Managing herbivory over space and time: consequences for vegetation and cattle responses in African rangelands

Alexander S Venter

VNTALE002

Thesis Presented for the Degree of

DOCTOR OF PHILOSOPHY

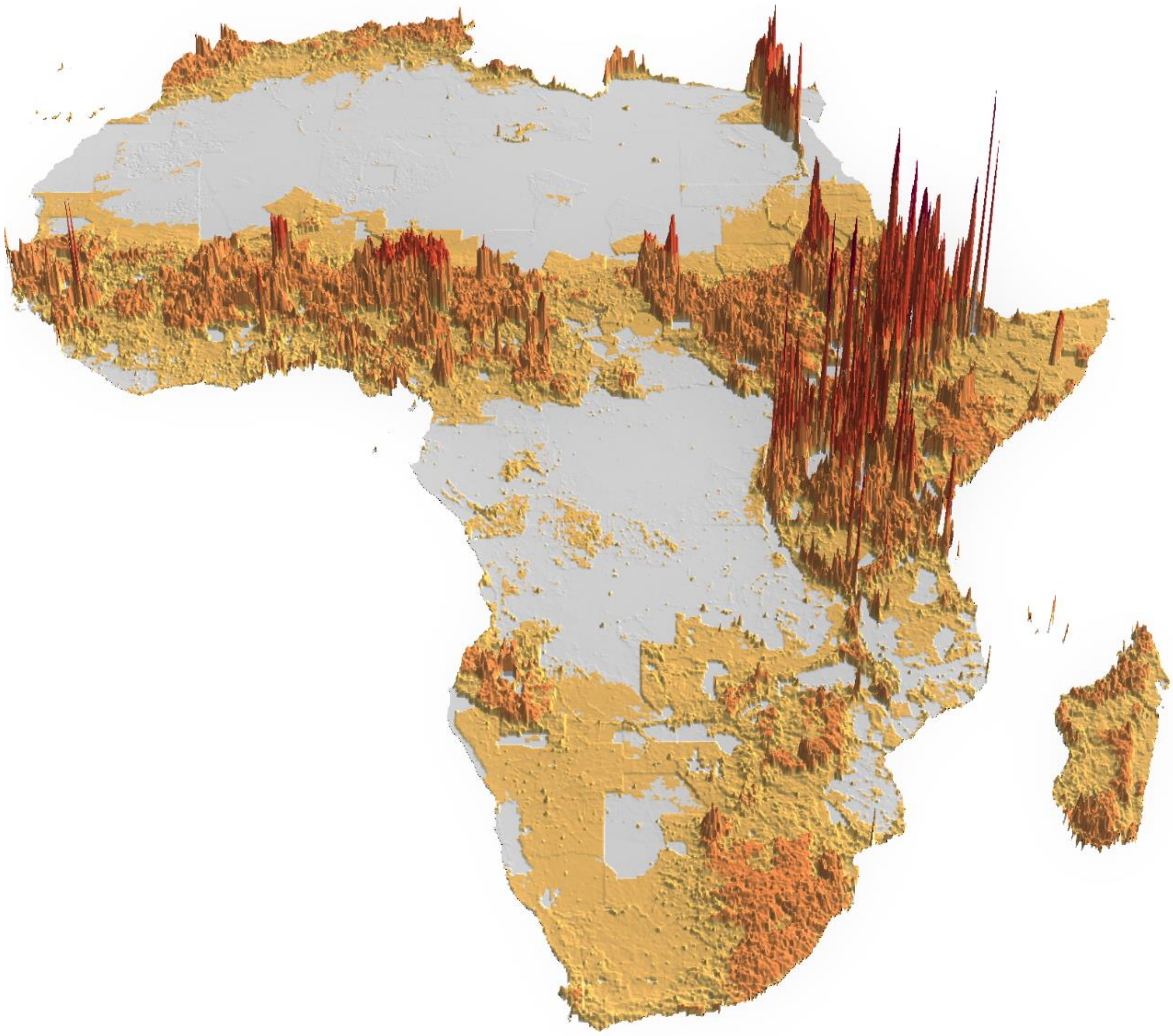
In the Department of Biological Sciences

UNIVERSITY OF CAPE TOWN

December 2018

Supervisors

Dr Heidi-Jayne Hawkins, Prof Michael D Cramer



Livestock biomass over Africa represented in 3D. Includes summed data for cattle, sheep and goats derived from Gilbert *et al.* (2018), processed in Google Earth Engine and rendered in RStudio. Follow this link to interact with the 3D map online: link to map.

Declaration

I know the meaning of plagiarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own. The thesis is submitted for the degree of Doctor of Philosophy in the Department of Biological Sciences, University of Cape Town. It has not been for any degree or examination at any other university.

I confirm that I have been granted permission by the University of Cape Town's Doctoral Degrees Board to include the following publication(s) in my PhD thesis, and where co-authorships are involved, my co-authors have agreed that I may include the publication(s):

Chapter 2: Venter, Z.S., Hawkins, H.-J. & Cramer, M.D. (2017) Implications of historical interactions between herbivory and fire for rangeland management in African savannas, *Ecosphere*, 8(10): 1-14.

Chapter 3: Venter, Z.S., Cramer, M.D. & Hawkins, H.J. (2018) Drivers of woody plant encroachment over Africa, *Nature Communications*, 9(1): 2272.

Chapter 4: Venter, Z.S., Hawkins, H.-J. & Cramer, M.D. (2019) Cattle don't care: Animal behaviour is similar regardless of grazing management in grasslands, *Agriculture, Ecosystems & Environment*, 272: 175-187.

Signed by candidate

Alexander S. Venter

VNTALE002

2018/12/21

Abstract

Mammalian herbivory is integral to determining vegetation structure, composition and ecosystem function in African rangelands, however the extent to which managing the movement of herbivores, specifically livestock, over time and space can sustain functioning and productive rangelands remains unclear. Previous research on forms of rotational grazing management are criticized for being limited to small-scale experimental trials that make untested assumptions about the effect of grazing density on animal behaviour and neglect measurements of landscape-scale pattern and process. Despite this, advocates of holistic planned grazing, a form of high density rotational grazing, claim that their practices can increase rangeland productivity and reverse climate change while doubling stocking rates. Thus, I tested the hypothesis that concentrating herbivores over space and moving them adaptively, primarily through forms of high density rotational grazing management, will reduce the overgrazing of palatable vegetation, increase vegetation cover and thereby enhance rangeland productivity. Given that the functional composition of herbivory over Africa has been simplified to one dominated by grazers, namely cattle, I first explored evidence from paleoecology, historical literature and savanna ecology to test the hypothesis that mid-Holocene African savannas were dominated by herbivory as a means of cycling nutrients and changing vegetation whereas fire perhaps played a lesser role than it does today. Currently, fire consumes 5.8 times more vegetation than herbivores do across sub-Saharan Africa, and charcoal deposits along with early colonial records suggest that herbivory was more prevalent in the past. I argue that the current balance might be shifted toward herbivory, fulfilling the functional role that fire plays in removing old biomass, while releasing less soil carbon and nitrogen to the atmosphere. However, shifting ecosystems to herbivore-dominance has been implicated in switching savannas into tree-dominated alternative stable states, characteristic of woody plant encroachment (WPE) although this has not been tested at regional sales. Using three decades of satellite imagery, I found that woody plant cover has increased by 8% over sub-Saharan Africa and a diversity of drivers, other than CO_2, were able to explain 78% of the spatial variation in this trend. High browser densities as well as high and/or low grazer densities have mitigated WPE, while declines in burned area along with warmer, wetter climates have driven WPE. To further explore the nuances of herbivore densities on vegetation change, I used an experimental trial in the grasslands of the Eastern Cape, South Africa, to isolate grazing from other disturbance and climatic drivers. I compared management practices including season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG). These treatments, reflecting a range of grazing densities (SLG < FCG < HPG) at a constant stocking rate, were applied over a period of 2.5 years in an experimental trial in a mesic grassland of South Africa. Cattle gained on average 0.2 ± 0.02 kg day^{-1} ha^{-1} and this did not differ between treatments. Grazing management had little effect on cattle herding and grazing behaviours including distance to neighbour (4.8 ± 2.6 m), proportional grazing time (37 ± 1.7 %), trampling (11 ± 2 steps m^{-2}), or plant species selection. At the grazing camp scale, HPG did, however, reduce selective foraging behaviour relative to SLG and consequently homogenized vegetation greenness as measured by the normalised difference vegetation index (NDVI). Cattle concentrations under SLG facilitated a reduction in the formation of bare ground by 6 ± 0.4 % on high nutrient, moist soils, however this effect was not apparent on relatively nutrient poor soils or under FCG or HPG. An experimental increase in defoliation frequency and severity on vegetation patches and potted grass plants reduced productivity, particularly in so-called unpalatable species, although this effect was mitigated with nutrient or dung addition. Overall, rotational grazing management did not enhance vegetation productivity or cover relative to less rotational practices. To address the limitations of drawing conclusions from shot-term grazing experiments, I performed a nation-wide farm management survey and a fence-line contrast study between farms that were largely aligned with HPG principles and their respective neighbours. Stocking rate, grazing density, and herbivore type had no consistent effect on remotely sensed NDVI, fractional bare ground, grass or woody plant cover.

This thesis presents evidence that vegetation and cattle productivity are largely unaffected by forms of rotational grazing management. Due to high infrastructure costs, adopting HPG might stunt farm profitability relative to alternative management practices in mesic grasslands. However, depending on the farm management goal, HPG may be used to homogenize vegetation cover, while free-ranging cattle under SLG show potential to increase vegetation heterogeneity and cover where soil nutrients are not limiting, akin to the establishment of grazing lawns in savannas. The continental increase in woody plant cover reported here confirms global greening trends and challenges widely held theories about declining terrestrial carbon balances and desert expansion. While climatic drivers like CO_2 may enhance the risk of WPE, incorporating browsers and fire along with grazers might mitigate WPE.

Acknowledgements

I find it difficult to claim any agency or honour for ‘my’ accomplishments in life knowing how dependent I am on those who have come before me and around me. The best account I can give for where I have ended up is some form of serendipitous grace. I am not one for giving personalised acknowledgements on public media, so without singling out any one person, I would like to thank all who have given me the opportunity to complete this work. I have thoroughly enjoyed it. I would hope that I have expressed my gratitude to relevant individuals in person.

Table of Contents

Chapter 1: General Introduction

The significance of rangeland as an agent of global change and provider of resources to humans becomes apparent when considering the magnitude and extent of its global footprint. Rangelands currently cover 36% of the earth's terrestrial surface (Fig. 1) and can be broadly defined as including shrubland, grassland, steppe and open woodland (Heady & Child 1999) that are uncultivated but provide the necessities of life for grazers and browsers (Holechek *et al.* 1989). In 1997 the dollar equivalent of ecosystem services provided by rangelands was estimated at 232 \$ ha^{-1} yr^{-1} (Costanza *et al.* 1997) which equates to 1.24 trillion dollars per annum globally. The literature on ecosystem services has expanded since then and rangelands are well-recognised for the provisioning of food and water, climate regulation, pollination, and aesthetic/recitational services (Sala *et al.* 2017). Given that the demand for these services has increased with population growth (Yahdjian *et al.* 2015), conserving the foundations of ecosystem services, namely biodiversity, habitat and primary production (Sala *et al.* 2017), is becoming increasingly important. Thus, managing rangelands to sustain ecosystem services requires an understanding of the environmental and anthropogenic factors inducing change in vegetation production and composition.

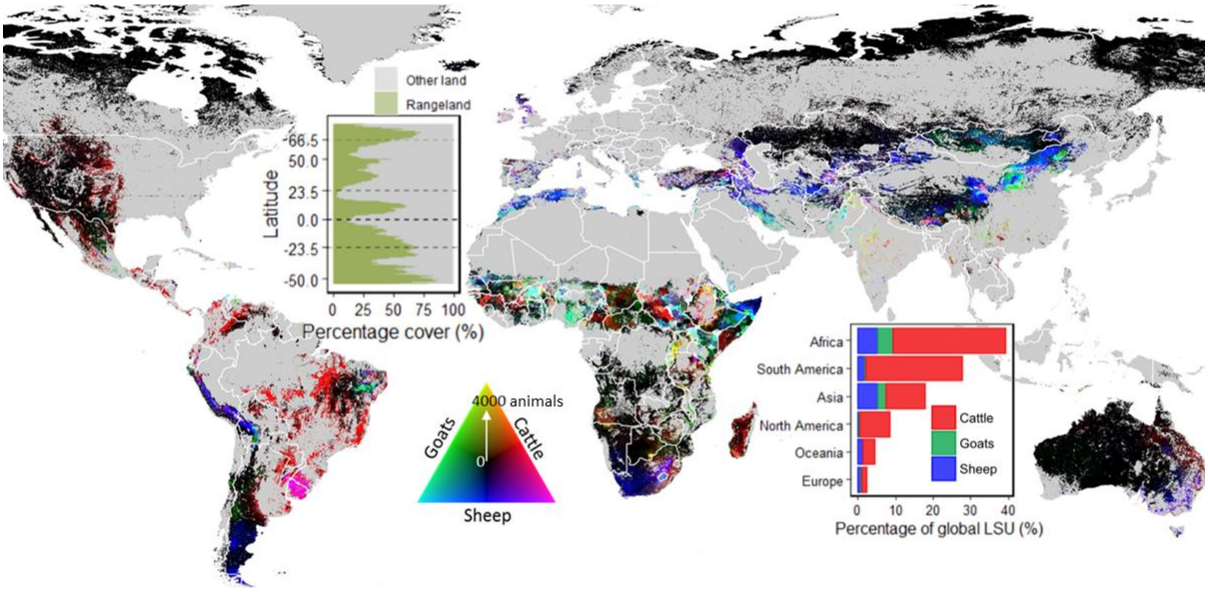


Figure 1.1 Global distribution of rangeland cattle, sheep and goat numbers. Here I have defined rangeland (non-grey land pixels) as shrubland, grassland (includes savanna) or tundra derived from a recent global landcover map at 30 m resolution (Chen *et al.* 2015). This aligns closely with the definitions outlined by Briske (2017) and the resulting total global coverage of 36% falls between the 26% coverage estimated by the FAO (2014) and 54% cited in Briske (2017). The percentage terrestrial surface covered by rangeland is displayed relative to latitude in the right inset graph. Livestock distributions of cattle, goats and sheep were derived from Gilbert *et al.* (2018) and expressed as total counts per 10 x 10 km pixel in red-green-blue colour space. After converting livestock numbers to large stock unit (LSU) equivalents, the percentage contribution of cattle, sheep and goats to the combined global herd mass (109 Mt) is displayed for each continent in the left graph inset.

The drivers of vegetation change in rangelands exist on a continuum of those that can be controlled by managers including fire and herbivory, to those largely out of rangeland managers' control including rainfall, temperature and atmospheric CO_2. The relative importance of these local and global drivers of change has been a matter of debate in rangeland ecology and management science over the past century (Vetter 2005; Briske 2017). Early conceptions of rangelands as equilibrium systems were born out of the concept of "the balance of nature" whereby livestock populations were viewed as density-dependent, exerting a strong feedback on vegetation composition, cover and productivity (Ellis & Swift 1988; Briske *et al.* 2003). Rangeland carrying capacity and stocking rate were management constructs that were developed within this paradigm based on the assumption that herbivory was the most important driver of vegetation change (Vetter 2005). Increasing herbivore numbers beyond the capacity of the forage resource base was predicted to revert climax ecosystem vegetation to a species composition representative of an early successional status (Dyksterhuis 1949). In the African context, this was associated with the narrative of desertification in which overgrazing of rangelands by communal indigenous pastoralists was leading to vegetation mortality, bare patch formation and the consequent expansion of desert into grassland and savanna (Sinclair & Fryxell 1985; Cowling 2000).

Later research in arid pastoral systems found evidence that rainfall extremes such as droughts override the effect of livestock numbers on vegetation and thus preclude livestock numbers from attaining the maximum carrying capacity (Ellis & Swift 1988). This opposed the equilibrium concepts of stocking rate, carrying capacity and the idea that livestock are the primary agents of rangeland degradation and desertification (Behnke 1994; Cowling 2000). Nonequilibrium theory was developed to incorporate the stochastic nature of climate and the spatial heterogeneity of forage resources to explain the complex nature of plant-herbivore interactions (Wiens 1984). Since then, others have argued for a balance between equilibrium and nonequilibrium theories given observations that herbivores are loosely coupled to wet-season resources but tightly coupled to dry-season resources (Illius & O'Connor 2000). Nonequilibrium theory is currently being replaced by resilience theory as the dominant framework for understanding rangelands because of the observation of both multiple equilibria and alternative stable states (Briske *et al.* 2017). This is an attempt to account for nonequilibrium dynamics over both space and time and quantify the variable thresholds that control these dynamics. Spatially, one might expect vegetation composition and structure to be relatively homogenous within a given climatic and edaphic envelope, however ecologists have identified sharp boundaries defining floristic turnover within ecosystems homogenous in climate (e.g. Staver *et al.* 2011; Cramer *et al.* 2018). Similarly, over time, a system might respond non-linearly to gradual trends in climate when thresholds of disturbance are surpassed. Resilience theory holds that an ecosystem might not return to its original equilibrium position following disturbance past a critical threshold in magnitude and thus may switch into an alternative stable state (Holling 1973; Gunderson 2000). In African rangelands, persistent grazing in the absence of browsing or fire can switch grasslands into alternative tree- and shrub-dominated stable states (O'Connor *et al.* 2014; Dantas *et al.* 2016). This process, also known as woody plant encroachment (WPE), is of importance in Africa where the diverse functional composition of wild herbivores has been largely replaced by domestic livestock (Hempson *et al.* 2017) dominated by grazers, namely cattle (Fig. 1.1). Nevertheless, woody plant encroachment has been observed in both browser-dominated (e.g. conservation areas) and grazer-dominated (e.g. agricultural rangelands) areas, suggesting climatic determinants are also involved (Stevens *et al.* 2016).

The transition within rangeland ecology from equilibrium to nonequilibrium theories has impacted the nature of rangeland management and the importance of biotic versus abiotic feedbacks (Vetter 2005). The role of herbivory as an agent of vegetation change was elevated to pivotal importance under the equilibrium theory, diminished in value relative to rainfall and climate in the nonequilibrium theory, and resurrected to equal standing relative to other disturbances including fire in resilience theory (Briske *et al.* 2017). The aspects of herbivory that rangeland managers can control include the type of livestock used (i.e. grazer, mixed feeder or browser), the quantity of the livestock (i.e. stocking rate), and the spatio-temporal movement of the livestock (i.e. grazing density). Stocking rate quantifies the number of animals stocked on a farm per year whereas grazing density refers to the number of animals per sub-unit of land per day, generally determined by the number of fenced grazing camps. With the shift to nonequilibrium and resilience theories, debates over adequate stocking rates have been nuanced by debates over how to achieve ideal grazing densities through forms of rotational grazing management, starting in the 1970s (Briske *et al.* 2011). In Africa the traditional transhumance (seasonal rotation) of livestock (Aryal *et al.* 2014) became constricted by settled farmers early on in the 20th century (Coughenour 1991). Thus, transhumance-based systems of season-long grazing were replaced by continuous grazing where the same vegetation would remain exposed to herbivory year-round. Later, the perceived degradation caused by this restricted mobility and continuous grazing led to the introduction or rotational grazing systems, inspired by the need to mimic grazing patterns of wild herbivores which consisted of intense defoliation followed by long periods of rest (Vetter 2005 and refs therein). This occurred despite the mis-match in spatial and temporal scale between farm grazing rotation and the regional rotation of grazing associated with transhumance. One of the most important functions assumed in rotational grazing systems was the prevention of selective overgrazing. The botanist John Acocks famously suggested that South African rangelands are "understocked but overgrazed" because animals were allowed to move freely and consequently overgraze palatable plant species even though there were less stock than the estimated carrying capacity of the rangeland (Acocks 1966).

To date the debate over the efficacy of rotational grazing management persists due to the inability of scientific research to capture both the social and biophysical components of complex adaptive systems in which rangeland management is practiced (Briske *et al.* 2011). It remains difficult to distil the complexity of rotational grazing management into one measurable variable as is the case for livestock type and quantity, both of which have been globally measured (Fig. 1.1). I suggest it is also because the causal mechanisms and plant-herbivore relationships assumed in rotational grazing approaches have been understudied. Despite the balance of the scientific literature showing no effect of rotational grazing on vegetation or animal productivity (Briske *et al.* 2008; Hawkins 2017), practices such as holistic planned grazing (Savory 1983; Savory & Butterfield 2016), synonymous with high density, time-controlled, or short-duration rotational grazing (Hawkins *et al.* 2017; Mann & Sherren 2018), remain advocated and practiced globally. The controversy over holistic planned grazing largely started due to the claim that it will permit a doubling of the recommended stocking rate without a loss in animal or plant production (Savory 1983). The controversy escalated recently when Allan Savory claimed that holistic planned grazing could sequester carbon and thereby reverse climate change (Savory 2013). Although scientists refute these claims, practitioners, farmers organisations, NGOs and policy makers require definitive guidance on the relevance of rotational grazing principles within a global but particularly African and South African context where many livestock owners are resource-poor (e.g. Musemwa *et al.* 2010).

In this thesis I aimed to use modern ecological theories and concepts, including resilience theory and alternative stable states, to give a new perspective on managing herbivores in African rangelands. I aimed to shed light on previously unresolved assumptions about animal behavioural mechanisms that are largely ignored in the experimental literature on rotational grazing (see studies cited in Hawkins 2017) leveraging recent advances in remote sensing and telemetry technologies. Finally, I aimed to perform these analyses using both short- and long-term data at spatial scales relevant to global, landscape and plant-level change. I hypothesised that concentrating herbivores over space and moving them adaptively, primarily through forms of high density rotational grazing management, will reduce the overgrazing of palatable vegetation, increase vegetation cover and thereby enhance rangeland productivity. In addition, I hypothesised that local scale disturbances including herbivory and fire are significant determinants of vegetation structure, heterogeneity, and productivity in African rangelands. To test these hypotheses, I set out four research chapters that explore the continental-scale historical and current interactions between herbivory and vegetation, and specific aspects of herbivore grazing management at various experimental scales in a South African grassland.

Given population growth in Africa and the concomitant increased impact of humans on the levels of herbivory and fire disturbance, and given claims that aspects of wildlife migratory patterns can be mimicked on managed rangelands (Savory & Butterfield 2016), it is of interest to gain perspective by comparing current with past fire and herbivory regimes. In the second chapter, I addressed the hypothesis that the influence of herbivory on vegetation relative to fire has been reduced by human intervention since the mid-Holocene (~5 kya). I used evidence from historical literature, savanna ecology and paleoecology, including previously published data on dry matter consumed by fire and herbivory over sub-Saharan Africa.

With numerous local-scale studies from across the globe, ecologists have identified a shift in savannas from grassy to woody alternative stable states. The extent and magnitude of continental WPE over Africa remains unquantified, and theories posing climatic factors, notably atmospheric [CO_2], as dominant drivers relative to fire and herbivory remain untested. I hypothesised that WPE is a continent-wide phenomenon and that changes in woody plant cover are equally determined by disturbance and climatic drivers. In the third chapter I tested this using three decades of satellite imagery to quantify the trends in woody plant cover over sub-Saharan Africa. I then attempted to explain the spatial variation in these trends using a suite of climatic, edaphic and disturbance (fire, herbivory, population growth) drivers.

The role of herbivory as an agent of vegetation change, including broad-scale WPE, depends on the type and function of local-scale herbivore pressures, typically determined by rangeland managers. In the fourth chapter I addressed the hypothesis that grazing management approaches, including high density rotational grazing, alter cattle grazing behaviours and thereby enhance farm productivity. To test this a grazing management trial was implemented for three years on a commercial farm in a mesic grassland of the Eastern Cape, South Africa. Management treatments included season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG), reflecting a range of grazing densities (SLG < FCG < HPG). Along with cattle production and farm profitability, I measured the spatio-temporal patterns of cattle behaviour, dietary composition, dung trampling, animal productivity, and vegetation normalised difference vegetation index (NDVI).

Recognising that grazing management approaches use fencing or herding to control the timing and period of grazing, I hypothesised that manipulating defoliation frequency and severity will alter plant growth responses and consequent basal cover and greenness. I supplemented remotely sensed data on vegetation NDVI and basal cover with measures of standing grass biomass. To test if the effects were consistent at multiple spatial scales and influenced by soil nutrients, I set up experimental defoliation and nutrient addition experiments with in situ grass plots on the farm and ex situ potted grasses in a glasshouse. I reported these results in the fifth research chapter of the thesis.

Finally, to overcome the limitations of drawing conclusions from a shot-term grazing experiment, I conducted a national grazing management survey and fence-line contrast study over South Africa. Using remotely sensed measures of vegetation cover, I tested the hypothesis that farms adopting highly rotational grazing management would have greater grass cover and less woody plant or bare ground cover than their neighbours. This has been reported in the sixth chapter.

Chapter 2: Implications of historical interactions between herbivory and fire for rangeland management in African savannas

This chapter has been published in *Ecosphere*:

Venter, Z.S., Hawkins, H.-J. & Cramer, M.D. (2017) Implications of historical interactions between herbivory and fire for rangeland management in African savannas, *Ecosphere*, 8(10): 1-14.

Abstract

Herbivory and fire are important drivers of ecosystem processes within African rangelands. I explore whether mid-Holocene African savannas were dominated by herbivory as a means of cycling nutrients, and whether fire perhaps played a lesser role than today. Evidence from savanna ecology, paleoecology, and historical literature indicate higher herbivore densities in mid-Holocene and pre-colonial times compared to present. While fire may increase or decrease forage availability for herbivores, depending on the nutrient status of the environment, herbivory tends to decrease fire intensity and frequency by decreasing fuel loads. Given this competitive relationship between fire and herbivory and the higher herbivore densities of the past, I suggest that some fire-dominated present-day savannas are the product of anthropogenic alterations in herbivore and fire regimes, including the increasing use of fire as a tool for managing ecosystems. I discuss whether managing for an alternative stable state dominated by herbivory could stimulate ecosystem processes, such as nutrient cycling and production, and whether this will achieve the same management objectives traditionally satisfied by fire. Management implications may include the adaptive manipulation of herbivore densities over time and space to maintain an appropriate carrying capacity for the rainfall and soil nutrient status of the area, occasional use of fire, and including a diversity of herbivore functional guilds.

Introduction

The notion of extant pristine ecosystems untouched by human influence is false (Denevan 1992). Humans have altered the earth’s ecosystems through the alteration of natural fire regimes over the last ca. 60 kyr (Diamond 2002), domestication and hunting over the last ca. 13 kyr (Thevenon *et al.* 2010) and more recently, through influences on climate change (Voosen 2016). In North America, all mammal species >1000 kg and over half of those >32 kg became extinct during the late Pleistocene and Holocene (Koch & Barnosky 2006). This mega-faunal collapse is paralleled in Eurasia and Australia and closely tracks human expansion across the planet (Barnosky *et al.* 2004; Burney & Flannery 2005). Estimates for mega-faunal extinction in Africa since the late Pleistocene range between 14% (Owen-Smith 1987) and 18% (Barnosky *et al.* 2004), however, looking further back in time (ca. 1 to 2 mya), it is likely that close to 40% have become extinct (Martin 1966). Although the rate of extinction of African megafauna is lower than on other continents, key drivers of ecosystem change, fire and herbivory, have been significantly modified by human activities (Archibald & Hempson 2016).

Parallels between fire and herbivory as consumers of biomass and ecosystem engineers have been drawn both globally (Bond & Keeley 2005) and within African savannas (Archibald & Hempson 2016). Reconstructing the past prevalence of fire or herbivory is challenging given limited data. Hempson *et al.* (2015a) use modelled data to suggest that current day herbivore densities exceed those of the past where the mean annual precipitation (MAP) is between 500 and 700 mm, and that the opposite is true for areas above 1000 mm MAP where soils tend to be leached and require fire to recycle nutrients (McNaughton 1985). Using evidence on the expansion and development of agropastoralism, along with paleocarbon charcoal data, Archibald *et al.* (2012) suggested that substantial human influence on fire regimes began ca. 40 kyr BP in closed/dissected landscapes and ca. 4 kya BP in open landscapes with an increase in fire frequency. These reconstructions contribute valuable baseline information to global change and ecological studies and their application to rangeland management is yet to be explored.

The recent progress in our understanding of how fire shapes ecosystems and the characterisation of “fire-prone” or “fire-adapted” systems (Bond & Keeley 2005; Bond *et al.* 2005; Lehmann *et al.* 2014) has informed the adoption of fire as a management tool in African rangelands. For example, fire in the Kruger National Park (KNP) has been actively managed since 1957 (van Wilgen *et al.* 2003), and is currently being managed to promote biodiversity and structural heterogeneity (van Wilgen *et al.* 2014). The translation of this understanding to managed commercial rangelands, without adequate consideration of how herbivory can be manipulated to fulfil some of the functions fire does, might result in a bias toward managing rangelands as fire-dominant ecosystems.

Ecologists have looked to the Pleistocene-Holocene for insights into restoring “lost” biodiversity and ecosystem function such as nutrient cycling, productivity and resilience. As a result, trophic “rewilding” (Svenning *et al.* 2016) has been proposed as a restoration strategy that uses species introductions to restore trophic interactions and promote self-regulating ecosystems. Perhaps the most widely known example of rewilding is the reintroduction of apex predators, wolves (*Canis lupus*), to Yellowstone National Park in the mid-1990s with consequences for trophic cascades (Laundré *et al.* 2001; Ripple *et al.* 2001). The principle has also been applied to restoring historical disturbance patterns associated with fire and herbivory, which have been dominant evolutionary processes. An emerging management practice, termed pyric herbivory, uses the interactive effects of fire and grazing to promote structural heterogeneity and conserve biodiversity within rangelands (Fuhlendorf *et al.* 2009). While practices such as pyric herbivory may make implicit assumptions about how prevalent fire and herbivory were in mid-Holocene ecosystems and imply that fire functions as a mega-herbivore (Bond & Keeley 2005), I question the equivalence of fire and herbivory. Furthermore, the interactions and trade-offs between fire and herbivory before colonial hunting and significant livestock domestication in Africa, have important implications for current managed rangelands. I hypothesise that herbivory was a more important driver of ecosystem function in mid-Holocene African savannas (ca. 5 kya) compared to present, and use evidence from savanna ecology, paleoecology, and historical literature to substantiate this. I then consider how rewilding of rangelands (defined as savannas and grasslands that are managed under commercial and communal land tenure for meat production) with the type, pattern and abundance of mid-Holocene herbivory may change rangelands from a fire-dominated to a herbivore-dominated stable alternative state. Lastly, I discuss the implications of a herbivore- versus a fire-dominated stable state for ecosystem processes and thus management of ecosystem services from rangelands.

