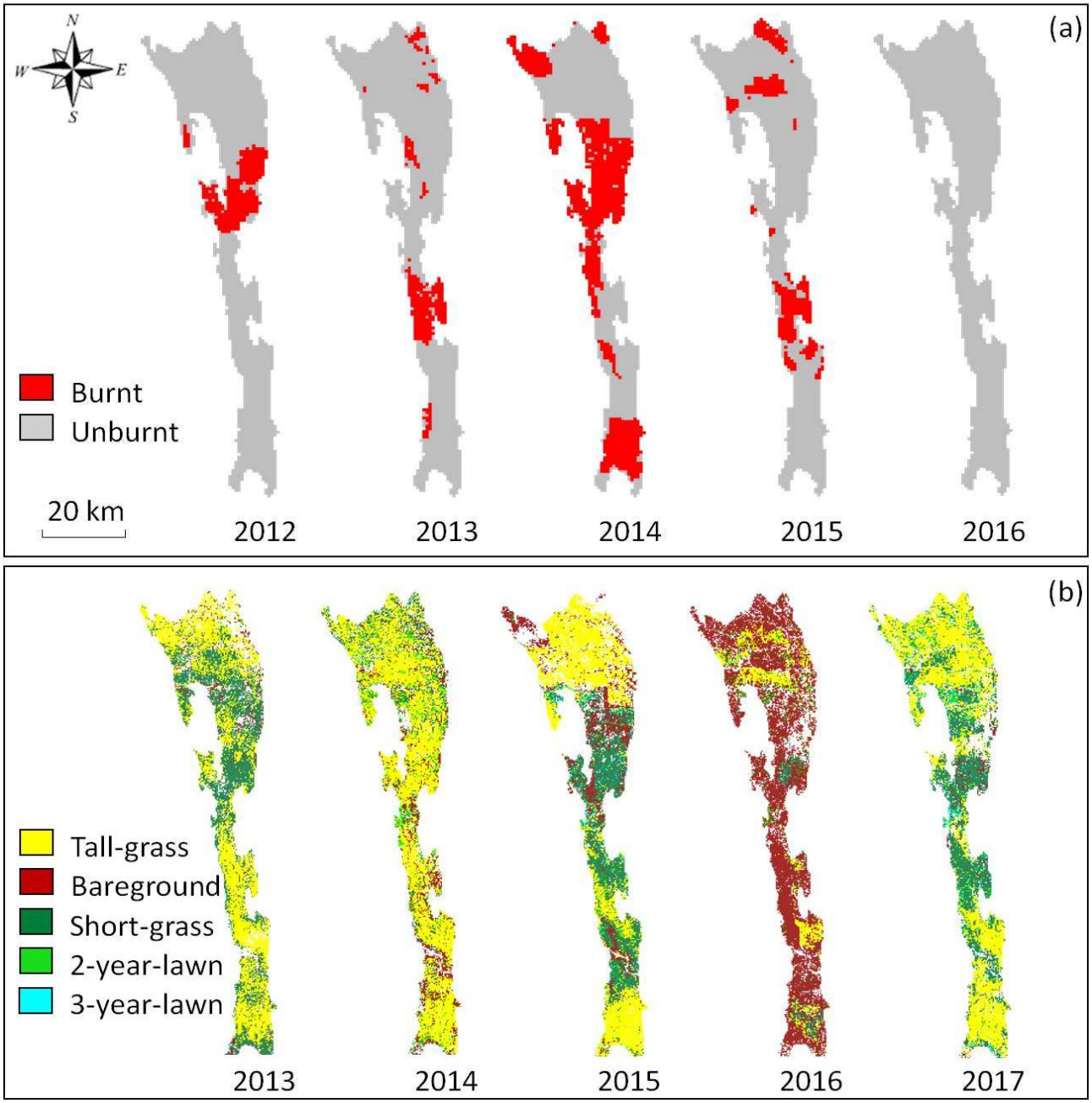


Figure 5.3. The position of fires from 2012 to 2017 (a) and tall-grass, short-grass and bare-ground for 2013 – 2017 (b) in the south-eastern section of Kruger National Park. Burnt area maps were accessed from the South African National Parks official annual burn scar layers. Grass distribution maps were created using Landsat 8 images and performing a supervised classification in ENVI 5.4 (*Exelis Visual Information Solutions, Boulder, Colorado*). These maps indicate the strong link between burnt area in the dry-season and short-grass distribution at the end of the following rainfall season due to pyric-herbivory.

The onset of drought changed the relationship between tall-grass communities and rainfall with GLMs indicating that fire (ES = 0.27, SE = 0.05) was the only fixed effect that changed the probability of tall-grass changing to short-grass from 2014-2015 (Figure 5.5). Thus, tall-grass areas that burned in 2014 had a high probability (0.75) of changing to short-grass in 2015. This effect had a strong impact on the landscape as a whole as 43% of the entire study system burnt in 2014 (Figure 5.3) resulting in a decline of ~ 418 km^2 in tall grass cover in the landscape by 2015 (Figure 5.4). The impact of burning observed in 2015 continued into 2016, fire once again increased the probability (ES = 0.35, SE = 0.17) that tall-grass areas in 2015 changed to short-grass or bare ground in 2016 (Figure 5.5). This intensified an already high probability (0.58) that tall-grass changed to short-grass during the drought even in the absence of fire. The effect of fire in combination with drought culminated in tall-grass covering the lowest percentage (15%) of the landscape during the course of the study (Figure 5.4).

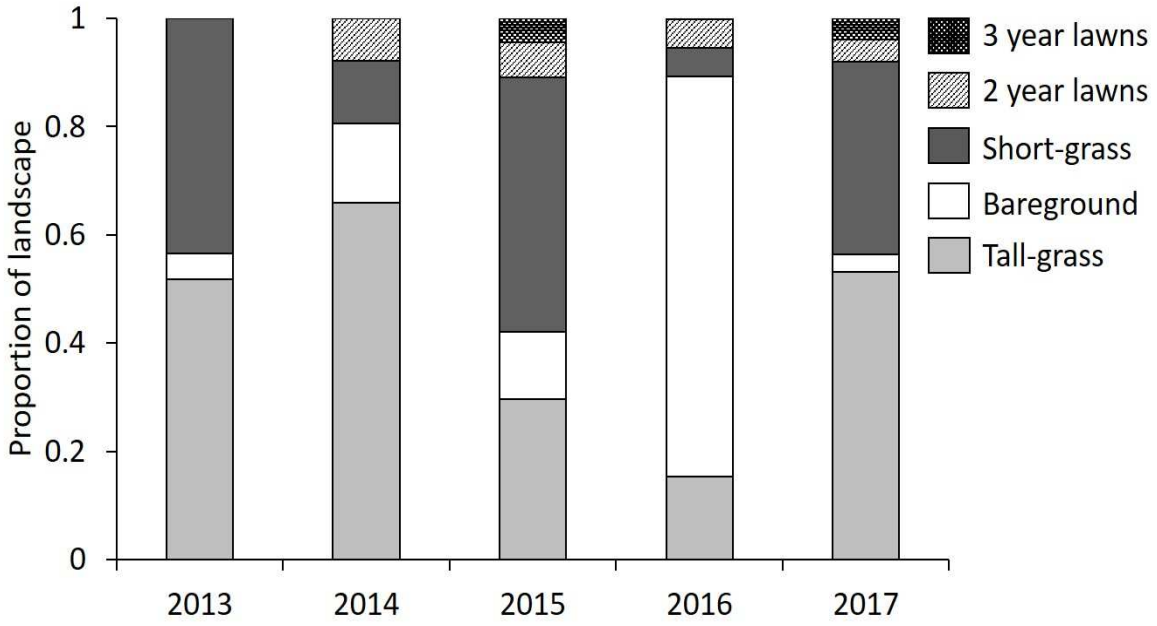


Figure 5.4. Proportional breakdown of tall-grass, bare ground, short-grass and two-year and three-year grazing lawns within the south-eastern section of Kruger National Park from 2013-2017. Proportions were calculated from maps of grass community distributions generated using Landsat 8 images (30 m^2 resolution) and classified in ENVI 5.4 (*Exelis Visual Information Solutions, Boulder, Colorado*).

At the end of the drought when rainfall returned, tall-grass communities quickly recovered to become the dominant landscape cover (53%). This was likely aided by the complete absence of fire in 2016 with areas that burnt in 2015 having no clear impact on the probability that tall-grass areas changed between 2016 and 2017 (Figure 5.5).

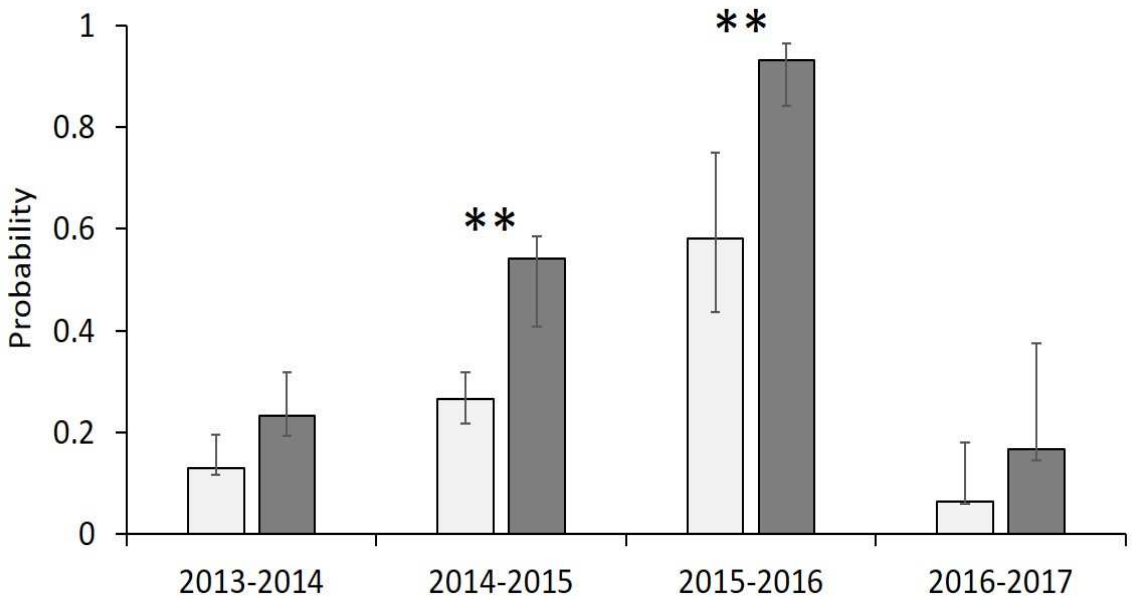


Figure 5.5. Probability (mean ±SE) that tall-grass areas (>15 cm) that are burnt (dark grey) or not burnt (light grey) change to short-grass (<15 cm) and bare-ground (<30% grass cover) the following season (**$p < 0.001$).

5 | Discussion

We know that both grazers and fire establish positive feedbacks within grass communities that stabilize grazing-lawns and fire-prone bunch grass communities both spatially and temporally (Archibald *et al.*, 2005; Hempson *et al.*, 2015). It is important to develop an understanding of how these established feedbacks are impacted by drought and whether drought can shift ecosystems from dominance by one consumer to the other. Recent work has provided evidence that drought impacts grazer-grass community feedbacks during drought events with implications for system productivity (**Chapter 4**). Our results align with these findings and indicate that the dynamics structuring vegetation in normal rainfall years changes at the onset of drought events

when productivity is reduced and pyric-herbivory, even on large burn-scars, limits the regrowth of tall-grass communities. However, no two droughts are the same and in this fire-dominated savanna we see little evidence of this drought event driving long term shifts in the dynamics of fire and grazers, with grazing-lawns and tall-grass communities returning abruptly to pre-drought proportions. Thus, our results stand contrary to our two original predictions with key implications for our understanding of consumer-grass feedbacks and for managers attempting to cope with increased drought events in wildlife protected areas.

We were unable to identify environmental drivers of lawn persistence and presence within the study region. Previous studies have shown that the presence, area covered and persistence of lawns is the result of biological processes rather than the underlying environmental conditions (Cromsigt and Olff, 2008; Waldram, Bond and Stock, 2008; Cromsigt and te Beest, 2014). Lawns in the Serengeti are a product of predator avoidance and feedbacks between the grass community and grazers rather than soil or rainfall (Mc Naughton, 1988; Anderson, Dong and Mc Naughton, 2006). Similarly, the cover of grazing lawns in KNP is strongly linked to the densities of white rhino and Cromsigt and Olff (2008) found no observable differences in the cover of lawns across a strong soil nutrient gradient when white rhino were present and similar results have been shown across a strong rainfall gradient (Waldram, Bond and Stock, 2008). All of these studies focused on systems with significantly larger environmental gradients than this region of KNP and our lack of links between environmental conditions and lawns in this area is not completely unexpected. However, this should not be mistaken as an unimportant finding and supports previous research showing that grazing lawns and fire-adapted grass communities can occupy the same environmental space and are only defined in the landscape by the biological and physical processes that govern them.

5.1 Influence of drought on grazing lawns

This study clearly shows that drought did not have an overwhelming negative impact on the feedbacks between grazing-lawns and grazers as was suggested in our first prediction. Certainly, we did not find evidence of a loss of established lawn communities through the drought and lawns present in 2014 were generally present and of similar size in 2017. This suggests that the drivers of established feedbacks between grazers and grazing-lawns are strong enough to withstand the dispersal of grazers (Riginos, 2015; Owen-Smith and Traill, 2017) away from

grazing-lawns during droughts. The strength of these feedbacks (even during the drought) in this area of the KNP suggests that grazing-lawns are assigned a high resource value by grazers. Cromsigt and Te Beest (2014) found very similar short grass cover (10.7%) in this area of KNP and estimated even lower established lawn cover (*c.* 1-2%) than we found in 2017 (*c.* 4%). It is clear that large fires burning through this landscape have shifted grass communities overwhelmingly in favour of repeat burning, even on soils and at rainfall conditions (<700 mm MAP) that would be expected to favour grazing lawns (Archibald and Hempson 2016; Venter, Cramer and Hawkins 2017). Thus, whatever feedbacks are maintaining grazing pressure on lawns are clearly strong enough to withstand regular dispersal of grazers into the broader landscape and onto fire-scars. Considering how heavily utilized grazing-lawns are by grazers in other savanna landscapes where lawns are more abundant resources (Mc Naughton, 1984; Kleynhans *et al.*, 2010), the attraction of grazers to the small number of long-term lawns in south-eastern KNP should be very strong and suggests an underrepresentation of grazing-lawn systems in the landscape, an issue raised in other areas of KNP (Yoganand and Owen-Smith, 2014) and in managed savannas more broadly (Venter, Hawkins and Cramer, 2017).