Herbivory and fire interactions

A direct and reliable comparison of current herbivore biomass and mid-Holocene herbivore biomass within Africa is confounded by the absence of reliable methods and the difficulty of comparing wildlife biomass of the past with a largely domesticated biomass of the present (Hempson *et al.* 2015a). Similarly, past fire regimes are difficult to model due to the complexity of how anthropogenic and natural drivers alter fire ignition frequency and extent (Archibald *et al.* 2012). However, ecological modelling, paleoecological proxies and, historic records provide some insights.

Hempson *et al.* (2015a) modelled the past distribution of herbivore biomass across Africa, showing that, since ca. 1000 years ago, there has been an increase within agricultural areas, but a decrease in areas with more than 1000 mm MAP. They relate the increase to the disease suppression and resource provision associated with livestock farming. However, the model included census data from wildlife reserves to estimate past densities. Although these reserves presumably approach an intact state, the wildlife populations within these reserves may, arguably, be depressed relative to the past due to colonial and pre-colonial hunting (Spinage 2012), and disruption of migration routes and habitat transformation. Therefore, past herbivore biomass may have been underestimated. Furthermore, global paleoecological studies provide evidence to suggest a decline in mega-faunal biomass since the Pleistocene, partially attributing this to the expansion of human populations on the earth and intensified fire regimes (Gill *et al.* 2009). The proxy for herbivore prevalence in such studies is the presence in lake and cave sedimentary deposits, of spores of the fungal genus *Sporormiella*, which requires herbivore digestion to complete its life cycle (Davis 1987). However, *Sporormiella* spore abundance cannot simply be equated to herbivore biomass since spore abundance is also influenced by climatic and topographic factors (Davis & Shafer 2006).

Nevertheless, early colonial records of herbivore populations, which were already reduced from hunting by indigenous peoples (e.g. Cramer & Mazel 2007; Spinage 2012), suggest higher animal numbers and densities compared to the present. Phrases used by early hunters to describe herds of game in southern Africa ca. 19th century include: “immense numbers”, “country swarmed with game”, “numbers impossible to estimate”, “thousands and tens of thousands”, “100 000 seen from a wagon at one time”, "half a million wildebeest within a circle of 12 miles in circumference" (Skead *et al.* 2007). Large densities were often reported during large migrations such as that of the "trekbokken" (springbuck) of the Karoo (South Africa). Fraser (1922), writing of a migration observed during 1849 stated "… we were awakened one morning … by the trampling of thousands of all kinds of game-wildebeest, blesbok, springboks, quaggas, elands, antelopes of all sorts and kinds ... as far as the eye could see covered the whole country, grazing off everything eatable before them … It took about three days before the whole of the trekbokken had passed". Although such reports may include hyperbole, the consistency between them suggests an element of truth. It would be hard to write similar stories about herbivore herds in reserves today, without the aid of hallucinogens.

Climate has been the dominant driver of fire prevalence since the last glacial maximum (Power *et al.* 2008). However, it is reasonable to conclude that humans have increased fire frequency (Bird & Cali 1998; Mouillot & Field 2005), and that mid-Holocene ecosystems were less fire-driven and more herbivory-driven than present managed rangelands. Indeed, paleoecological studies that use multiproxy analyses associate increased charcoal densities in sedimentary deposits with human expansion across the globe (Thevenon *et al.* 2010). In Africa, deposits from Lake Masoko in Tanzania indicate a major influx of charcoal deposits synchronous with the Late Iron Age and agricultural innovations between 1.8 and 0.6 kyr BP (Thevenon *et al.* 2003). Apart from increasing fire ignition frequency (Bowman *et al.* 2011), humans contributed to releasing fire from its competitive relationship with herbivory through increased hunting. For example, in Australia (Rule *et al.* 2012) and America (Robinson *et al.* 2005; Gill *et al.* 2009), vegetation change during the Pleistocene-Holocene has been attributed to the indirect effect of relaxed herbivory pressure induced by human hunting and consequent increases in fire. However, widespread declines in fire over the past century suggest that agriculture and intensive grazing might have reduced fire spread more recently (Archibald *et al.* 2012; Marlon *et al.* 2013).

It is thought that the fire and herbivory interactions in near-pristine African wildlife reserves approximate mid-Holocene ecosystems (Hempson *et al.* 2015a), in contrast to intensively managed rangelands where the form and function of fire and herbivory have been altered. In wildlife reserves, the interaction between herbivory and fire is partly facilitative, but largely competitive (Archibald & Hempson 2016). Fire non-selectively removes both unpalatable and palatable herbaceous biomass (Spasojevic *et al.* 2010), thereby excluding herbivory. However, burn scars facilitate nutrient-rich grass regrowth with increased leaf:stem ratios (Van de Vijver *et al.* 1999), which is of particular nutritive value to herbivores during the dry season (McNaughton 1985). Grazers compete with fire by removing the herbaceous layer that is fuel for fire. However large browsers, such as elephants, open up relatively closed-canopy woody savannas, thereby promoting herbaceous growth and consequently greater fuel loads (Beuchner & Dawkins 1961; Staver *et al.* 2009; Bond & Van Wilgen 2012).

African shrub-dominated grasslands and tree-dominated savannas have been shown to exist as alternative stable states driven as much by disturbance regimes, such as fire and herbivory, as they are by climate and soil (Dantas *et al.* 2016). For example, within a climatic envelope suitable for both grasslands and savannas, any factors acting to reduce fire (e.g. grazing) will increase the probability of a savanna (McNaughton 1984). Similarly, fire-prone tall-grass and herbivore-prone short-grass alternative stable states within the savanna herbaceous layer have been identified and experimentally manipulated (Donaldson *et al.* 2017). Given that the herbivory-fire interaction is more competitive than facilitative (Archibald & Hempson 2016), I expect these two alternative stable states to be driven by thresholds of herbivory, beyond which fire will be largely excluded from a system, and *vice versa*. The two states are thus likely to contain structurally and compositionally different vegetation in the herbaceous and woody layers.

The herbaceous layer of a herbivore-dominated alternative state within savannas is characterised by herbivory-adapted, perennial shrubs and grasses with low-growth forms (Dublin *et al.* 1990; Liedloff *et al.* 2001; Anderson *et al.* 2007; Asner *et al.* 2009; Sankaran *et al.* 2013). The dominant species in this herbivore-dominated stable state are characterised by traits enabling rapid recovery from herbivory, such as stoloniferous (e.g. *Digitaria eriantha*) or rhizomatous (e.g. *Setaria incrassata*) grasses (Diaz *et al.* 2007; O'Connor *et al.* 2014). The nutrient-rich regrowth following defoliation encourages repeated herbivory and establishes grazing lawns (McNaughton 1984; Staver *et al.* 2012; Hempson *et al.* 2015b). In addition, the lower C:N ratios decrease foliar structural carbon and plant bulk density, thereby inhibiting flammability (Schwilk 2015). A fire-dominated alternative state would promote a herbaceous layer characterised by fire-tolerant taller bunch grass species (e.g. *Hyparrhenia filipendula*) that re-sprout vigorously from stored reserves after a fire (Archibald *et al.* 2005; Anderson *et al.* 2007). These grasses are of low nutritive quality (due to lower leaf:stem ratios) and inhibit herbivory, resulting in high levels of standing biomass to fuel fires and thereby enforcing a positive feedback loop, promoting a fire-driven system (McNaughton 1985).

The consequences of herbivore- or fire-dominance for the woody vegetation layer are contested in the debate about the ecological drivers of woody plant encroachment. Relaxing herbivore pressure and increasing that of fire has been proposed as method to prevent woody encroachment (Bond & Midgley 2001; Roques *et al.* 2001; Wiegand *et al.* 2005). However, a four-decade fire manipulation experiment in four different savanna ecosystems in KNP found no significant change in woody cover density (Higgins *et al.* 2007). This may be due to the interactive effects of herbivory and fire on seedling emergence, survival and recruitment which can both increase and decrease woody encroachment (van Wilgen *et al.* 2003). Furthermore, 41-year herbivore exclusion experiments in KNP, South Africa, resulted in an 11-fold increase in woody canopy cover (Asner *et al.* 2009). Indeed, herbivory, specifically in the form of browsing, is suggested to have been a key driver in the historical evolution of savannas, suppressing trees and releasing grasses (Charles-Dominique *et al.* 2016). Herbivory-driven states can reduce woody encroachment if both grazing and browsing act to simultaneously prevent seedling establishment and reduce recruitment of woody plant species (Van Langevelde *et al.* 2003; O'Connor *et al.* 2014). For example, Augustine & McNaughton (2004) showed that a community of native browsers ranging from selective species (e.g. dik-diks; *Madoqua* spp.) to large bulk feeders (elephants; *Loxodonta africana*) can supress shrub encroachment on commercial rangeland in Kenya.

The transition of one stable state to another occurs when a critical threshold is reached in response to a shift in a climatic or biotic driver (Hirota *et al.* 2011). The resilience to this transition between fire- and herbivore-dominated stable states, might be strongly mediated by spatiotemporal variation in water and nutrient availability (Krawchuk & Moritz 2011). Fire has been observed as a dominant driver of vegetation structure above ca. 650 mm annual rainfall over African savannas (Sankaran *et al.* 2005). Currently, fire consumes 5.8 times more dry matter than herbivory across sub-Saharan Africa which equates to 103 g m^{-1} (Fig. 2.1). The median regression line of this relationship changes across the rainfall gradient, where herbivores consume more biomass under ca. 700 mm MAP, which is very close to the threshold reported by Sankaran *et al.* (2005). Fire-dominance peaks between ca. 700 and 1500 mm MAP which are mesic savannas in central and east Africa (Fig. 2.1). In mesic savannas, leached low-nutrient soils support unpalatable vegetation with high C:N ratios (Bell 1982; East 1984), thereby inhibiting herbivory and promoting fire (Du Toit 1995). Thus, mesic fire-dominated rangelands may be resilient to change and resist switching to a herbivore-dominated alternative stable state (Fig. 2.2A and red areas in Fig. 2.1). The opposite is true for arid, less leached, nutrient-rich savannas with palatable vegetation that sustains an abundance of herbivores, which keep fuel loads down and prevent the occurrence and spread of fire (McNaughton 1984; Du Toit 1995). Consequently, semi-arid grasslands at ca. 700 mm MAP, which are currently neither herbivore nor fire-dominant (grey areas in Fig. 2.1), may switch faster to a herbivore-dominated stable state (Fig. 2.2B and light green areas in Fig. 2.1) under increased herbivore pressure.

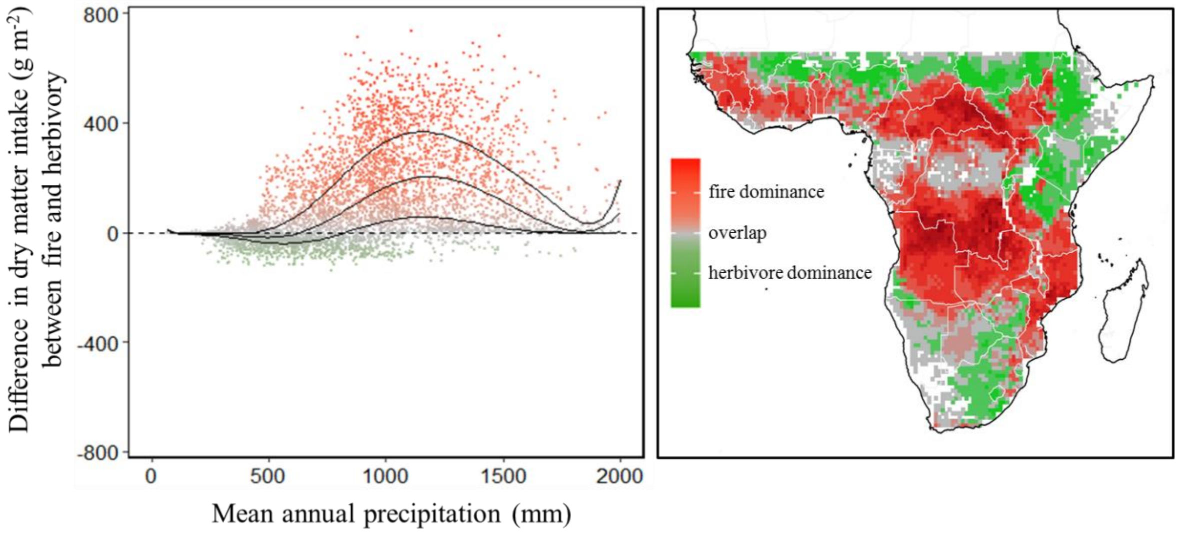


Figure 2.1 The difference in dry matter intake (g m^{-2}) between fire and herbivory for each quarter-degree-square over Africa, represented across mean annual precipitation (left) and spatial (right) gradients. The 25, 50 and 75% quantiles are represented by solid black lines (left). The data, supplied by Archibald & Hempson (2016), was derived from satellite imagery, and wildlife and livestock census data.

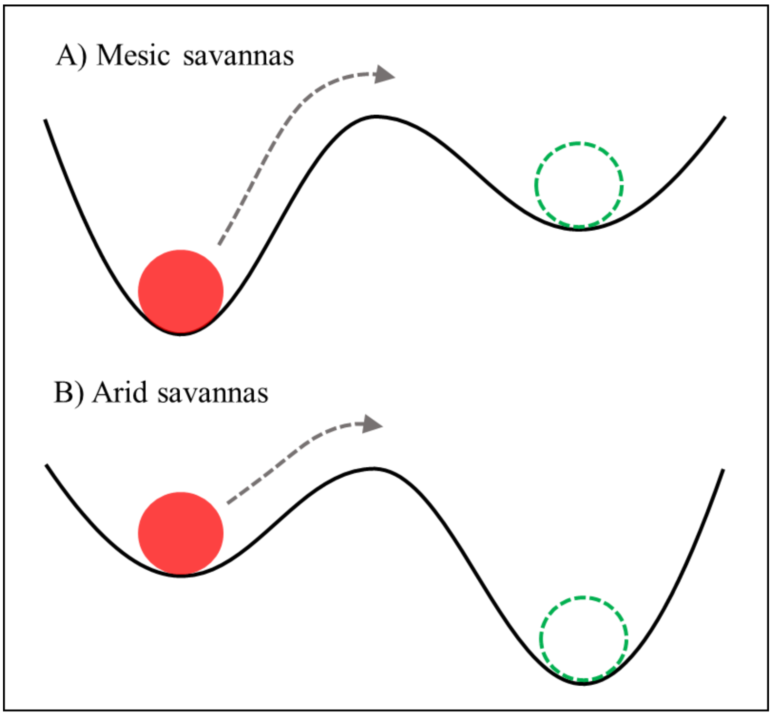


Figure 2.2 Two-dimensional ball-in-cup diagrams comparing notional resilience to a shift in alternative stable states within mesic and arid savannas. (A) Mesic savannas contain leached, nutrient-poor soils, which are prone to fire, and may thus display greater resilience to shifting to herbivore-dominance. A greater increase in herbivory is required to push the ball out of the cup. (B) In arid savannas, nutrient-

rich soils support higher quality forage which promotes herbivory and consequently reduces fuel for fire. In arid savannas that currently exist as fire-dominated stable states, less change in herbivory is indicated to be required to shift the ball out of the cup into a herbivore-dominated state. Thus, fire-dominated states are more stable in mesic than arid savannas. I suggest that grey and light-red areas on the map, characterising co-dominant and slightly fire-dominant states, respectively, can be switched to herbivore-dominance through less management intervention than would be required for heavily fire-dominated areas. Management intervention may include adaptive manipulation of herbivore densities over time and space to maintain an appropriate carrying capacity for the rainfall and soil nutrient status of the area, occasional use of fire, and including a diversity of herbivore functional guilds.

Rewilding and ecosystem function

The principle of rewilding ecosystems with extirpated species (Rosenzweig 2003; Svenning *et al.* 2016) or evolutionary disturbances (Fuhlendorf *et al.* 2009; Scasta *et al.* 2016) has not been directly considered for African rangelands. An obvious commercial benefit of promoting a herbivory-dominant alternative state is potentially greater animal production and profits, whereas benefits to other ecosystem services are dependent on abiotic and edaphic conditions. As we have seen, the effects of herbivory-dominance may vary over time and space along nutrient and rainfall gradients (Archibald & Hempson 2016). As an example, I will compare the effects of fire and herbivory on nutrient cycling in African savannas to explore whether a herbivore-dominant alternative state may improve ecosystem function.

The mechanisms through which herbivory enhances nutrient cycling include dung and urine deposition and trampling (McNaughton *et al.* 1988; Singh *et al.* 1991), litter deposition and changes in stochiometric feedbacks (Krumins *et al.* 2015), plant physiological responses (Holland *et al.* 1992), and changes in species composition (Anderson *et al.* 2007). Plants exhibit compensatory growth after grazing and, after passing through the herbivore gut, this biomass returns to the soil in a form (dung and urine) that enhances substrate decomposition and mineralisation rates. Plant litter contributed to the detrital pool through “sloppy” or partial feeding enhances microbial-mediated metabolism and N mineralisation (Krumins *et al.* 2015). This is further mediated through concomitant changes in soil temperature and moisture associated with litter cover which increases microbial activity and mineralisation (Sitters & Venterink 2015). At a larger scale, herbivory has been shown to be associated with higher plant nutritive quality relative to fire, due to a change in species composition favouring lower-biomass species with lower C:N and C:P ratios (Anderson *et al.* 2007).

Fire causes a loss of C and N in soil through volatilisation (Kauffman *et al.* 1994; Bustamante *et al.* 2006; Chen *et al.* 2010), and a conservation of Na and P (among other elements) through pyromineralisation (Hartshorn *et al.* 2009). Using satellite-derived estimates, Chen *et al.* (2010) found that fire emissions in savannas account for a net N loss equivalent to 22% of biological N-fixation. Although some nutrients (e.g. P) are less volatile under fire than others, these may not become available in soils due to wind displacement of ash, leaching, or changes in soil structure (DeBano & Conrad 1978; Anderson *et al.* 2007; Resende *et al.* 2011). Consequently, because mycorrhiza are strongly linked to P acquisition in plants, P cycling to plants would be limited (Koide & Kabir 2000). Also, the strong negative relationship between fire frequency and the mycorrhizal colonisation of perennial grass roots in African savanna may be due to soil crusting, increased run-off and decreased moisture following fire (Hartnett *et al.* 2004).

Long-term decadal studies directly comparing the effects of fire and herbivory on nutrient cycling at different intensities do not exist (Pellegrini *et al.* 2015). However, in a two-year manipulation experiment in tallgrass prairie, Hobbs *et al.* (1991) calculated that using herbivory instead of fire to remove biomass saves ca. 1 g m^{-2} yr^{-1} N that would otherwise have been lost as a result of volatilisation during burning. Assuming that cattle need 0.014 g N per gram of fresh body weight (Berg & Butterfield 1976), and that animals could potentially utilise 50% of standing plant biomass (Cordova *et al.* 1978) and efficiently convert it to body weight, this equates to 357 kg meat productivity lost per hectare burnt instead of grazed. Apart from N, ca. 45 million ton of grassland biomass is burned every year in southern Africa (Scholes *et al.* 1996). Assuming grazing livestock in Africa have a feed-use efficiency of ca. 1 ton of dry grass matter per kilogram of mean (Herrero *et al.* 2013) this represents a maximum potential loss of 45 thousand tons of meat production per year. However, this calculation relies on the assumption that all burnt vegetation biomass is palatable to livestock. In mesic savannas, much of the burned biomass is tall tussock grasses that are not palatable to domestic livestock, and in arid areas, a large portion of grass biomass that is burned might be constituted of unpalatable stems. Even if one assumes that the burnt biomass was likely to be largely unpalatable, particularly in mesic areas, and that it would only be moderately utilised (e.g. 25-50%, Hart et al. 1993), this is still a significant economic loss.

Comparing studies on the independent effects of fire and herbivory on soil nutrient pools reveals that herbivory conserves more soil C and N. In a meta-analysis of 115 published studies from around the globe, Zhou *et al.* (2016) found that livestock grazing decreased soil C and N pools by 10.3 and 13.4%, respectively, relative to ungrazed controls, whilst increasing N mineralisation and nitrification by 22 and 24%. Equivalent meta-analyses for fire effects do not exist, but a 58 year annual fire experiment in the KNP of South Africa produced soils depleted of C and N by 25 and 62% relative to unburnt plots (Pellegrini *et al.* 2015). This equates to at least a two-fold and four-fold conservation of soil C and N, respectively, when savannas are grazed instead of being burnt. Although herbivory and fire both deplete soil nutrient pools relative to an undisturbed control, grazing enhances mineralisation whereas fire does not have consistent effects on N (Coetsee *et al.* 2008) or P (Hartshorn *et al.* 2009; Holdo *et al.* 2012) mineralisation.

Management implications

The management implications of rewilding savannas with mid-Holocene herbivore densities are difficult to ascertain because the exact type and spatiotemporal patterns of herbivory that occurred in mid-Holocene ecosystems are unknown. Some resource managers have attempted to derive grazing practices based on ecological principles from observations of supposedly intact ecological systems, e.g. pyric herbivory (Fuhlendorf *et al.* 2009), opportunistic management (Westoby *et al.* 1989), holistic planned grazing (Savory 1983), and other forms of time-controlled, short-duration rotational grazing (Table 2.1 and 2.2; Media Gallery P1). I distil a few basic principles from these management practices, the colonial records, and research within near-pristine wildlife reserves and suggest these principles are necessary to sustain a herbivory-dominant ecosystem state without compromising rangeland productivity and ecosystem services.

Table 2.1 Summary of existing grazing management systems.

System	Description	Reference
Continuous grazing; season-long grazing	Access to all or half of grazing areas for at least a full season. Particularly common in communal rangelands and wildlife areas.	De V. Booysen 1967; Tainton 1999
Rotational grazing	Grazing area divided into multiple paddocks to create reoccurring periods of grazing and rest. Generally managed according to a fixed or adaptive rotation plan.	Merrill 1954; Tainton 1999; Briske *et al.* 2008
High- and ultra-high density grazing; cell grazing; holistic planned grazing; short-duration grazing; non-selective grazing	A variant of rotational grazing with higher stocking densities (more camp divisions and shorter grazing durations) of hundreds or thousands of animals per hectare. Often associated with an adaptive management approach.	Acocks 1966; Savory 1983; Voisin 1988; Briske *et al.* 2008
Opportunistic management; pyric herbivory	A non-equilibrium approach where grazing management decisions are made in response to spatiotemporal patterns in resource availability at varying scales. Fire may be used to create a shifting mosaic of heavily-grazed burnt patches among taller undisturbed patches. Water points may be moved to achieve similar effects.	Westoby *et al.* 1989; Illius & O'Connor 1999; Vetter 2005; Fuhlendorf *et al.* 2009; Laca 2009; Limb *et al.* 2011; Fynn 2012

Table 2.2 Cont.

System	Claimed benefits	Criticisms
Continuous grazing; season-long grazing	Increased grazing selectivity for palatable plants and subsequent increased animal production; low management inputs	Increased woody plant encroachment through reduced competition from grass; overgrazing and loss of palatable species
Rotational grazing	Increased forage utilisation; reduced grazing selectivity and subsequent loss of palatable species; sustained species diversity	Lack of empirical evidence; existing evidence displays large variation and is often confounded by other variables; reduced selection for palatable plants results in animal weight loss
High- and ultra-high density grazing; cell grazing; holistic planned grazing; short-duration grazing; non-selective grazing	Increased forage utilisation; reduced grazing selectivity and subsequent loss of palatable species; increased trampling and subsequent enhanced water infiltration and soil nutrient cycling; reduced woody plant encroachment through seedling mortality	Lack of empirical evidence; increased trampling damages biological soil crusts and increases soil compaction; higher infrastructure costs; potential for increased animal stress and reduced fecundity
Opportunistic management; pyric herbivory	Results in functional heterogeneity and consequent resilience to environmental stresses; conservation of biodiversity; increased forage quality on post-burn grazing patches	Adaptive approach makes experimental testing difficult; lack of empirical evidence for increased production; loss of species and soil erosion on heavily-grazed patches

Diversifying the type of herbivory through introducing mixed livestock herds has not been directly accounted for in the dominant rangeland management strategies (Table 2.1 & 2.2). Mixed herbivory may approximately imitate the large variation in herbivore functional types that would have been present in mid-Holocene savannas (Du Toit & Cumming 1999). Currently, higher rainfall savannas support a much lower herbivore biomass than in the past (Hempson *et al.* 2015a). This is largely due to the loss of large browsers in farmed rangelands, which has also been identified as a contributing factor to widespread woody plant encroachment across southern Africa (O'Connor *et al.* 2014). Furthermore, a comparison between domestic cattle herbivory and wildlife herbivory in the KNP of South Africa found that mono-specific herbivory led to increased tree cover and lower grass foliar N content relative to multi-species herbivory (Baumgartner *et al.* 2015). A possible improvement could involve introducing a combination of grazers, browsers and generalist livestock along with wildlife (Augustine *et al.* 2011; Fynn *et al.* 2016) onto rangelands to sustain a productive herbivore-dominant stable state.

The strong herding behaviour of wild herbivores, that evolved in response to predatory pressures and the need for migration (Savory 1983), is perceived to be less evident in domesticated livestock and this may have significant effects on foraging patterns and soil and vegetation responses. It may be effective to increase herbivore density per unit time through intensive rotational grazing management (Table 2.1 & 2.2). Claims that the rotational grazing strategies will increase productivity whilst maintaining ecosystem processes have been contested and are currently both supported (e.g. Teague *et al.* 2013) and contradicted (e.g. Briske *et al.* 2008; Briske *et al.* 2011). Savory (1983) and others propose increasing grazing densities to increase animal “hoof impact”, which would promote nutrient and water cycling through litter cover, soil surface chipping and dunging. However, other studies have shown that high grazing densities can cause soil compaction, reduce water infiltration and damage biological soil crusts (Warren *et al.* 1986; Du Toit *et al.* 2009; Carter *et al.* 2014). The effects of animal densities on soil are minor compared to the defoliation effects (Greenwood & McKenzie 2001), and the rotational grazing debate has largely centred around grazing selectivity and the resulting long-term changes in species composition. Species composition responds strongly to stocking rate (O'Reagain & Turner 1992), but is largely unaffected by the grazing management system (Morris & Tainton 1996; Hickman *et al.* 2004; Dowling *et al.* 2005). This may be because it is difficult to reduce animal selectivity at the feeding station scale (Kirby & Webb 1989; Walker *et al.* 1989; Morris & Tainton 1996). However, at the patch and landscape-scale, rotational grazing can reduce selectivity and shows potential to reduce loss of palatable species (Teague *et al.* 2004). Thus, introducing a variety of animal densities through rotational grazing to imitate the herding behaviour of wild herbivores may benefit long-term rangeland production.

Alternatives to traditional rotational grazing strategies (Table 2.1 & 2.2) that attempt to reduce selection and vegetation heterogeneity are emerging primarily in the rangeland conservation literature. The maintenance of ecosystem function and biodiversity in historical ecosystems have often been attributed to landscape heterogeneity (Christensen Jr 1997). Diversifying disturbance patterns to change vegetation structure over the landscape may imitate the high levels of ecosystem function and biodiversity that were present in mid-Holocene ecosystems (Fuhlendorf & Engle 2001). This might involve adopting an adaptive and opportunistic management framework that implements variable herbivore pressures over time and space to shift non-equilibrium rangelands into desired alternative states (Westoby *et al.* 1989). Movable watering points can achieve something similar through imitating ephemeral water resources that characterised mid-Holocene savannas. Small fires may also be used in this regard to create a mosaic of nutrient-rich regrowth patches over the landscape, possibly leading to grazing lawns (Archibald *et al.* 2005). Manipulating grazing return-periods from a day (as would be the case on grazing lawns) up to a year or longer (as would be the case with seasonal migrations) depending on the vegetation composition present will utilise the suite of plant phenotypes that evolved during the mid-Holocene.

There is a balance to be found between the competing equilibrium and non-equilibrium paradigms in ecology and rangeland management (Vetter 2005). The density-dependent regulation of livestock numbers (equilibrium theory) should be adaptable to stochastic factors such as rainfall and fire (non-equilibrium theory). For example, de-stocking during drought and re-stocking in high rainfall years imitates the natural fluctuation in wild populations and prevents over-utilisation of forage (Skovlin 1987; Westoby *et al.* 1989; Jakoby *et al.* 2014). Instead of managing for livestock numbers to be in equilibrium with the ecological carrying capacity, there is potential for rangeland managers to maintain equilibrium dynamics within alternative stable states (Briske *et al.* 2017). John Acocks once remarked that African rangelands might be “understocked and overgrazed” due to a perceived lack of grazing management leading to high selectivity for, and consequent overgrazing of, palatable species (Hoffman & Cowling 2003). Altering the spatiotemporal pattern of herbivory may afford an increase in overall abundance and stocking rate over a landscape without causing rangeland degradation. Although matching the stocking rate to the carrying capacity (forage base) of an area remains, and should remain, a guiding principle in rangeland management (Briske *et al.* 2017), a landscape can be maintained under a mosaic of animal densities leading to multiple fire- and herbivore-dominant stable states depending on the rangeland managers objectives. The resilience of current fire-driven systems to a shift to herbivore-dominance will determine the lag-time for the change to take effect, and the intensity with which the above-mentioned practices should be implemented. For example, in a mesic, fire-dominant system, more intense herbivory and fire suppression might be required over a longer time to shift the system to herbivore-dominance (Fig. 2.2). In arid rangelands the shift might be faster.

Conclusion

I thus question the widespread assumption that frequent fires are a necessary and “natural” management tool to address ecosystem problems such as woody plant encroachment, induced by reduced diversity and density of herbivores. Prolonged rewilding of some African rangelands with mid-Holocene herbivory pressure and diversity may shift a system into an alternative stable state which, relative to a fire-dominant state, may enhance nutrient cycling, conserve soil nutrient pools and benefit productivity. The conservation of nutrients and alteration of vegetation communities might have long-term consequences on the global carbon budget and climate change. However, the shift to a herbivore-dominant state should not imply the suppression of fire, particularly in mesic savannas where fires facilitate herbivory by removing unpalatable forage biomass. Although briefly considered here, the conversion of biomass, particularly outside of mesic areas, that would otherwise have been burnt, into meat may have economic and societal impact of global significance. Sustaining this intense herbivory may involve diversifying livestock feeding guilds, increasing herding densities and spatiotemporal herbivory patterns, and promoting adaptive heterogeneous management practices.

Chapter 3: Drivers of woody plant encroachment over Africa

This chapter has been published in *Nature Communications*:

Venter, Z.S., Cramer, M.D. & Hawkins, H.J. (2018) Drivers of woody plant encroachment over Africa, *Nature Communications*, 9(1): 2272.

Abstract

While global deforestation induced by human land use has been quantified, the drivers and extent of simultaneous woody plant encroachment (WPE) into open areas are only regionally known. WPE has important consequences for ecosystem functioning, global carbon balances and human economies. Here I report, using high-resolution satellite imagery, that woody vegetation cover over sub-Saharan Africa increased by 8% over the past three decades and that a diversity of drivers, other than CO_2, were able to explain 78% of the spatial variation in this trend. A decline in burned area along with warmer, wetter climates drove WPE, although this is mitigated in areas with high population growth rates, and high and low extremes of herbivory, specifically browsers. These results confirm global greening trends, thereby bringing into question widely-held theories about declining terrestrial carbon balances and desert expansion. Importantly, while global drivers such as climate and CO_2 may enhance the risk of WPE, managing fire and herbivory at the local-scale provides tools to mitigate continental WPE.

Introduction

Continental-scale changes in woody plant cover have been mapped for forests >5 m in height (Hansen *et al.* 2013), indicating an overwhelming deforestation trend induced by human land use (Foley *et al.* 2005). A less well-known, yet equally important global trend is gradual woody plant encroachment (WPE), occurring in non-forest biomes (Stevens *et al.* 2017). In Africa, WPE has been identified as a concern for rangeland management since the early 20th century and has the potential to reduce rangeland carrying capacities of wild and domestic grazers through the displacement of herbaceous forage by trees and shrubs. On the other hand, WPE may significantly contribute to forage for wild and domestic browsers, household fuel-wood provision, and may lead to increased carbon sequestration, with consequences for global carbon budgets and climate change (Archer *et al.* 2017). In order to manage the effects of WPE on these diverse local and global ecosystem services, we need to understand what is driving it.

The drivers of WPE are poorly-understood compared to those of deforestation where human-induced clearing is dominant. Rising atmospheric CO_2 (Bond & Midgley 2000; Buitenwerf *et al.* 2012) and associated climatic changes, coupled with changing fire and herbivore management regimes, have been proposed as dominant drivers (O'Connor *et al.* 2014; Archer *et al.* 2017; Devine *et al.* 2017; Stevens *et al.* 2017). While homogenous global CO_2 enrichment may enhance tree growth (Ainsworth & Long

2005), the trends in WPE are spatially variable, suggesting other local- or regional-scale drivers. For example, increases in rainfall have been shown to correlate with WPE, while the influence of trends in temperature are less clear (Brandt *et al.* 2017). Agriculturally-induced transformation of Africa's unique set of functional herbivore guilds (Hempson *et al.* 2017), and the alteration of fire regimes (Archibald *et al.* 2012) may shift systems into tree-dominated states at the local-scale. However, quantifying these drivers at continental scales has been limited by the paucity of local-scale studies (Stevens *et al.* 2017) or continental analyses relying on low resolution remotely sensed data (Brandt *et al.* 2017). The lack of spatially explicit measures of the magnitude and scale of WPE has made it difficult to draw generalised conclusions about its causes, and to identify the potential for the use of local drivers (i.e. fire, herbivory and human disturbance) as management tools to mitigate the putative effects of global (i.e. climatic) drivers on WPE.

I mapped change in woody plant cover, excluding closed forest (more than 40% cover by trees taller than 5 m), at 30 m resolution for Africa over the past three decades. I considered a suite of potential drivers to explain this change, including CO_2 as a global driver and other local- or regional-scale drivers that have received less attention (Fig. S3.1). I report that non-forest biomes in Africa have undergone a net 8% increase in woody plant cover over the past three decades, although the magnitude and direction of this trend was spatially variable. During the same period there have been significant increases in CO_2, rainfall and herbivory, and reductions in burned area. I develop a machine learning model to elucidate these complex correlations and find that a diversity of drivers other than atmospheric CO_2 are able to explain 78% of the spatial variation in African woody cover change. WPE has been exacerbated by warming and wetting climates associated with global climate change, but local changes in fire, herbivory and direct anthropogenic disturbance (e.g. deforestation) predominate. Altering fire and herbivory management regimes thus has the potential to mitigate WPE.

Methods

Fractional woody cover prediction

The study area included sub-Saharan Africa, totalling 20.5 Mkm^2, equivalent of 22.8 billion Landsat pixels. Woody plant cover was defined as fractional woody cover of 30 x 30 m squares, defined by the Landsat pixel grid. The dynamics of tree cover change have been comprehensively explored using remote sensing techniques for forest biomes (Hansen *et al.* 2013). Given that the potential for WPE to occur in areas already saturated with tree cover is negligible and that my aim was to investigate WPE and its drivers, I excluded the forest biome from my analysis. Pixels with >40% cover by trees of >5 m in height were considered as closed forest (FAO 2001; Bastin *et al.* 2017) and excluded using data from the Global Land Cover Facility (Sexton *et al.* 2013). Tree cover may be unable to fully distinguish forests from densely wooded savannas (Griffith *et al.* 2017), however, these ecotonal boundary areas are relatively small compared to the total area occupied by true non-forest biomes. Thus, the erroneous masking of densely wooded savannas was expected to have little effect on the continent-wide analysis. Forestry areas were defined as pixels that have both lost and gained woody cover between 2000 and 2015 using global forest cover change data derived from Hansen *et al.* (2013) and were excluded from analysis. Urban, water, wetland, cropland, and natural-cropland mosaics were also excluded from the analysis using the MODIS landcover product (Friedl *et al.* 2010). This combined pixel mask (Fig. S3.2) was applied to all Landsat- and MODIS-derived data in this analysis.

The remote sensing analysis was performed using the Google Earth Engine cloud computing platform for earth observation data analysis (Gorelick *et al.* 2017). The near-complete set of Landsat surface reflectance data available for Africa (1986-2016) from the USGS Earth Resources Observation and Science archive (Woodcock *et al.* 2008) were analysed to identify change in fractional woody cover. I analysed six epochs of Landsat data between 1986 and 2016 (Fig. S3.1). Landsat 5 Thematic Mapper (TM) was used for the 1986-1991, 1991-1996, and 1996-2001 epochs. Landsat 7 Enhanced Thematic Mapper Plus (ETM+) was used for the 2001-2006, 2006-2011, and 2011-2016 epochs. Data gaps in the 2011-2016 epoch were filled by merging the Landsat 7 ETM+ collection with the Landsat 8 Operational Land Imager (OLI) collection using published cross-calibration coefficients for surface reflectance (Roy *et al.* 2016). A cloud mask and confidence quality assessment data were used to create cloud-free image collections which were used to derive per-pixel time-series spectral metrics for each epoch. Temporal reflectance data were derived from visible, near infrared, and shortwave infrared bands, as well as three vegetation indices, namely normalised difference vegetation index (Tucker 1979), soil-adjusted vegetation index (Huete 1988), and enhanced vegetation index (Liu & Huete 1995). Vegetation indices have been used extensively in vegetation cover mapping and landcover classification (Gómez *et al.* 2016). Time-series metrics derived from these included the minimum, maximum and selected percentile values (10, 25, 50, 75 and 90% percentiles) and the mean reflectance values for observations between selected percentiles (10-25%, 25-50%, 50-75%, 75-90%, and 25-75%). Similar time-series metrics have been successfully used in forest cover mapping using Landsat data (Broich *et al.* 2011; Potapov *et al.* 2012; Hansen *et al.* 2013). To further assist in differentiating between woody and herbaceous cover, which have different phenological metrics (Helman *et al.* 2015), I derived the variance and range in vegetation indices.

Time-series metric data were used to train a Random Forest (RF) regression model to predict fractional woody plant cover for each 5-year epoch (Fig. S3.1). RF is a supervised classification and prediction tool that has been extensively used because it avoids overfitting and can incorporate non-parametric data (Belgiu & Drăguţ 2016). Training data were derived from image interpretation methods using very high spatial resolution images derived from Google Earth. I generated 4000 randomly scattered 30 x 30 m sampling quadrats, aligning with the Landsat pixel grid, within the unmasked areas for the given Landsat epoch collection. I manually classified the fractional woody plant cover of each sampling quadrat by identifying woody plant canopies using texture, colour and canopy shadows as identification cues (Fig. S3.9). I estimated the woody plant cover to the closest percentile class (0, 0.25, 0.5, 0.75, 1). Sampling quadrats were excluded if the image acquisition date fell outside of the epoch date range or if there was any uncertainty in designating a fractional woody plant cover value. A separate RF classifier was trained for Landsat 5 TM, Landsat 7 ETM+, and gap-filled Landsat 7 ETM+ with Landsat 8 OLI collections. RF accuracy assessment traditionally employs internal cross-validation between in-bag samples used to train the trees, and out-of-bag samples used for model validation (Breiman 2001). However, recent literature suggests internal cross-validation may over-estimate model accuracy, and suggest validation against a testing dataset independent of that used in model construction (Fassnacht *et al.* 2014; Belgiu & Drăguţ 2016). The RF regression models produced high accuracies when using both internal and independent hold-out datasets for validation (Table S3.2).

The RF models were used to predict fractional woody plant cover across Africa at 30 m resolution for each epoch. Pixel-level change was defined by the slope of the linear regression between fractional woody cover and year. This is the same metric of change employed by other remote sensing analyses of forest cover change (Hansen *et al.* 2013). Although the response variable in the linear regression was bounded (i.e. proportional woody cover), the model assumptions were checked and satisfied, thus data were not transformed prior to fitting the model. Nevertheless, the analysis of drivers of woody cover change was performed on both untransformed and logit-transformed woody cover data, and both yielded similar results. Estimates of data quality were calculated for each pixel based on the number of available Landsat time-points for the linear regression, and the total number of pixels used to derive time series metrics (Fig. S3.10).

Environmental covariates

To explain the change in fractional woody cover I obtained a broad set of climatic, edaphic, biotic, and demographic explanatory variables (Fig. S3.6 and S3.7). All variables were sourced and analysed within the Google Earth Engine platform, except for herbivore density, protected area status and soils data, which were obtained from sources documented below and analysed within R (RCoreTeam 2016) and Quantum GIS (QGIS 2014).

High temporal resolution climatic data were obtained from the Global Land Data Assimilation System (GLDAS) produced by NASA at 0.25° every 3 h between 1986 and 2016 (Rodell *et al.* 2004). Variables included were surface temperature, air temperature, rainfall, potential evaporation rate, soil moisture, and wind speed. Additional rainfall data were obtained from the Tropical Rainfall Measuring Mission (Huffman *et al.* 2010) and Climate Hazards Group (CHIRPS; Funk *et al.* 2014) for comparison with GLDAS. Annual counts of extreme rainfall events, defined as any 5-day rainfall amount that exceeded the 95th percentile of all measurements for that grid cell (Zhai *et al.* 2005), were calculated. Rainfall variability was calculated as the standard deviation across both yearly and 5-hourly time-series. The extent to which rainfall is evenly distributed through the year was calculated as the precipitation concentration index (Oliver 1980) using data from the CHIRPS dataset. For each variable, I calculated the long-term average and the slope of the linear trend over time. WorldClim rainfall and temperature min, max, mean values for the driest, wettest, warmest and coldest quarters, and seasonality were also included (Hijmans *et al.* 2005).

Mid-troposphere daily CO_2 concentration data at 2 x 2.5° resolution were obtained from Atmospheric Infrared Sounder between 2010 and 2017 (Texeira 2009). The means and trends were calculated per grid cell, but after consideration were not included in the modelling procedure for the following reasons: the data were collected at lower spatial resolution than all other explanatory variables; they were collected for the mid-troposphere and thus the relevance to ambient ground-level CO_2 was questionable; and, unlike other bio-climatic variables, the range in the means (2 ppm) and temporal trends in CO_2 (0.35 ppm yr^{-1}) concentrations were very small (Fig. S3.11) in comparison to the CO_2 enrichment values necessary (>160 ppm) to induce significant changes in woody plant growth (Körner 2006). An attempt was also made to include the long-term CO_2 trend in the model, however, because this is spatially homogenous it had very low explanatory power and was thus excluded.

Edaphic data were derived from the 'SoilsGrid 1 km' global dataset (Hengl *et al.* 2014). These included depth to bedrock (R horizon); bulk density (kg m^3); cation exchange capacity (cmol kg^{-1}); clay and sand content (% gravimetric); soil organic carbon content (g kg^{-1}) and pH (in H_2O). The data for six soil depths were aggregated by depth-weighted averaging (i.e. averaged by weighting values for each depth-interval). Digital elevation at 30 m resolution from the Shuttle Radar Topography Mission (Farr *et al.* 2007) was used to calculate a terrain ruggedness index (Riley 1999), which measures the sum change in elevation between a pixel and its eight neighbouring pixels.

Herbivory data were supplied by Archibald & Hempson (2016) at 0.5° resolution. These included modelled grazer, browser, mixed feeder and total herbivore densities using the FOA livestock data (Robinson *et al.* 2014) and indigenous wildlife census data from reserves across Africa. To obtain a change layer for herbivore density, I constructed a boosted regression tree (BRT) model (see methods in following section) to hind- and forecast herbivore densities. The FAO reference year used in the dataset was 2005, thus the 2001-2006 epoch was used as the starting point for hind- and forecasting. The model was able to explain 72% of the total deviance in herbivore density. Explanatory variables included population density, normalised difference vegetation index, longitude, latitude, temperature, and rainfall, which contributed 25, 24, 22, 21, 5, and 3% to the explanatory power of the model, respectively. The slope of the linear trend in modelled herbivore density was calculated for each 0.5° grid cell. Despite the uncertainty in deriving herbivory trends, I found that its removal/addition in woody cover change models did not unduly influence model explanatory power. Removing change in herbivory from the model presented in Fig. 3.3 reduced the explanatory power by only 4%.

Fire data from the MODIS (MCD45A1.051) burned area monthly product at 500 m resolution (Roy *et al.* 2008) were used to derive the annual average and annual trend in mean annual burned area, fire frequency, and burn date per 0.5 x 0.5º square between 2000 and 2017. Due to technical problems on the MODIS satellite experienced during 2001 (Justice *et al.* 2002), I decided to exclude burned area for 2001 in my analysis. To derive trends in fire data that are representative of the study period (1986 – 2016), I followed the same approach as with herbivory and hindcast fire data using a BRT model. The model, trained on the mean fire data between 2000 and 2017, was able to explain 70% of total deviance. For further validation, a separate model, trained on 2006-2011 mean data, was used to predict burned area for 2001-2006 and 2011-2016 mean data. The adjusted R^2 of the linear regression between observed and predicted burned area for 2001-2006 and 2011-2016 was 0.66 and 0.72, respectively, thus corroborating the predictive capability of the model used for hindcasting. Explanatory variables included in the model were latitude, normalised difference vegetation index, population density, longitude, rainfall, and temperature, which contributed 24, 22, 17, 15, 14, and 8% to the explanatory power of the model, respectively. The equivalent analyses were conducted on fire intensity data from the Fire Information for Resource Management System dataset (Davies *et al.* 2009). All fires that fell within the data mask (Fig. S3.1) used in the woody plant cover analysis were excluded.

I determined the proportion of each 0.5º square covered by protected areas using data from Protected Planet (www.wdpa.org; Juffe-Bignoli *et al.* 2014). Half degree squares were classified into vegetation type (White 1983), ecoregion, and biome (Olson *et al.* 2001) based on the centroid of each grid cell. The average and trend in African population density between 2000 and 2015 at 1 km resolution was obtained from the Gridded Population of the World, Version 4 (GPWv4) dataset (CIESIN 2005).

Boosted regression tree modelling

To assess the interactions between explanatory variables and fractional woody cover change, I used BRTs (Fig. S3.1), which have been used extensively in ecological studies to analyse complex systems, including drivers of woody plant cover (Sankaran *et al.* 2008). BRTs are an advanced form of machine learning that iteratively fit and combine multiple regression tree models to improve predictive performance (Elith *et al.* 2008). An advantage of BRTs is their ability to ingest explanatory variables of multiple classes to model complex interactions with a given response without making assumptions about variable interactions, as is often the case with other forms of linear and non-linear modelling (Elith *et al.* 2008). All BRTs were fitted in R (RCoreTeam 2016), using the ‘dismo’ library following the procedure outlined by Elith *et al.* (2008).

Variables used in the modelling exercise were aggregated up to a common spatial resolution of 0.5°. Raw data with a resolution >500 m were resampled to 0.5° using bilinear resampling, and those with a resolution ≤500 m were reduced to the mean value per 0.5° grid cell. Data points were assigned a quality weighting based on the 30 m per-pixel quality layers (Fig. S3.10) and the number of unmasked pixels per 0.5° cell. This was used as a weighting variable by assigning it to the "site.weights" call in the BRT model to prevent low quality data with small samples sizes from having an undue influence on the model fitting and prediction. Data with a quality score less than the 0.25 percentile value were excluded from the BRT analysis.

Combined and separate models were fitted with explanatory variables termed "drivers" and "facilitators" of woody cover change. I distinguished between explanatory variables with a temporal component (e.g. slope of linear trend in precipitation) and called these drivers, and those without a temporal component (e.g. average precipitation) and called these facilitators of WPE. Prior to fitting the models, I identified a limited set of strongly collinear variable groups with an $r > 0.7$ (Dormann *et al.* 2013; Fig. S3.12) and removed variables within these groups that were deemed less likely to be influential for woody cover change. Nevertheless, the excluded collinear variables were kept in mind during the analysis of model results. Further, no trend variables were collinear, making interpretation of the model with drivers of woody cover change simpler. Following parameter optimisation, I used family=Gaussian, tree complexity=5, learning rate=0.01, bag fraction=0.5 and cross-fold validation=10 as model parameters. The initial BRT models were simplified using procedures described by Elith *et al.* (2008), and only the variables with the highest explanatory power were included and analysed for interactions with change in fractional woody cover. To ensure that the BRT results were not a product of chance, I randomly assigned woody cover change values for all 0.5° grid cells and re-ran the model. The model failed to resolve, thus confirming the initial results were not a product of chance. The relative importance of predictors was determined based on the number of times it was selected for splitting, weighted by the squared improvements to the model, averaged over all trees (Friedman & Meulman 2003). The final models for the simplified set of 31 combined, 25 facilitator (Fig. S3.6) and 12 driver (Fig. S3.7) explanatory variables explained 78%, 75% and 51% of the total deviance in woody cover change, respectively. Further to this, I reduced the trend model to include only drivers that are most often inferred in woody encroachment literature (i.e. fire, herbivory, population density, rainfall and temperature trends). This final model included five predictors and explained 34% of the total deviance in woody cover change.

Results and discussion

Broad-scale trends in woody plant cover

Over the past three decades, 7.5 million km^2 (55%) of non-forest biomes (see data mask in Fig. S3.2) in sub-Saharan Africa underwent significant net gains in woody plant cover (Fig. 3.1, 3.2A, and Fig. S3.3). This is more than triple the 2.2 million km^2 (16%) significant decrease in woody plant cover, confirming local-scale studies indicating increases in WPE over the last century (Stevens *et al.* 2017). Woody cover loss was prevalent in parts of the Sahel, East Africa and much of Madagascar, but WPE dominated the central-interior of Africa. Countries exhibiting a mean fractional increase >30% were

Cameroon, Central African Republic, South Sudan, and Uganda (Table S3.1). Almost all other countries experienced net encroachment, with only Congo, Kenya, Madagascar, Niger, and Somalia undergoing a net decline in woody cover. The highest rates of encroachment occurred in areas with moderate initial woody cover (i.e. 30 to 60%) in 1986 (Fig. S3.4). Areas with more than 75% initial cover experienced highest rates of loss, probably due to human-induced clearing (e.g. Fig. S3.3). There was little difference between WPE inside (13.9%) and outside of (12.5%) protected areas. Encroachment trends were lowest in shrublands (3.5 ± 0.4% increase) and highest in Caesalpinioid savannas (20 ± 0.4% increase), but were pronounced across all vegetation types (Fig. S3.5), indicating that the drivers of this change are globally available, but act regionally allowing WPE in some areas and deforestation in others.

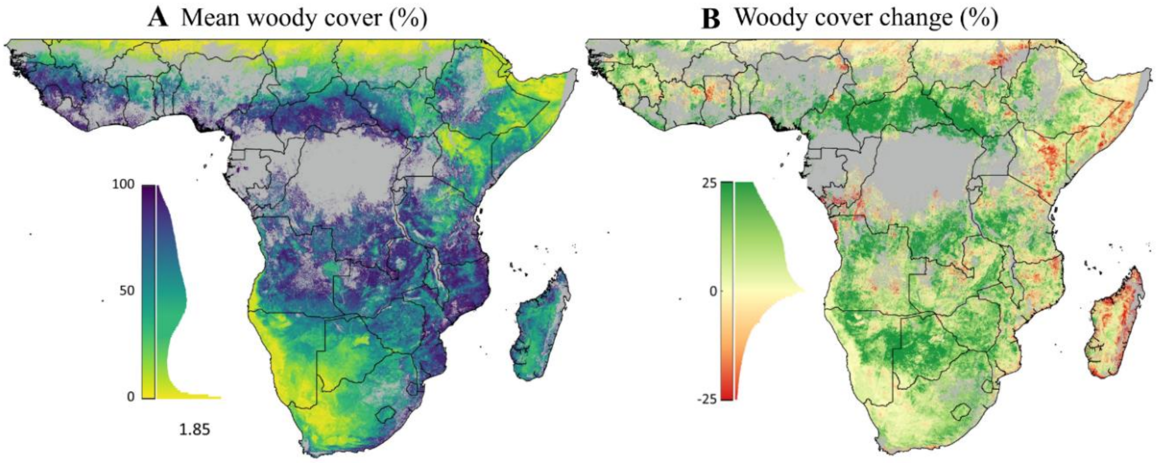


Figure 3.1 Woody plant cover dynamics over sub-Saharan Africa. Satellite observations of 30 years of fractional woody plant cover (A) reveal a dominant increasing trend (derived from the slope of the linear trend line between 1986 and 2016, (B). Histograms alongside colour scales indicate data distributions. Grey areas were masked from the analysis and represent urban, wetland, cropland, and forest (areas >40 % cover by trees >5 m). Maps constructed in Google Earth Engine (Gorelick *et al.* 2017).

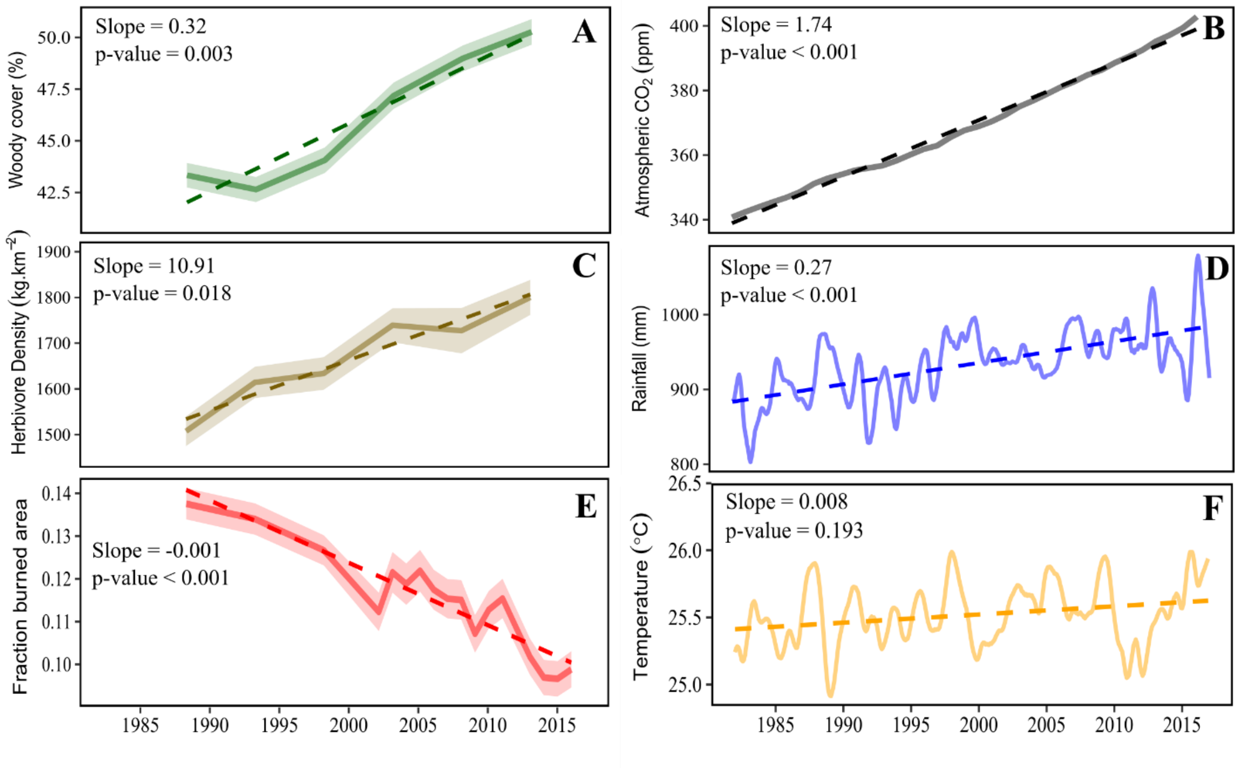


Figure 3.2 Time series data for woody cover and select environmental covariates averaged over Africa. Solid lines represent the mean value with 95% confidence interval ribbons based on using 0.5° grid cells as replicates (n = 6255). Linear trend lines are indicated with dashed lines. The slope of the trend line and p-value of the linear regression are displayed for each plot. Solid lines for rainfall and temperature indicate inter-annual trends once seasonality has been removed. Inflection points for lines in A and B are plotted at the median timepoint for each epoch.

Drivers of woody plant cover change

The widespread trend in WPE correlates with a significant rise in atmospheric CO$_2$ and rainfall (Fig. 3.2B and D), but also a significant increase in herbivore densities and decline in burned area (Fig. 3.2C and E). To avoid drawing conclusions about drivers of WPE from such continental-scale correlations (Fig. 3.2) without acknowledging the spatial variation in trends (i.e. some areas have increased in rainfall or woody cover while others have decreased), I employed the established machine learning technique of boosted regression tree modelling (De'Ath 2007; Elith *et al.* 2008) to investigate the relative importance of and interactions between a set of >60 explanatory variables (climatic, edaphic and disturbance) and woody cover change.

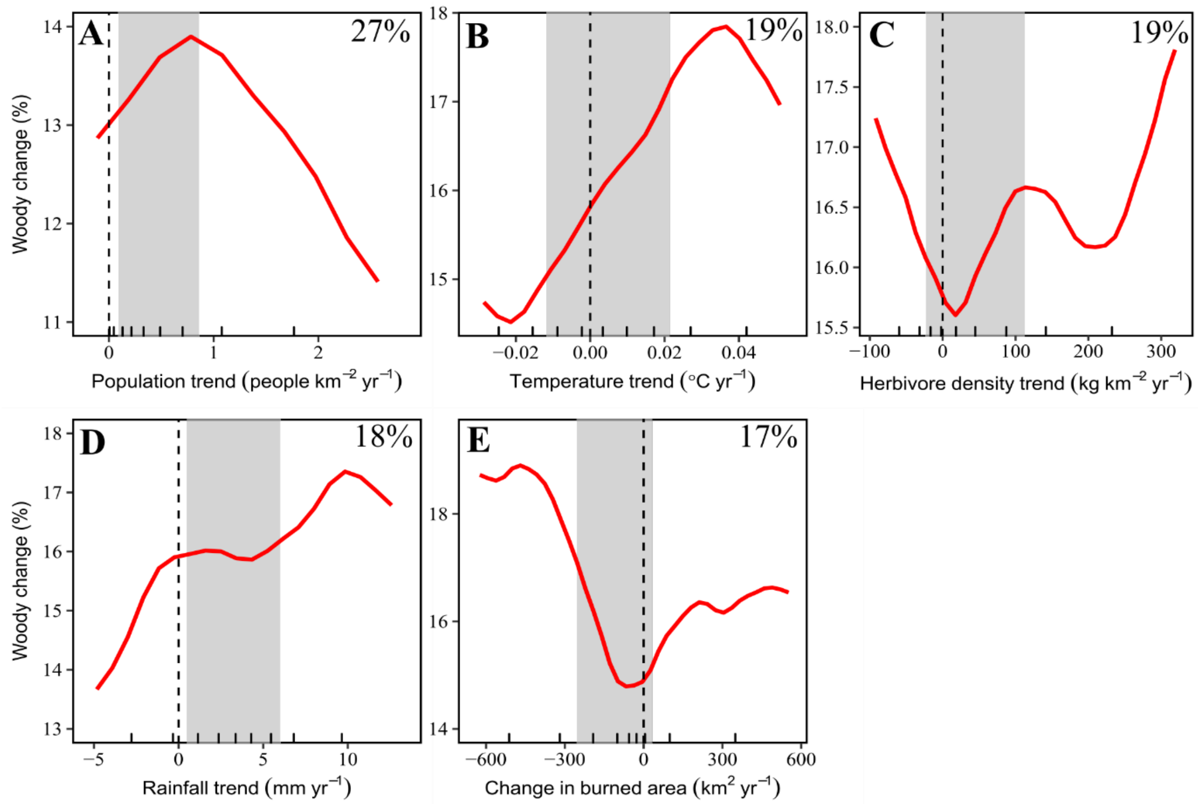


Figure 3.3 Most important drivers of woody plant cover change. Boosted regression tree partial dependence of fractional woody cover change on selected explanatory variables, when accounting for the average effect of all other driver variables (see Fig. S3.7). See Fig. S12 for strength of interactive effects of explanatory variables. The red lines are smoothed representations of the responses, with fitted values (model predictions based on the original data) for each 0.5° grid cell over sub-Saharan Africa. The trend of the line, rather than the actual values, describes the nature of the dependence between response and explanatory variables. Small bats on the x-axis represent data deciles, and grey bands indicate data between the 25th and 75th percentile. The x-axis was clipped to the 5th and 95th percentile to highlight trends in the bulk of the data. The full model explained 51% of the total deviance in woody cover change, and the relative contribution (%) of each explanatory variable is indicated.