The expansion of lawns both in size and landscape cover during 2015 is likely to be the effect of grazers using lawns as areas of safety from predation and moving into the surrounding tall-grass to feed during the day (Owen-Smith and Traill, 2017). This would increase lawn size as grazers balance food requirements and predation risk (Riginos, 2015; Owen-Smith and Traill, 2017) and increasing short grass at the edge of lawns. The reduction in their size during the second season of drought is unsurprising as grazing-lawns would be expected to have limited or no cover when rainfall fails as they generally do even in normal dry-seasons (Bonnet *et al.*, 2010). The reason that lawns did not increase back to the size and cover of 2015 when rainfall returned in 2017 is less intuitive. One potential explanation is that die-off of grazers during the drought meant the standing grazer biomass in 2017 was too low to maintain pressure on larger lawns. This combined with large areas of the landscape experiencing fresh regrowth would have reduced the need for grazers to intensively graze on lawn edges. This is an important observation for grazer-fire feedbacks as, in non-migratory systems, grazing lawns are unlikely to increase in landscape cover in response to drought as long as rainfall returns to previous conditions within a relatively short time span. In such situations grazer populations are unlikely to be large enough nor able to

recruit fast enough in the immediate aftermath to limit regrowth of areas grazed short during the drought event itself and fire, which can respond immediately, will return.

5.2 Influence of drought on tall grass communities

Prior to the drought there were limited impacts of pyric-herbivory on the grass height over the majority of the landscape with the few areas that changed from tall to short related to low rainfall rather than burning. This supports the theory that large fires do not result in pyric-herbivory intense enough to limit grass re-growing and burning repeatedly (Archibald *et al.*, 2005). Indeed, certain areas of the landscape regained enough biomass after burns to carry fires for three consecutive seasons. At the onset of drought this changed considerably and a strong pattern of pyric-herbivory severely limiting regrowth in 2015 continued into 2016, indicating a shift in the functioning of the system as grasses on larger burnt patches could be kept short for a full season. Moreover, the proportion of grass communities that were maintained in a short-grass cropped state for longer than a single season increased in 2015 and the size of contiguous also patches increased in a predictable fashion when considering more arid savannas are dominated by grazer processes (Archibald and Hempson, 2016). While not apparently effective during short periods of drought, pyric-herbivory is a process by which large savanna areas could shift quickly from fire to grazer dominated, if a long-term climatic trend towards declining rainfall becomes established. However, in the case of short-term drought events our results indicate that when rainfall returns the system is likely to return quickly to a fire dominated landscape due to fires ability to respond immediately to an increase in resources when compared to biologically limited grazers.

5.3 Conclusion

It is evident from our study that areas burnt and grazed during the drought recovered biomass readily when rainfall returned and are able to carry fire in the following dry season. This supports previous recent research that found increases in grazing by herbivores within intact tall-grass communities during drought does little to impact their productivity following drought (**Chapter 4**). Clearly grazers that were unable to maintain large areas of the landscape in a short state beyond a single season prior to the drought could not maintain the large lawns created during the drought after rainfall returned. The long-term effects of this drought on consumer-grass feedbacks seems relatively minor at least at the structural level. Thus, established

feedbacks appear to give the system some level of resilience to drought events as long as they do not represent a more permanent, chronic change to lower rainfall conditions in which case pyric-herbivory will drive an accelerated change to a grazer dominated state.

Chapter 6 | General discussion and synthesis

1 | General overview

In his concluding remarks Bond (2005) stated "The interaction between fire and herbivory as shapers of vegetation has received remarkably little attention." Over the past decade there have been numerous studies addressing this short fall, particularly in grassland and savanna systems where both consumers are well represented (Archibald *et al.*, 2005; Fuhlendorf *et al.*, 2009; Holdo *et al.*, 2009; Archibald and Hempson, 2016; Burkepile *et al.*, 2016). My thesis has been inspired by this growing body of literature and I focused on further developing theory around grazer-fire interactions and the feedbacks that structure savanna grass communities. In **Chapters 2 - 5** my results add support to several already established theories on the role of consumer-grass feedbacks in maintaining distinct grazer-dominated and fire-dominated grass communities in savanna systems. Beyond the support of previous work, I have also tested (in a free roaming wild herbivore system) key concepts regarding the role of drought events in changing consumer-grass feedbacks and how this changes ecosystem function both at the local and landscape scale. Here I underline how my results have supported past ideas and theory and where I have added novel insights.

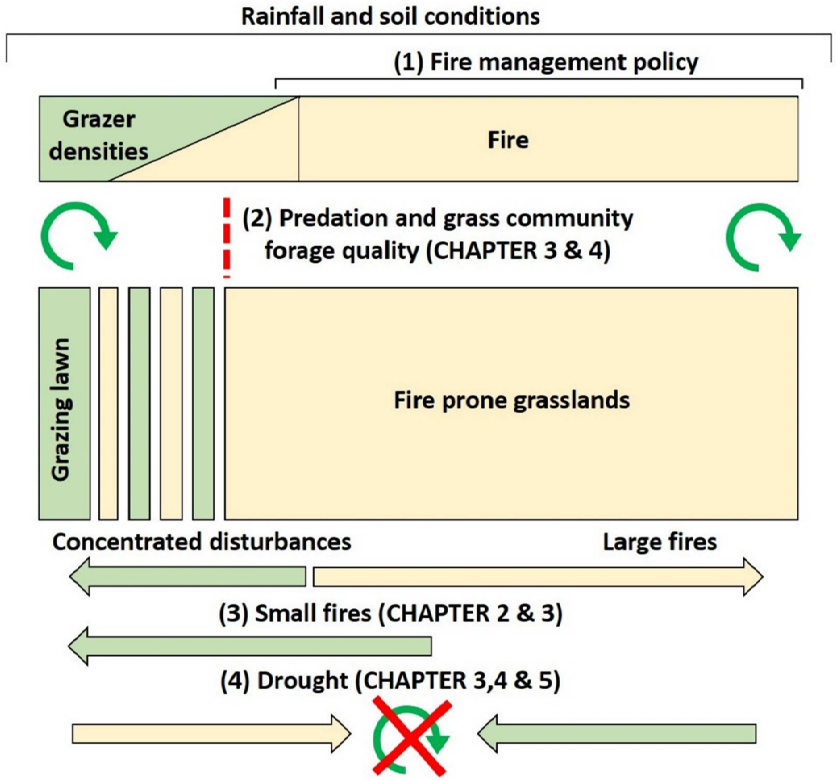
1.1 Fire – inferior competitor but dominant consumer

The effect of fire on savannas is constrained by its physical limitations with fires only able to burn when fuel quantity is high, continuous in space and dry enough to combust (Archibald *et al.*, 2009). In contrast, herbivores can consume biomass throughout the season and feed continuously through time, if grazer densities are high enough they can limit the extent of fires in the landscape (Holdo *et al.*, 2009). Thus, Archibald and Hempson (2017) suggested that fire is the "inferior competitor" as it only has access to biomass left behind by grazing herds. Despite this, of the two consumers, fire has a greater affect on vegetation structure at the global scale (Bond, Woodward and Midgley, 2005) and under current conditions consumes more biomass across Africa (Archibald and Hempson, 2016). At higher rainfalls (>800 mm) this may be expected as grass biomass builds up too fast for grazers to remove and there is sufficient fuel to support repeat burning on a regular time scale. This trend is exacerbated by the high carbon, low protein grasses that grow in high rainfall areas and constrain the majority of medium and small herbivores which cannot survive on the plentiful but poor quality forage (Owen-Smith and Novellie, 1982). In contrast, at lower rainfalls (400 – 800 mm) in areas where abiotic conditions

do not predispose grasslands to burning or grazing, it could be expected that grazers outcompete fires, but this is not what has been observed at the continental scale (Archibald and Hempson, 2016). **Chapter 5** of my thesis highlights the absence of this trend at a more local scale as I found burning dominated the dynamics of south-eastern Kruger National Park (KNP) with only ~ 4% of the landscape appearing to be driven by grazer dynamics while up to 40% of the landscape burnt within a single season, with fire return times of ~ 3 years experienced by the majority of landscape. This amount of grazing lawn cover agrees with past estimates made for KNP (Cromsigt and te Beest, 2014) and highlights a remarkably low grazing-lawn cover when compared to other wildlife managed African savannas where large scale migrations are still present (Mc Naughton, 1988), or white rhino densities more contiguous (Archibald, 2008). Thus, maps of grass communities prior to the drought in **Chapter 5** supports suggestions by Venter, Hawkins and Cramer (2017) that fire adapted grass communities are currently over represented in certain managed savannas (Figure 6.1).

The clear landscape domination by fire in KNP raises two closely related questions: (1) how is a supposedly inferior competitor dominating savanna grass community processes? And (2) why do grazers not limit fire by consuming more biomass in tall-grass communities during the wet season? My thesis in combination with several previous studies (Burkepile *et al.*, 2013, 2016; Yoganand and Owen-Smith, 2014; Owen-Smith and Traill, 2017) indicate that strong barriers exist in tall, fire-prone grass communities that limit their value to smaller-bodied grazers and in doing so make large areas of the landscape sub-optimal habitat for many herbivores that would otherwise directly compete with fire for biomass. These negative feedbacks to medium-sized-grazers manifest as positive feedbacks for fires that burn repeatedly in the largely unfrequented areas of the landscape. The process that establishes these feedbacks in the landscape is linked to fire size (Archibald *et al.*, 2005) and my thesis has further developed theory around the specific mechanisms that enhance positive fire feedbacks in frequently burnt savannas. We know that large fires disperse grazing animals over broad areas as they respond to the high quality graze available on burn scars in what has been termed pyric-herbivory (Archibald and Bond, 2004; Fuhlendorf *et al.*, 2009). The “thinning” of large mammal herds over wide ranges after a fire decreases concentrated grazing and allows grass to accumulate biomass and ultimately encourages repeat burning (Archibald *et al.*, 2005). Importantly, the post-fire environment on large burn scars with low grazing pressure results in a short period where resources are high for

grasses and results in an environment that favours resource competitive grass species that can grow fast and accumulate biomass quickly (Simpson *et al.*, 2016).Grasses associated with frequently burnt systems resprout vigorously and have high stem to leaf ratios, high leaf C : N ratios and accumulate biomass that does not break down readily (Anderson *et al.*, 2007; Simpson *et al.*, 2016). Ultimately this means the quality of forage in repeatedly burnt systems decreases in the long term as grass community composition switches to favour species with minimal nutritional gain for grazing species. Moreover, the height of these grasses and their continued accumulation of moribund material results in a habitat that conceals predators (Burkepile *et al.*, 2013). Thus, low quality, tall-grass systems are poor habitat for small bodied grazing mammals that need high protein forage to survive and reproduce (Owen-Smith and Novellie, 1982; Owen-Smith and Ogutu, 2013) and are susceptible to predation (Owen-Smith and Mills, 2008). Previous research has shown that smaller bodied grazers (<1000 kg) avoid tall-grass areas in favour of grazing lawns where higher nutrition and better predator detection provide more adequate habitat (Anderson *et al.*, 2010; Yoganand and Owen-Smith, 2014; Owen-Smith and Traill, 2017). In my study I found evidence of both these processes limiting grazer utilization of tall-grass areas. In **Chapter 3**, tall grass communities in areas with low grazer presence were dominated by low nutrient grass species (high C : N). Moreover, mesoherbivores remained on lawns in high numbers even after two seasons of failed rainfall when forage was almost completely absent and the only benefit could have been structural with higher predator detection on open patches when compared to tall-grass areas (**Chapter 3 and 4**). This finding is contrary to previous work done in East-Africa where grazers left grazing lawns and moved into high-risk tall grass systems during drought and sacrificed fear for food (Riginos, 2015). My results suggest that in systems where predator numbers are higher and foraging in tall-grass carries a higher risk of mortality grazers will continue to use open patches to avoid predators even when there is no nutritional gain (Owen-Smith and Traill, 2017). The key finding from this set of results is that the well documented positive feedbacks between fires and fast growing, resource competitive grass species manifests itself in savanna landscapes as a strong barrier to grazing in tall grass areas by mesoherbivores that cannot cope with the low quality, high risk fire adapted habitat. Ultimately, these fire adapted grass communities are largely protected from continuous intensive grazing by barriers to mesoherbivores that arise in systems where large fires persist (Figure 6.1).



1) In **Chapter 5** of my thesis I found that large areas of south-eastern Kruger National Park are governed by positive fire-grass community feedbacks that were likely established during periods when large-intense fires burnt through this region of KNP.
2) High predation risk and low quality forage in tall-grass fire-prone grass communities act as barriers to intense mesoherbivore grazing in these areas (**Chapter 3 and 4**). These barriers promote the maintenance of alternate grass community states in the landscape once feedbacks are established and are likely key drivers in the temporal stability of grass communities.
3) In **Chapter 2 and 3** I found unlike large-fires that disperse grazing across broad areas, small-fires concentrate grazing and can drive a local area to shift towards a grazer driven savanna state. This in turn leads to the establishment of positive grazer-grass community feedbacks in the form of improved predator detection and higher quality graze. The exact fire size that results in this response will be unique to the grazing population and rainfall of each system with smaller-fires required in lower herbivore or higher rainfall areas. Moreover, drought impacts this relationship by increasing the size of fires that can be kept short by the existing grazing population (**Chapter 5**).
4) I found that droughts result in a convergence of grass community trait space as grazers feed more intensively in fire-adapted communities allowing for invasion by annual species (**Chapter 3**). Grazers can also be forced to completely leave grazing lawns and if they do not return when droughts end this can result in grazing lawns growing tall and there is the potential that these areas burn over longer periods. I did not find evidence for long-term changes in grass community distribution within the landscape as positive consumer feedbacks appear to result in some resistance to the effects of drought (**Chapter 5**). However, it is clear that drought events that do have long-term impacts will do so by affecting the feedbacks maintaining consumer-grass feedbacks in savanna systems.

Figure 6.1. Schematic diagram summarizing key findings of the chapters in this thesis.

It is worth noting that larger bodied grazers in the form of buffalo did not favour grazing-lawns on my experimental sites and prior studies have not shown them to select lawns (Kleynhans *et al.*, 2010). It is possible that buffalo and the three largely predator free mega-herbivores elephant, hippopotamus and white rhino could "invade" fire-adapted grass communities and drive a switch to a more grazer-controlled system. However, buffalo and elephant have not been linked to the formation of lawns (Hempson *et al.*, 2015), and in the context of KNP the current white-rhino population in this area do not appear to be high enough to increase the proportion of lawn-cover (Cromsigt and te Beest, 2014). Hippopotamus form grazing lawns readily (Verweij *et al.*, 2006), but are restricted by their life strategies to only impact areas close to rivers where fire is already limited. Thus, the past fire management of KNP that either allowed or implemented large burns on the eastern basalts (Govender, Trollope and Van Wilgen, 2006) appear to have promoted positive feedbacks that encourage repeat burning. This represents a clear mechanism for fire dominance in large savanna landscapes where fire policy needs to account for the practicality of managing fires over substantial areas. In areas where large mammal migrations are absent and white rhino populations limited, the implementation of fire regimes will have severe repercussions on the long-term dynamics of grazing communities. If large fires are burnt regularly in these systems, tall frequently-burnt grasslands will become a barrier to local mesoherbivores and established feedbacks are unlikely to be reversed without external intervention.