The final model explained 78% of the deviance in spatially-explicit woody cover trends. WPE expresses a hump-shaped response to human population growth (Fig. 3.3A). At high population growth rates, WPE was inhibited, presumably due to clearing, emphasising that deforestation trends (Hansen *et al.* 2013) are not limited to the forest biome. Low population growth rates had a negligible effect on curbing WPE, potentially due to a covariance with human-induced landscape fragmentation and the subsequent reduction in fire spread (Archibald *et al.* 2012). Local disturbances by fire and herbivory are known to maintain open savannas in areas that could climatically support closed-canopy forest (Lehmann *et al.* 2011). This analysis confirms that local disturbance patterns can have continental consequences for WPE and are of equal importance to edaphic and climatic variables in explaining the spatial variation in woody cover change (Fig. S3.6 and S3.7). Large reductions in burned area in Africa, consistent with the global trend (Andela *et al.* 2017), have driven larger WPE rates (Fig. 3.3E). Decreases in fire reduces tree mortality and consequently reduces competition from the grass layer and facilitates tree recruitment, which further reduces the grass fuel load for fires, creating a negative feedback loop (Van Langevelde *et al.* 2003). Fire intensity is an important determinant of tree mortality in savannas where intense fires area able to reach tree canopies and cause “top-kill” (Govender *et al.* 2006). Fire may thus be ineffective at reducing WPE in areas under extensive livestock management and some conservation areas where fires are managed for safety by burning during seasons that facilitate low-intensity fires.

The bulk of the data for trends in herbivory suggest that increasing herbivore intensity exacerbates WPE (shaded area in Fig. 3C). Grazing herbivores, which dominate most African rangelands (Robinson *et al.* 2014; Hempson *et al.* 2015a), reduce grass competition with woody plants and reduce fuel loads for fires, thereby releasing woody plants from the fire trap (Roques *et al.* 2001; O'Connor *et al.* 2014). However, WPE might also be facilitated in areas with large declines in herbivory (Fig. 3.3C). These contradictory herbivore-induced effects on WPE are likely due to differing livestock management contexts coupled with the widespread loss of mid-Holocene herbivore functional guilds, such as browsers (Hempson *et al.* 2015a; Venter *et al.* 2017). Browsers play an important role in regulating woody plant populations through direct mortality (e.g. elephant impact; Daskin *et al.* 2016; Skowno *et al.* 2016; Stevens *et al.* 2016; Hempson *et al.* 2017) or by inhibiting shrub and tree growth rates and thereby increasing vulnerability to fire (Van Langevelde *et al.* 2003; Augustine & McNaughton 2004). Indeed, I found that areas with high browser densities experienced lower encroachment rates (Fig. S3.8A). In contrast, grazers reduce fuel loads for fire and thus enhance WPE (Van Langevelde *et al.* 2003), however, I found that extreme grazer densities may inhibit WPE (Fig. S3.8B). One possible way that high grazer densities may reduce WPE is through consumption and trampling of coppicing and young woody plants.

Areas experiencing increases in rainfall underwent greater WPE than those where rainfall has decreased (Fig. 3.3D), confirming rainfall as a potent determinant of tree cover (Sankaran *et al.* 2008; Staver *et al.* 2011). Although rises in temperature have been shown to enhance WPE at local scales through declines in frost-induced tree mortality, the regional-scale interaction between changes in temperature and woody cover are less well understood for Africa (O'Connor *et al.* 2014). Here I show that changes in WPE with rising temperatures mirrored the effect of increases in rainfall (Fig. 3.3B), suggesting that WPE may be set to continue under global warming scenarios. The detrimental effects of increased transpiration and drought stress under warmer temperatures may be mitigated by wetter climates and enhanced water use efficiency induced by rising atmospheric CO_2 (Lu *et al.* 2016; Devine *et al.* 2017). Experimental evidence also exists for increased seedling establishment under warmer climates for some savanna woody species (Stevens *et al.* 2014).

Apart from the interactive effect with temperature and water use efficiency, rising atmospheric CO_2 levels might contribute to continental WPE through enhanced C_3 woody plant photosynthetic rates and post-fire resprouting capabilities, relative to C_4 grasses (Hoffmann *et al.* 2000; Bond & Midgley 2012). The lack of spatial variability in atmospheric CO_2 trends precluded it from being incorporated into my model. Notwithstanding, the changes I observe between 1986 and 2016 might reflect the legacy effects of post-industrial revolution CO_2 trends, although the shape of continental trend lines suggests that the temporal variation in WPE rate is not directly linked to that of CO_2 (Fig. 3.2A and B). While experimental studies have noted a positive growth response in trees to elevated CO_2 (Ainsworth & Long 2005; Kgope *et al.* 2010), the strength of this response relative to herbaceous plants is variable, especially when considered in isolation from nutrient limitations and competitive interactions present in natural systems but commonly absent in experimental set-ups (Körner 2006; Ainsworth *et al.* 2008). Nevertheless, possibly the most compelling evidence for CO_2-driven WPE is that it has been observed in both conservation and agricultural areas where browsing and fire levels vary across land-use classes (Stevens *et al.* 2016). While CO_2 may contribute to WPE, the global trend in atmospheric CO_2 has not led to homogenous trends in WPE (Fig. 3.1B). Thus, the other climatic and disturbance drivers assessed here are important in determining the direction of vegetation change and determining the magnitude of WPE.

Implications

The widespread continental increase in woody plants shown here corroborates global trends of increasing leaf area index (Zhu *et al.* 2016) and vegetation greenness (Fensholt *et al.* 2012) in semi-arid areas, thereby challenging the long-held desertification narrative (Reynolds *et al.* 2007). The inclusion of spatially-explicit greening trends into global carbon budgets have previously relied on low resolution (>250 m) estimates of net primary productivity in semi-arid areas (Poulter *et al.* 2014). The present dataset of decadal woody cover change might aid in more accurately quantifying the extent to which WPE contributes to the global carbon sink, potentially offsetting the carbon losses from deforestation. Despite the potential benefits to the global carbon budget, the local-scale disadvantages (e.g. reduced grazing capacity) and their effects on rural livelihoods has motivated substantial governmental investment into clearing alien and native invasive woody plants (e.g. ca. 100 million US$ per annum in South Africa; van Wilgen & Wannenburgh 2016). Initial indications from my models suggest that WPE management interventions will be most needed in areas that are expected to increase in temperature and rainfall under future climate change scenarios. More importantly, manipulating local disturbance patterns has the potential to override climatic effects and significantly mitigate WPE. Management interventions may include increasing fire using heterogenous management regimes (Fuhlendorf *et al.* 2009), or through rewilding savannas with historical herbivory pressures (Hempson *et al.* 2017; Venter *et al.* 2017), and diversifying herbivore functional guilds by incorporating more browsers (Hempson *et* *al.* 2015a). Thus, while global drivers such as climate and CO_2 may enhance the risk of WPE, the realisation of WPE is largely dependent on management decisions.

Chapter 4: Cattle don’t care: Animal behaviour is similar regardless of grazing management in grasslands

This chapter has been published in *Agriculture, Ecosystems & Environment*:

Venter, Z.S., Hawkins, H.-J. & Cramer, M.D. (2019) Cattle don’t care: Animal behaviour is similar regardless of grazing management in grasslands, *Agriculture, Ecosystems & Environment*, 272: 175-187.

Abstract

It is well known that rangelands lose productivity and ecosystem function under excessive rates of livestock stocking, however the role of the spatiotemporal distribution of grazing density remains debated. Multiple studies show that managing grazing for high livestock density has little effect on plant and livestock productivity, yet fewer explore animal behaviour as a mechanism that would explain these observations. I hypothesised that increasing cattle grazing densities under equivalent stocking rates would cause animals to concentrate more, spend more time grazing and thereby increase utilisation of forage, and reduce selection for palatable vegetation patches and species. I compared season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG) over three years in an experimental trial in a mesic grassland of South Africa reflecting a range of grazing densities (SLG < FCG < HPG). I measured the spatiotemporal patterns of cattle behaviour, dietary composition, dung trampling, animal productivity, and normalised difference vegetation index (NDVI). The management approach did not change the time allocated to different animal behaviours, trampling of dung, nor the selection for particular plants. HPG cattle grazed at closer distances to one another than SLG but not FCG, and herds were equally concentrated when resting and walking. HPG cattle spent less time in patches of high vegetation NDVI compared to SLG, thereby reducing the spatial heterogeneity of NDVI over time. Cattle gained 0.2 ± 0.02 kg day^{-1} ha^{-1}, and this did not differ between management approaches. The HPG approach is costly to set up and is predicted to take twice as long as FCG and SLG to become profitable. Depending on the management goal, HPG could reduce selection for palatable patches, possibly preventing overgrazing and formation of bare patches over the long-term. Alternatively, SLG could increase selection for palatable patches and initiate the formation of grazing lawns and, in combination with fire, commonly used in FCG, might enhance biodiversity.

Introduction

Globally, livestock grazing is one of the most widespread land uses, occupying 36% of the terrestrial earth surface (Chapter 1). After fire, wild and domestic herbivores (vertebrate and invertebrate) are the most prevalent consumers of biomass globally (Bond & Keeley 2005; Estes *et al.* 2011; Archibald & Hempson 2016), and can alter ecosystem function, for example, through reducing competition for invasive unpalatable herbs (Milton 2004) and woody plants (O'Connor *et al.* 2014; Venter *et al.* 2018). New paradigms in rangeland management identify the importance of managing the spatial and temporal distribution of herbivory for maintaining ecosystem services and biodiversity conservation (Fuhlendorf *et al.* 2017). In ecosystems relatively untransformed by human impact, the movement patterns of grazing herbivores track seasonal or ephemeral patterns of resource availability (McNaughton 1993). This is evident from the seasonal migrations of wildebeest in the African Serengeti (McNaughton 1985) or the way bison herds concentrate on post-fire vegetation regrowth in North American prairies (Fuhlendorf *et al.* 2009). Grazing management approaches in rangelands have drawn from these ecological observations and developed methods to reintroduce periods of rest from grazing (Briske *et al.* 2008).

Reviews of rangeland management literature over the last century have found that manipulating grazing densities via grazing management systems is of minor importance relative to stocking rate in determining vegetation and animal production (Sampson 1951; Heady 1961; Van Poollen & Lacey 1979; O'Reagain & Turner 1992; Briske *et al.* 2008). Stocking rate refers to the number of large stock units (LSUs) per hectare of available rangeland, whereas grazing density (sometimes referred to as “stock density”) is the number of LSUs per subunit of area at any point in time on that rangeland so that two farms may have the same stocking rate but different densities depending on the number of defined camps or paddocks in which stock are held per unit time. Grazing management approaches such as rotational grazing attempt to manipulate grazing densities by altering the duration of vegetation exposure to livestock with the aid of fencing (see Media Gallery P1) or herding (Heitschmidt & Taylor Jr 1991). Such approaches exist on a continuum of grazing density ranging from season-long continuous, where animals are moved once a year, to high or ultra-high density grazing, where animals are moved daily or multiple times a day. Season-long continuous grazing was traditionally and remains to some extent the conventional approach in the USA (Briske *et al.* 2008) and is very similar to the “rotational rest” approaches adopted in Middle-East, African and Asian rangelands based on transhumance (seasonal rotation; Makarewicz & Tuross 2012; Aryal *et al.* 2014; Morokong 2016). At the other end of the grazing density spectrum are practices such as short duration grazing and holistic planned grazing (Savory 1978; Tiedeman 1986; Tainton 1999; Savory & Butterfield 2016). These approaches move animals using electric fencing or herding between small paddocks at high frequencies based on an adaptive management framework.

Despite the theory, the balance of experimental studies shows little effect of rotational grazing practices (Briske *et al.* 2008) or high density practices in particular (Hawkins 2017) on vegetation basal cover, biomass, or animal gain compared to season-long grazing. The debate about rotational grazing effects persists due to a mismatch between experimental evidence and anecdotal experiences of practitioners (Briske *et al.* 2011), and possibly, a lack of nuanced research that captures less obvious consequences of rotational grazing. For example, assumptions about animal behaviour under different grazing densities have been largely ignored. Testing the assumptions implicit in arguments for high density grazing is important given that it has been advocated to policy makers as a solution to climate change (Sherren *et al.* 2012; Briske *et al.* 2014a). High density grazing approaches, including holistic planned grazing, are based on the assumption that animals concentrated in space and time would behave differently resulting in (1) increased proportion of available plants that are grazed, (2) homogenisation of grazing severity across species and vegetation patches, and (3) increased distribution of plant litter, dung and urine into the soil via hoof trampling (Savory & Butterfield 2016). In lower density management approaches, overgrazing of highly palatable plants leads to mortality and may cause the competitive release of less palatable species that may consequently encroach or become invasive (Anderson & Briske 1995). The loss of palatable species can also increase soil exposure and reduce overall vegetation basal cover (Thurow 1991; Fuls 1992; Ash & Smith 1996; Teague *et al.* 2011). This is predicted to feedback negatively into animal production and farm profitability. While the causal links between increasing animal numbers (i.e. stocking rates) and the loss of ecological function and species richness (degradation) on rangelands have been corroborated (Briske 2017), few studies have investigated the changes in animal behaviour induced by increasing grazing densities at the same stocking rate. This might be important in explaining farm productivity responses, or lack thereof, to rotational grazing.

The primary behavioural mechanism assumed to be distinctive in high density grazing practices is the spatial utilisation of and selectivity for palatable plants and forage patches within a defined area (Barnes *et al.* 2008; Bailey & Brown 2011). In a comprehensive review of the literature (Hawkins 2017), only one study compared forage utilisation under rotational and continuous grazing management (Hart *et al.* 1993) and they found no difference in the proportional grazing of available plants. A few studies have found that increasing grazing densities can prevent animals from selecting for palatable vegetation patches (Smith & Owensby 1978; Charles *et al.* 1985; Volesky 1994), however, qualitative reviews of the literature have also argued that rotational grazing has no consistent effect (Launchbaugh & Howery 2005; Soder *et al.* 2009; Bailey & Brown 2011). Rather, other factors such as watering points, topography and stocking rates are stronger determinants of selection at the patch-scale. Similarly, selection at the plant-scale is largely unaffected by rotational grazing management (Kirby *et al.* 1986; Kreuter & Tainton 1988; Olson & Malechek 1988) because animals choose to eat plants based on nutritional status and digestibility regardless of how tightly they are concentrated (Bailey & Brown 2011). However, recent work has found exceptions in African rangelands where active herding reduces selection for palatable taxa in cattle (Odadi *et al.* 2018) and sheep/goat (Samuels *et al.* 2016) systems. Thus, grazing management apparently has no effect on dietary selection at the patch-scale while results are contradictory at the plant-scale.

A second behavioural mechanism potentially triggered by concentrating animals under high density grazing is the allocation of time and energy to grazing, walking and resting. Typically, herbage quality and availability determine the time livestock spend grazing (Ungar & Noy-Meir 1988), however the literature also highlights the potential trade-offs between energy savings and adverse effects of herd concentration and frequent moving. In wild ungulates such as Alaskan moose, increasing herd size and density can promote foraging efficiency by reducing vigilance for predators, but may also reduce time spent grazing due to intraspecific competition for forage resource (Molvar & Bowyer 1994). In African rangelands, increasing cattle herd size can reduce foraging efficiency due to intraspecific competition (Odadi & Rubenstein 2015), yet this effect may be counteracted by forcing herds to concentrate more closely and thereby prevent energy losses from walking longer distances to search for preferred forage (Odadi *et al.* 2018). Experimental trials show that frequent movements between fenced areas can cause animal agitation and stress and, combined with reduced ability to select for palatable forage that meets animal requirements and a sudden decline in forage availability (Cox *et al.* 2017), can lead to declines in animal performance and conception rates (Worthington 1984; McCollum III *et al.* 1999; Badgery *et al.* 2017). The time animals allocate to walking has consequences for step rates and trampling behaviour. Rotational grazing management has been shown to increase the density of cattle walking trails (Walker & Heitschmidt 1986), but has also been found to have little effect on step rates and distances walked (Hart *et al.* 1993). Understanding the effect of management on trampling behaviour and consequent hoof impact has important implications for soil hydrology and nutrient cycling and may conceivably promote or inhibit plant growth and consequently animal production (Byrnes *et al.* 2018).

The effects of rotational grazing, particularly holistic planned grazing on animal behaviour has been identified as a research gap (Hawkins *et al.* 2017). I set up an experimental trial on a working farm in a mesic grassland of the Eastern Cape, South Africa, to test the effects of a range of grazing densities on animal responses, implemented via three management approaches including season-long grazing, four-camp grazing and holistic planned grazing. I predicted that increasing animal grazing density using fencing would cause (1) tighter concentration of animal herds; (2) altered time spent grazing, resting and walking; (3) increased utilisation of available forage; (4) reduced selectivity for palatable patches and plants; (5) increased trampling of dung; and (6) increased animal production per unit area and farm profitability.

Methods

Study site

The Merino Walk experimental trial was located approximately 5 km north of Cedarville, Eastern Cape, South Africa (30° 21’ 8’’ S; 29° 3’ 29’’ E) at an altitude of 1440 m above sea level. Half of the trial was located on north-facing slopes covered by East Griqualand Grassland and the other half was located on low-lying flats covered by Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands (Mucina & Rutherford 2006). Dominant grasses included *Themeda triandra* and *Eragrostis plana*, respectively. The area is underlain by mudstones and sandstones of the Elliot and Molteno Formations

(Mucina & Rutherford 2006). Flats consist of poorly-drained and nutrient-rich haplic lixisols with high clay contents whereas slopes contain relatively nutrient-poor haplic acrisols (Hengl *et al.* 2014). Long-term (1960-2000) mean annual rainfall and temperature was 760 mm and 15°C (Hijmans *et al.* 2005), with most rainfall occurring during austral summer months.

Experimental design

Three grazing management treatments, occupying 219 ha of land on the Merino Walk farm, were initiated as an experimental trial in December 2015. Prior to this, the land had been managed under conservative stocking rates as a commercial cattle and sheep farm. Initial vegetation and soil measurements allowed us to determine how management legacy affected variation across the treatments prior to commencement of the trial (Table S4.1), and to express changes relative to these initial measures.

Treatments included season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG) and were deliberately assigned non-randomly to control for watering points, topography and vegetation as far as possible (Fig. S4.1). Each treatment had one replicate on a sloped and flat area of the farm respectively, where the sloped area was more suitable for cattle during winter due to reduced frost and lack of flooding. This study, like many other experimental trials was limited to one treatment replicate due to limited resources. For this reason, I sampled intensively across the farm prior to and during the study. A regularly-spaced sampling grid of points 90 m apart was generated over the farm producing 209 sampling locations which were revisited over time for dung and vegetation sampling (see Media Gallery P2). The treatments differed primarily in the number of camp divisions, and consequently the relative grazing densities (Table 4.1). In SLG grazing, one camp is grazed for an entire growing-season and then cattle are moved to a second camp, with accumulated biomass, for the non-growing season. In FCG, cattle are rotated amongst three camps while one camp is left to rest for an entire year. In subsequent years, the camp allocated to annual rest is the first camp to be grazed, and conventionally this is proceeded by burning (Venter & Drewes 1969). I chose to exclude burning from this system because of difficulties in distinguishing and comparing fire and grazing behaviour effects across treatments. I recognised that this could bias against plant productivity in the FCG approach relative to working farms using this approach. For this study, HPG refers to a high intensity grazing approach similar to short duration (Tiedeman 1986), cell grazing (McCosker 2000), and holistic planned grazing (Savory & Butterfield 2016). I followed the adaptive management protocol of Holistic Management (HM, Savory & Butterfield 2016) for the duration of the study and across all treatments. In HM, a flexible grazing plan is constructed outlining animal movements between multiple small camps based on forage availability, seasonal temperature and flooding, with the aim of increasing animal densities and thereby increasing even utilisation and reducing overgrazing while increasing animal gain. The farm manager and research team undertook an intensive 3 d training course by an accredited HM trainer familiar with the South African context. This was done in order to adhere to HM principles and follow the correct HM planning procedure. The same trainer oversaw the development and implementation of grazing plans in the first year of the study. Portable electric fencing was employed to construct grazing strips of between one and two hectares in size. All treatments were stocked with year-old Bonsmara-Boran steers at a moderate stocking rate of 0.53 LSU ha^{-1} yr^{-1} i.e. similar to the government recommended rate of 0.55 LSU ha^{-1} yr^{-1} (Avenant 2016).

Table 4.1 Characteristics of three grazing management treatments, including season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG), implemented at the Merino Walk experimental trial. Stocking rate refers to the number of large stock units (LSUs) per hectare of available rangeland, whereas grazing density refers to the number of LSUs per fenced subunit area at any point in time on the rangeland.

Variable	SLG	FCG	HPG
Stocking rate (LSU ha^{-1} yr^{-1})	0.53	0.53	0.53
Number of camp divisions	2	4	70
Grazing density (LSU ha^{-1} d^{-1})	1	2.1	36.8
Grazing period (d $camp^{-1}$)	180	21-28	1
Recovery period (d $camp^{-1}$)	180	15-180	60
Between season rest	Yes	Yes	No
Within season rest	No	Yes	No
Adaptive management	Yes	Yes	Yes

The trial stocked cattle destined for the meat market and was managed as a commercial operation. Stock remained on the trial between 12 and 18 months depending on market-related factors and animal weight gains. Over the duration of the trial, three sets of cattle were introduced and at each intake, individual cattle were randomly allocated to management treatments. Ten of each new herd intake were tagged and monitored for weight gain over the course of their occupancy. Cattle were managed according to livestock agricultural best practices and national guidelines for the care and use of animals (University of Cape Town ethical clearance certificate no. 2016/v14/HH).

Herd observations

During Jun 2017 and Jan 2018, I performed behavioural sampling to identify how concentrated or spread-out herds were during grazing, resting and walking behaviours. Grazing behaviour was considered as the act of searching for (movement of <5 m between bites) and consuming grass. Walking was defined as a continuous forward movement without grazing. Resting was defined as standing or lying down without consuming food. Observations took place over 2 d in summer and 2 d in winter.

Three observers concurrently monitored cattle in a treatment for 2 h recording behaviour every 5 min, and rotated between all treatments. Observers recorded the behaviour and proximity to nearest neighbour of ten individuals in the herd. Proximity to nearest neighbour was estimated at five intervals between 0, 5, 10, 15, 20, >25 m.

Triaxial accelerometers

I deployed triaxial accelerometers (Fig. S4.2) on randomly selected cattle for 30 d during Jun 2017 and Jan 2018. MicroPython pyboards with triaxial accelerometers were programmed to take recordings of movement along the X-, Y- and Z-axes every 0.5 s. The monitors weighing 464 g were attached alongside the GPS devices (see below) to nylon collars of 7 cm in width, and fastened with an adjustable buckle (see Media Gallery P2). I successfully retrieved data from 18 of the 22 devices deployed, resulting in an average of 3 replicates per treatment per sampling occasion. At each sampling occasion, the devices collected data for a mean of 15 ± 1 d. During the Jun 2017 deployment, observational measurements of grazing, resting and walking took place to calibrate the accelerometer readings (see below). A mobile phone with a clock synchronous to the triaxial accelerometers was used to record exact timestamps for switches between grazing, resting and walking using CyberTracker (https://www.cybertracker.org/). Each collared individual was observed for at least 120 contiguous seconds in each behavioural state. The post-processing of the raw accelerometer data and calibration with observational data was conducted in R (RCoreTeam 2016) following methods outlined in Alvarenga *et al.* (2016). Briefly, a machine learning Random Forest (RF) model (Liaw & Wiener 2002) was developed to classify behavioural states from the accelerometer data. The raw X, Y and Z axis values were used to calculate feature vectors specifically designed to classify animal behaviour from accelerometer readings (Campbell *et al.* 2013). The feature vectors included the signal magnitude, movement variation, energy, entropy, pitch, roll and inclination using formulae described in Alvarenga *et al.* (2016) for each 5 s epoch. Along with the mean values, I also calculated the standard deviation, minimum and maximum for each epoch. This produced 44 explanatory variables which were used in the RF model to predict the observed behaviour. This data subset was split into 70% for training the model using calibration data (evaluation) and 30% for testing the predictions of the model. The accuracy of the model was assessed by calculating a confusion matrix of the observed and predicted behavioural classes. Finally, the trained model was used to predict behavioural states over the duration of the accelerometer readings.

Dung counts

At each sampling location (Fig. S4.1) trampled and untrampled dung pats were counted in a 10 x 2 m belt transect every six months from Jan 2016 to Jan 2018 (see Media Gallery P2). A dung pat was defined as any intact dung with a diameter >10 cm. Old dung pats which had disintegrated and had no clear boundary were excluded. A trampled pat was considered as one with clear evidence of a cattle hoof print. This technique was developed for the purposes of this experimental trial. The repeatability of the method was investigated by comparing camp-level means of total annual dung counts to verify that there was little variance between years and bias between dung samplers.

Vegetation patch selectivity

GPS collars were deployed on randomly selected cattle for 60 d on two summer (Jan 2017 and 2018) and two winter (June 2016 and 2017) sampling occasions. GPS devices (Perthold Engineering LCC, Richardson, Texas, USA) were set to log a position every 5 min and attached to nylon belts fastened around the animals' necks. I deployed enough collars to obtain an average replication of three collars per treatment per sampling date. Three devices were placed at a known location and left for three weeks to test the spatial accuracy of the GPS. This revealed a median error of 5.4 m with 95% of the data points occurring within 22.5 m of the actual location (Fig. S4.3). GPS devices remained active for an average of 29 ± 2.4 days per sampling occasion.

To assess the cattle selection for vegetation patches over the landscape, the GPS data from each replicate animal was analysed as a spatial point pattern using the 'spatstat' package in R (Baddeley *et al.* 2015). I used GPS points from all treatments over the period in which the HPG cattle were moved through one complete management unit. The GPS points were clipped to the boundaries of the camps occupied during the sampling period after applying a negative buffer of 10 m to each camp to account for the effects of fences on the cattle behaviour. Given that resting behaviour is not expected to influence grazing heterogeneity, I excluded GPS points at which cattle were resting. To do this, I defined active GPS locations (grazing or walking) as consecutive points (5 min apart) >22.5 m from one another which, according to this assessment (Fig. S4.3), reflects 95% certainty that the animal was not resting. I quantified the clustering of GPS point patterns using $L(r)$, a transformation of Ripley's K-function (Besag 1977). Ripley's K function (Ripley 1976) calculates the density of points at a given distance r of the typical point. It is calculated across a range of distances defined by the extent of the point pattern. I used Monte Carlo simulations to derive confidence intervals around the $L(r)$ curve for a completely random point process (Wiegand & Moloney 2004). I then plotted the observed $L(r)$ curve for a GPS point pattern and quantified the deviation of this pattern from randomness as the area between the $L(r)$ curve and the upper confidence envelope for a random point pattern (Fig. S4.4).

Satellite-derived estimates of vegetation quality were obtained using the Google Earth Engine cloud computing platform (Gorelick *et al.* 2017). The normalised difference vegetation index (NDVI, Tucker 1979) has been widely used as an indicator of vegetation productivity, quality and vigour in rangelands (Svoray *et al.* 2013; Ali *et al.* 2016). I extracted the median NDVI values over the farm from the Landsat 7 Enhanced Thematic Mapper Plus (ETM+) dataset at 30 m resolution for the three years prior to the start of the trial. This served as a spatial template of the forage quality distribution. To establish the association between cattle and vegetation quality, I related the kernel ("gaussian") smoothed density of locations to the farm NDVI. For each 30 m Landsat pixel I calculated the GPS point density per animal replicate. To assess how the heterogeneity in vegetation NDVI changed through time under the management treatments, I created annual median mosaics of NDVI for 2015-2018. For each annual mosaic, I estimated heterogeneity by assigning to each pixel the standard deviation of the eight neighbouring pixels (Fig. S4.5). The initial (2015) measure was calculated from Landsat 7 ETM+ and Landsat 8 Operational Land Imager data after correcting for inter-sensor discrepancies using published calibration coefficients (Roy *et al.* 2016). For 2016, 2017 and 2018 I used Sentinel 2 Multi Spectral Instrument, Level-1C data (Drusch *et al.* 2012) because this has a higher spatial resolution (10 m) and would thus capture vegetation heterogeneity in more detail. To compare treatments whilst accounting for the initial baseline heterogeneity, I calculated the trend in heterogeneity as the slope of the linear trend line between 2015 and 2018 for each pixel over the farm. I then sampled this trend image at each of the 209 sampling locations.

Vegetation utilisation

After clipping GPS locations to camp boundaries and isolating those defining grazing behaviour, I extracted a random subset of 1000 points per GPS collar. To estimate the percentage of forage space utilised by the cattle I created a 5 m buffer around each location (Fig. S4.4), representing the potential "footprint" of the animal's consumption at that point. Cattle that repeatedly visit the same grazing patch will use less of the available forage space than cattle that seldom return to the same grazing patch. Given that the cattle in different treatments occupied camps of slightly different sizes, I standardised the number of randomly extracted points to equal 66 points per hectare. This value was the maximum number of random points per hectare that could be extracted across all collars based on the available sample sizes. I calculated utilisation as the percentage of the camp covered by the footprint of buffered GPS points.

Dietary selection

Vegetation in camps occupied by cattle within the preceding six months were sampled in Jan (2017 and 2018) and Jun (2016 and 2017) for bite marks. At each sampling location (Fig. S4.1), a Levy Bridge (Levy & Madden 1933) was used to sample 10 descending points spaced 25 cm apart (see Media Gallery P2). At each point, the plant species were identified and height, basal cover, and percentage of leaves with bite marks recorded. To assess diet selectivity, I first established a forage palatability rating for the available plant species. I used Jacob's (1974) index of selection, $D_i = (r_i - p_i)/(r_i + p_i - 2r_ip_i)$, where r_i and p_i are the proportions of plant species i in diet (from bites) and in vegetation, respectively. Each forage species was assigned an index score which ranged from -1 (avoided) to 1 (preferred). The species were also categorised as preferred (D > 0.08) and avoided (D < 0.08) according to thresholds suggested by Lamoot *et al.* (2005). The proportion of available plant area grazed was calculated based on basal cover in each grazing camp.

Five random dung samples per treatment were collected monthly from fresh (moist) dung pats between Jan and Jun 2017 and immediately frozen at -20 °C. Samples for summer (Jan to Mar) and winter (Apr to Jun) were then blended together, oven dried at 60 °C, milled to a fine powder and sent to Inqaba Biotechnical industries (Pretoria, South Africa) for DNA extraction and sequencing. The genomic DNA was extracted from samples using the ZymoBIOMICS (Zymo Research,USA) extraction kit. A portion of the chloroplast trnL intron was amplified from each DNA sample using the c and h trnL truseq tailed primers. Amplicons libraries were purified using the Agencourt Ampure XP bead (Beckman Coulter, USA) protocol. Library concentration was measured using Nebnext Library quant kit (New England Biolabs, USA) and quality validated using Agilent 2100 Bioanalyser (Agilent Technologies, USA). The samples were pooled in equimolar concentrations and diluted to 4 nM based on library concentrations and calculated amplicon sizes. The library pool was sequenced on a MiSeq using a MiSeq Reagent kit V2 300 cycles PE (Illumina, USA). The final pooled library was at 9 pM with 30% PhiX (nucleotide library derived from the well-characterised bacteriophage PhiX genome) as a control for run quality. The DNA sequence data was analysed by Jonah Ventures (Colorado, USA) following methods outlined in Craine *et al.* (2016) yielding operational taxonomic unit (OTU) counts from the GenBank database. The top 50 OUT counts per sample were converted to proportions of total count and the selectivity index calculated using the same protocol outlined for animal bites.

Animal production and profitability

The 10 randomly tagged cattle per treatment were weighed monthly. Auction sales records and purchase invoices for set up infrastructure (fencing and water) and running costs (labour, feed, fuel and electricity) were used to calculate gross income and expenditure for each management treatment. The gross income and expenditure from the first two years was used to forecast annual net profits over a five-year time horizon. Using the forecast figures, I calculated the five-year return on investment (ROI) as the net returns as a percentage of the cumulative cost of investment (E): $ROI = \frac{G-E}{E} x\ 100$, where G is the cumulative gross income.

Statistical tests of significance

To establish whether grazing management approach was a significant predictor of cattle responses, I used linear mixed-effects modelling (Harrison *et al.* 2018) with the ‘lme4’ package in R (Bates *et al.* 2014). Grazing management treatment was considered a fixed effect and variables designating non-independence of replicates (e.g. repeated measures) were considered random effects. In animal location, behaviour and production data each animal was considered a replicate. The GPS point complete spatial randomness statistics were calculated for each season, and thus season index was considered as the random intercept. For the model explaining time spent under different behavioural states, I calculated the proportion of each 24-hour day spent in each behavioural state and, in this case, day index was assigned to a random intercept. Proportional response variables were left untransformed if the distribution of model residuals met the assumptions of linear models. The animal production data were collected monthly, and thus month was assigned to the random intercept.

For dung trampling and plant selectivity data, camp-level averages were calculated and added to a model that included season and camp (Fig. **S**4.1) as random effects. Data from scan sampling of herd behaviours were aggregated into morning and afternoon samples which were treated as pseudo-replicates and assigned to a random intercept in the model.

Results

Cattle behaviour

I found HPG cattle grazed closer together than SLG but not FCG cattle (Table 4.2), whereas management did not affect herd densities during resting or walking. Cattle were more dispersed when walking during winter compared to summer (Table 4.2). The RF model correctly classified the activities grazing, resting and walking from triaxial accelerometer readings 91%, 95%, and 84% of the time (Table S4.2). Grazing management did not affect how much time was spent on each behaviour (Table 4.2). Cattle spent more time grazing under HPG than FCG but not SLG in winter, while in summer there were no differences between treatments (Table 4.2). Grazing behaviour followed a diurnal pattern across all treatments (Fig. 4.1). Grazing commenced at ca. 06h00 and ceased at ca. 20h00 with a small grazing bout, exaggerated during winter, around 23h00. A short cessation of grazing at mid-morning during summer and at midday during winter coincided with observed rumination activity. Cattle spent more time grazing and less time resting during summer compared to winter (Table 4.2) and cattle appeared to walk in between grazing and resting throughout the day (Fig. 4.1).

Table 4.2 Animal responses (means ± standard errors) for three grazing management treatments, season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG), implemented at the Merino Walk experimental trial. Results from linear mixed-effects models are reported for individual treatment, season, and vegetation type terms, along with interaction terms, where they applied. Vegetation types constitute flats and slopes characterised by low-lying *Eragrostis plana* dominated by Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands, and higher-lying *Themeda triandra* dominated by East Griqualand grasslands, respectively. Spatial forage utilisation was a relative measure of the proportion of grazing area covered by GPS locations buffered by a 5m radius. The forage bite mark utilisation was measured as the proportion of sampled plants with evidence of bite marks. The integrated measure of complete spatial randomness is the area between the L(r) curve for observed GPS point pattern and the upper confidence envelope for a random point pattern, where L(r) is a transformed Ripley's K-function. The larger the area, the greater the deviation from randomness. The change in NDVI heterogeneity is the slope of the linear trend line between 2015 and 2018 and is represented in heterogeneity units per decade instead of year to reduce decimal values.

Attribute	SLG	FCG	HPG	Significance (p value)				
				Treatment	Season	Vegetation	Treatment x Season	Treatment x Vegetation
Distance to neighbour (m)								
Grazing	6.8^{a} ± 0.5	5.0^{ab} ± 0.5	4.2^{b} ± 0.4	$p < 0.001$**	0.109	-	0.201	-
Resting	3.0 ± 0.6	3.5 ± 0.4	3.0 ± 0.7	0.819	0.933	-	0.221	-
Walking	6.6 ± 1.3	6.4 ± 1.3	4.1 ± 0.6	0.155	0.02*	-	0.942	-
Activity budget (% day)								
Grazing	36.4 ± 0.7	36.4 ± 1.1	37.4 ± 0.7	0.915	$p < 0.001$**	-	0.014*	-
Resting	54.5 ± 0.8	52.7 ± 1.0	53.9 ± 0.8	0.806	$p < 0.001$**	-	0.191	-
Walking	8.9 ± 0.5	10.7 ± 0.6	8.5 ± 0.3	0.777	0.164	-	0.104	-
Spatial forage utilisation (%)	15.6^{b} ± 0.1	16.0^{a} ± 0.09	15.8^{ab} ± 0.09	0.001*	$p < 0.001$**	0.388	0.271	0.295
Forage bite mark utilisation (%)	30.1 ± 11.6	33.1 ± 5.5	33.6 ± 8.6	0.793	-	0.084	-	0.742

Significance is indicated at $p < 0.05$* and $p < 0.001$**. For direct treatment effects, significant differences are indicated with letters.

Table 4.2 Cont.

Attribute	SLG	FCG	HPG	Significance (p value)				
				Treatment	Season	Vegetation	Treatment x Season	Treatment x Vegetation
Selectivity								
Patch-scale								
Integrated spatial randomness score	1514.0 ± 366.1	2068.0 ± 284.5	1218.1 ± 190.6	p < 0.001**	0.005*	0.004*	p < 0.001**	0.002*
Change in NDVI heterogeneity (units decade^{-1})	0.9^{a} ± 0.8	-0.2^{ab} ± 0.3	-1.0^{b} ± 0.4	0.043*	-	0.297	-	0.778
Plant-scale								
Bite marks (% of plants)								
Preferred	21.8 ± 5.7	18.7 ± 6.0	18.7 ± 4.9	0.885	-	0.088	-	0.713
Avoided	4.4 ± 4.4	5.6 ± 2.2	1.4 ± 0.8	0.218	-	0.724	-	0.673
Faecal DNA (% of plants)								
Preferred	60.3 ± 25.8	60.6 ± 9.7	50.4 ± 18.5	0.78	-	-	-	-
Avoided	4.8 ± 3.1	6.1 ± 4.3	2.8 ± 1.2	0.654	-	-	-	-
Dung trampling (pats ha^{-2})	407.9 ± 212.5	347.1 ± 63.1	379.9 ± 67.0	0.918	0.468	0.056	0.181	0.044*
Dung produced (pats ha^{-2})	913.8 ± 109.3	900.2 ± 78	786 ± 159.6	0.517	0.393	0.489	0.879	0.983
Step counts (steps m^{-1})	8.9 ± 1.2	14.3 ± 3.8	10.5 ± 1.2	0.187	0.784	-	0.156	-
Animal production (kg day^{-1} ha^{-1})	0.2 ± 0.02	0.2 ± 0.0	0.2 ± 0.0	0.605	p < 0.001**	-	0.294	-

Significance is indicated at p < 0.05* and p < 0.001**. For direct treatment effects, significant differences are indicated with letters.

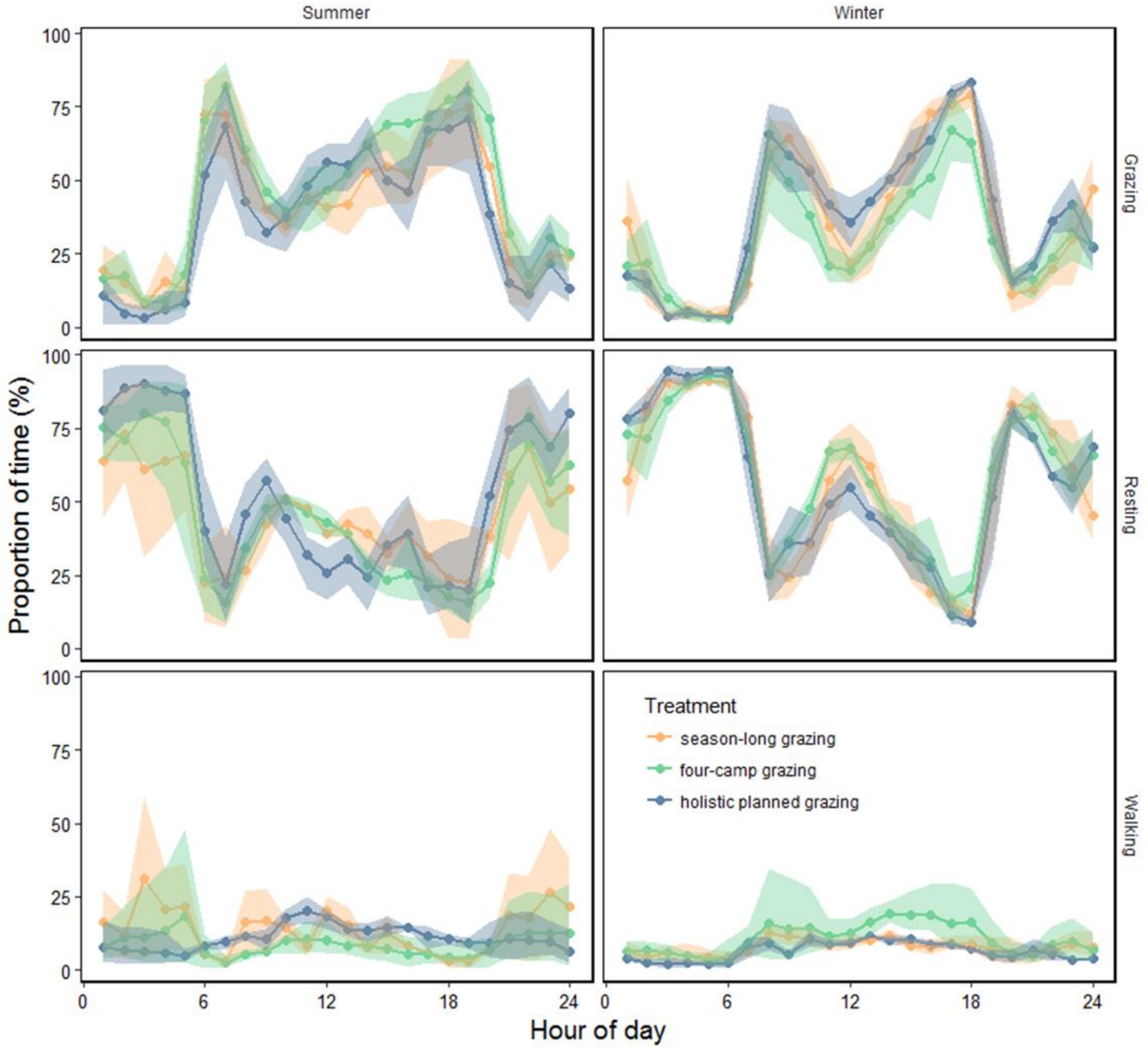


Figure 4.1 Hourly activity budgets over an average 24-hr day for cattle under three grazing management systems during winter and summer at the Merino Walk experimental trial. The mean proportion of each hour spent grazing, resting and walking is reported with points and solid lines with 95% confidence intervals defined by ribbons.

Based on behavioural observations, cattle took an average of 11 ± 2 steps per minute and trampled 23% (378 ± 114) of the 1658 ± 115 dung pats found per hectare. There was no difference in the step rate, the number of dung pats produced or trampled between grazing management treatments (Table 4.2). This was corroborated by accelerometer recordings of walking and grazing behaviour which showed no management effect on the time allocated to these behavioural states (Fig. 4.1, Table 4.2). Both walking and grazing require steps and thus one would expect no difference in dung trampling between treatments.

Vegetation utilisation and selectivity

The percentage of available plant foliar cover with evidence of grazing bite marks, a proxy for forage utilisation, was 33% overall, and did not differ between treatments (Table 4.2). The alternative measure of spatial forage utilisation using GPS points revealed that cattle utilised only 0.5% more of their grazing camps in summer (16.3 ± 0.06%) relative to winter (15.8 ± 0.06%) and that cattle utilised more of available forage area under FCG compared to SLG, but HPG was not different from either (Table 4.2). Treatment and season both affected the clustering of cattle GPS points, measured by the integrated spatial randomness score (SRS), at the patch-scale (Table 4.2). The clustering of GPS points during winter was lower under HPG (1125 ± 270 SRS) relative to FCG (2590 ± 392 SRS) but not SLG (1189 ± 832 SRS), and in summer there was no treatment effect (Table 4.2). Thus, assuming that the clustering of GPS points is a good proxy for selective grazing behaviour (see GPS animation in Media Gallery P3), I found that HPG had no effect on reducing patch selectivity relative to SLG but was more effective than FCG. In addition, when accounting for the existing spatial variation in forage NDVI, I found a treatment effect on selection for patches of high NDVI. In both summer and winter, SLG cattle GPS point densities were positively correlated to vegetation NDVI (Fig. 4.2). This correlation was less apparent in FCG and HPG grazing treatments. Consistent with the increased selection for patches of high NDVI under SLG, I found that SLG increased the spatial heterogeneity of NDVI, whereas HPG reduced it (Fig. 4.3).

The effect of HPG on reducing NDVI heterogeneity at the pixel neighbourhood (ca. 1 ha area) was significantly different to SLG but not to FCG (Table 4.2). FCG and HPG reduced heterogeneity in 2016 relative to the baseline (see dip in Fig. 4.3A) presumably due to homogenous grazing patterns at the trial outset, whereas SLG further entrenched existing baseline heterogeneity in 2016. The large variation in SLG heterogeneity is itself a further indication of heterogeneity at the landscape-scale. The trend (relative to the baseline) in NDVI variation at the grazing camp scale (ca. 20 ha area) was not different between treatments (Fig. S4.7). All treatments exhibited a very little change in NDVI heterogeneity over the course of the trial, although SLG did exhibit a very gradual increase.

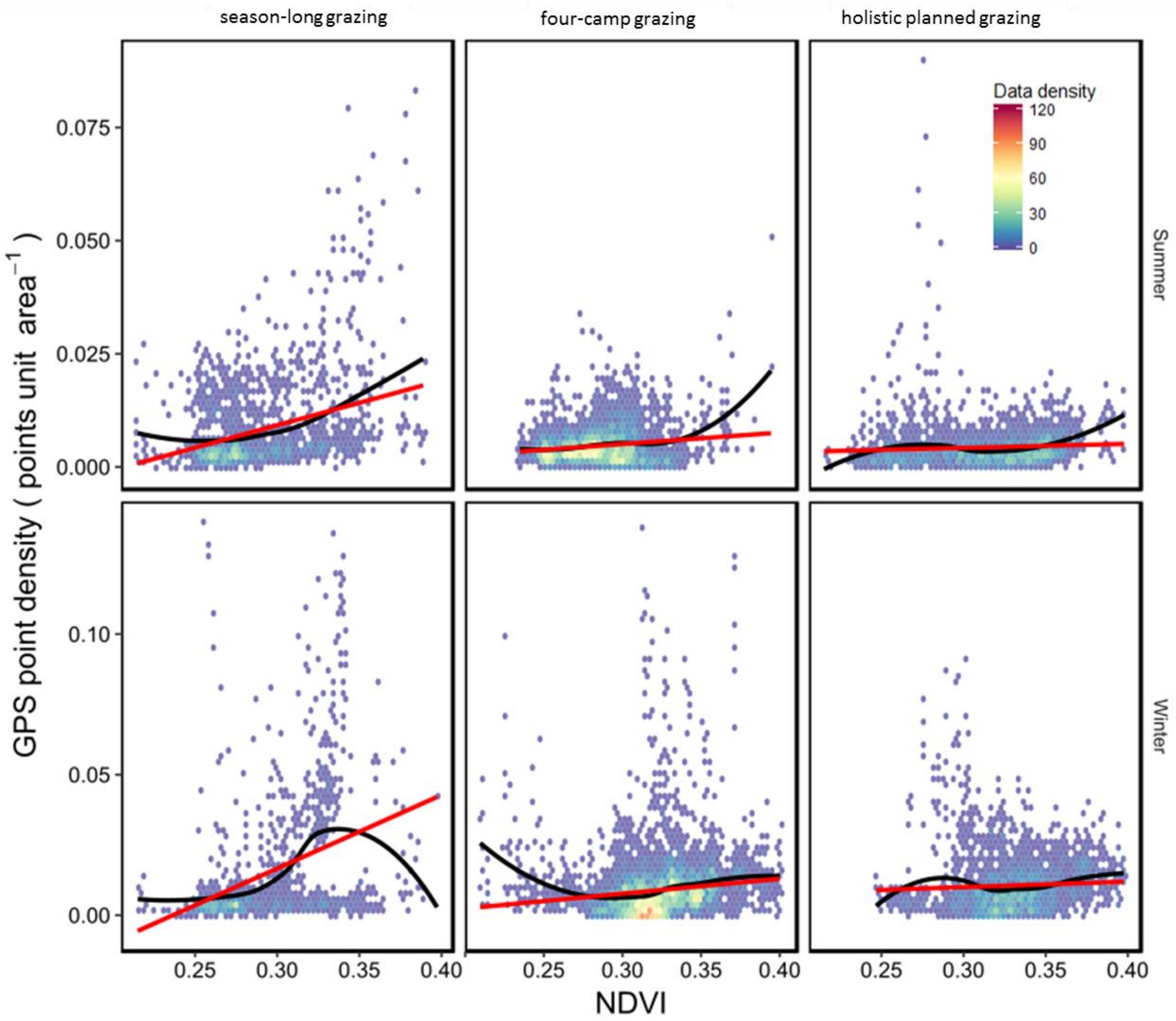


Figure 4.2 The relationship between cattle GPS point density and normalised difference vegetation index (NDVI). GPS densities are based on GPS data collected from cattle (n = 3) during two summer and two winter sampling occasions. The NDVI values are derived from a Landsat mosaic for the year preceding the trial implementation. Data point densities are represented by coloured hexagons, with each data point representing a 30 x 30 m Landsat pixel. Linear and loess trend lines have been fitted in red and black, respectively.

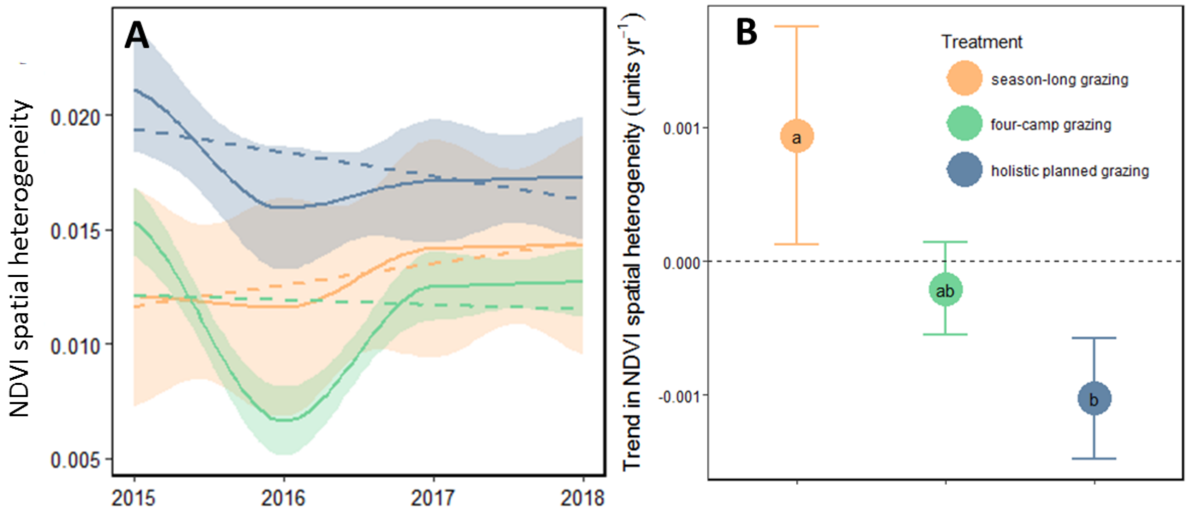


Figure 4.3 Vegetation heterogeneity over grazing camps at the Merino Walk experimental trial between 2015 and 2017 (A). The trial was implemented from 2016 onward. Heterogeneity is determined by calculating the normalised difference vegetation index (NDVI) for a satellite image mosaic, and then assigning each pixel with the standard deviation in its eight neighbouring pixels. Linear trend lines (dotted) and Loess regression lines with 95% confidence intervals (solid lines and ribbons) are plotted in A. The slope of the linear trend in heterogeneity was calculated for each grazing camp to determine significant differences between treatments (B).

At the plant-scale, the extent to which cattle selectively grazed species did not differ between treatments (Table 4.2). Cattle displayed positive selection for a variety of forbs and grasses including *Eragrostis capensis*, *Andropogon appendiculatus*, *Harpochloa flax*, *Sporobolus africanus* and *Setaria incrassata* (Fig. S4.6). Some of the strongly avoided species included *Elionurus muticus*, *Heteropogon contortus* and *Aristida junciformis*. The proportion of available preferred and avoided plant species bitten or found in faecal DNA did not differ between treatments (Table 4.2). Indeed, when expressed as a continuous variable, the selectivity index of forage species was positively correlated to the proportion utilised across all treatments (Fig. 4.4). This was true for data from both bite mark sampling and faecal DNA.

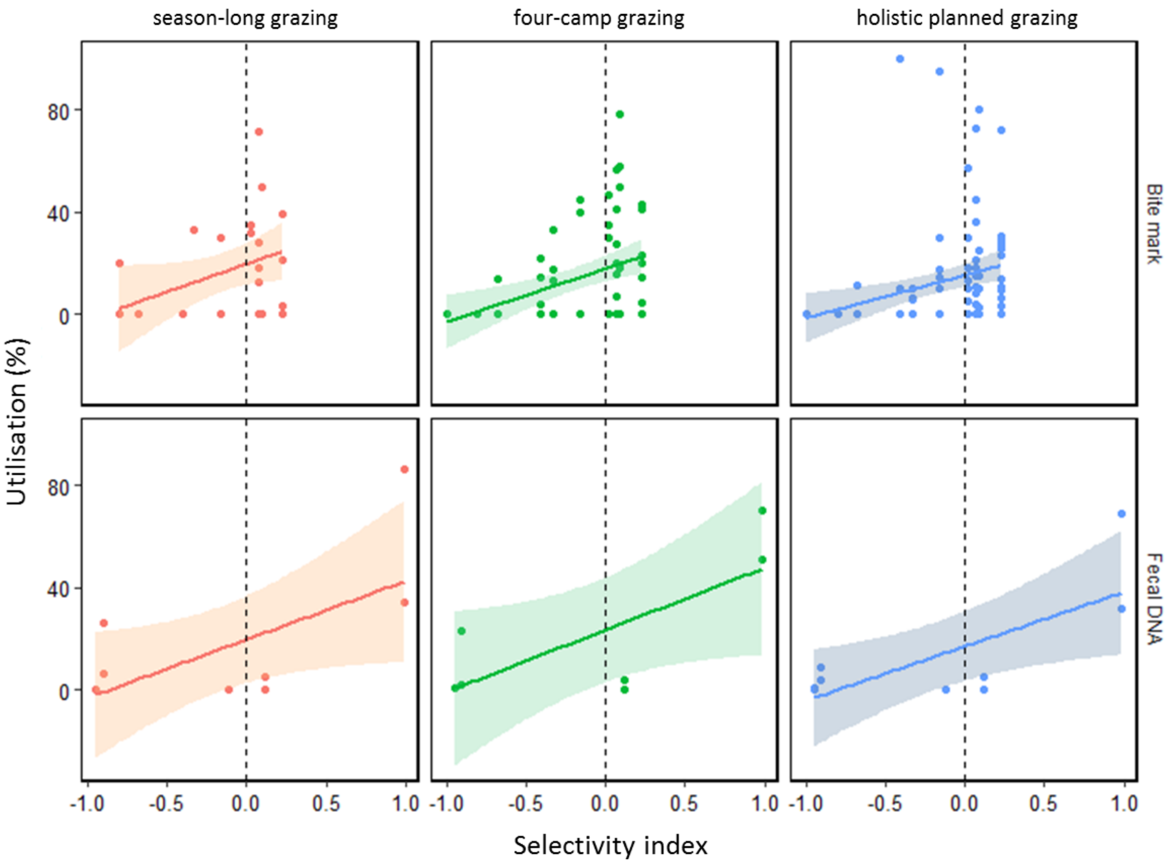


Figure 4.4 Cattle utilisation of forage taxa in relation to selectivity indices derived from farm-level measurements for the same forage taxa. Data from two methods of measurement (rows) are presented across three grazing management treatments (columns) at the Merino Walk experimental trial. Data points represent vegetation taxa per grazing camp for bite mark data (top row) and faecal DNA data (bottom row). Utilisation for bite mark data is the fraction of plants bitten as a percentage of the fraction of plants available. Utilisation for faecal DNA data is the fraction of plants found in dung as a percentage of fraction plants available. Linear trend lines and 95% confidence interval ribbons are plotted.

Animal production and profitability

Average daily weight gain for all cattle was 0.2 ± 0.02 kg day^{-1} ha^{-1}. Animal weight fluctuations tracked the seasonal vegetation productivity cycle (Fig. 4.5; see video in Media Gallery P3), differing significantly between seasons (Table 4.2). In summer cattle gained 0.4 ± 0.02 kg day^{-1} ha^{-1} whereas in winter they lost 0.1 ± 0.02 kg day^{-1} ha^{-1}. Over the duration of the trial weight gain did not differ between management treatments (Table 4.2), although HPG cattle from the first intake underperformed relative to FCG and SLG cattle during the winter months (Fig. 4.5). During the second intake, SLG cattle outperformed HPG and FCG cattle over summer months. These group-specific differences disappeared when averaging across all groups. Revenue generated from two years of auction sales was 81, 80 and 79 $ ha^{-1} yr^{-1} for SLG, FCG and HPG treatments, respectively. The HPG approach was the most expensive to set up (Fig. 4.6A). Fencing and water infrastructure exceeded that of FCG and SLG. The excess running costs under HPG relative to SLG and FCG constituted fuel, labour and electric fencing. After accounting for expenses, I forecast SLG, FCG and HPG management approaches to start making a net profit after 20, 24 and 48 months, respectively (Fig. 4.6B). The return of investment for SLG (116%) over five years is predicted to be substantially higher than that for FCG (70%) and HPG (9%).