1.2 Switching states – grazing in fire driven savannas

In **Chapter 2** of this thesis I found it was possible to change the major consumer of local grass communities from fire to grazing by burning small-repeated fires and concentrating pyric-herbivory pressure in an otherwise tall-grass fire dominated landscape. Initially this manifested as a structural response with concentrated grazing on burn scars maintaining the previously tall grass sward in a cropped state. Once the structural barriers of tall-grass communities were broken down grazers continued to use these patches and the consistent defoliation drove changes in the grass community composition that resulted in a more generally palatable grass sward than had originally occurred (**Chapter 3**). The process of grazing lawn formation and positive feedbacks linked to higher grass quality on grazing lawns has been tested previously in African savannas (Cromsigt and Olff, 2008). However, here I experimentally linked changes in herbivory pressure at the landscape scale to a shift in the functional trait space of grass communities that

would directly and positively benefit the local grazing community. This is unique to this study as previous experimental work on grazing lawn formation in free-roaming systems has either required the addition of nutrients to attract grazers (Cromsigt and Olff, 2008) or not directly tested changes in the trait space related to grass species compositional shifts (Archibald *et al.*, 2005). Moreover, this experiment managed to identify these processes at larger scales (up to 25 ha) than has been achieved in previous studies. The directional shift to higher graze quality on patches in response to grazing over areas of this size demonstrates a clear positive feedback between grazers and grasses that can drive the establishment and maintenance of lawns across African savannas even in the absence of obvious climatic and edaphic controls (Mc Naughton, 1984; Waldram, Bond and Stock, 2008).

The change towards a more palatable grass community in response to grazing on experimental patches was the result of both an increase in the cover of more palatable grass species and a decrease in less palatable species (**Chapter 5**). The trend of a general improvement of grass community graze quality has obvious positive feedbacks to wild grazers that can select palatable patches to graze rather than seeking out individual palatable plants (Ben-Shahar and Coe, 1992). However, if grazing lawns are to become resistant in time to changes and fluctuations of grazer numbers in the system it is the decline of less palatable high C : N species that is important. The most notable declines in species cover under heavy grazing was for *Bothriochloa radicans* and *Themeda triandra* with the latter known to respond similarly to increased grazing in other systems. Both of these species are associated with frequent burning within KNP (Trollope, Potgieter and Zambatis, 1989) and have poor leaf nutrient and low leaf moisture content when mature, while resprouting vigorously after fire and building up dead biomass over time. These species thus represent high quality fuel for fires and their local extinction should create similar barriers to fire on grazing lawns to those experienced by mesoherbivores in unpalatable fire-dominated grasslands i.e. in grazing systems where grazing results in the local extinction of good fire fuel species, it may take several growing seasons without grazers before fire can spread through these systems. Waldram *et al*. (2008) showed that lawns grew tall in the absence of white rhinos under high rainfall but not low rainfall conditions. Further, work in the Serengeti has shown that lawns grow tall in the absence of grazing (Mc Naughton, Banyikwa and Mc Naughton, 1997). However, considering these feedbacks and the potential effects of grass community traits on fire spread, it appears that the time taken for grazing lawns to burn after

grazers are removed will have important repercussions for the resilience of grazing systems to external perturbations that impact grazer populations.

Changes in consumer dominance between grazing and fire in savannas have well documented cascading impacts on ecosystem function (Holdo *et al.*, 2009). It is therefore pertinent that we identify how long it takes for barriers between alternate consumer-dominated states to be overcome and for novel feedbacks to establish in savanna systems. My thesis has demonstrated that a strong concentrating agent which changes the physical structure of grass communities can enable mesoherbivores to overcome barriers of predation risk and low-quality forage generally found in tall-grass savannas (**Chapter 2**). Positive feedbacks between grazers and grass communities in the form of short grass structure (**Chapter 2**) and improved grass community palatability (**Chapter 3**) can establish within only a few rainfall seasons once barriers are overcome and grazing remains high. However, newly established grazing lawns will be at risk of repeat burning if intense grazing is removed unless grass communities have switched to a state where species that represent good fuel for fires become locally extinct. Our understanding of when grazing lawns switch to fire adapted grass communities requires more understanding and specifically the development of datasets that show how long it takes for different grazing systems to burn after grazers are removed. If this is achieved, it will go some way in solidifying the elusive definition of an "established" grazing lawn in African savannas.

1.3 Drought

Grazers changed their foraging behaviour through the 2015 - 2016 drought and the feedbacks that governed the grazer-grass community relationship pre-drought changed as animals were forced initially to feed in tall-grass communities before having to leave the area completely (**Chapter 4**). This changed the post-drought relationship between grazers and grass communities with negative repercussions for grazing-lawn productivity. Ultimately, grazer responses to drought in free-roaming grazing systems will be dependent on a unique set of drought conditions that drive grazer behaviour. This limits the value of detailed experimental work on drought and productivity in savanna ecosystems, which have largely assumed uniform grazing during and after drought events (Koerner and Collins, 2014). Rather, understanding the potential impacts of droughts on savanna productivity and function requires further development of theory on what triggers grazers to feed on different grass communities at different periods in a drought. If we

can better understand at what body condition different grazer species risk predation to feed in tall-grass communities and what drives the long distance relocation of herds of grazers during droughts – then we could more accurately predict when barriers between grass communities will be crossed, and when established feedbacks will break down leading to changes in savanna function during droughts.

Prior to drought there were limited impacts of pyric-herbivory on the inter-seasonal grass height and productivity within the KNP study system (**Chapter 5**). However, this changed considerably at the onset of drought with a strong pattern of pyric-herbivory severely limiting regrowth in 2015 (**Chapter 5**), which continued into 2016 (**Chapter 4**). Thus, there was a clear shift in system function as grasses on larger burn scars could be kept short for a full season after burning due to lower grass productivity (**Chapter 4 and 5**). Moreover, the effect of pyric-herbivory that removed all available foliage on burnt bunch grasslands during the most intense period of drought (2016) resulted in a more severe reduction in the basal cover of tussocks on burnt patches compared to unburnt bunch grasslands (**Chapter 4**). This in turn appears to have negatively affected grass productivity on burnt bunch grasslands the following season when rainfall returned. In cases where rainfall takes longer to return than in the studied drought event, higher basal cover die-off on burnt patches would be expected (O'Connor, 1995). Although not observed in my study, a longer drought may shift large burnt areas towards states where productivity is kept low for several seasons after rainfall returns. Moreover, in savanna systems where the long-term rainfall trend is expected to decline, pyric-herbivory has the potential to suddenly shift large areas from fire-dominated grasslands to grazer dominated states as productivity declines (**Chapter 5**). Thus, rather than a gradual change in savanna dynamics that may be expected from a transition to a lower productivity scenario, my results imply that changes to savanna function may happen over short periods as grasses on larger burn scars are kept short by grazing mammals and repeat burning is limited. Both increasing drought frequency and intensity as well as a shift in rainfall patterns to fewer but larger rainfall events is predicted for much of southern Africa under current trends of increasing atmospheric CO_2. All of these predictions will negatively affect grass productivity (Briggs and Knapp, 1995; Fay *et al.*, 2003; Buis *et al.*, 2009). Land managers should be aware that a sudden transition from fire- to grazer-dominated savanna dynamics will likely occur at some threshold productivity, where pyric-herbivory by the standing grazer population manages to keep large fires short enough to exclude

repeat burning. In my case study of KNP this change was initiated at a 50% decrease in year on year rainfall (**Chapter 5**) at which point grazers were able to keep grass short for a full season on burn scars from landscape scale fires.

1.4 Management implications

Chapter 2 and 3 demonstrated that ecological theory on the feedbacks driving grass community structure and function could be practically implemented to shift the dominant consumer from fire to grazing and in doing so exclude fire locally. Importantly, this is the first study that I am aware of that actively sought to test whether large and small fires impact grazer-grass feedbacks in a divergent manner and broadened our understanding of how fire management policies can influence savanna ecosystem functions. It is clear from this work that fires of different sizes have very different impacts on grazer communities and fire management implemented for specific wildlife management goals should incorporate an understanding that large fires disperse grazers while small fires concentrate them and both can influence governing savanna dynamics. Across African savannas, fire represents a key tool for land managers looking to control bush encroachment (Roques, O'Connor and Watkinson, 2001), manage graze for livestock and reduce tick loads (Tainton, 1999; Butz, 2009), and to open landscapes and manipulate the movement of wild herds for tourism (Eriksen, 2007) – it is important in these situations that the feedbacks to grazing communities are considered, especially in areas where migratory herds and white-rhino are absent. In such situations the repeated ignition of large fires in the landscape will likely drive grass communities towards a state that favours repeat burning with negative repercussions for mesoherbivores. Once a fire dominated state has established my results indicate that it is difficult to reverse without direct management intervention.

2 | Conclusion

The main aim of this study was to investigate the processes involved in the establishment and break-down of grass-consumer feedbacks and understand how these dictate the balance of fire and grazer driven grass communities in an African savanna. Through **Chapter 2-5** I have added to existing theory on how grazers and fire interact to structure grass communities with feedbacks that spatially and temporally stabilize savanna landscapes (Figure 6.1). Clearly, fire and herbivory need to be considered in conjunction and understanding the state of a given grass community can only be done by assessing the governing grass-consumer relationship. Drought

represents a good example of this, changes in the short-term abiotic conditions within a savanna appear to have little impact on savanna function and structure unless it drives changes in the positive feedback loops that govern the distribution of grazer-driven and fire-driven grass communities within the landscape. Fires remain one of the only major management tools in large protected savannas and my thesis underlines the need to manage them by considering how fire influences grass-grazer dynamics and not simply use fire as a ubiquitous method for improving graze quality in the short-term.

BIBLIOGRAPHY

Allred, B. W., Fuhlendorf, S. D., Engle, D. M. and Elmore, R. D. (2011) Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*, 1, pp. 132–144.

Amin, R., Thomas, K., Emslie, R. H., Foose, T. J. and Van Strien, N. (2006) An overview of the conservation status of and threats to rhinoceros species in the wild. *International Zoo Yearbook*, 40, pp. 96–117.

Anderson, T. M., Ritchie, M. E., Mayemba, E., Eby, S. L., Grace, J. B. and Mc Naughton, S. J. (2007) Forage nutritive quality in the Serengeti ecosystem: the roles of fire and herbivory. *The American Naturalist*, 170, pp. 343–57.

Anderson, T. M., Hopcraft, J. G. C., Eby, S. L., Ritchie, M., Grace, J. B. and Olff, H. (2010) Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology*, 91, pp. 1519–29. Available at: http://www.ncbi.nlm.nih.gov/pubmed/20503883.

Anderson, T. M., Kumordzi, B. B., Fokkema, W., Fox, H. V. and Olff, H. (2013) Distinct Physiological Responses Underlie Defoliation Tolerance in African Lawn and Bunch Grasses. *International Journal of Plant Sciences*, 174, pp. 769–778.

Anderson, T. M., Dong, Y. and Mc Naughton, S. J. (2006) Nutrient acquisition and physiological responses of dominant Serengeti grasses to variation in soil texture. *Journal of Ecology*, 94, pp. 1164–1175.

Archibald, S., Bond, W. J., Stock, W. D. and Fairbanks, D. H. K. (2005) Shaping the landscape: Fire-grazer interactions in an african savanna. *Ecological Applications*, 15, pp. 96–109.

Archibald, S. (2008) African grazing lawns: How fire, rainfall, and grazer numbers interact to affect grass community states. *Journal of Wildlife Management*, 72, pp. 492–501.

Archibald, S., Roy, D. P., Van Wilgen, B. W. and Scholes, R. J. (2009) What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology*, 15, pp. 613–630.

Archibald, S., Lehmann, C. E. R., Gómez-dans, J. L. and Bradstock, R. a (2013) Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America*, 110, pp. 6442–6447.

Archibald, S. and Bond, W. J. (2003) Growing tall vs growing wide: tree architecture and allometry of Acacia karroo in forest, savanna, and arid environments. *Oikos*, 102, pp. 3–14.

Archibald, S. and Bond, W. J. (2004) Grazer movements: Spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, 13, pp. 377–385.

Archibald, S. and Hempson, G. P. (2016) Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, p. 20150309.

Archibald, S., Staver, C. A. and Levin, S. A. (2012) Evolution of human-driven fire regimes in Africa. *Proceedings of the National Academy of Sciences*, 109, pp. 847–852.

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

Augustine, D. J. and Derner, J. D. (2014) Controls over the strength and timing of fire-grazer interactions in a semi-arid rangeland. *Journal of Applied Ecology*, 51, pp. 242–250.

Augustine, D. J. and Mc Naughton, S. J. (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, 41, pp. 45–58.

Augustine, D. J. and Mc Naughton, S. J. (2007) Ungulate Effects on the Functional Species Composition of Plant Communities : Herbivore Selectivity and Plant Tolerance Invited Paper. *Journal of Wildlife Management*, 62, pp. 1165–1183.

Augustine, D. J. and Mcnaughton, S. J. (2006) Interactive effects of herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems*, 9, pp. 1242–1256.

Augustine, D. J., McNaughton, S. J. and Frank, D. A. (2003) Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications*, 13, pp. 1325–1337.

Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 325, pp. 883–885.

Ben-shahar, R. and Coe, M. J. (1992) The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. *Oecologia*, 90, pp. 422–428.

Benjamini, Y. and Hochberg, Y. (1995) Controlling the false discovery rate : a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society*, 57, pp. 289–300.

Biggs, H. C. and Potgieter, A. L. F. (1999) Overview of the fire management policy of the Kruger National Park. *Koedoe*, 42, pp. 101–110. Available at: http://www.koedoe.co.za/index.php/koedoe/article/view/227%5Cnpapers2://publication/doi/10.4102/koedoe.v42i1.227.

Biondini, M. E., Patton, B. D. and Nyren, P. E. (1998) Grazing intensity and ecosystem processes in northern-mixed grass prairie, USA. *Ecological Applications*, 8, pp. 469–479.

Blanchet, F. G., Legendre, P. and Borcard, D. (2008) Forward selection of spatial explanatory variables. *Ecology*, 89, pp. 2623–2632.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. and White, J.-S. S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, pp. 127–35.

Bond, W. J. (2005) Large parts of the world are brown or black: A different view on the ‘ Green World ’ hypothesis. *Journal of Vegetation Science*, 16, pp. 261–266.

Bond, W. J. and Keeley, J. E. (2005) Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, 20, pp. 387–94.

Bond, W. J., Woodward, F. I. and Midgley, G. F. (2005) The global distribution of ecosystems in a world without fire. *The New phytologist*, 165, pp. 525–37.

Bonnet, O., Fritz, H., Gignoux, J. and Meuret, M. (2010) Challenges of foraging on a high-quality but unpredictable food source: the dynamics of grass production and consumption in savanna grazing lawns. *Journal of Ecology*, 98, pp. 908–916.

Boone, R. B. (2007) Effects of fragmentation on cattle in African savannas under variable precipitation. *Landscape Ecology*, 22, pp. 1355–1369.

Briggs, J. M. and Knapp, A. K. (1995) Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic, and fire as determinants of aboveground biomass.

American Journal of Botany, 82, pp. 1064–1069.

Briske, D. D. (1995) Strategies of plant survival in grazed systems: A functional interpretation. in Hodgson, J. G. and Illius, A. W. (eds) *The Ecology and Management of Grazing Systems*. CAB International, pp. 37–67.

Briske, D. D., Fuhlendorf, S. D. and Smeins, F. E. (2005) State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management*, 58, pp. 1–10.

Bucini, G. and Hanan, N. P. (2007) A continental-scale analysis of tree cover in African savannas. *Global Ecology and Biogeography*, 16, pp. 593–605.

Buis, G. M., Blair, J. M., Burkepile, D. E., Burns, C. E., Chamberlain, A. J., Chapman, P. L., Collins, S. L., Fynn, R. W. S., Govender, N., Kirkman, K. P., Smith, M. D. and Knapp, A. K. (2009) Controls of aboveground net primary production in mesic savanna grasslands: An inter-hemispheric comparison. *Ecosystems*, 12, pp. 982–995.

Burkepile, D. E., Burns, C. E., Tambling, C. J., Amendola, E., Buis, G. M., Govender, N., Nelson, V., Thompson, D. I., Zinn, A. D. and Smith, M. D. (2013) Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. *Ecosphere*, 4, pp. 1–19.

Burkepile, D. E., Thompson, D. I., Fynn, R. W. S., Koerner, S. E., Eby, S. L., Govender, N., Hagenah, N., Lemoine, N. P., Matchett, K. J., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K. and Smith, M. D. (2016) Fire frequency drives habitat selection by a diverse herbivore guild impacting top–down control of plant communities in an African savanna. *Oikos*, 125, pp. 1636–1646.

Butz, R. J. (2009) Traditional fire management: historical fire regimes and land use change in pastoral East Africa. *International Journal of Wildland Fire*, 18, pp. 442–450.

Chase, J. M., Leibold, M. A., Downing, A. L. and Shurin, J. B. (2000) The effect of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, 81, pp. 2485–2497.

Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., de Ruiter, D., Sealy, J., Grant, R. and Fourie, N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, 273, pp. 21–29.

Collier, P., Conway, G. and Venables, T. (2008) Climate Change and Africa. *Oxford Review of Econimic Policy*, 24, pp. 337–353.

Collins, S. L. and Wallace, L. L. (1990) *Fire in North American Tallgrass Prairies*. Edited by S. L. Collins and L. L. Wallace. London: University of Oklahoma Press.

Congalton, R. G. (2001) Accuracy assessment and validation of remotely sensed and other spatial information. *International Journal of Wildland Fire*, 10, pp. 321–328.

Core Team, R. (2016) R: A Language and Environment for Statistical Computing. Vienna, Austria. Available at: https://www.r-project.org/.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Steege, H., Morgan, H. D., Van Der Heijden, M. G. A., Pausas, J. G. and Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, pp. 335–380.

Crawley, M. J. (2012) *The R Book*. Edited by M. J. Crawley. West Sussex: John Wiley and Sons.

Cromsigt, J. P. G. M., Rensburg, S. J., Etienne, R. S. and Olff, H. (2009) Monitoring large herbivore diversity at different scales: comparing direct and indirect methods. *Biodiversity and Conservation*, 18, pp. 1219–1231.

Cromsigt, J. P. G. M. and te Beest, M. (2014) Restoration of a megaherbivore: Landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. *Journal of Ecology*, 102, pp. 566–575.

Cromsigt, J. P. G. M. and Olff, H. (2008) Dynamics of grazing lawn formation: An experimental test of the role of scale-dependent processes. *Oikos*, 117, pp. 1444–1452.

Dai, A. (2013) Increasing drought under global warming in observations and models. *Nature Climate Change*. Nature Publishing Group, 3, pp. 52–58.

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

Davis, A. L. V. (1996) Seasonal dung beetle activity and dung dispersal in selected South African habitats: implications for pasture improvement in Australia. *Agriculture, Ecosystems &*

Environment, 58, pp. 157–169.

Davis, A. L. V., Scholtz, C. H., Kryger, U., Deschodt, C. M. and Strümpher, W. P. (2010) Dung Beetle Assemblage Structure in Tswalu Kalahari Reserve: Responses to a Mosaic of Landscape Types, Vegetation Communities, and Dung Types. *Environmental Entomology*, 39, pp. 811–820.

Díaz, S., Lavorel, S., Mc Intyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. and Campbell, B. D. (2007) Plant trait responses to grazing - a global synthesis. *Global Change Biology*, 13, pp. 313–341.

Dolédec, S., Chessel, D., ter Braak, C. J. F. and Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics*, 3, pp. 143–166.

Donaldson, J. E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z. and Parr, C. L. (2017) Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*, pp. 1–11.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S. and ter Braak, C. J. F. (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, 95, pp. 14–21.

Dray, S. and Legendre, P. (2008) Testing the species traits-environment relationships : the fourth-corner problem revisited. *Ecology*, 89, pp. 3400–3412.

Dublin, H. T., Sinclair, A. R. E. and McGlade, J. (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology*, 59, pp. 1147–1164. Available at: http://www.jstor.org/stable/5037.

East, R. (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, 22, pp. 245–270.

Eby, S. L., Burkepile, D. E., Fynn, R. W. S., Burns, C. E., Govender, N., Hagenah, N., Koerner, S. E., Matchett, K. J., Thompson, D. I., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K. and Smith, M. D. (2014) Loss of a large grazer impacts savanna grassland plant communities similarly in North America and South Africa. *Oecologia*, 175, pp. 293–303.

Ekblom, A., Gillson, L., Risberg, J., Holmgren, K. and Chidoub, Z. (2012) Rainfall variability and vegetation dynamics of the lower Limpopo Valley, Southern Africa, 500 AD to present. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 363.

Ellis, J. E. and Swift, D. M. (1988) Stability of African pastoral ecosystems : Alternate paradigms and implications for development AND. *Journal Of Range Management*, 41, pp. 450–459.

Eriksen, C. (2007) Why do they burn the 'bush'? Fire, rural livelihoods, and conservation in Zambia. *The Geographical Journal*, 173, pp. 242–256.

Estes, R. D., Atwood, J. L. and Estes, A. B. (2006) Downward trends in Ngorongoro Crater ungulate populations 1986-2005: Conservation concerns and the need for ecological research. *Biological Conservation*, 131, pp. 106–120.

Farr, T., Rosen, P., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D. and Alsdorf, D. (2007) The shuttle radar topography mission. *Reviews of Geophysics*, 45, pp. 1–33.

Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M. and Collins, S. L. (2003) Productivity responses to altered rainfall patterns in a C4 -dominated grassland. *Oecologia*, 137, pp. 245–251.

Fensham, R. J., Holman, J. E. and Cox, M. J. (1999) Plant species responses along a grazing disturbance gradient in Australian grassland. *Journal of Vegetation Science*, 10, pp. 77–86.

Fortin, D., Boyce, M. S., Merrill, E. H. and Fryxell, J. M. (2004) Foraging costs of vigilance in large mammalian herbivores. *Oikos*, 107, pp. 172–180.

Fowler, C. and Konopik, E. (2007) The history of fire in the southern United States. *Human Ecology Review*, 14, pp. 165–176.

Fuhlendorf, S. D., Engle, D. M., Kerby, J. and Hamilton, R. (2009) Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, 23, pp. 588–598.

Fuhlendorf, S. D. and Engle, D. M. (2001) Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns. *BioScience*, 51, p. 625.

Fynn, R. W. S. (2012) Functional resource heterogeneity increases livestock and rangeland productivity. *Rangeland Ecology and Management*, 65, pp. 319–329.

Gadd, M. E. (2012) Barriers , the Beef Industry and Unnatural Selection : A Review of the Impact of Veterinary Fencing on Mammals in Southern ... Barriers , the Beef Industry and Unnatural Selection : A Review of the Impact of Veterinary Fencing on Mammals in Southern Afric. in Sommers, M. J. and Hayward, M. W. (eds) *Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes?* New York: Springer, pp. 153–186.

Georgiadis, N., Hack, M. and Turpin, K. (2003) The influence of rainfall on zebra population dynamics : implications for management. *Journal of Applied Ecology*, 40, pp. 125–136.

Gertenbach, W. P. D. (1983) Landscapes of the Kruger National Park. *Koedoe*, 26, pp. 9–121.

Gizaw, M. S. and Gan, T. Y. (2017) Impact of climate change and El Niño episodes on droughts in sub‐Saharan Africa. *Climate Dynamics*. Springer Berlin Heidelberg, 49, pp. 665–682.

Gordan, I. J. and Illius, A. W. (1996) The nutritional ecology of ruminants: a reinterpretation.pdf. *Journal of Animal Ecology*, 65, pp. 18–28.

Govender, N., Trollope, W. S. W. and Van Wilgen, B. W. (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, pp. 748–758.

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

Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P. G. M. and Berger, J. (2009) Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, 7, pp. 55–76.

Hawkins, H.-J., Short, A. and Kirkman, K. P. (2017) Does Holistic Planned Grazing™ work on native rangelands? *African Journal of Range and Forage Science*, 34, pp. 59–63.

Hema, E. M., Di Vittorio, M., Barnes, R. F., Guenda, W. and Luiselli, L. (2017) Detection of interannual population trends in seven herbivores from West African savannah: a comparison between dung counts and direct counts of individuals. *African Journal of Ecology*, 55, pp. 609–617.

Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., Kruger, L. M., Moxley, C., Owen-Smith, N., Peel, M. J. S., Smit, I. P. J. and Vickers, K. J. (2015) Ecology of grazing lawns in Africa. *Biological Reviews*, 90, pp. 979–994.

Hempson, G. P., Archibald, S. and Bond, W. J. (2015) A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science*, 350, pp. 1056–61.

Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S. and Kempen, B. (2017) SoilGrids250m: Global gridded soil information based on machine learning. *Plos One*, 12, p. e0169748.

Hill, A. M. O. and Smith, A. J. E. (1976) Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon*, 25, pp. 249–255. Available at: http://www.jstor.org/stable/1219449.

Hobbs, N. T., Schimel, D. S., Owensby, C. E. and Ojima, D. S. (1991) Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology*, 72, pp. 1374–1382.

Hoffmann, W. A., Adasme, R., Haridasan, M., De Carvalho, M. T., Geiger, E. L., Pereira, M. A. B., Gotsch, S. G. and Franco, A. C. (2009) Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology*, 90, pp. 1326–1337.

Holdo, R. M., Sinclair, A. R. E., Dobson, A. P., Metzger, K. L., Benjamin, M., Ritchie, M. E. and Holt, R. D. (2009) A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biology*, 7, p. e1000210.

Holdo, R. M., Holt, R. D. and Fryxell, J. M. (2009) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, 173, pp. 431–445.

Homewood, K. and Lewis, J. (1987) Impact of drought on pastoral livestock in Baringo , Kenya. *Journal of Applied Ecology*, 24, pp. 615–631.

Hutchinson, M. F. (1998) Interpolation of Rainfall Data with Thin Plate Smoothing Splines -Part II: Analysis of Topographic Dependence. *Journal of Geographic Information and Decision Analysis*, 2, pp. 152–167.

Illius, A. W. and O'Connor, T. G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos*, 89, pp. 283–294.

Jones, A. (2000) Effects of cattle grazing on North American arid ecosystems: a quantitative review. *Western North American Naturalist*, 60, pp. 155–164.

Kleynhans, E. J., Jolles, A. E., Bos, M. R. E. and Olff, H. (2010) Resource partitioning along multiple niche dimensions in differently sized African grazers. *Oikos*, 120, pp. 591–600.

Klop, E. and van Goethem, J. (2008) Savanna fires govern community structure of ungulates in Bénoué National Park, Cameroon. *Journal of Tropical Ecology*, 24, pp. 39–47.

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

Knapp, A. K., Conrad, S. L. and Blair, J. M. (1998) Determinants of soil CO2 flux from a sub-humid grassland: Effect of fire and fire history. *Ecological Applications*, 8, pp. 760–770.

Knapp, A. K. and Smith, M. D. (2001) Variation among biomes in temproal dynamics of aboveground primary productivity. *Science*, 291, pp. 481–484.

Koerner, S. E., Burkepile, D. E., Fynn, R. W. S., Burns, C. E., Eby, S. L., Govender, N., Hagenah, N., Matchett, K. J., Thompson, D. I., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K. and Smith, M. D. (2014) Plant community response to loss of large herbivores differs between North American and South African savanna grasslands R eports. *Ecology*, 95, pp. 808–816.

Koerner, S. E. and Collins, S. L. (2014) Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, 95, pp. 98–109.

Krook, K., Bond, W. J. and Hockey, P. A. R. (2007) The effect of grassland shifts on the avifauna of a South African savanna The effect of grassland shifts on the avifauna of a South African savanna. *Ostrich*, 78, pp. 271–279.

Legendre, P. and Gallagher, E. D. (2001) Ecologically meaningful transformations for ordination

of species data. *Oecologia*, 129, pp. 271–280.

Legendre, P. and Legendre, L. F. J. (2012) *Numerical Ecology*. 3rd edn. Amsterdam: Elsevier Ltd.

Lock, J. M. (1972) The effects of Hippopotamus grazing on grasslands. *Journal of Ecology*, 60, pp. 445–467.

Macandza, V. A., Owen-Smith, N. and Cross, P. C. (2004) Forage selection by African buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research*, 34, pp. 113–121.

Marques, F. F. C., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A. and Peace, A. J. (2001) Estimating deer abundance from line transect surveys of dung: Sika deer in southern Scotland. *Journal of Applied Ecology*, 38, pp. 349–363.

Mazancourt, C. de and Loreau, M. (2000) Effect of herbivory and plant species replacement on primary production. *The American Naturalist*, 155, pp. 735–754.

Mc Naughton, S. J. (1976) Serengeti migratory wildebeest: Facilitation of energy flow by grazing. *Science*, 191, pp. 92–94.

Mc Naughton, S. J. (1979) Grazing as an optimization process : Grass-ungulate relationships in the Serengeti. *The American Naturalist*, 113, pp. 691–703.

Mc Naughton, S. J. (1984) Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist*, 124, pp. 863–886. Available at: http://www.jstor.org/stable/2461305 .

Mc Naughton, S. J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, 55, pp. 259–294. Available at: http://www.jstor.org/stable/1942578 .

Mc Naughton, S. J. (1988) Mineral nutrition and spatial concentrations of African ungulates. *Nature*, 334, pp. 343–345.

Mc Naughton, S. J., Banyikwa, F. F. and Mc Naughton, M. M. (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science*, 278, pp. 1798–1800.

Mc Naughton, S. J., Milchunas, D. G. and Frank, D. A. (1996) How can net primary productivity be measured in grazing ecosystems? *Ecology*, 77, pp. 974–977.