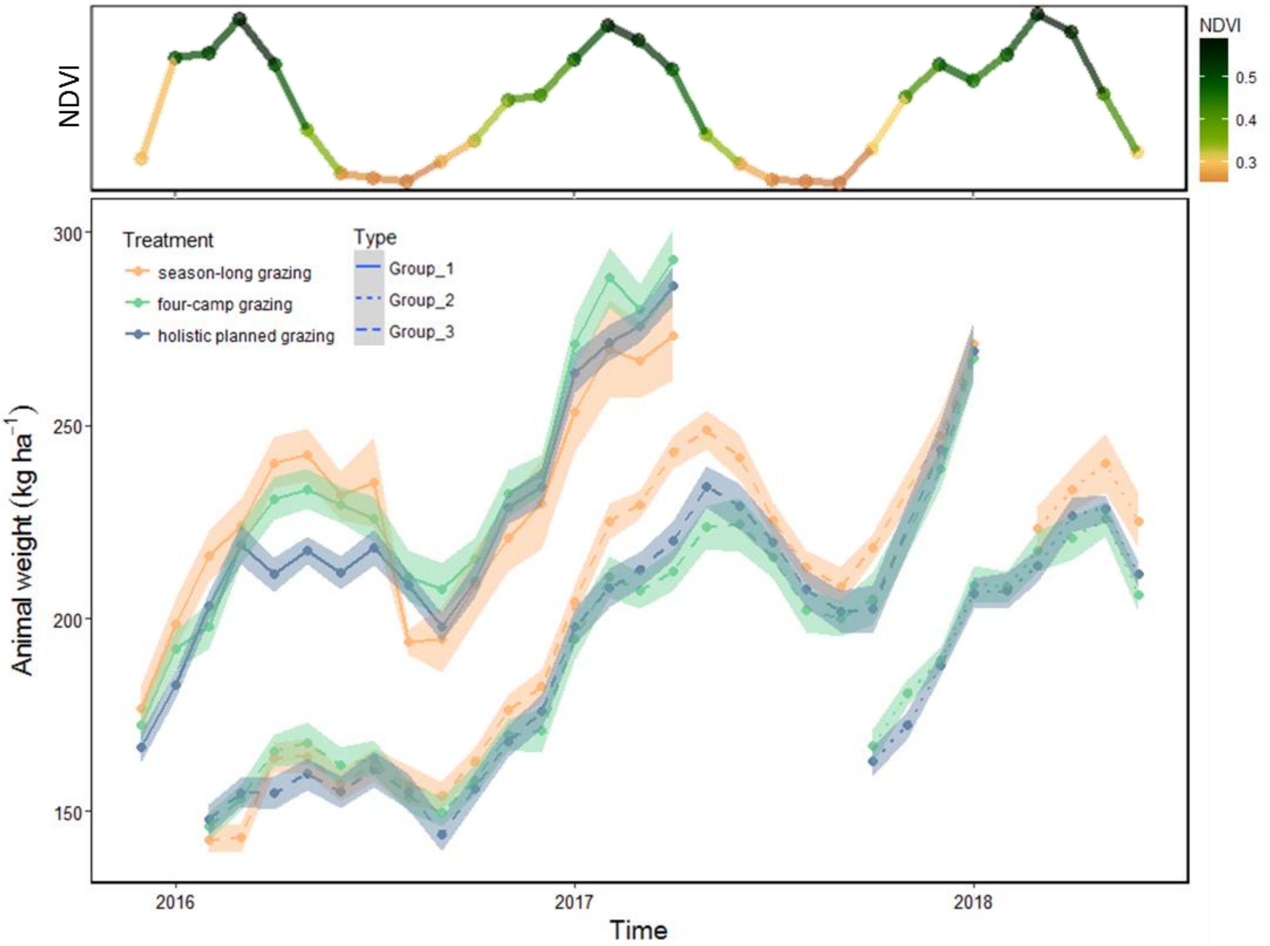


Figure 4.5 Monthly cattle weights for three grazing management treatments over the duration of the Merino Walk experimental trial. Each group of lines (differentiated by line styles) represents a set of 10 oxen which were bought onto the farm and monitored for weight gain before being sold. Lines and ribbons reflect a means and 95% confidence intervals. Mean monthly normalised difference vegetation index (NDVI) values over the farm, derived from Landsat satellites, are plotted above to indicate the seasonality of vegetation production.

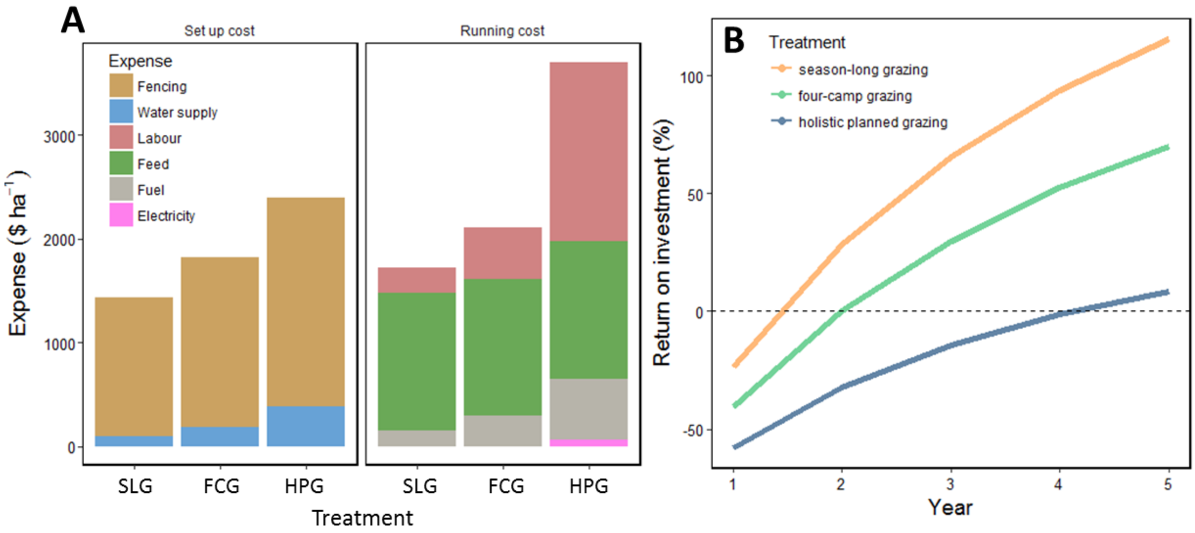


Figure 4.6 Farm expenses (A) and profitability (B) of the Merino Walk experimental trial management approaches including season-long (SLG), four-camp (FCG) and holistic planned (HPG) grazing. Expenses are separated into set up costs incurred at the initiation of the trial, and running costs, incurred on an annual basis. Using cattle sales records from the first two years of the trial, combined with cumulative expenses, I forecast the return on investment over five years for each management treatment.

Discussion

Increasing animal densities with rotational grazing management practices (i.e. FCG and HPG) did not increase cattle productivity or profitability relative to low-density SLG in a mesic grassland of South Africa. I found that HPG did not affect cattle herding proximities, time spent grazing, forage utilisation, forage species selection, or dung trampling. I did, however, find evidence to support the hypothesis that increasing animal densities reduces the selection for palatable vegetation patches within a grazing camp, and that this can reduce the spatial heterogeneity in vegetation vigour over time.

A striking finding was that constraining cattle with electric fencing did not cause cattle to concentrate more tightly relative to cattle that are allowed to range freely in a camp when averaging across all behavioural states. This is a key assumption of high density grazing practices (Brunson & Burritt 2009; Savory & Butterfield 2016). SLG and FCG cattle performed all activities at similar distances to neighbours compared to HPG cattle although HPG cattle did graze at greater proximities than SLG cattle. These results might vary considerably over time depending on the shape and size of grazing camps occupied and thus more intensive sampling effort might yield different outcomes. Studies on wild herbivore sociality have found that intraspecific competition for forage increases with herd density (Molvar & Bowyer 1994). This competition may drive individuals to spend more time grazing or increase intra-specific aggression and thereby reduce time spent grazing (Krebs & Davies 2009). In African rangelands, when animal densities were increased through active herding, cattle benefitted through enhancing foraging efficiency because they spent less time actively searching for forage and thereby expending energy (Odadi *et al.* 2018). Given that there was no difference in observed herding densities in this study, it follows that there were unlikely to be differences in time allocated to grazing behaviour. Indeed, data from triaxial accelerometers revealed no management effect on time allocated to grazing, resting or walking. A study testing Holistic Resource Management (Savory 1983), an earlier version of HPG, also found no effect on cattle behavioural patterns on an experimental range in Wyoming, USA (Hart *et al.* 1993). Consequently, grazing management approach produced no effect on the cattle utilisation of available forage and thus, animal weight gain was unaffected. Similarly, cattle in this study spent similar time grazing, utilised the same amount of available forage and gained similar weight across all three management approaches. Other studies have even reported declines in animal production (Worthington 1984; Anderson 1988; McCollum III *et al.* 1999; Badgery *et al.* 2017) and conception rates (Worthington 1984) under high density grazing due to increased stress from continuous movements and the rapid depletion of pasture and restrictions in diet quality associated with mature forage at the time of grazing. These results show no such effect possibly because all cattle spent the same proportion of time walking.

Another mechanism through which walking was proposed to influence animal production is hoof impact on soil and vegetation (Savory & Butterfield 2016). Trampling of dung and urine into soil is predicted to enhance nutrient and water cycling, vegetation cover and consequently animal production. The number of trampled dung pats, steps taken, and time spent walking under HPG did not differ to FCG or SLG in this trial. Previous experimental trials in the USA have found that increasing paddock numbers may reduce (Hepworth *et al.* 1991), increase (Walker & Heitschmidt 1986) or have little effect (Hart *et al.* 1993) on distances walked and ground trampled by cattle. Despite the diverse grazing management effects on trampling, rotational grazing enhances soil organic carbon and reduces bulk density relative to year-long continuous grazing (Byrnes *et al.* 2018), although whether the same is true for season-long continuous is not clear. Practitioners of HPG suggest that increased hoof impact and trampling can be induced by placing supplemental feed cubes in a field or using active herding with horses and dogs (Savory & Butterfield 2016), although whether this will be beneficial for soil hydrological processes has been debated in the literature (Briske *et al.* 2008). It is possible that rotational grazing may enhance the trampling effect when a threshold grazing density is exceeded, highlighting the scope for testing a broader range of animal densities.

A common criticism of experimental trials is that they do not have sufficient herd sizes or densities to induce the “herd effect” (see comments in Venter 2017). Discerning what grazing densities or herd sizes constitute high density grazing is difficult because it varies across socio-ecological contexts depending on factors like vegetation productivity and decision making paradigms (Mann & Sherren 2018). Further, there are virtually no recommendations for specific grazing densities in training materials produced by well-known HPG organisations apart from phrases like “maximum density for minimum time” (Global

Savory Network, 2015; Savory and Butterfield, 2016). A global meta-analysis found that no studies on variants of high density grazing implemented grazing densities exceeding 12 LSU ha^{-1} (Hawkins 2017). This trial took place on a working farm and implemented HPG with average grazing densities of 36 LSU ha^{-1}. This was characteristic of high density grazing practitioners in the area according to the local farmer (Nel, G. *pers comm* 2016) and accredited HM trainer (Lambrechts, J. *pers comm* 2016).

The animal behaviour most commonly associated with high density grazing in the literature is reduced selective foraging under high animal density. These results support this proposition that concentrating animals and rotating grazing pressure over the farm reduces the selection for palatable vegetation at the patch-scale. Although HPG did not distribute grazing pressure more randomly than SLG in summer or winter, HPG cattle were restrained from focussing on more palatable (or more green) vegetation patches relative to SLG. SLG cattle were able to spend more time in areas of high vegetation greenness/vigour. A rotational grazing trial in Australia also found that high intensity rotations prevented sheep from selecting quality forage and in this case it resulted in a decline in per head productivity (Badgery *et al.* 2017). In European (Probo *et al.* 2014) and American (Charles *et al.* 1985) pastures, rotational grazing has also been shown to reduce the patchiness of grazing behaviour, however others have found that the location of watering points, topography and stocking rates override any effect of rotational grazing (Launchbaugh & Howery 2005; Soder *et al.* 2009; Bailey & Brown 2011). Because I controlled for these variables in this trial, I was able to detect the effect of manipulating animal densities. To my knowledge, this study is the first experimental trial to report on changes in the heterogeneity of vegetation in response to high density grazing. Using satellite data, I provided evidence that even over three years, high density grazing reduced the spatial heterogeneity of vegetation vigour (NDVI), probably because cattle were prevented from overgrazing palatable patches and further entrenching existing patchiness. The land allocated to HPG had higher NDVI heterogeneity at the commencement of the trial compared to FCG but not SLG (Table S4.1). Thus, the magnitude of treatment differences might have been reduced or increased given equal starting points, nevertheless, assuming the trends persist, over the long-term, HPG could possibly prevent bare patch formation (Thurow 1991; Fuls 1992). Alternatively, homogenising vegetation might open up a niche vulnerable to invasion by non-palatable herbaceous (Milton 2004) and woody (O'Connor *et al.* 2014; Venter *et al.* 2018) species.

Recent advances in the understanding of natural disturbance patterns in rangelands suggest that managing for patchiness and heterogeneity is beneficial for biodiversity and productivity (Fuhlendorf *et al.* 2017). The use of fire and herbivory to create diversity in vegetation structure and function over the landscape is known as pyric herbivory (Fuhlendorf *et al.* 2009). This heterogeneity can provide niches for a greater variety of species to occupy, thereby increasing the resilience of rangeland to stress such as drought (Briske *et al.* 2017), and benefitting ranchers that enter into incentive-based land stewardships where the maintenance of biodiversity is desired (Reed *et al.* 2015). Furthermore, the repeated grazing of burned patches can, along with nutrient import from dung, maintain grasses in palatable vegetative states that constitute grazing lawns (Hempson *et al.* 2015b; Porensky & Veblen 2015), a common occurrence in African savannas. Here grass communities can convert within a few years to stoloniferous, low-growth forms with low C:N ratios, sustaining palatable forage for livestock (Donaldson *et al.* 2017). Although fire was not included as a factor in this trial, GPS collar and satellite NDVI data showed that SLG cattle repeatedly visited palatable patches over the grazing camp. This appeared to increase the patchiness of vegetation vigour over time, a result possibly akin to that achieved with pyric herbivory. Further, allowing cattle to select for palatable, more nutritious forage may explain why SLG cattle gained more weight than HPG cattle over several months of the year.

The influence of management practice on cattle selection for palatable vegetation at the patch-scale was not mirrored at the plant-scale. Both bite mark sampling as well as faecal DNA analysis revealed that cattle actively selected for palatable forbs and grasses, and that increasing grazing densities did not reduce this selectivity. Assuming this remains consistent over time, HPG is not projected to result in a more favourable species composition (more palatable species) over the long-term compared to forms of low density grazing. Indeed, a 24-year simulated rotational grazing trial showed no effect of grazing treatment on floristic composition in South Africa (Morris & Tainton 1996). Thus, this contradicts a central tenant in high intensity rotational grazing (Briske *et al.* 2008). However, Odadi *et al.* (2018) found that increasing animal densities through herding (instead of fencing) reduced the selectivity for palatable grass species in savanna. Similarly, a study in more arid rangelands of the Karoo, South Africa, found that herded sheep consumed less annual herbs and more non-succulent shrubs than free-ranging sheep (Samuels *et al.* 2016). Herding at large spatial scales moves animals across a range of vegetation communities and prevents them from lingering in any one type. It is possible that the vegetation species communities on this farm, a grassland, are more evenly distributed over space relative to those in Karoo and savannas and thus forcing animal movements over space did little to change the diversity of their dietary intake. This may also be the case for other experimental trials revealing no rotational grazing effects on plant species selectivity (Kirby *et al.* 1986; Kreuter & Tainton 1988; Olson & Malechek 1988). Herbivore dietary choices will always be largely determined by factors intrinsic to plant physical and chemical structure that characterise nutritional status and digestibility (Bailey and Brown 2011), however distributing grazing across plant communities at the landscape-scale can reduce over utilisation of palatable species vulnerable to overgrazing.

It is important to note that the dynamics of cattle behaviour change over spatial scales (Bailey *et al.* 1996; Soder *et al.* 2009) and the results of this study might not be directly applicable to other management contexts. For example, in more arid rangelands where stocking rates are lower and grazing areas are larger, the effect of fencing on increasing spatial forage utilisation and reducing overgrazing of patches may be enhanced. Furthermore, this study included only steers. Social hierarchies are important determinants of grazing patterns (di Virgilio & Morales 2016) and these results may have differed with herds constituted of breeding animals or a diversity of age classes. Cow-calf operations, where conditioning to electric fencing is maintained through multiple generations, as opposed to fattening operations, where new animals are bought onto the farm every year might prevent possible drops in production caused by stress (Brunson & Burritt 2009). Incorporating mixed herds with a diversity of functional guilds may diversify the utilisation of available plant taxa (Hempson *et al.* 2017; Venter *et al.* 2017). For example, introducing browsers, such as goats with grazers in savannas can mitigate woody plant encroachment (Venter *et al.* 2018). Finally, replicating this study in both similar and different vegetation types will improve the scope of these findings, based as they are on a large-scale trial on a working commercial farm with associated limitations on replication and randomisation in the design. Despite this I find that these conclusions here are well founded because these results agree with the literature where there was commonality and I reduced limitations on experimental design by having similar vegetation and soil characteristics between treatments at the start of the trial, by sampling intensively, and by accounting for pseudo-replication using a mixed modelling approach.

Conclusion

These results suggest that adopting rotational grazing practices or variants of high density grazing do not enhance animal productivity relative to season-long continuous grazing in mesic grasslands over the short-term. This has significant economic consequences given the capital investment in setting up electric fencing and watering infrastructure for high density grazing. An economic analysis, although context-specific, revealed that conventional approaches like SLG and FCG will become profitable after one to two years, whereas HPG will take around four years to offset the higher setup and maintenance costs. Over the long-term this may change, especially if vegetation heterogeneity becomes so entrenched under SLG that it leads to rangeland degradation and declines in animal production. Managers who wish to homogenise grazing over space by adopting rotational grazing might consider reducing infrastructure costs by replacing the function of fencing with active herding, especially in rural African rangelands where traditional herding activities have played a functional role in savanna ecosystems for millennia (Marshall *et al.* 2018). Alternatively, managers who wish to enhance vegetation heterogeneity and possibly initiate the formation of grazing lawns might consider adopting SLG which, in combination with fire, commonly used in FCG, may enhance biodiversity.

Chapter 5: Does defoliation frequency and severity influence plant productivity? The role of grazing management and soil nutrients

Abstract

Rangeland management approaches, including forms of high density rotational grazing, rely on assumptions about plant growth responses to the intensity, or severity (sward height) plus frequency, of defoliation. I hypothesised that grass growth responses would be reduced under more frequent and severe defoliation but that this would be mitigated under elevated soil nutrients, in line with the Compensatory Continuum Hypothesis which predicts that compensatory growth will increase across an increasing fertility gradient. To test this at the farm-, patch- and plant-scale, I set up a grazing management trial on the Merino Walk experimental farm in an Eastern Cape mesic grassland of South Africa along with field plot and glasshouse pot manipulation experiments. The grazing trial tested season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG) at equivalent stocking rates over three years thereby enforcing a range of grazing densities (SLG < FCG < HPG). Potted plants exhibited higher relative growth rates under elevated nutrients, while both the frequency and severity of defoliation suppressed regrowth. Similarly, in the field plot experiment, dung application suppressed the negative effects of defoliation by enhancing vegetation basal cover and greenness (as measured by the normalised difference vegetation index, NDVI). In the farm trial, SLG, which theoretically causes high frequency, low severity defoliation, reduced bare ground cover and increased NDVI with increasing defoliation intensity on *Eragrostis plana* dominated nutrient-rich soils. This effect was not present under FCG or HPG and disappeared under very high defoliation intensities and on relatively water- and nutrient-poor soils dominated by *Themeda triandra*. This supports the Compensatory Continuum hypothesis and demonstrates how soil nutrient status modulates the impact of planned grazing and may be indicative of a grazing lawn effect, common in wildlife areas. Grazing lawns could potentially be induced through fertilisation (natural or artificial) of grassland paired with high frequency grazing. Managers adopting more intensive rotational grazing might try maximizing grazing frequency on nutrient-rich soils, and grazing recovery on nutrient-poor soils. These findings highlight potential to restore degraded rangeland to higher levels of basal cover and forage palatability by matching the soil resource status to the appropriate grazing management approach.

Introduction

The sustained defoliation of vegetation beyond its capacity to regrow degrades productivity and ecosystem functioning in heavily stocked rangelands across the globe (Fernández 2002; FAO 2010). Indeed, stocking rate, defined as the number of large stock units (LSUs) per hectare of available rangeland, is the most important management variable in determining vegetation and animal production

(Van Poollen & Lacey 1979; Briske *et al.* 2008). The role of grazing management strategy, whereby grazing densities are controlled across a management unit using fencing or herding, is less influential on farm productivity (Sampson 1951; Heady 1961; O'Reagain & Turner 1992). Despite the consensus of experimental evidence, the debate over the efficacy of rotational grazing relative to continuous or season-long grazing persists (Briske *et al.* 2011). This is possibly because rotational grazing should be able to maximise sward growth by some combination of defoliation duration, frequency and timing (McNaughton 1983). Nevertheless, plant basal cover and plant biomass are unaffected by forms of high density rotational grazing such as holistic planned grazing (Hawkins 2017). To help resolve these inconsistencies between theory and praxis, I investigated plant growth responses to defoliation intensity, defined as a combination of frequency and severity, through controlled manipulative studies and compared these to responses observed in a farm-scale grazing management trial. For the purposes of this study, grazing is defined as, and includes the activities of defoliation, trampling and dung deposition.

Expansion of photosynthetic tissues is primarily a response to plant level resource sinks characterised by organs with increased demand for carbon (Wardlaw 1990; Paul & Foyer 2001; White *et al.* 2016). This sink regulation of photosynthetic rate determines foliar growth, and is the primary mechanism explaining grass responses to defoliation (McNaughton 1979). Removing foliar material from grasses triggers changes in both intrinsic (physiology and development) and extrinsic (resource availability) factors (McNaughton 1983), which often result in greater relative growth rates (Hilbert *et al.* 1981). Some of the internal plant mechanisms explaining this include an increase in light-saturated photosynthetic rates and associated carboxylating enzymes (Hodgkinson 1974; Detling *et al.* 1979; Lee *et al.* 2011), a surge of plant growth promoting hormones from roots to shoots (Avery & Lacey 1968; Iqbal *et al.* 2012), and reallocation of assimilate from storage organs to meristems (Gifford & Marshall 1973; Ryle & Powell 1975; Dawson *et al.* 2004; Machado *et al.* 2013). This is associated with a root pruning and a reduction in root growth (Crider 1955; Oswalt *et al.* 1959; Wilson 1988) to re-establish a root to shoot balance, however as foliar material is recovered the weight allocation is shifted back toward shoots (Dunn & Engel 1971; McNaughton 1983). In older, less photosynthetically active leaves, partial defoliation particularly reduces stomatal and mesophyll resistance and thereby increases the intake of carbon dioxide and water vapor, essential for photosynthesis (Thorne & Koller 1974; McCormick *et al.* 2006). Extrinsic resources may also be more accessible in the post defoliation environment. Defoliation reduces shading and may increase water use efficiencies due to a reduction in leaf transpiration surface area (Baker & Hunt 1961; McNaughton 1979; White *et al.* 2016).

Plant growth responses to defoliation range from under-compensation, or partial replacement of lost foliar tissue, to over-compensation whereby plants regrow more foliar material than is lost during defoliation (McNaughton 1983; Belsky 1986). Reviews of the literature on compensatory growth have found under- or equal-compensation to be the norm because defoliation removes valuable photosynthetic material and thus reduces the capacity to produce carbohydrates (Belsky 1986; Georgiadis *et al.* 1989; Hawkes & Sullivan 2001; Wise & Warren G. Abrahamson 2007). The exceptions to this norm are found when extrinsic or intrinsic factors that limit plant growth are reduced or inhibited through defoliation (McNaughton 1983; Wise & Warren G. Abrahamson 2007). For example, grasses in the Serengeti exhibit over-compensation of lost foliage (McNaughton 1979) and unchanged root biomass (McNaughton *et al.* 1998) partly because the grass species are a product of strong evolutionary selection for grazing tolerance and partly because nutrients and water are seldom limiting in this environment. It was this tropical savanna ecosystem that inspired McNaughton (1979) to develop the Grazing Optimisation Hypothesis which posits that above ground productivity of grazed plants is increased at low to moderate grazing intensities until productivity is maximised at an optimal grazing intensity, beyond which it begins to fall. While some have argued that this hypothesis is true in an evolutionary sense (Hilbert *et al.* 1981), others have found no evidence to support it in rangeland management settings especially where resources are lacking (Belsky 1986).

In nutrient- and water-limited rangelands, grasses may fail to compensate for defoliation and thus the Grazing Optimisation Hypothesis breaks down. Simulated defoliation and nutrient limitation experiments have shown soil N (Hamilton III *et al.* 1998) and P (Chapin & McNaughton 1989) to limit Serengeti grass growth responses to defoliation. Under-compensation in nutrient limited soils is exacerbated by the negative effects of defoliation on grass roots, which are vital for nutrient and water acquisition. In a quantitative review of experimental literature, Ferraro & Oesterheld (2002) found that defoliation of grasses reduced root biomass by 32% across all plant sizes. This may lead to eventual plant mortality and the formation of bare ground patches (Thurow 1991; Fuls 1992), or where herbivores select for palatable species, the invasion of less palatable species (Ellison 1960) with a concomitant decline in primary productivity, forage quality and animal production. The decline in vegetation greenness and increase in bare ground induced by overgrazing in arid rangelands has been observed using satellite imagery in Africa (Munyati & Makgale 2009), South America (Blanco *et al.* 2008) and Asia (Hilker *et al.* 2014). In these examples, defoliation intensity exceeds the capacity vegetation has for compensatory growth often reducing vegetation basal cover and enhancing erosion and bare ground formation.

The extent to which resource availability mediates plant compensatory growth responses to herbivory has been encapsulated in the Compensatory Continuum Hypothesis (Maschinski & Whitham 1989). Here tolerance to defoliation is predicted to be greater in high resource, low competition or otherwise benign environments. For example, fertile, moist soils facilitate fast regrowth after grazing (Hawkes & Sullivan 2001). This, combined with enhanced foliar nutrient concentrations (Bryant *et al.* 1983; Jones & Hartley 1999) and consequent palatability, attracts further herbivory, which promotes faster nutrient cycling via the animal gut and urine and dung deposition compared to slower microbial or physical decomposition and oxidation of plant material (Hobbs 1996; Frank & Groffman 1998; Bardgett &

Wardle 2003). This process reinforces a positive feedback loop sustaining high soil and plant nutrient levels and has been suggested as one of the mechanisms behind the formation of grazing lawns in African savannas, characterised by productive, highly palatable and grazing tolerant grass species (McNaughton 1979; Hempson *et al.* 2015b). Indeed, grazing lawns have been experimentally induced with nutrient addition, thereby corroborating the Compensatory Continuum Hypothesis (Cromsigt & Olff 2008).

Plant responses to a range of defoliation frequencies are seldom studied (Tiffin 2000) and the interaction between defoliation severity, frequency and soil nutrient levels even less so. I investigated these interactions experimentally at three different scales including a commercial farm grazing management trial, and in situ field plot, and ex situ potted plant defoliation experiments with bunch grasses from a mesic grassland of South Africa. I hypothesised that increasing defoliation intensity (frequency x severity) will reduce grass growth responses and that this would be mitigated under elevated soil nutrients, thereby supporting the Compensatory Continuum Hypothesis. Specifically, I predicted grazing intensity would reduce relative growth rates, below ground productivity, shoot:root ratios, foliar greenness, and basal vegetation cover (the inverse of bare ground cover).

Methods

Farm grazing trial

Merino Walk experimental trial was located approximately 5 km north of Cedarville, Eastern Cape, South Africa (30° 21’ 8’’ S; 29° 3’ 29’’ E) at an altitude of 1440 m above sea level. Half of the trial was located on north-facing slopes covered by East Griqualand Grassland and the other half was located on low-lying flats covered by Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands (Mucina and Rutherford 2006). Dominant grasses included *Themeda triandra* and *Eragrostis plana*, respectively. The area is underlain by mudstones and sandstones of the Elliot and Molteno Formations (Mucina & Rutherford 2006). Flats consist of poorly-drained and nutrient-rich haplic lixisols with high clay contents whereas slopes contain relatively well-drained and nutrient-poor haplic acrisols (Hengl *et al.* 2014). Long-term (1960-2000) mean annual rainfall and temperature is 760 mm and 15 °C (Hijmans *et al.* 2005), with most rainfall occurring during austral summer months.

To verify the nutrient status of the farm soils, I took 14 and 19 evenly spaced soil samples on the slopes and flats respectively before the grazing trial was initiated. Using a 7 cm diameter soil auger, I collected four cores to a depth of 20 cm per sampling location. Samples were bulked, air-dried and sieved to 2 mm. A subsample of each was sent to Bemlab (Somerset West, South Africa) for analysis of total N by the combustion method using a Leco-FP528 N analyser (Leco, St. Joseph, MI). For the determination of total P, K, Ca, and Mg, a subsample was analysed using a Spectro Xepos X-ray fluorescence (XRF) analyser (Spectro, Amatek materials analysis division, Kleve, Germany) after grinding soil to a powder.

Measurements were conducted in a helium atmosphere using a silicon drift detector and were calibrated using a standard certified by the National Research Centre for Certified Reference Materials, Beijing, China.

Three grazing management treatments, occupying 219 ha of land on the Merino Walk farm, were initiated as an experimental trial in Dec 2015. Prior to this, the land had been managed under conservative stocking rates as a commercial cattle and sheep farm. Baseline vegetation and soil measurements were taken to account for variation in legacy management effects across the treatments. Treatments included season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG), and were assigned to existing farm camps non-randomly due to management limitations (Fig. 5.1). All treatments were stocked with year-old Bonsmara-Boran steers at a moderate stocking rate of 0.53 LSU ha^{-1} yr^{-1}, which is similar to the government recommended rate of 0.55 LSU ha^{-1} yr^{-1} (Avenant 2016). While stocking rate was kept constant, treatments differed primarily in the number of camp divisions, and consequently the relative grazing densities, defined as the number of LSUs per subunit of area at any point in time on the rangeland. Equivalent stocking rates, but varying grazing densities, theoretically result in a range of defoliation frequencies (the inverse of recovery period from grazing) and severities (the quantity of foliage removed in one defoliation event). Rotational grazing approaches are suggested to enforce short bursts of intense and severe defoliation followed by extended periods of rest (Briske *et al.* 2011; Bork *et al.* 2017). Assuming cattle consumed equal annual forage biomass, the treatments lie on a continuum from high frequency, low severity (SLG) to low frequency, high severity (HPG), with FCG producing moderate frequencies and severities (Fig. 5.2). However, SLG does not necessarily represent a high frequency, low severity type of grazing regime. The cattle in this management regime have more opportunity to express foraging behaviors, which may or may not result in high frequency of grazing on individual plants. It is entirely possible that under SLG, individual plants may mostly only be bitten once over the course of a growing season. Although experimental clippings likely simulated a wider range of defoliation frequencies and intensities than would be found in the farm trial of the direction of the defoliation severity and frequency gradients are comparable to those applied in both plot and plot clipping experiments (see below).