Mc Pherson, G. R. (1997) *Ecology and Management of North American Savannas*. Edited by G. R. Mc Pherson. Tuscon: University of Arizona Press.

McGranahan, D. A., Hovick, T. J., Elmore, R. D., Engle, D. M., Fuhlendorf, S. D., Winter, S. L., Miller, J. R. and Debinski, D. M. (2016) Temporal variability in aboveground plant biomass decreases as spatial variability increases. *Ecology*, 97, pp. 555–560.

McIver, D. K. and Friedl, M. A. (2002) Using prior probabilities in decision-tree classification of remotely sensed data. *Remote Sensing of Environment*, 81, pp. 253–261.

Milchunas, D. G., Sala, O. E. and Lauenroth, W. K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist*, 1, pp. 87–106.

Mucina, L. and Rutherford, M. C. (2006) *The vegetation of South Africa, Lesotho and Swaziland*. Edited by L. Mucina and M. C. Rutherford. Pretoria: South African National Biodiversity Institute.

O'Connor, T. G. (1994) Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology*, 31, pp. 155–171.

O'Connor, T. G. (1995) Transformation of a savanna grassland by drought and grazing. *African Journal of Forage Science*, 12, pp. 53–60.

Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N. and Reid, R. S. (2008) Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *Journal of Animal Ecology*, 77, pp. 814–829.

Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N. and Reid, R. S. (2009) Dynamics of Mara-Serengeti ungulates in relation to land use change. *Journal of Zoology*, 278, pp. 1–14.

Ogutu, J. O., Owen-Smith, N., Piepho, H. P. and Said, M. Y. (2011) Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977-2009. *Journal of Zoology*, 285, pp. 99–109.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B. and Wagner, H. (2016) vegan: Community Ecology Package Software.

Oliva, G., Cibils, A., Borrelli, P. and Humano, G. (1998a) Stable states in relation to grazing in

Patagonia: a 10-year experimental trial. *Journal of Arid Environments*, 40, pp. 113–131.

Oliva, G., Cibils, A., Borrelli, P. and Humano, G. (1998b) Stable states in relation to grazing in Patagonia: a 10-year experimental trial. *Journal of Arid Environments*, 40, pp. 113–131.

Ottichilo, W. K., De Leeuw, J., Skidmore, A. K., Prins, H. H. T. and Said, M. Y. (2000) Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. *African Journal of Ecology*, 38, pp. 202–216.

van Oudtshoorn, F. (1999) *Guide to Grasses of South Africa*. Edited by F. van Oudtshoorn. Pretoria: Briza Publications.

Owen-Smith, N. (1987) Pleistocene extinctions : The pivotal role of megaherbivores. *Paleobiology*, 13, pp. 351–362. Available at: http://www.jstor.org/stable/2400736.

Owen-Smith, N. (1989) Megafaunal extinctions: The conservation message from 11 000 years B.P. *Conservation Biology*, 3, pp. 405–412. Available at: http://www.jstor.org/stable/2386221.

Owen-Smith, N. (2004) Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology*, 19, pp. 761–771.

Owen-Smith, N., Mason, D. R. and Ogutu, J. O. (2005) Correlates of survival rates for 10 African ungulate populations: Density, rainfall and predation. *Journal of Animal Ecology*, 74, pp. 774–788.

Owen-Smith, N. and Mills, M. G. L. (2008) Predator – prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, 77, pp. 173–183.

Owen-Smith, N. and Novellie, P. (1982) What should a clever ungulate eat? *The American Naturalist*, 119, pp. 151–178.

Owen-Smith, N. and Ogutu, J. O. (2013) Controls over reproductive phenology among ungulates : allometry and tropical-temperate contrasts. *Ecography*, 36, pp. 256–263.

Owen-Smith, N. and Traill, L. W. (2017) Space use patterns of a large mammalian herbivore distinguished by activity state: fear versus food? *Journal of Zoology*, 303, pp. 281–290.

Parr, C. L., Robertson, H., Biggs, H. C. and Chown, S. L. (2004) Response of African savanna ants to long term fire regimes. *Journal of Applied Ecology*, 41, pp. 630–642. Available at: http://onlinelibrary.wiley.com/doi/10.1111/j.0021-8901.2004.00920.x/full.

Peterson, D. W. and Reich, P. B. (2001) Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications*, 11, pp. 914–927.

van der Plas, F., Zeinstra, P., Veldhuis, M., Fokkema, R., Howison, R. and Olff, H. (2013) Responses of savanna lawn and bunch grasses to water limitation. *Plant E*, 214, pp. 1157–1168.

Polis, G. A. (2007) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Polis*, 86, pp. 3–15.

Prendini, L., Theron, L., Merwe, K. Van Der and Owen-smith, N. (1996) Abundance and guild structure of grasshoppers (Orthoptera : Acridoidea) in communally grazed and protected savanna. *South African Journal of Zoology*, 31, pp. 120–130.

Prins, H. H. T. and van der Jeugd, H. (1993) Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology*, 81, pp. 305–314. Available at: http://www.jstor.org/stable/2261500.

Ratnam, J. V., Behera, S. K., Masumoto, Y. and Yamagata, T. (2014) Remote effects of El Nino and Modoki events on the austral summer precipitation of southern Africa. *American Meteorological Society*, 27, pp. 3802–3816.

Ribeiro, P. J. and Diggle, P. J. (2016) Package ‘geoR’.

Richard, Y., Fauchereau, N., Poccard, I., Rouault, M. and Trzaska, S. (2001) 20th century droughts in southern Africa: Spatial and temporal variability, teleconnections with oceanic and atmospheric conditions. *International Journal of Climatology*, 21, pp. 873–885.

Riginos, C. (2015) Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84, pp. 124–133.

Ripley, B., Visser, V., Pascal-Antoine, C., Archibald, S., Martin, T. and Osborne, C. P. (2015) Fire ecology of C 3 and C 4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type Fire ecology of C 3 and C 4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology*, 96, pp. 2679–2691.

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terbough, J. and Van Valkenburgh, B. (2015) Collapse of the world’s largest herbivores.

Science Advances, 1, pp. 1–12.

Roques, K. G., O'Connor, T. G. and Watkinson, A. R. (2001) Dynamics of Shrub Encroachment in an African Savanna : Relative Influences of Fire , Herbivory , Rainfall and Density Dependence Author (s): K . G . Roques , T . G . O ' Connor , A . R . Watkinson Published by : British Ecological Society Stable URL : h. *Journal of Applied Ecology*, 38, pp. 268–280.

Sala, O. E., Parton, W. J., Joyce, L. A. and Lauenroth, W. K. (1988) Primary production of the central grassland region of the United States. *Ecology*, 69, pp. 40–45.

Samways, M. J. and Kreuzinger, K. (2001) Vegetation , ungulate and grasshopper interactions inside vs . outside an African savanna game park. *Biodiversity and Conservation*, 10, pp. 1963–1981.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J. V., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Roux, X. Le, Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J., *et al.* (2005) Determinants of woody cover in African savannas. *Nature*, 438, pp. 8–11.

Saura-Mas, S. and Lloret, F. (2007) Leaf and shoot water content and leaf dry matter content of Mediterranean woody species with different post-fire regenerative strategies. *Annals o*, 99, pp. 545–554.

Sensenig, R. L., Demment, M. W. and Laca, E. A. (2010) Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology*, 91, pp. 2898–2907.

Serneels, S. and Lambin, E. F. (2001) Impact of land-use changes on the wildebeest migration in the northern part of the Serengeti-Mara ecosystem. *Journal of Biogeography*, 28, pp. 391–407.

Shackleton, S. E., Shackleton, C. M., Netshiluvhi, T. R., Geach, B. S., Ballance, A. and Fairbanks, D. H. K. (2002) Use Patterns and Value of Savanna Resources in Three Rural Villages in South Africa. *Economic Botany*, 56, pp. 130–146.

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

Smit, I. P. J. (2011) Resources driving landscape-scale distribution patterns of grazers in an

African savanna. *Ecography*, 34, pp. 67–74.

Smit, I. P. J., Govender, N., Linder, H. P. and MacFadyen, S. (2013) Rainfall, geology and landscape position generate large-scale spatiotemporal fire pattern heterogeneity in an African savanna. *Ecography*, 36, pp. 447–459.

Smith, E. P. (2002) BACI design. in El-Shaarwi, A. H. and Piegorsch, W. W. (eds) *Encyclopedia if Environmetrics*. Chichester, UK: John Wiley and Sons, pp. 141–148.

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

Stige, L. C., Stave, J., Chan, K., Ciannelli, L., Pettorelli, N., Glantz, M., Herren, H. R. and Stenseth, N. C. (2006) The effect of climate variation on agro-pastoral production in Africa. *Proceedings of the National Academy of Sciences of the United States of America*, 103, pp. 3049–3053.

Tainton, N. M. (1972) The relative contribution of overstocking and selective grazing to the degeneration of tall grassveld in natal. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 7, pp. 39–43.

Tainton, N. M. (1999) *Veld Management in South Africa*. Pietermaritzberg: Natal University Press.

Therneau, T. and Atkinson, B. (2018) rpart: Recursive partitioning and regression trees. Available at: https://cran.r-project.org/package=rpart.

Thonicke, K., Venevsky, S., Sitch, S. and Cramer, W. (2001) The role of fire disturbance for global vegetation dynamics: Coupling fire into a dynamic global vegetation model. *Global Ecology and Biogeography*, 10, pp. 661–677.

Thornes, J. B. (1985) The ecology of erosion. *Geography*, 70, pp. 222–235.

du Toit, J. T. (2003) Large herbivores and savanna heterogeneity. in du Toit, J. T., Rogers, K. H., and Biggs, H. C. (eds) *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. 1st edn. Washington: Island Press, pp. 292–309.

Tomor, B. M. and Owen-Smith, N. (2002) Comparative use of grass regrowth following burns

by four ungulate species in the Nylsvley Nature Reserve, South Africa. *African Journal of Ecology*, 40, pp. 201–204.

Traill, L. W. (2004) Seasonal utilization of habitat by large grazing herbivores in semi-arid Zimbabwe. *South African Journal of Wildlife Research*, 34, pp. 13–24.

Trenberth, K. E., Dai, A., Van Der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R. and Sheffield, J. (2014) Global warming and changes in drought. *Nature Climate Change*, 4, pp. 17–22.

Trollope, W. S. W. (1982) Ecological effects of fire in South African savannas. in Huntley, B. J. and Walker, B. H. (eds) *Ecology of Tropical Savannas*. Berlin: Springer, pp. 292–306.

Trollope, W. S. W. (1995) *Report on the fire ecology of the Ngorgoro Conservation Area in Tanzania with particular reference to the Ngorogoro Crater*. *Report to NCAA Conservator*.

Trollope, W. S. W., Potgieter, A. L. F. and Zambatis, N. (1989) Assessing veld condition in the KNP using key grass speciespdf. *Koedoe*, 32, pp. 67–93.

Turner, M. G., Gardner, R. H. and O'Neill, R. V. (2001) *Landscape ecology in theory and practice*. New York: Springer.

Veldhuis, M. P., Howison, R. A., Fokkema, R. W., Tielens, E. and Olff, H. (2014) A novel mechanism for grazing lawn formation: large herbivore-induced modi fi cation of the plant – soil water balance. *Journal of Ecology*, 102, pp. 1506–1517.

Venter, F. J., Scholes, R. J. and Eckhardt, H. C. (2003) The abiotic template and its associated vegetation pattern. in Du Toit, J. T., Rogers, K. H., and Biggs, H. C. (eds) *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Washington: Island Press, pp. 83–129.

Venter, Z. S., Hawkins, H.-J. and Cramer, M. D. (2017) Implications of historical interactions between herbivory and fi re for rangeland management in African savannas. *Ecosphere*, 8.

Verweij, R. J. T., Verrelst, J., Loth, P. E., Heitko, I. M. A. and Brunsting, A. M. H. (2006) Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. *Oikos*, 114, pp. 108–116.

Vetter, S. (2013) Development and sustainable management of rangeland commons – aligning

policy with the realities of South Africa's rural landscape. *African Journal of Range & Forage Science*, 30, pp. 1–9.

Van de Vijver, C. A. D. M., Poot, P. and Prins, H. H. T. (1999) Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plant and Soil*, 214, pp. 173–185.

Van der Wal, R., Egas, M., Van der Veen, A. and Bakker, J. (2000) Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology*, 88, pp. 317–330.

Waldram, M. S., Bond, W. J. and Stock, W. D. (2008) Ecological Engineering by a Mega-Grazer : White Rhino Impacts on a South African Savanna. *Ecosystems*, 11, pp. 101–112.

Walker, B. H., Emslie, R. H., Owen-Smith, N. and Scholes, R. J. (1987) To cull or not to cull: Lessons from a Southern African drought. *The Journal of Applied Ecology*, 24, pp. 381–401.

Wang, S. and Loreau, M. (2014) Ecosystem stability in space: a, b and y variability. *Ecology Letters*, 17, pp. 891–901.

Warui, C. M., Villet, M. H., Young, T. P. and Jocque, R. (2005) Influence of grazing by large mammals on the spider community of a Kenyan savanna biome. *The Journal of Arachnology*, 33, pp. 269–279.

Westoby, M., Walker, B. and Noy-Meir, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal Of Range Management*, 42, pp. 266–274.

Whyte, I. J. and Joubert, S. C. J. (1988) Blue wildebeest population trends in the Kruger National Park and the effects of fencing. *South African Journal of Wildlife Research*, 18, pp. 78–87.

Van Wilgen, B. W., Biggs, H. C., O'Regan, S. P. and Mare, N. (2000) A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Sciences*, 96, pp. 167–178.

Van Wilgen, B. W. and Govender, N. (2004) Response of savanna fire regimes to changing fire-management policies in a large African national park. *Conservation Biology*, 18, pp. 1533–1540.

Van Wilgen, B. W., Govender, N. and Macfadyen, S. (2008) An assessment of the implementation and outcomes of recent changes to fire management in the Kruger National Park.

Koedoe, 50, pp. 22–31.

Williams, R. J., Cook, G. D., Gill, A. M. and Moore, P. H. R. (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology Ecology*, 24, pp. 50–59.

Williamson, D. T. and Mbano, B. (1988) Wildebeest mortality during 1983 at Lake Xau, Botswana. *African Journal of Ecology*, 26, pp. 341–344.

Yahdjian, L. and Sala, O. E. (2006) Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology*, 87, pp. 952–962.

Yoganand, K. and Owen-Smith, N. (2014) Restricted habitat use by an African savanna herbivore through the seasonal cycle: Key resources concept expanded. *Ecography*, 37, pp. 969–982.

Zambatis, N., Zacharias, P., Morris, C. and Derry, J. (2006) Re-evaluation of the disc pasture meter calibration for the Kruger National Park, South Africa. *African Journal of Range & Forage Science*, 23, pp. 85–97.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. and Smith, G. M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. *Springer*. New York.

Appendix A

An overview of fire management in Kruger National Park

Kruger National Park management in South Africa has actively managed fire for at least the past 90 years (Van Wilgen and Govender, 2004). Over that period several different fire management policies were attempted to achieve management goals. Initially (1926 – 1947) fire management was largely informal with fires used mainly to promote fresh grass growth for grazing. During the next phase (1948 – 1956) managers attempted to limit the frequency of fires within the same area and applied prescribed burns at regular intervals (Van Wilgen *et al.*, 2000). Importantly, this management practice led to the setup of large 'burn blocks' ~ 4000 ha in size that was separated by a network of fire breaks (Van Wilgen *et al.*, 2000; Govender, Trollope and Van Wilgen, 2006). Although fire management practices within KNP have shifted these burn blocks remain a key feature of fire management within the landscape and were used to limit the impact of fire on the experiment described in **Chapter 2** and **3** (Van Wilgen and Govender, 2004).

A major change in KNP fire management policy occurred from 1981 to 1991 when burning was carried out based on rainfall, fuel loads and time since last fire (Govender, Trollope and Van Wilgen, 2006). Season of fire ignition was altered to develop variation in burn intensity, but the area burnt across the park was largely determined by mean annual rainfall. Again this policy was changed in 1991 and only fires ignited by lightning strikes were allowed to burn until 2001. Fires ignited by lighting were allowed to burn freely and aided in crossing firebreaks while those resulting from human ignitions were extinguished when possible. While the annual area burned within KNP during this period did not change, this policy resulted in larger, more intense fires burning during the late dry-season (Govender, Trollope and Van Wilgen, 2006).

The fire policy within KNP since 2002 has returned to igniting fires in areas where fuel loads and management goals dictate the fires should be applied with an upper limit of annual area burned defined by rainfall during the past two wet seasons (Van Wilgen and Govender, 2004; Govender, Trollope and Van Wilgen, 2006). Lightning fires are allowed to burn while unplanned fires are extinguished in areas where fire does not form part of the management plan (Van Wilgen, Govender and Macfadyen, 2008). This plan has been adopted in an attempt to create landscape level heterogeneity across the KNP as different fire practices result in variable tree/grass

densities with variation in ecosystem functioning expected to follow (Van Wilgen, Govender and Macfadyen, 2008).

Fires within the Satara land system 2012 - 2017

The experiment described in detail in Chapters 2 and 3 was setup in the Satara land system after consultation with fire management in the KNP. During this period it was decided that the experiment should be setup within a single burn block with the four neighboring burn blocks used to buffer it from fires during the course of this study (Figure S2.1). Considering each burn block is ~ 4000 ha and that these areas span two separate land management units, keeping fire out of this area for several years during the experiment was a considerable request. Any further buffer was therefore unrealistic and would have substantially impacted fire management policies within the Satara and N'wanetsi management units.

Fires were kept out of the experimental burn block and all adjacent buffer burn blocks in 2012, 2013 and 2014 (Figure S2.1). Despite this, two large fires burnt in 2014 within two-burn blocks of the experimental burn block (Figure S2.1). Thus, freshly burned areas were present 2.5 km to the north-west of the most northerly positioned experimental plots and 5 km to the south of the most southerly positioned plots during the 2015 rainfall season (Figure S2.1). These distances are traversable by the key mammalian herbivore species focused on during this study and thus the potential impact of these fires in reducing grazer populations in the area of our experiment cannot be discounted. However, there were little observable differences in dung counts between 2013 and 2014 and animals only appeared to migrate out of the study system in late 2016 when food resources were severely limited.

The low rainfall during the 2015/2016 rainfall season resulted in high fire risk across the KNP and several lightning fire ignitions during late October 2015 burnt fires within the experimental burn block and two of the adjacent buffer burn blocks. These fires burnt two of the no-burn 5 ha plots and two of the 0.25 ha plots effectively halving the sample size of this treatment. While none of the burn treatment plots had enough fuel to carry the fire, exactly half of all burn-treatments were positioned within the fire scar and impacted by the proximity to alternative fresh regrowth. It is worth noting that these fire scars were extremely limited in their green-up after burning due to the very low rainfall through the season. No further fires burned in the study system during the remainder of the experiment.

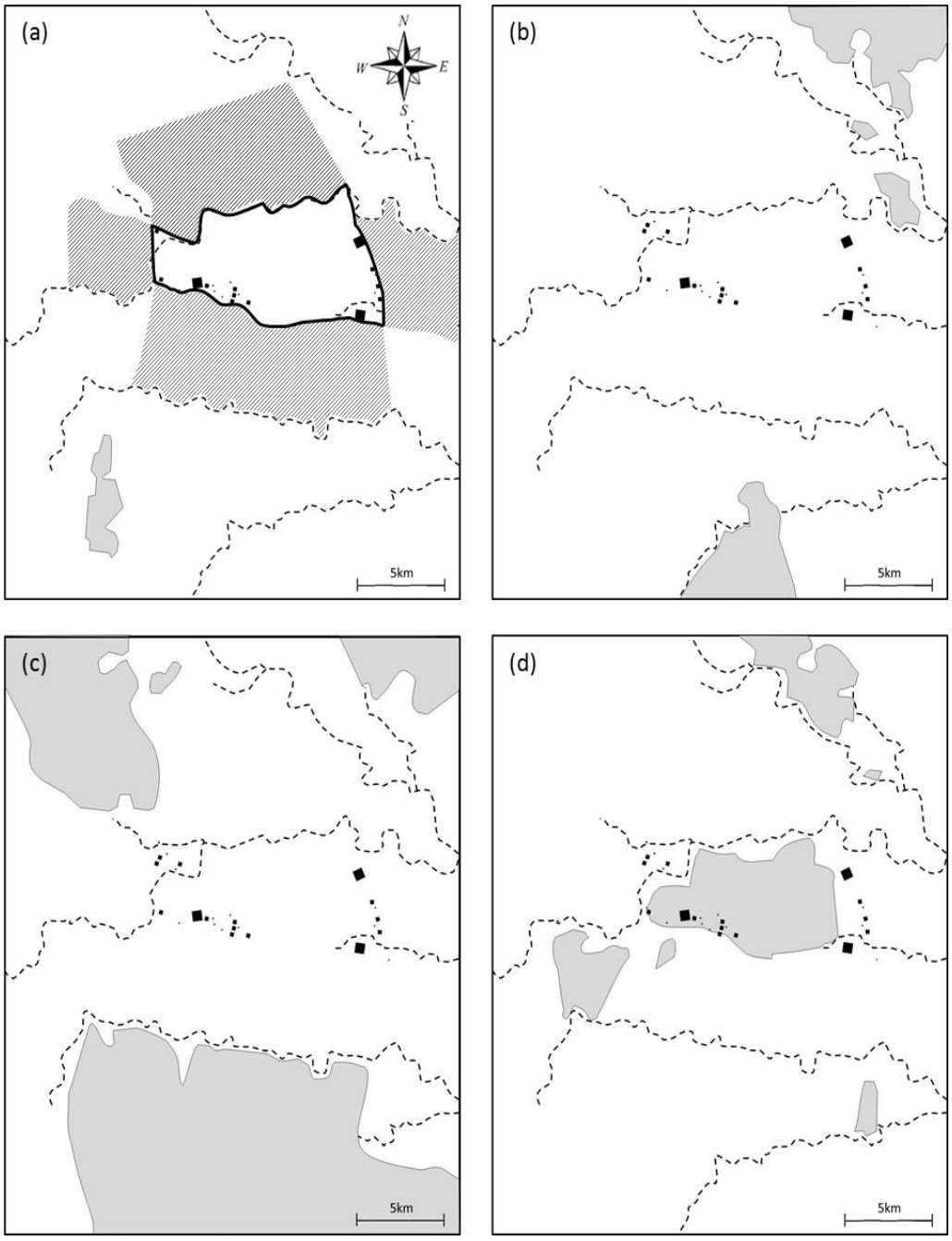


Figure S2.1. Fires burnt in the Satara land system in Kruger National Park during 2012 (a), 2013 (b), 2014 (c) and 2015 (d). Black squares represent plots used for data collection in the fire experiment described in **Chapter 2, 3** and **4**. Attempts were made to limit all non-experimental fires (light grey) from the experimental burn block (black outline) and adjacent buffer burn blocks (hatched). This was successful until a lightning fire burnt through the main experimental burn block in October 2015. No non-experimental fires burnt during 2016 and thus no map is presented here. Data provided by South African National Parks.

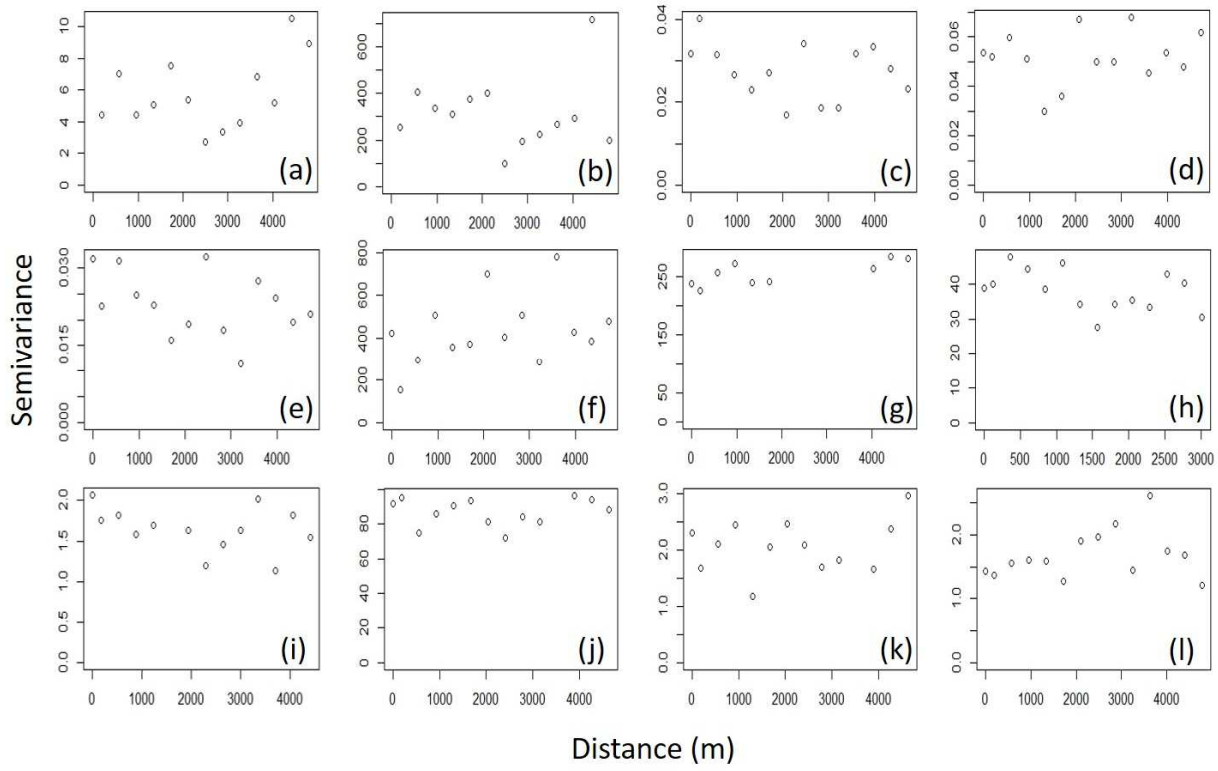


Figure S2.2. Semivariograms indicating no spatial autocorrelation is inherent in raw dung (a) and grass height data (b) or the residuals of selected models. Residual semivariograms labelled by the response variable: wildebeest dung (c); impala dung (d); zebra dung (e); buffalo dung (f); grass height on unburned plots (g); all dung on early-burns for the year 2013 (h); grass height on early-burns (i); all dung on late-burns for the year 2013 (j); grass height in late-burns (k); grass height on all plots for the year 2015 (l).

Table S2.1. Extant grazers of African savannas as defined by Hempson, Archibald & Bond (2015)

Latin name	Common name	Short grass (<5 cm) specialist	Evidence of active short grass selection	Reference
Aepyceros melampus	Impala	No	Yes	Kleynhans et al. 2010
Alcelaphus buselaphus	Red hartebeest	No	No	
Antidorcus marsupialus	Springbok	No	No	
Ceratotherium simum	White rhinoceros	Yes	Yes	Kleynhans et al. 2010
Connochaetes gnou	Black wildebeest	Yes	Yes	Von Richter 1971
Connochaetes taurinus	Blue wildebeest	Yes	Yes	Kleynhans et al. 2010
Damaliscus lunatus	Tsessebe	No	No	
Damaliscus pygargus	Bontebok	Yes	Yes	Luyt 2005
Equus africanus	African wild ass	No	No	
Equus grevyi	Grevy's zebra	No	No	
Equus quagga	Common zebra	No	Yes	Burkepile et al. 2016
Equus zebra	Cape mountain zebra	No	No	
Eudorcas albonotata	Mongalla gazelle	No	No	
Eudorcas thomsonii	Thompson's gazelle	No	No	
Hippopotamus amphibius	Hippopotamus	Yes	Yes	Lock 1972
Hippotragus equinus	Roan	No	No	
Hippotragus niger	Sable	No	No	
Kobus ellipsiprymnus	Waterbuck	No	No	
Kobus kob	Kob	No	No	
Kobus leche	Lechwe	No	No	
Kobus megaceros	Nile lechwe	No	No	
Kobus vardonii	Puku	No	No	
Nanger granti	Grant's gazelle	No	No	
Oryx beisa	East African oryx	No	No	
Oryx gazella	Gemsbok	No	No	
Ourebia ourebi	Oribi	No	No	
Phacochoerus aethiopicus	Desert warthog	No	No	
Phacochoerus africanus	Common warthog	No	Yes	Kleynhans et al. 2010
Redunca arundinum	Reedbuck	No	No	
Redunca fulvorufula	Mountain reedbuck	No	No	
Redunca redunca	Bohor reedbuck	No	No	
Syncerus caffer	Cape buffalo	No	No	