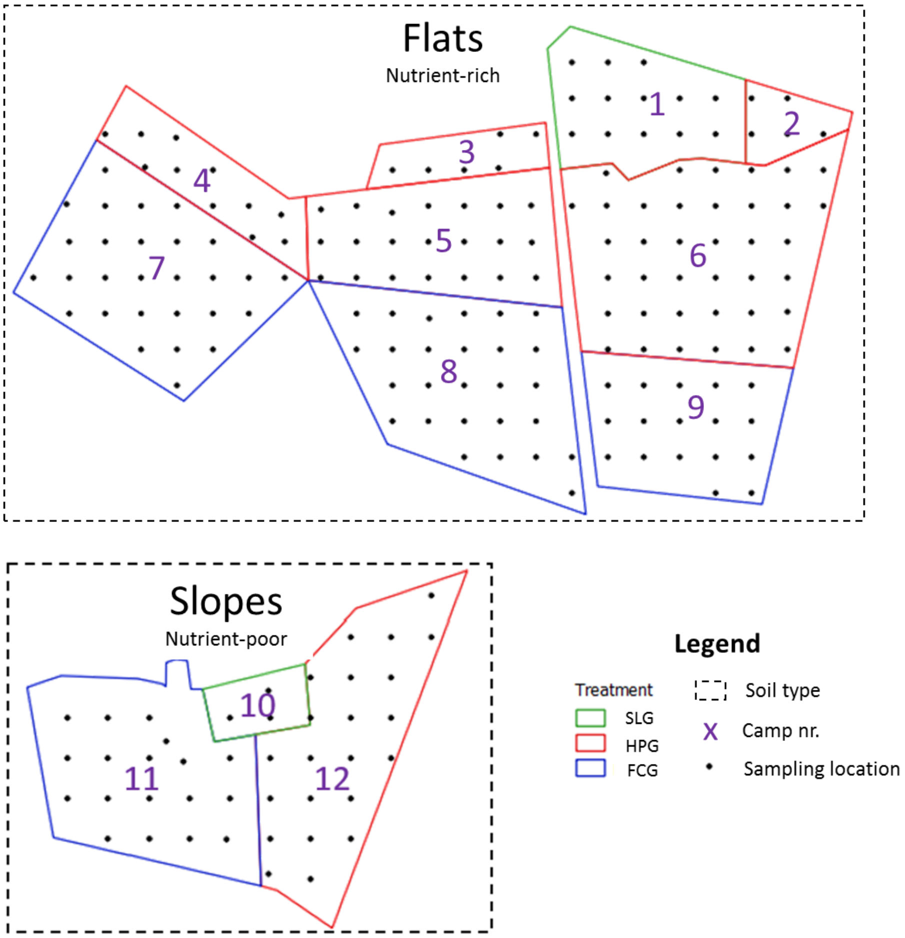


Figure 5.1 Merino Walk experimental trial layout for three grazing management treatments, season-long grazing (SLG), four-camp grazing (FCG), and holistic planned grazing (HPG). Vegetation biomass sampling locations are indicated with solid points. Half of the trial is covered by the East Griqualand Grassland vegetation type (Slopes), dominated by *T. triandra*. The other half is located on low-lying relatively nutrient-rich soils of the Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands vegetation types, dominated by *E. plana*.

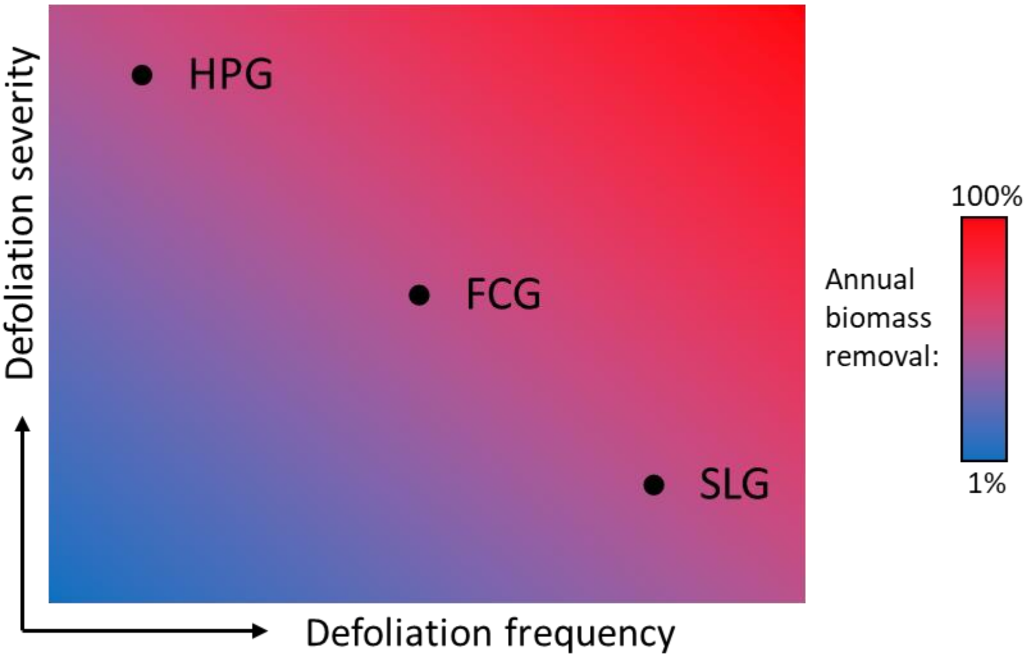


Figure 5.2 Theoretical defoliation severity (amount of plant removed in one grazing evet) and frequency (the inverse of recovery between grazing events) experienced by a parcel of land or individual plant on the Merino Walk experimental trial at a theoretical 50% biomass removal. Season-long grazing (SLG) theoretically allows animals to range freely and thus repeatedly graze vegetation regrowth within a grazing season resulting in high defoliation frequencies, however while SLG allows animals to forage freely this may not mean repeated grazing of the same tillers. Holistic planned grazing (HPG) is at the other extreme because it restricts grazing area per day with electric fencing or herding and, in the case of my trial, enforces a minimum 60 d recovery period, resulting in low defoliation frequency. Assuming cattle remove equivalent annual biomass, defoliation severity and frequency must be inversely related. Hypothetically, SLG cattle might take one bite of a plant (low severity) and return a few days later to regraze the new regrowth, whereas the same plant might be defoliated several times within one day (high severity) due to higher cattle densities but will only be regrazed after 60 d recovery. Four-camp grazing (FCG) lies in between SLG and HPG.

In SLG grazing, one camp is grazed for an entire growing season and then cattle are moved to a second camp for the non-growing season. In FCG, cattle are rotated amongst three camps at varying levels of intensity while one camp is left to rest for an entire year. In subsequent years the camp allocated to annual rest is the first camp to be grazed, and conventionally this is preceded by burning (Venter & Drewes 1969). I chose to exclude burning from this system because of difficulties in distinguishing and comparing fire and grazing behaviour effects across treatments. For this study, HPG refers to a high intensity grazing approach similar to short duration (Tiedeman 1986), cell grazing (McCosker 2000), and holistic planned grazing (Savory & Butterfield 2016). In the study I followed the adaptive management protocol of Holistic Management (HM) in which a flexible grazing plan is constructed outlining animal movements between multiple small camps (see Media Gallery P1) with the aim of increasing animal densities and thereby increasing even utilisation and reducing overgrazing (Savory & Butterfield 2016). Portable electric fencing was employed to construct grazing strips of between one and two hectares in size. The farm manager and research team undertook an intensive three-day training course by an accredited HM trainer familiar with the South African context. This was done in order to adhere to HM principles and follow the correct HM planning procedure.

To quantify the spatial distribution of defoliation intensities, I deployed GPS collars (see Media Gallery P2) on randomly selected cattle for 60 d on two summer (Jan 2017 and 2018) and two winter (Jun 2016 and 2017) sampling occasions. GPS devices (Perthold Engineering LCC, Richardson, Texas, USA) were set to log a position every 5 min and attached to nylon belts fastened around the animals' necks. I deployed enough collars to obtain an average replication of three collars per treatment per sampling date. Three devices were placed at a known location and left for three weeks to test the spatial accuracy of the GPS. This revealed a median error of 5.4 m with 95% of the data points occurring within 22.5 m of the actual location. GPS devices remained active for an average of 29 ± 2.4 days per sampling occasion. I analysed the data from each GPS collar as a spatial point pattern using the 'spatstat' package in R (Baddeley *et al.* 2015). For each sampling occasion I included GPS points from all treatments over the period in which the HPG cattle were moved through one complete management unit (see camps in Fig. 5.1). The GPS points were clipped to the boundaries of the camps occupied during the sampling period after applying a negative buffer of 10 m to each camp to account for the effects of fences on the cattle behaviour. I then defined GPS locations relevant to grazing pressure as consecutive points (5 min apart) greater than 22.5 m from one another which, according to my accuracy assessment reflects 95% certainty that the animal was not resting (i.e. grazing or walking). To estimate the spatial distribution of grazing pressure I then calculated the kernel (gaussian) smoothed density of the remaining locations, after standardising the number of points per hectare, using the 'density' function in spatstat.

A regularly-spaced sampling grid of points 90 m apart was generated over the farm producing 209 sampling locations which were revisited every austral summer and winter between 2015 and 2018 to measure standing grass biomass. I used a disc pasture meter (DPM), which relates grass biomass to the height of a disc dropped on the sward (Bransby & Tainton 1977). The DPM was calibrated by collecting and drying grass clippings directly under the disc at 60 evenly spaced points within the sampling grid. These weights were regressed on the DPM readings ($R^2 = 0.78$) and the linear regression coefficients were used to calculate standing biomass for all subsequent readings. I took DPM readings every metre along a 10 m line transect at each sampling point every season. To correct for baseline variations in biomass between treatments, I calculated the trend in biomass at each point as the slope of the linear regression line between 2015 and 2018.

Satellite-derived estimates of vegetation greenness and bare ground cover were obtained using the Google Earth Engine cloud computing platform (Gorelick *et al.* 2017). The normalised difference vegetation index (NDVI, Tucker 1979) has been widely used as an indicator of vegetation productivity, quality and vigour in rangelands (Svoray *et al.* 2013; Ali *et al.* 2016). I extracted the NDVI values over the farm from the Landsat 7 Enhanced Thematic Mapper Plus and Landsat 8 Operational Land Imager surface reflectance products at 30 m resolution after correcting for inter-sensor discrepancies using published calibration coefficients (Roy *et al.* 2016). Once clouds were masked using the 'pixel_qa' band, I calculated the slope of the linear trend line for each pixel by regressing NDVI on time. As with standing biomass (above), this gives a relative measure of change, accounting for any baseline differences in NDVI between treatments. To detect fractions of bare ground cover I used four high resolution (3-5 m) cloud free scenes obtained from Planet (PlanetTeam 2017) RapidEye and PlanetScope satellites during Aug (winter) each year (2015-2018). The Planet data were converted to top-of-atmosphere reflectance using the calibration coefficients provided for each scene. Spectral unmixing techniques (Bateson *et al.* 2000) were used to derive fractional bare ground cover within each image pixel. Spectral mixing models are based on the understanding that each pixel contains a mixture of information from several spectrally distinct surface components or 'endmembers'. I created a mosaic of all Planet scenes and defined pixels characterising pure bare ground and pure vegetation cover. The mean reflectance value over these pixels for each spectral band was obtained and these values were used as endmembers in a mixing model to discriminate pixel fractions of bare ground and vegetation. After determining fractional bare ground for each winter season, and NDVI for each month, I calculated the change in both variables for each pixel over the farm as the slope of the linear trend line between 2015 and 2018.

Field plot experiment

I set up an in situ defoliation and dung addition experiment on Merino Walk (see Media Gallery P4) to discern interactions between defoliation severity and frequency in a more controlled environment, which allowed for more precise sampling of vegetation responses than what the farm-scale trial allowed for. One hectare of homogenous East Griqualand Grassland, which had not been grazed for the previous three years, was fenced off from livestock. After baseline vegetation sampling in 2015, I found the dominant grasses to be *T. triandra*, *Tristachya leucothrix*, and *Harpochloa flax*, with a basal cover of 18, 26, and 23%, respectively. *T. tiandra* is considered palatable, while *T. leucothrix* and *H. flax* are less palatable and are known to increase under grazing pressure. All three species are perennial tussock grasses. I divided the area into 5 x 5 m plots. Four levels of defoliation frequency (15, 30, 60 and 90 d) were crossed with two levels of defoliation severity (defoliation to 10 or 5 cm above ground) and three randomly allocated replicate plots per treatment. The 60 d recovery by 10 cm defoliation height treatment was replicated another three times to introduce a nutrient addition treatment. I randomly assigned three undefoliated plots as controls for both experiments. Defoliation was carried out using a sit-on lawn mower, the height of which was manipulated to achieve 10 and 5 cm mowing heights. Clipped plant material was raked to the side of each plot following defoliation. Fresh cattle dung collected from the surrounding farm camps was mixed with water into a slurry and applied randomly and not homogenously to the nutrient addition treatment every 60 d following a 10 cm defoliation. The slurry was applied randomly to mimic the patchy distribution of dung pats over a rangeland. To determine how many dung pats to apply I laid out 200 regularly spaced belt transects (1.5 x 10 m) over the farm and counted dung pats. I observed an average of 0.28 dung pats per square meter and thus applied 3 dung pats per application to a 3 x 3 m square within each 5 x 5 m plot. This 1 m buffer was created to prevent nutrient contamination of neighbouring plots. The addition of dung after clipping was meant to more fully simulate the effect of grazing by cattle.

I implemented the defoliation and nutrient addition treatments between Feb 2016 and Aug 2018 and measured bare ground cover and vegetation NDVI. To measure percentage bare ground I used a Levy Bridge (Levy & Madden 1933) to sample 10 descending points spaced 25 cm apart. The Levy Bridge was randomly dropped inside each plot three times during Jan of 2017 and 2018. I counted the number of point intercepts with bare ground or plant material and calculated bare ground as a percentage of the sum of all dropped points. To measure NDVI, I used the GreenSeeker Handheld Crop Sensor (Trimble, CA, USA). The device was held 100 cm above the ground and an integrated NDVI measurement was taken by walking in a spiral pattern from the edge of the plot inward with the device's trigger held down for 30 s (see Media Gallery P4). This measurement was repeated every two weeks for the duration of the experiment.

Glasshouse pot experiment

To study plant-level responses to defoliation intensity and soil nutrient levels, I set up a glasshouse pot experiment with a 3 x 3 factorial design, with three species and three levels of defoliation frequency (20, 40 and 60 d). I selected three perennial bunch grass species, including *T. triandra*, *E. plana*, and *Elionurus muticus*, from the same farm in which the field experiment and grazing trial took place (see Media Gallery P5). Empirical evidence from previous studies shows *T. triandra* decreases in abundance under heavy or selective grazing whereas *E. plana* and *E. muticus* increase (Foran *et al.* 1978; Tainton *et al.* 1980). *T. triandra* is generally considered the most important grass in sub-Saharan African rangelands due to its widespread abundance and palatability (Snyman *et al.* 2013). *E. muticus* and *E. plana* are both relatively unpalatable grazing-resistant grasses, which proliferate in over-utilised grassland (Brockett 1983; Barnes 1990). Because *E. plana* is the most abundant species on the farm, I chose it to apply two levels of defoliation severity (10 and 5 cm) and two nutrient addition levels (low and high).

Treatments were replicated six times. Plants of basal diameter >10 cm were randomly selected in the field, removed with 30 cm of soil, and transported to a glasshouse at the University of Cape Town (33°

57’ 21’’ S; 18° 27’ 43’’ E). Plugs containing 5-10 tillers were transplanted into plastic pots, 18 cm in diameter, filled with a mixture of course and fine grain sand (1:1). Haifa Multicote 12 month slow-release fertilizer (Haifa Chemicals Ltd, South Africa) containing 14-7-14 N:P:K (97%) with Mg (2%), Fe, Mn, Cu, Mo, Zn, B, and Ca (1% cumulative) was mixed with soil in the top half of each pot. Nutrient additions were calculated from foliar N accumulation rates for *T. triandra* reported in Anderson *et al.* (2013). I applied 100% (6 g fertilizer) of the minimum nutrient requirement calculated for *T. triandra* over 360 days to each pot. For the nutrient high treatment applied to *E. plana*, I used 150% (9 g fertilizer) of the minimum nutrient requirement. Plants were initially clipped to 10 cm to stimulate root establishment and left to regrow under irrigation for 6 months prior to the implementation of defoliation treatments.

Plants were defoliated between Oct 2016 and May 2017 with secateurs and the clipped biomass was oven dried at 70 °C for one week and then weighed. The biomass removed at the first (W_1) clipping and the cumulative biomass removed at the final (W_2) clipping was used to calculate relative growth rate (RGR, Fisher 1921) for each plant, where $RGR = \frac{\ln W_2 - \ln W_1}{t_1 - t_2}$. As a relative response, RGR accounts for the potential confounding effect of baseline plant sizes. After the final harvest, roots were washed, dried and weighed and added to cumulative foliar harvest to obtain total plant biomass production.

In addition to measures of plant biomass I measured foliar NDVI every 20 days using a MAPIR Survey 2 camera, which measures reflectance in visible and near-infrared wavelengths. NDVI has been shown to correlate well to plant foliar C:N ratios, crude protein and plant vigour (Pettorelli *et al.* 2005; Beeri *et al.* 2007; Ali *et al.* 2016), all characteristics of forage palatability. Pots were placed within a 60 x 60 cm cardboard box covered in red paper and photos were taken from a height of 100 cm above the box using a tripod. Images were captured in RAW format and pre-processed using Image J FIJI software with the MAPIR plugin, whereby image reflectance values were corrected for solar radiance using values from a calibration target (supplied by MAPIR) measured at each sampling occasion. The purpose of the red paper background was to isolate image pixels constituting plant leaves. Using the ‘raster’ package in R (RCoreTeam 2016), I applied a threshold of 0.3 to mask out background pixels before calculating mean foliar NDVI (see Media Gallery P5).

Statistical tests of significance

I used linear mixed models (Harrison *et al.* 2018) to analyse the effects of treatments on response variables in pot, plot and farm trial experiments. Due to practical limitations on the farm trial the spatial distribution of camps was not randomised although I made efforts to standardise access to water and allocate equal treatment areas to the two soil and vegetation types defined by slopes and flats (Fig. 5.1). To account for this, and the spatial autocorrelation in remotely sensed variables, I assigned camp number as a random intercept in the model, and balanced sample sizes between treatments by extracting a random subsample of pixels stratified by treatment. Management approach, soil type, and cattle density were added as fixed effects in separate models explaining biomass, bare ground, and NDVI trends. Similarly, in field plot experiments, repeated measures of bare ground and NDVI create potential temporal autocorrelation in the data. To account for this, I assigned plot number as a random intercept in the model, with defoliation frequency, severity and dung application as fixed effects. Finally, baseline plant sizes in the glasshouse pot experiment varied between treatments, thus, after testing that it was not significant as a main effect, initial plant weight was added as a random intercept in the model to control for this. Defoliation frequency, severity, species and nutrient addition were added as fixed effects in separate models explaining each growth response variable. Model residuals were inspected for violations of linear mixed model assumptions before resorting to logit (proportional data) or log (continuous data) transformation procedures as a corrective measure. All mixed models were performed in R (RCoreTeam 2016) using the 'lme4' package (Bates *et al.* 2014).

Results

Nutrient addition in the glasshouse pot experiments had the strongest (highest χ^2 values) positive effect on total biomass, shoot:root biomass production ratios and NDVI relative to declining defoliation frequency and severity while frequency had a greater influence on RGR and root biomass (Table 5.1a; Fig. 5.3A-E). In the field plot experiments, dung addition at 60 d defoliation frequency completely prevented the formation of bare ground and significantly enhanced NDVI relative to both clipped and unclipped treatments without dung (Table 5.2b; Fig. 5.4B and D; Fig. S5.1). In the pot experiment, the positive effect of nutrient addition on root and total biomass was enhanced at lower clipping frequencies but was unaffected by defoliation severity (Table 5.1a, Fig. 5.3B and C). In contrast to this, when considering shoot biomass alone (as foliar RGR), the effect of nutrient addition was enhanced under more severe defoliation but unaffected by defoliation frequency (Table 5.1a; Fig. 5.3A). Increasing defoliation frequency (60 to 20 d) and severity (10 to 5 cm) generally reduced RGRs, total biomass and root production, whereas this effect was not apparent for shoot:root biomass or NDVI. Severe defoliation enhanced shoot:root biomass independent of frequency (Table 5.1a; Fig. 5.3D), while frequent defoliation at low severity resulted in a relatively enhanced NDVI within each nutrient level (Fig. 5.3E). In the field plot experiments, bare ground cover and NDVI were unaffected by defoliation frequency, however, severe defoliation increased bare ground cover across all levels of defoliation frequency while it increased NDVI at 15 d frequency alone (Table 5.2a; Fig. 5.4A and C).

Table 5.1 The effects of defoliation frequency (20, 40 or 60 d), severity (10 or 5 cm sward height) and nutrient addition (high or low) on the growth response of potted *E. plana* (a), and effects of defoliation frequency on the growth responses of three species (*E. plana*, *E. muticus*, and *T. triandra*) under low nutrients and low defoliation severity (b) in a glasshouse pot experiment. Results are based on linear mixed models explaining plant responses.

(a) Frequency x Severity x Nutrients				(b) Frequency x Species			
	χ^2	*df*	*p*		χ^2	*df*	*p*
RGR (g g^{-1} d^{-1})				RGR (g g^{-1} d^{-1})			
Frequency	109.1	2	< 0.001*	Frequency	102.9	2	< 0.001*
Severity	22.7	1	< 0.001*	Species	52.5	2	< 0.001*
Nutrients	27.5	2	< 0.001*	Frequency x Species	8.1	4	0.087
Frequency x Severity	5.89	2	0.053	Total biomass (g)			
Frequency x Nutrients	2.2	2	0.333	Frequency	21.3	2	< 0.001*
Severity x Nutrients	8.1	1	0.004*	Species	75.3	2	< 0.001*
Total biomass (g)				Frequency x Species	14.6	4	0.005*
Frequency	103.2	2	< 0.001*	Root biomass (g)			
Severity	12.1	1	< 0.001*	Frequency	261.3	2	< 0.001*
Nutrients	285.7	1	< 0.001*	Species	31.1	2	< 0.001*
Frequency x Severity	0.8	2	0.658	Frequency x Species	12.3	4	0.016*
Frequency x Nutrient	27.1	2	< 0.001*	Shoot:root biomass ratio			
Severity x Nutrients	2.5	1	0.11	Frequency	1120.9	2	< 0.001*
Root biomass (g)				Species	460.6	2	< 0.001*
Frequency	77.8	2	< 0.001*	Frequency x Species	60.7	4	< 0.001*
Severity	21.4	1	< 0.001*	NDVI			
Nutrients	13.1	1	< 0.001*	Frequency	1.9	2	0.393
Frequency x Severity	1.4	2	0.501	Species	813.8	2	< 0.001*
Frequency x Nutrients	8.4	2	0.015*	Frequency x Species	0.6	4	0.963
Severity x Nutrients	3	1	0.082				

RGR stands for relative growth rate

χ^2 is the chi-square statistic

$p < 0.05$ indicated by *

Table 5.1 Cont.

(a) Frequency x Severity x Nutrients			
	χ^2	*df*	*p*
Shoot:root biomass ratio			
Frequency	0.7	2	0.692
Severity	6	1	0.014*
Nutrient	272.3	1	< 0.001*
Frequency x Severity	1.4	2	0.495
Frequency x Nutrient	1.6	2	0.443
Severity x Nutrient	2.9	1	0.087
NDVI			
Frequency	14.3	2	< 0.001*
Severity	0.8	1	0.371
Nutrient	23.1	1	< 0.001*
Frequency x Severity	8.5	2	0.014*
Frequency x Nutrient	6.4	1	0.011*
Severity x Nutrient	1.3	2	0.001*

NDVI is the normalised difference vegetation index

χ^2 is the chi-square statistic

$p < 0.05$ indicated by *

Table 5.2 The effects of defoliation frequency (15, 30, 60 or 90 d) and severity (10 or 5 cm) on percentage bare ground cover and NDVI (a) in the field plot experiments as modelled with linear mixed models. The effects of dung application (versus no application) to plots defoliated every 60 d to 10 cm sward height were also modelled (b).

(a) Frequency x Severity			
	χ^2	*df*	*p*
Bare ground (%)			
Frequency	8.9	4	0.062
Severity	17.9	1	< 0.001*
Frequency x Severity	3.2	3	0.364
NDVI			
Frequency	10.9	2	0.004*
Severity	10	3	0.018*
Frequency x Severity	8.9	3	0.031*

(b) Dung			
	χ^2	*df*	*p*
Bare ground (%)			
Dung	9	2	0.011*
NDVI			
Dung	28.9	2	< 0.001*

NDVI is the normalised difference vegetation index

χ^2 is the chi-square statistic

$p < 0.05$ indicated by *

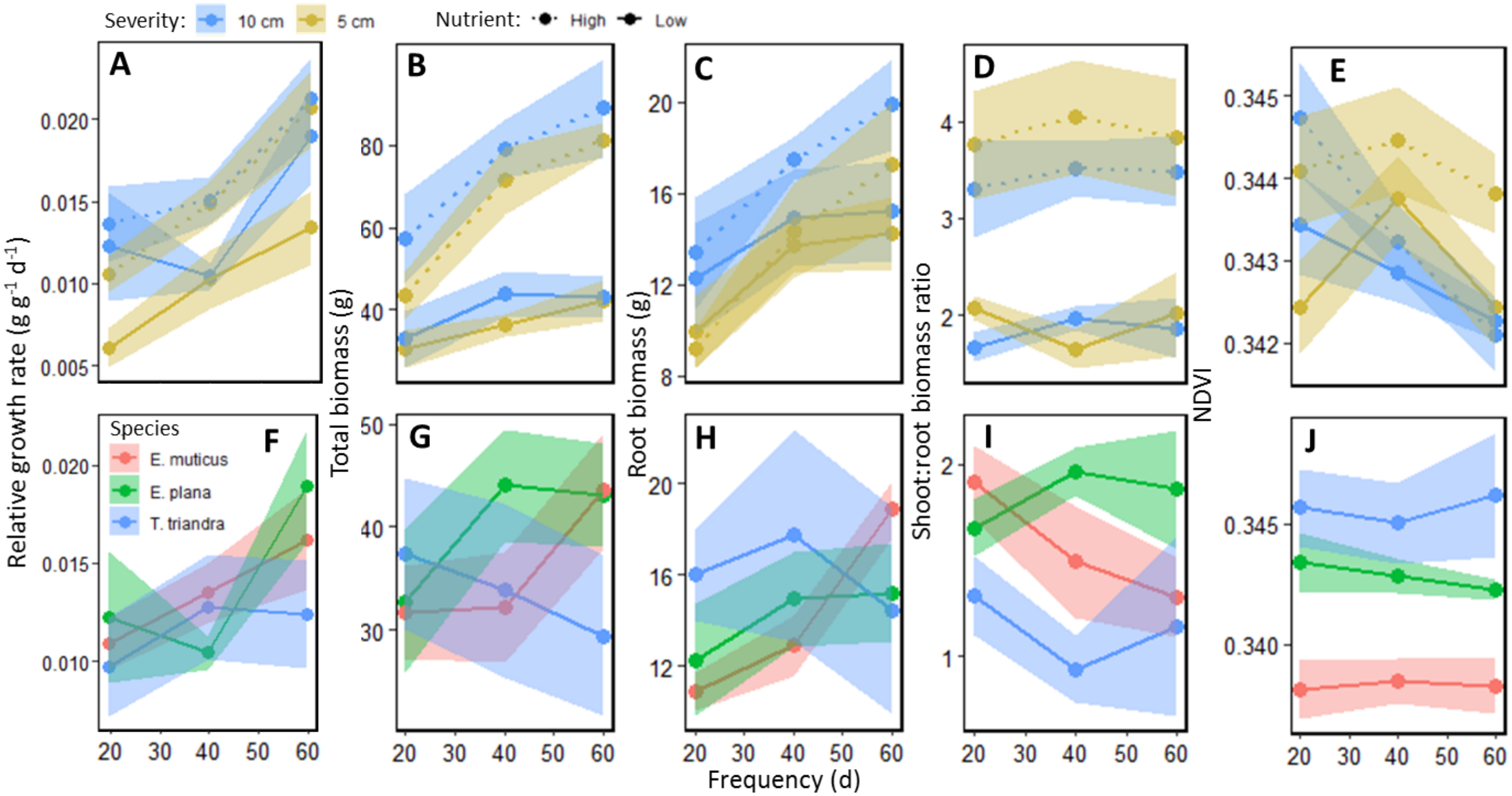


Figure 5.3 Plant growth responses from a glasshouse pot experiment with three bunch grasses removed from Merino Walk experimental farm. Experimentally induced defoliation frequency, severity and nutrient input was applied to *E. plana* (top row). The defoliation frequency treatment was applied to three grass species (*E. plana*, *E. muticus* and *T. triandra*) at 10 cm severity and low nutrient levels to assess species-specific responses (bottom row). Growth responses included relative growth rates (A, F), total cumulative plant biomass at harvest (B, G), root biomass (C, H), shoot:root biomass ratios (D, I), and foliar greenness as measured by the normalised difference vegetation index (NDVI, E, J). Data points and colour ribbons represent treatment means (n = 6) and 95% confidence intervals, respectively.