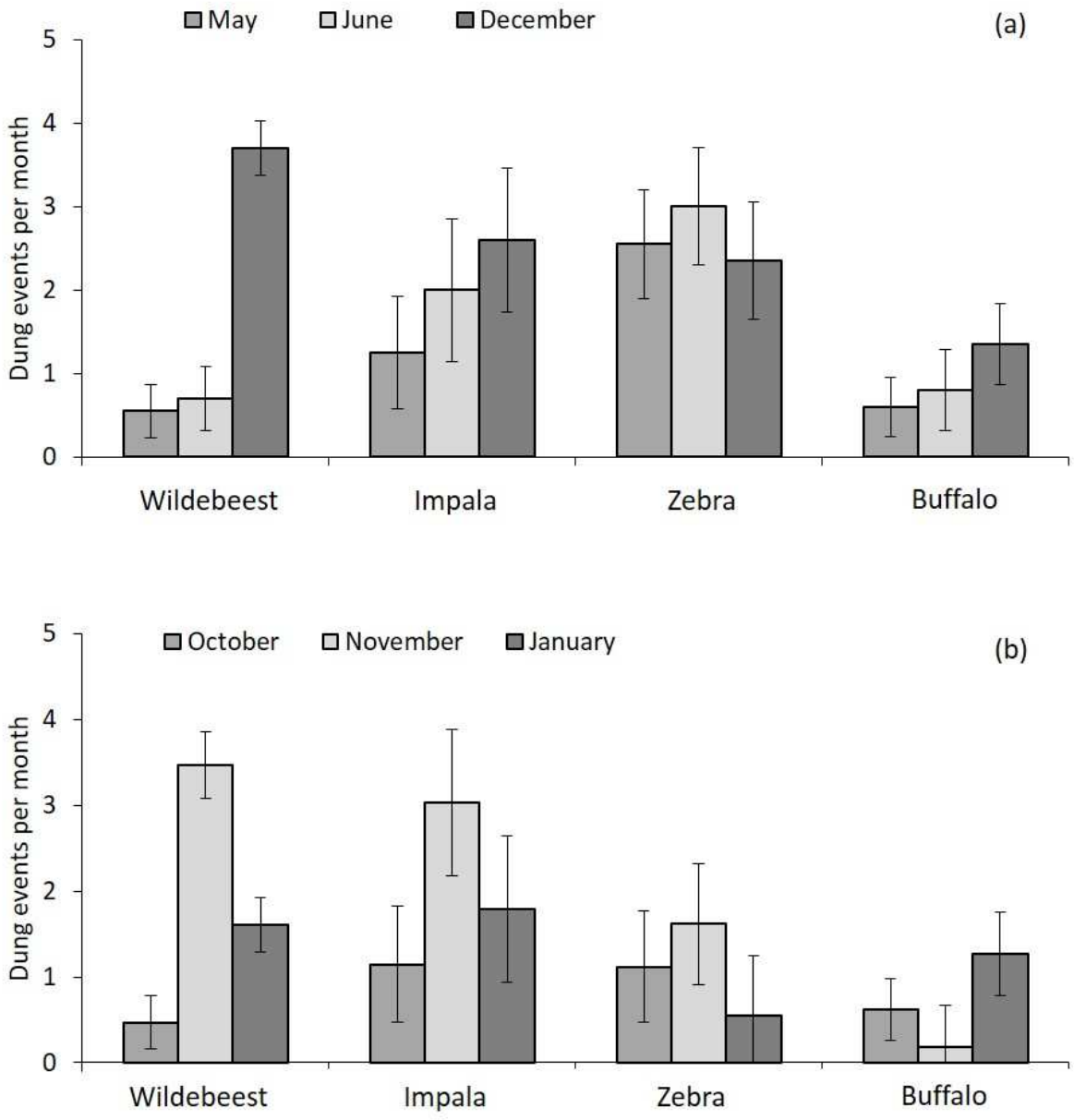


Figure S2.3. Dung deposition per month (mean ± SE) by focal grazer species (wildebeest, impala, zebra, and buffalo) on early-burn (a) and late-burn treatments (b) plots during 2013 and early 2014. Data was sampled on early-burn plots prior to fire application in May and after burn treatments in June and December. Similarly, late-burn plots were sampled before fire application in October and after fire in November and January.

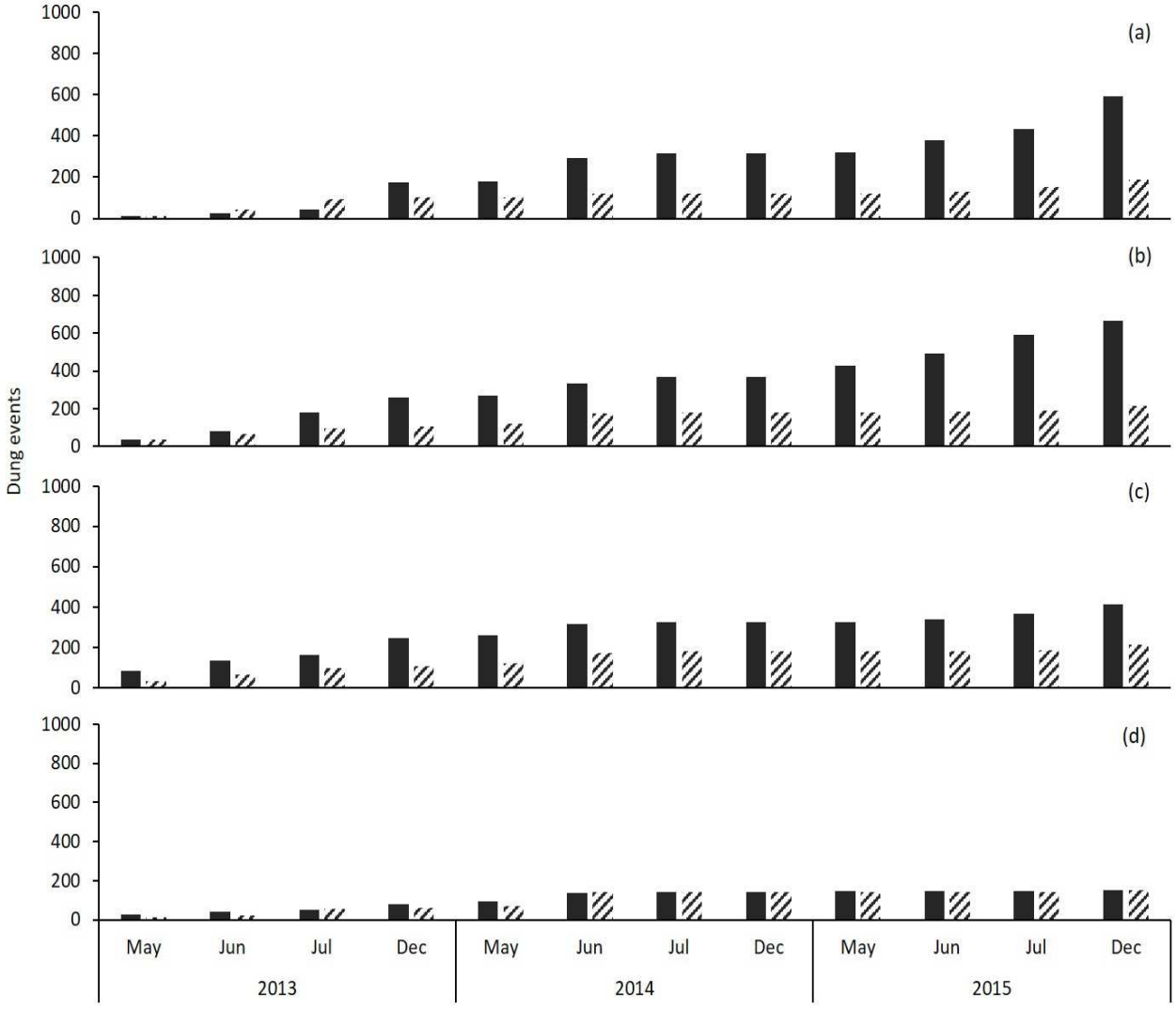


Figure S2.4. Cumulative total dung deposition for early-burn (black) and no-burn (hatched) treatments by focal species: wildebeest (a), impala (b), zebra (c) and buffalo (d) over a three-year period. Data are only presented from months when collection was synchronised on both early-burn and no-burn plots. Data for December 2015 are from only two 5ha and two 0.25 ha plots per treatment due to November 2015 lightning fires.

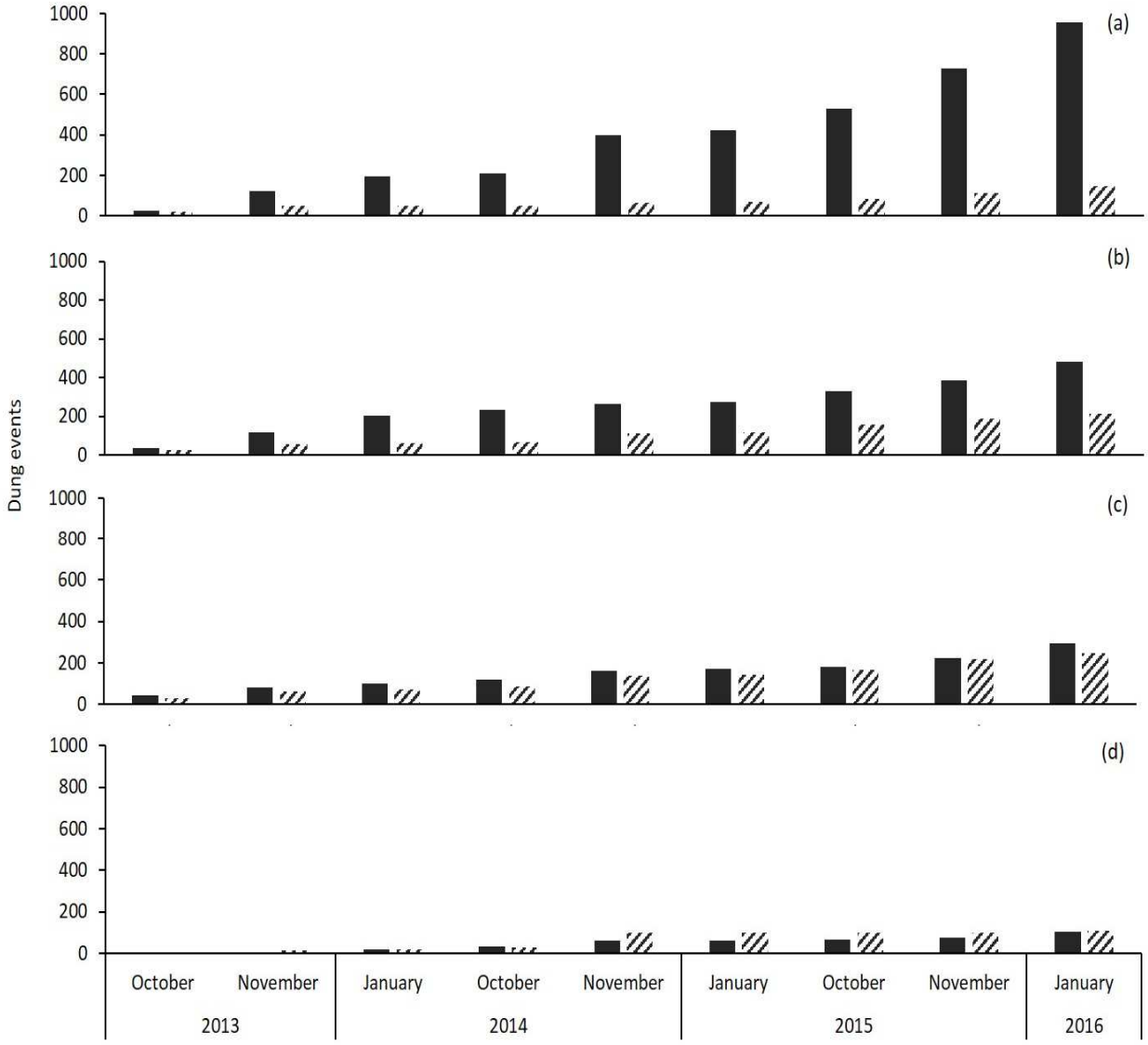


Figure S2.5. Cumulative total dung deposition for late-burn (black) and no-burn (hatched) treatments by focal species: wildebeest (a), impala (b), zebra (c) and buffalo (d) over a three-year period. Data are only presented from months when collection was synchronised on both late-burn and no-burn plots. Data for January 2016 are from only two 5ha and two 0.25 ha plots per treatment due to November 2015 lightning fires.

Appendix B

Analyses of leaf carbon and nitrogen content for all grass species were done on a Flash HT Plus elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer by ConFlo IV interface (all equipment supplied by ThermoFisher, Bremen, Germany). Carbon and nitrogen isotope values were corrected against in-house standard (Merck Gel) and a Urea Working Standard (IVA Analysentechnik e.K., Meerbusch, Germany). Laboratory standards and blaks were run after every 24 unknown samples.

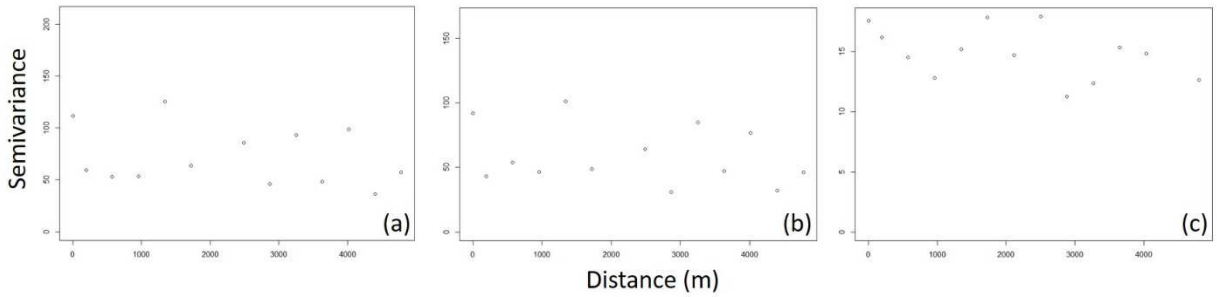


Figure S3.1. Semivariograms indicating no spatial autocorrelation is inherent in the residuals from the generalized linear mixed model for all grass tussocks basal area (a), *Bothriochloa radicans* tussock basal areas (b), and proportion of plots bitten from different treatments (c).

Table S3.1. Grass species traits for all species identified at the experimental plots described in **Chapter 3**. Stolons refers to the presence of stolons on any plants assessed throughout the study. Life history was defined by Van Outsdoorn (1991). Grazing columns refer to plants measured in the presence of grazing while no grazing refers to plants measured in exclosures. For all measured values three individual plants were measured. Flowering height refers to height of the lowest flower. Methods for measuring C : N are described in detail in **Chapter 3**. Culm orientation is the mean angle of 3 culms per plant. Internode length is the mean internode length of 3 internodes on 3 culms per plant. Mean leaf length is the mean leaf length of five leaves per plant.

						Culm orientation (cm)		Internode length (cm)		Leaf length (cm)	
Species	Life history	Stolons	Flowering Height (cm)	Leaf Table Height (cm)	C:N ratio	No grazing	Grazing	No grazing	Grazing	No grazing	Grazing
Aristida congesta congesta (Roem. & Schult)	Perrenial	Absent	79.44	50.88	34.45	80.00	39.17	11.62	3.48	19.44	8.22
Brachiaria eruciformis (Sm.)	Annual	Absent	32.11	25.80	16.93	51.78	1.50	5.39	3.19	11.12	4.06
Bothriochloa radicans (Lehm.)	Perrenial	Present	100.33	80.12	33.23	84.67	73.56	9.73	3.70	19.50	7.84
Cenchrus ciliaris (L.)	Perrenial	Present	77.90	85.02	33.64	77.17	No value	2.94	No value	28.15	No value
Chloris virgata (Sw.)	Perrenial	Present	93.20	68.71	30.68	71.56	26.00	9.49	4.17	14.46	5.76
Digitaria eriantha (Steud.)	Perrenial	Present	98.79	45.77	39.03	83.11	26.11	14.12	8.46	38.22	25.12
Eragrostis cilianensis (All.)	Annual	Absent	53.49	40.90	31.69	78.22	59.11	6.31	5.56	15.09	7.26
Eragrostis superba (Pehr.)	Perrenial	Absent	81.22	63.45	30.65	77.00	4.00	12.63	3.78	28.12	5.81
Heteropogon contortus (L.)	Perrenial	Absent	74.09	49.85	45.34	83.05	54.89	15.42	3.83	14.46	3.42
Panicum coloratum (L.)	Perrenial	Present	106.36	90.85	27.82	79.33	23.28	10.92	4.84	29.46	7.91
Panicum maximum (Jacq.)	Perrenial	Present	103.09	78.30	20.54	85.44	56.89	10.08	7.59	35.91	17.93
Schmidtia pappophoroides (Steud.)	Perrenial	Present	60.03	41.13	32.77	86.78	No value	8.27	No value	17.62	No value
Setaria incrassata (Hochst.)	Perrenial	Absent	106.16	75.29	33.64	81.00	80.00	11.96	7.29	49.03	26.74
Sorghum versicolor (Anderss.)	Annual	Absent	120.81	92.61	25.37	85.00	80.33	12.39	6.01	28.66	14.44
Themeda triandra (Forssk.)	Perrenial	Absent	113.11	88.95	37.36	48.11	14.33	3.50	2.21	3.37	2.43
Tragus berteronianus (Schult)	Annual	Present	23.70	14.79	20.46	79.00	57.50	14.38	6.57	24.29	8.98
Urochloa mosambicensis (Hack.)	Perrenial	Present	96.85	74.53	21.81	80.89	1.75	7.12	4.04	27.70	3.75

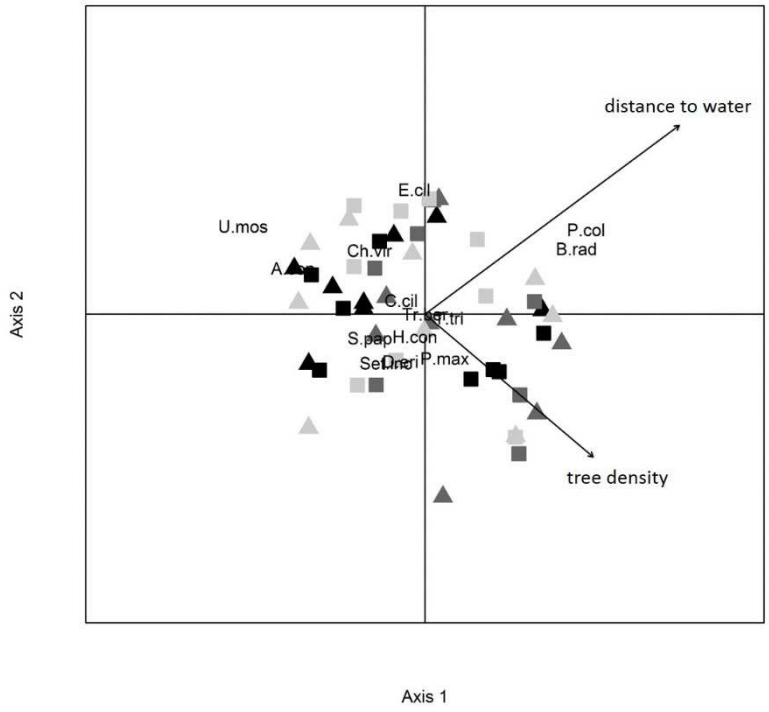


Figure S3.2. Correlation biplots based on RDA ordination of the grass species aerial cover on no-burn (black), early-burn (dark-grey) and late-burn (light-grey) treatment plots for 2013 constrained by the environmental variables. Environmental factors shown with arrows did not show any significant structuring of plots by treatment (p = 0.189). A. con = *Aristida congesta*, B. eru = *Brachiaria eruciformis*, B. rad = *Bothriochloa radicans*, C. cil = *Cenchrus ciliaris*, Ch. vir = *Chloris virgate*, D. eri = *Digitaria eriantha*, E. cil = *Eragrostis cilianensis*, E. sup = *Eragrostis superba*, H. con = *Heteropogon contortus*, P. col = *Panicum coloratum*, P. max = *Panicum maximum*, S. inc = *Setaria incrassata*, Sc. pap = *Schmidtia pappophoroides*, So. ver = *Sorghum versicolor*, T. tri = *Themeda triandra*, Tr. ber = *Tragus berteronianus*, U. mos = *Urochloa mosambicensis*.

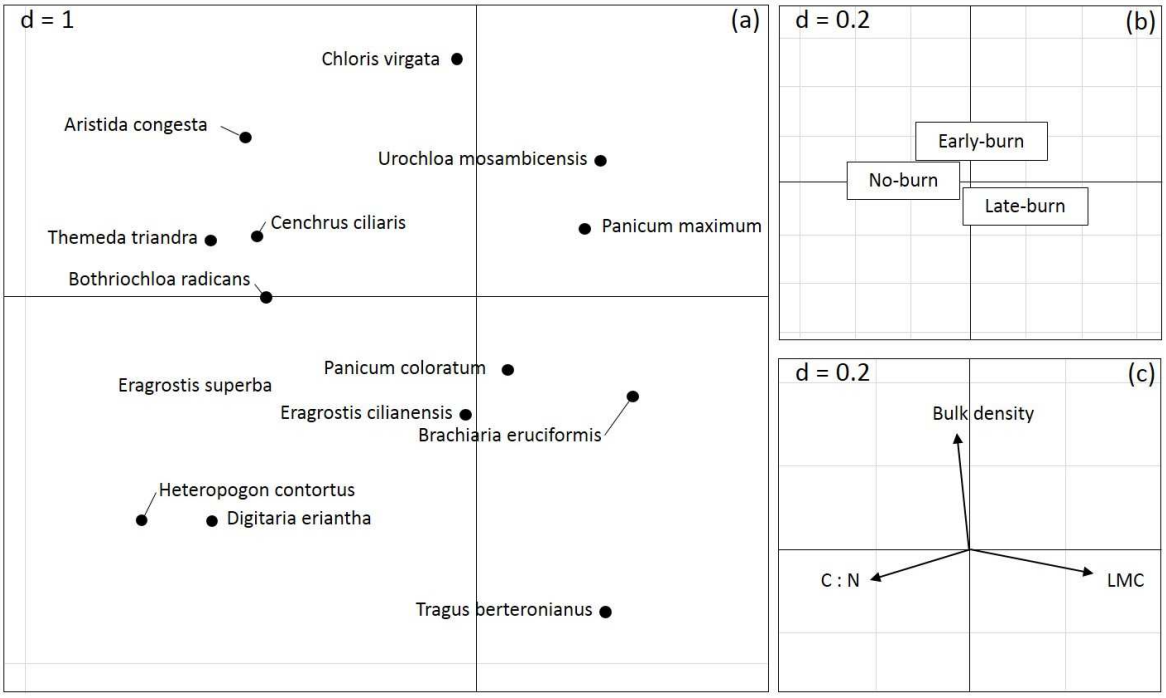


Figure S3.3. Results of the first two axes of R-mode linked to Q-mode (RLQ) analysis for 2017: the RLQ space maximizes the relationships between traits and environments. The positions of species in the RLQ space are shown in (a), environmental factors in (b) and species traits in (c). The 'd' values give the grid size for scale comparison across the three figures. C : N ratio and leaf moisture content (LMC) appear to be negatively and positively associated with heavily grazed late-burn plots respectively, but this was not statistically supported by permutation tests (p=.09).

Appendix C

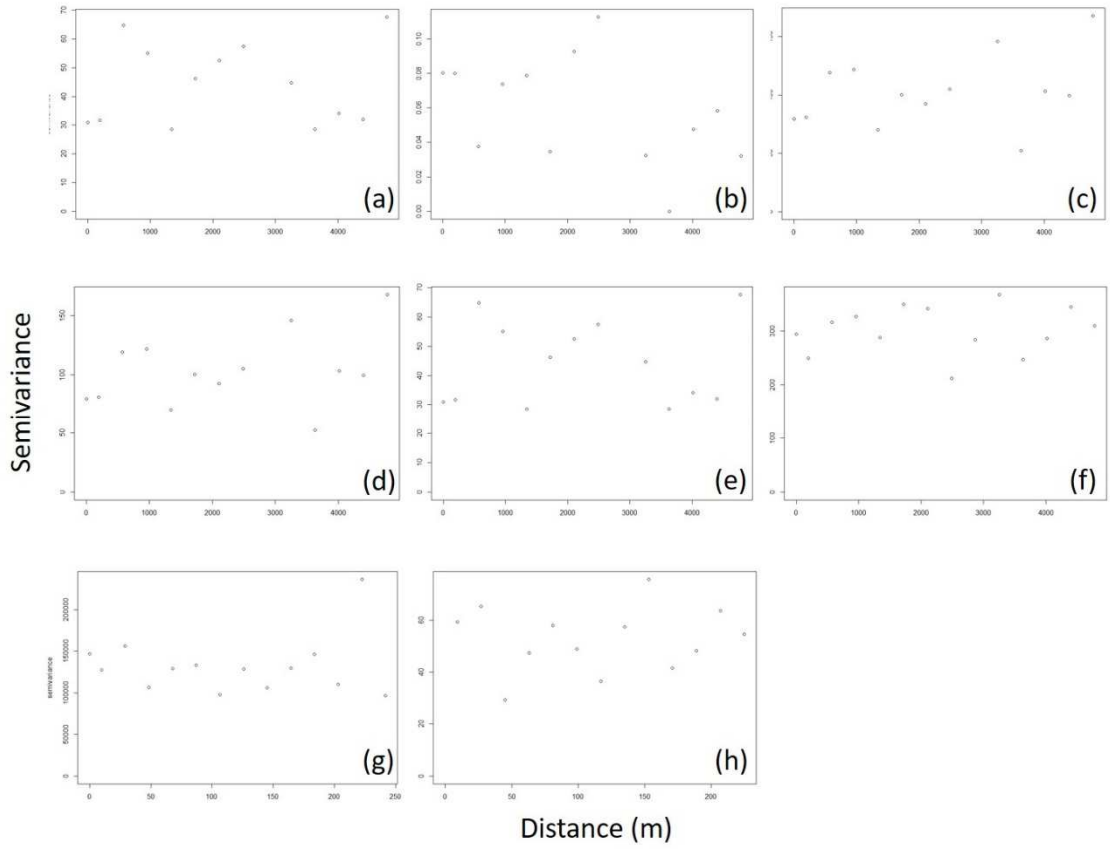


Figure S4.1. Semivariograms indicating no spatial autocorrelation is inherent in all grazers dung (a); wildebeest dung (b); impala dung (c); zebra dung (d); buffalo dung (e); bites per subplot (f); dry-grass growth (g); and established tussock growth (h).

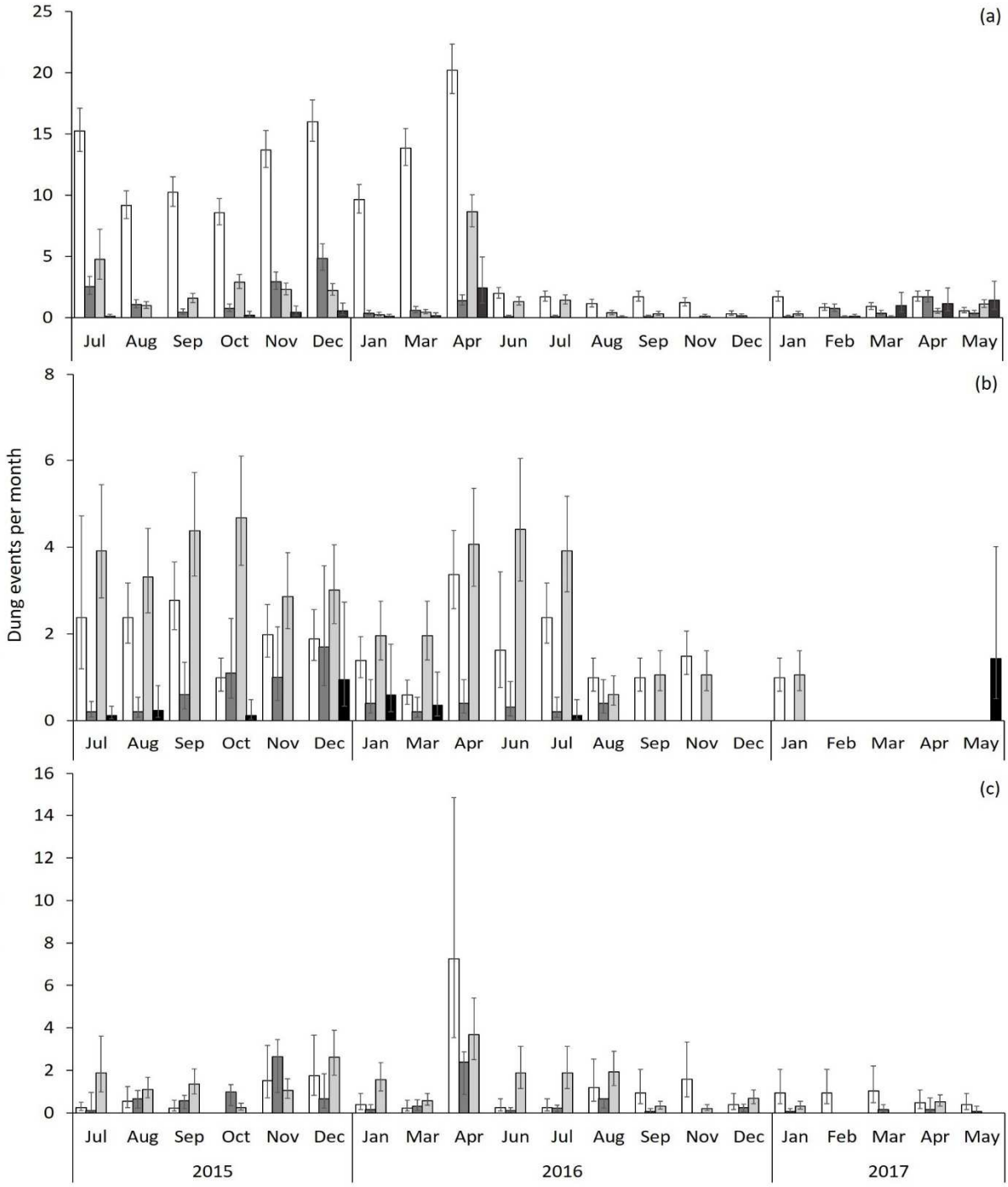


Figure S4.2. Dung deposition (mean ± SE) for wildebeest (clear), impala (dark grey), zebra (light grey), and buffalo (black) on grazing lawns (a), tall-grass patches (b) and burnt areas (c) over the entire study period (2015-2017).