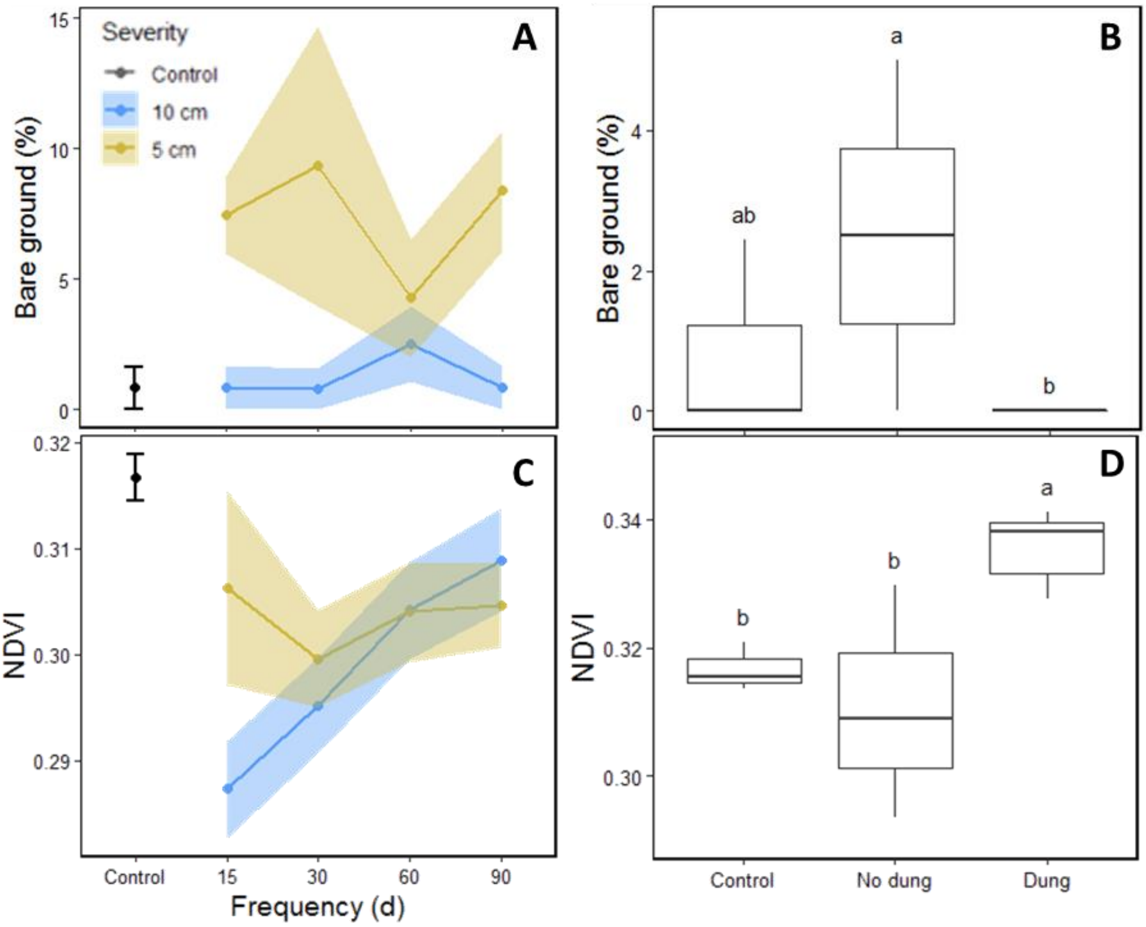


Figure 5.4 Percentage bare ground (A, B) and vegetation greenness (C, D), as measured by the normalised difference vegetation index (NDVI), for experimental plots located on the Merino Walk (Goedehoop section) experimental farm. Responses to defoliation frequency and severity (A, C), and dung application with 60 d defoliation at 10 cm severity (B, D) are shown in contrast to control plots that did not receive defoliation or dung. In A and C, data points and colour ribbons represent treatment means (n = 3) and 95% confidence intervals, respectively. In C and D, data medians are represented as horizontal lines within boxes which stretch to the 25th and 75th data percentiles. Whiskers extend to the largest and smallest values no further than 1.5 times the inter quartile range.

Grass species in glasshouse pot experiments differed in their response to defoliation frequencies for all response variables (Table 5.1b; Fig. 5.3 F-J). Growth responses and NDVI of *T. triandra* were unresponsive to defoliation frequency whereas RGR and total biomass production in *E. muticus* and *E. plana* were reduced under 20 d relative to 60 d defoliation frequencies (Fig. 5.3 F and G). *T. triandra* produced lower total biomass at 60 d recovery compared to *E. muticus* and *E. plana* (Fig. 5.3 G). Increasing defoliation frequency reduced root biomass and increased shoot:root production in *E. muticus*, whereas these responses were unaffected in *E. plana* and *T. triandra* (Fig. 5.3 H and I). Species foliar NDVI increased with increasing palatability (*E. muticus* < *E. plana* < *T. triandra*, Fig. 5.3J), where palatability was inferred from previous empirical studies on grazing tolerance (Tainton *et al.* 1980). Foliar NDVI was unaffected by defoliation frequency (Table 5.1b).

At the farm-scale, cattle density was unrelated to changes in standing biomass, and this did not change across management approaches or soil types (Table 5.3; Fig. 5.5A-C). Soil analyses confirmed that the flats were significantly richer in N and P compared to slopes (Table 5.4), confirming a priori soil type classifications. Over the course of the trial, bare ground increased more on nutrient-poor compared to nutrient-rich soils, where the extent of this effect increased with increasing cattle densities in SLG and HPG (Table 5.3; Fig. 5.5D-F). Although cattle density had no overall effect on bare ground, higher densities (under SLG) reduced bare ground on high nutrient soils and increased bare ground on low nutrient soils (Fig. 5.5D) where relatively high and low nutrient soils were dominated by grass species *E. plana* and *T. triandra* respectively. The reduction in bare ground under increasing SLG cattle densities on nutrient-rich soils saturated at very high densities and was not apparent under FCG or HPG. The response in NDVI trends to cattle densities (Fig. 5.5G-I) were inversely related to those of bare ground, but only under SLG (Fig. 5.5G), where NDVI was enhanced with increasing cattle density on high nutrient soils. This effect also plateaued at very high cattle densities. NDVI was measured during both growing and non-growing seasons and displayed positive trends over the entire farm, whereas bare ground, measured during the non-growing season alone due to data limitations, increased in some areas and decreased in others. Although NDVI trends were positive over the entire farm, the magnitude of this increase was unaffected by cattle density across all treatments on low nutrient soils. The pot experiment corroborates the finding on the farm trial in that the growth responses, including NDVI, of *T. triandra* (the dominant species on low nutrient soils) were resilient to defoliation frequency.

Table 5.3 The effects of cattle density (GPS points m^{-2}), grazing management (season-long, four-camp, or holistic planned grazing), and soil type (nutrient-rich *E. plana* dominated areas on the flats, or relatively nutrient-poor *T. triandra* dominated areas on the slopes) on vegetation biomass, bare ground and NDVI trends on the Merino Walk experimental trial. Results are based on linear mixed models explaining vegetation responses.

	χ^2	*df*	*p*
Biomass trend (kg ha^{-1} yr^{-1})			
Cattle density	0.3	1	0.581
Grazing management	0.2	2	0.888
Soil type	0.7	1	0.389
Cattle density x Grazing management	1	2	0.612
Cattle density x Soil type	2	1	0.161
Grazing management x Soil type	1.8	2	0.401
Bare ground trend (% yr^{-1})			
Cattle density	0.01	1	0.789
Grazing management	1.3	2	522
Soil type	8.1	1	0.004*
Cattle density x Grazing management	39.6	2	< 0.001*
Cattle density x Soil type	19.1	1	< 0.001*
Grazing management x Soil type	0.7	2	0.712
NDVI trend (units yr^{-1})			
Cattle density	32.5	1	< 0.001*
Grazing management	0	2	0.999
Soil type	2.2	1	0.138
Cattle density x Grazing management	43.2	2	< 0.001*
Cattle density x Soil type	0.5	1	0.489
Grazing management x Soil type	0	2	0.998

NDVI is the normalised difference vegetation index

χ^2 is the chi-square statistic

$p < 0.05$ indicated by *

Table 5.4 Soil nutrient concentrations on the flats and slopes of Merino Walk experimental farm. The flats are covered by Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands (Mucina & Rutherford 2006) with poorly-drained haplic lixisols with high clay contents (Hengl *et al.* 2014). The slopes are covered by East Griqualand Grassland with relatively well-drained haplic acrisols. Soil nutrient concentration means ± standard errors are reported. Different letters after standard errors represent significant differences between flats and slopes. ANOVA results are also reported.

Soil nutrient	Flats			Slopes			*F*	*df*	*p*
N (%)	0.14	±	0.006^{a}	0.096	±	0.003^{b}	14.97	1	< 0.001
P (%)	0.044	±	0.002^{a}	0.038	±	0.002^{b}	4.3	1	0.043
K (%)	1.03	±	0.019^{b}	1.21	±	0.052^{a}	16.13	1	< 0.001
Ca (%)	0.535	±	0.036	5.54	±	0.212	0.019	1	0.89
Mg (%)	0.148	±	0.026	0.144	±	0.079	0.005	1	0.945

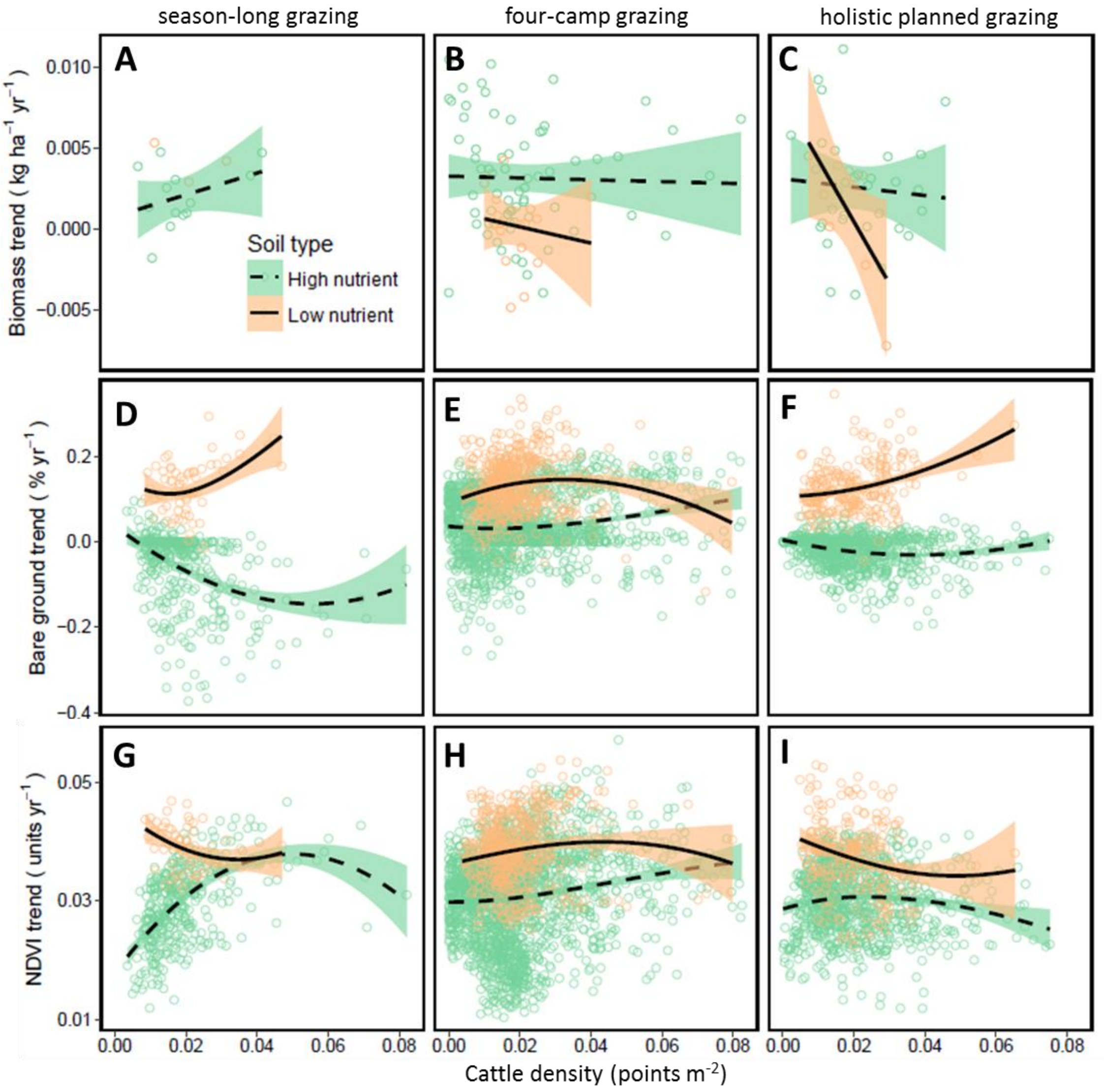


Figure 5.5 Vegetation cover responses (panel rows) in relation to observed cattle grazing densities on low and high nutrient soils on the Merino Walk experimental farm. Management approaches (panel columns) included season-long grazing, four-camp grazing and holistic planned grazing. Grazing densities were inferred from the density of GPS collar locations over the farm. The kernel smoothed densities of GPS points were rasterised and related to satellite derived raster images of NDVI and bare ground trends, whereby each data point represents a 30 x 30 m raster pixel over the farm. Biomass trends were derived from seasonal disc pasture meter readings at points along a defined sampling grid. Grazing density values were extracted for each biomass trend sampling location. Trend values were calculated as the slope of the linear trend line through all available time points for each vegetation response from 2015 to 2018. Lines plotted through bare ground and NDVI trend data are loess regressions. Linear regressions produced a better fit to the data for biomass trend data. The trend line was excluded for low nutrient soils in A due to deficient data. Coloured ribbons indicate 95% confidence intervals.

Discussion

Increasing defoliation intensity (frequency x severity) generally reduced grass growth responses across glasshouse-, field- and farm-scale experiments. This supports the well-established principle that plant compensatory growth is inhibited at excessive levels of defoliation (McNaughton 1979). Few studies explore the interaction between defoliation frequency and severity even though grazing management decisions require an understanding of how plants respond to various combinations of grazing frequency and severity. The bulk of studies testing a range of defoliation frequencies have found reduced plant growth under high frequency defoliation whereas those investigating the effect of defoliation height (severity) have found no changes in growth response (Ferraro & Oesterheld 2002). A review of ryegrass responses to defoliation showed that re-grazing grasses before they have recovered two leaves per tiller retards regrowth because plants are unable to recover sufficient photosynthetic surface area (Fulkerson & Donaghy 2001). Nevertheless, grazing severity can be as significant as frequency, depending on the height of defoliation. For example, Snyman *et al.* (2013) found that seed production and biomass can be drastically reduced in *T. triandra* but only if defoliation is severe enough to remove the apical meristems of tillers, which are located close to the soil surface.

The most consistent finding in this study was that higher soil nutrients mitigated the negative effects of defoliation on plant growth. This supports the Compensatory Continuum Hypothesis, which predicts that compensatory growth will increase across an increasing fertility gradient (Maschinski & Whitham 1989). In contrast to this, a review of 16 defoliation experiments found that both high and low soil N levels led to a more severe reduction in growth by defoliation relative to moderate N levels (Ferraro & Oesterheld 2002). N limitations reduce the capacity for plants to replenish N stores that are removed during severe defoliation (McNaughton & Chapin 1985; Augustine & McNaughton 2006). Conversely, when N is abundant, plants grow at high growth rates anyway and thus defoliation would not promote compensatory growth (Georgiadis *et al.* 1989). The Limiting Resource Model is perhaps better at capturing these nuances than the Compensatory Continuum Hypothesis because it predicts that plant responses to grazing are dependent on whether defoliation exacerbates any one of multiple growth-limiting nutrient resources (Wise & Abrahamson 2005). For example, P deficiency reduced plant ability to replenish nutrient and biomass losses to grazers in the Serengeti (Chapin & McNaughton 1989). Further, Zhao *et al.* (2008) concluded that the lack of growth response to N addition in their study was likely because their N application did not surpass a critical threshold of N availability. Globally, grasslands have been found to be predominantly N-limited (LeBauer & Treseder 2008). Given the ratio between N and P in the present study did not differ greatly between nutrient-rich and poor soils, it is likely that growth responses were inhibited by a co-limitation of N and P in nutrient-poor soils. Further, the inhibited growth found at elevated nutrients by Ferraro & Oesterheld (2002) is arguably an artefact of experimental manipulations applying nutrient levels in excess of that which is commonly found in natural settings.

The influence of soil nutrient status on plant growth responses to defoliation in the pot experiment were corroborated by measures of vegetation basal cover and biomass production in the field plot experiment and farm trial. Bare ground formation increased with defoliation frequency, but this was completely and partially mitigated by dung addition and soil nutrient status in the field plots and farm trial, respectively. A reduction in bare ground is likely a result of increased compensatory growth to defoliation because of increased basal vegetation cover. Other studies have found similar effects when livestock are corralled into small areas, thereby concentrating dung and enhancing vegetation basal cover (Muchinu *et al.* 2009; Porensky & Veblen 2015) or mitigating woody plant encroachment (Veblen 2013). Soil moisture, a factor not tested in my pot experiments, is likely also a significant contributor to growth responses in the field plot and farm trial experiments where dung application and soil type both enhanced moisture availability in association with enhanced nutrients. Cattle dung decreases soil crusting and bulk density thereby enhancing soil infiltration and water holding capacity (Haynes & Naidu 1998). Further, the farm trial flats, where a significant reduction in bare ground occurred under SLG, have high clay contents and thus a higher water holding capacity than the slopes (Hengl *et al.* 2014). Given that water and nutrient availability enhance plant growth rates, it is not surprising that plants in environments with abundant resources can recover faster from defoliation than those in resource-limited environments (Hawkes & Sullivan 2001).

Despite the importance of resource availability, the grazing management debates remain focussed on the trade-offs between grazing severity and frequency induced by forms of rotational grazing. One of the main aims of rotational grazing is to extend rest periods (reduce defoliation frequency) between grazing events, and therefore by necessity increase the grazing severity per grazing event (Derner *et al.* 1994; Volesky 1994). A study in Canadian mixed grass prairie reported no difference in forage yields between high frequency, low severity grazing, and low frequency, high severity grazing (Bork *et al.* 2017). Similarly, my results reveal no direct trade-off between grazing severity and frequency, although soil fertility on the farm trial mediated an indirect trade-off where increasing the density of grazing pressure under SLG (high frequency, low severity) reduced bare ground cover and increased vegetation NDVI on soils where nutrients and moisture were abundant. In contrast, forms of rotational grazing, FCG and HPG, showed no such effect. Likewise, in the pot experiments, increasing defoliation frequency enhanced NDVI under elevated soil nutrients. Although I did not measure foliar nutrients directly, NDVI has been shown to correlate with a range of forage quality and digestibility indices including foliar N and crude protein content (Svoray *et al.* 2013; Ali *et al.* 2016). This effect on NDVI may be similar to the formation of grazing lawns observed in African savannas (Augustine *et al.* 2003; Augustine & McNaughton 2006; Hempson *et al.* 2015b). Grazing lawns establish with the frequent re-grazing of grasses which, combined with concentrated dung deposition, stimulates palatable grass regrowth, eventually changing species composition and shifting the system into an alternative stable state. *Eragrostis* and *Themeda* grasses, abundant on the flats and slopes of the farm trial respectively, include facultative lawn grass species which can switch growth forms to prostrate growth or form caespitose lawns of small cushion-like plants under regular defoliation (Hempson *et al.* 2015b). Indeed, *T. triandra* displayed stronger tolerance to frequent defoliation in the pot experiments as well the highest NDVI values (Fig. 5.3J), supporting the idea that grazing lawns might induce a shift to grazing tolerant and more palatable species. Inducing this effect might be possible with rangeland fertilization (e.g. Augustine *et al.* 2003), which in the case of this farm trial might require elevating N and P by 0.05 and 0.006% (maintaining an N:P ratio of 3:1) on the slopes to match the nutrient concentrations of the flats, where the greatest grazing lawn-like response was evident.

In the farm trial, the positive effect of SLG on vegetation NDVI trends and reducing bare ground disappeared at very high grazing pressures on high nutrient soils and was absent on low nutrient soils. Given that root biomass was significantly reduced under frequent defoliation in the pot experiment, I expect that the grazing lawn effect under SLG might not be sustainable over the long-term if root biomass becomes insufficient to sustain the nutrient and water demands of compensatory growth. Although most regrowth after defoliation results from current photosynthesis, and not root carbon reserves (Richards & Caldwell 1985), sustained defoliation may lead to the preferential allocation of photosynthates to leaf growth instead of root growth and thereby reduce root biomass assuming resources become limiting (Harper 1989; Dawson *et al.* 2004). For example, a number of studies on African grassland species have attributed the decline in grass cover under heavy grazing to the loss of non-structural carbohydrate reserves in root and/or crown material (Opperman *et al.* 1970; Danckwerts & Gordon 1990; Oosthuizen & Snyman 2003). However, the reduction in root biomass under defoliation is highly variable across studies from around the world (Ferraro & Oesterheld 2002), depending on context-specific factors such as resource availability, defoliation intensity and most importantly, plant species. A study on 35 studies from Australian rangelands including 829 species showed that 41% of these species responded inconsistently to grazing (Vesk & Westoby 2001). Thus, although persistent frequent grazing may deplete root reserves and degrade rangeland through bare patch formation and invasion of unpalatable species, further research is required to ascertain how resilient different rangelands and their grazing lawn-like systems are to frequent grazing (Hempson *et al.* 2015b).

I also found variable regrowth responses to defoliation frequency between the three bunch grass species selected for my glasshouse pot experiment. Contrary to a priori definitions of grazing tolerance, where increaser species thrive and decreaser species decline under grazing pressure (Tainton *et al.* 1970; Vesk & Westoby 2001; Del-Val & Crawley 2005), I found that the decreaser species *T. triandra* was remarkably resilient to frequent defoliation compared to supposed grazing tolerant *E. muticus* and *E. plana*. In the farm trial, *E. muticus* is avoided by cattle while *T. triandra* and *E. plana* are relatively selected for by cattle (Fig. S4.6). Given that *T. triandra* is resilient to grazing frequency and *E. plana* is less so, we would expect *T. triandra* to exhibit higher long-term survival. Another defoliation experiment on South African grassland species (Morris 2016) also found that palatable decreasers such as *T. triandra* are no more intolerant of grazing than increaser species, however they are more likely to be persistently selected for by grazers (Snyman *et al.* 2013). In the case of increaser species, chemical and structural strategies for grazing avoidance (e.g. tannins, lignin, awns) are more important than grazing tolerance (Briske 1996). Although some studies do provide empirical evidence for the correspondence between grazing tolerance and the increaser-decreaser continuum (Del-Val & Crawley 2005), they highlight the importance of environmental pressures on plant fitness such as competition, moisture or nutrient limitations. For example, *T. triandra* is notoriously sensitive to high soil nutrient levels (Snyman *et al.* 2013) and can be out-shaded by taller grasses under fertilizer application in the absence of defoliation (Fynn & O'Connor 2005). Yet, under frequent defoliation, it loses fewer nutrient reserves than taller grasses and can thus gain the competitive advantage, especially when competing for a limiting soil nutrient (Fynn *et al.* 2005). In my farm trial, the biomass of *T. triandra* dominated areas (nutrient-poor slopes) was unaffected by cattle densities suggesting *T. triandra* is resilient to defoliation in the competitive in situ context.

Conclusion

I find evidence across multiple experimental scales that increasing both defoliation severity and frequency retards growth responses in bunch grasses of a mesic South African grassland but that this effect is mitigated at elevated soil nutrient levels under season-long grazing management that enforces frequent defoliation. Managers who are able to manipulate grazing frequency and severity using forms of high intensity rotational grazing should maximise grazing frequency on nutrient-rich soils, and grazing recovery on nutrient-poor soils. Further, it would be worth testing whether the grazing lawn effect might be induced by rangeland managers through fertilisation paired with high frequency grazing, and whether this would lead to sustained productivity. Despite the interactive effect of grazing approach and defoliation intensity on bare ground on high nutrient soils, my farm trial revealed no direct rotational grazing effect on combined vegetation responses, supporting the thesis that grazing management approach is less important than stocking rate as a determinant of rangeland productivity. Finally, my study challenges widespread assumptions that grazing pressure exacerbates indicators of rangeland degradation such as bare ground formation. On moist, fertile soils dominated by grasses able to switch growth form in response to herbivory, high frequency grazing at moderate cattle densities might restore degraded rangeland to higher levels of basal cover and vegetation palatability.

Chapter 6: Rotational grazing management in South Africa has little effect on remotely-sensed vegetation characteristics

Abstract

The balance of experimental studies around the world show rotational grazing management has little effect on vegetation cover and animal productivity. Critics claim that experimental trials fail to capture the complexity of adaptive management decisions that bring about long-term vegetation changes at the landscape-scale. Thus, I used a nation-wide farm survey and fence-line contrast study in South Africa, coupled with remotely-sensed vegetation indices, to test the hypothesis that rotational grazing sustains higher animal numbers while increasing grass cover and reducing bare ground and woody plant cover. Reports from 48 farms under consistent management for 15 ± 0.8 years (mean ± standard error) revealed that farm stocking rates were 59 ± 12% higher than those recommended by government and that adopting extremes of rotational grazing management did not affect this. Fence-line differences (n = 23) in rotational grazing densities (85 ± 5% relative difference) were unrelated to differences in normalised difference vegetation index (NDVI), fractional bare ground, grass or woody plant cover. Similarly, fence-line differences in farm stocking rate (30 ± 7%) and livestock type (55 ± 16%) had no consistent effect on differences in vegetation cover. This regional analysis corroborates the conclusion drawn from multiple experimental studies on rotational grazing and adds weight to it by including a diversity of rotational grazing intensities ranging from continuous grazing to extreme forms of ultra-high density grazing. However, commonly observed negative effects of excessive stocking rates on vegetation cover were not evident possibly due to relatively small fence-line differences. Further, the previously untested hypothesis that rotational grazing inhibits woody plant encroachment was not supported. Continued advocacy for extreme forms of rotational grazing management appears unfounded.

Introduction

Global meat and dairy consumption is set to increase with the projected increase in per capita gross domestic product, which would place increasing pressure on rangeland managers to preserve the ecosystem services flowing from rangelands (Tilman & Clark 2014). Understanding the interaction between various management practices and vegetation and animal responses that form the basis of ecosystem function and services is thus important. However, rangelands are dynamic and complex systems in which vegetation responses to some management interventions (e.g. herbivore stocking and fire) are strongly mediated by fluctuations in climate (Vetter 2005; Gillson & Hoffman 2007). Despite this, stocking rate has long been considered the most important management variable in maintaining palatable vegetation production within rangelands (Skovlin 1987; Ralphs *et al.* 1990; Willms *et al.*

1990; Gillen *et al.* 1998; Briske *et al.* 2008; Derner *et al.* 2008). Stocking rate refers to the number of large stock units (LSUs) per hectare of available rangeland and, maintaining stocking rates higher than the capacity for vegetation to recover leads to mortality of palatable plant species and consequent rangeland degradation. It has been argued that stocking rate has a stronger effect on vegetation and animal productivity than the grazing management approach adopted (Briske *et al.* 2011; Hawkins 2017). Grazing management approaches define the spatio-temporal pattern or rotation of livestock movements, typically using fencing to achieve desired livestock grazing densities (Briske *et al.* 2008). Grazing density, sometimes referred to as "stock density", is the number of LSUs per subunit of area at any point in time on that rangeland so that two farms may have the same stocking rate but different densities depending on the number of defined camps in which stock are held per unit time.

Vegetation composition, productivity, and basal cover are predicted to respond to the varying duration and timing of exposure to defoliation by herbivores, imposed by different rotational grazing management approaches. In the absence of grazing rotation, or under free-range continuous grazing, animals are predicted to utilise a landscape heterogeneously, repeatedly grazing palatable vegetation patches and species (Fuls 1992; Kellner & Bosch 1992; Andrew W Illius & Tim G O'Connor 1999; WallisDeVries *et al.* 1999; Teague *et al.* 2004). Subsequent selective overgrazing leads to plant mortality and may cause the competitive release of less palatable species that may consequently encroach or become invasive (Anderson & Briske 1995; Parker *et al.* 2006). Population growth and associated livestock farming in Africa has simplified the functional composition of herbivores to one dominated by grazers, namely cattle (Hempson *et al.* 2017). In Africa, overgrazing has been implicated as a driver of woody plant encroachment into grassy areas (O'Connor *et al.* 2014; Stevens *et al.* 2016; Venter *et al.* 2018), which can alter hydrological cycles and reduce the carrying capacity of the range (Archer *et al.* 2017). Grazers reduce herbaceous biomass and allow for the competitive release of woody plants, primarily through the reduction of fuel loads for fires, thereby releasing woody plants from the fire trap (Roques *et al.* 2001; O'Connor *et al.* 2014). Incorporating browsers combined with high density grazing and the supposed reduced ability for herbivores to selectively overgraze palatable vegetation might suppress woody plant encroachment (Venter *et al.* 2018).

Overgrazing under excessive stocking rates, and selective overgrazing under continuous (non-rotational) grazing management, is also proposed to increase soil exposure and reduce overall vegetation basal cover (Thurow 1991; Fuls 1992; Ash & Smith 1996; Teague *et al.* 2011). The sacrifice zones around farm watering points (a type of piosphere) offer a magnified example of where localised stocking rates cause loss of vegetation cover, increased soil exposure, compaction and erosion (Andrew 1988; Jeltsch *et al.* 1997). Despite such examples, proponents of Holistic Management maintain that adopting forms of high density grazing can enhance rangeland productivity while doubling stocking rates (Savory 1983; Butterfield *et al.* 2006). The balance of the evidence from experimental trials investigating rotational grazing systems, including holistic planned grazing (HPG), shows no consistent effect on vegetation production, basal cover, or animal gain (Briske *et al.* 2008; Briske *et al.* 2011; Hawkins 2017).

Experimental trials are often implemented over small spatial and temporal scales, failing to capture the landscape-scale and long-term consequences of complex management decisions that constitute a grazing management system (Teague *et al.* 2013). To overcome this, some have attempted to use multiple cross-site comparisons of working farms (Teague *et al.* 2011), while others have employed the use of satellite remote sensing to monitor landscape-scale long-term changes in vegetation cover, quality and even composition (Booth & Tueller 2003; Palmer & Fortescue 2004; Svoray *et al.* 2013; Ali *et al.* 2016). Satellite remote sensing has been used previously to distinguish degraded from non-degraded rangeland in South Africa, typically using the normalised difference vegetation index (NDVI) as a proxy for vegetation productivity (Botha & Fouche 2000; Archer 2004; Wessels *et al.* 2004; Munyati & Makgale 2009). However, these studies have limited their analysis to the influence of stocking rates and have largely ignored possible interactions with the adoption of rotational grazing management. Further, few studies have investigated the effects of rotational grazing management across a range of rotational intensities (Hawkins 2017) on vegetation response variables other than NDVI.

Using a national grazing management questionnaire survey, along with a fence-line comparison study, I investigated the effects of grazing management on remotely-sensed fractions of vegetation cover. I hypothesised that increasing grazing densities through forms of rotational grazing management facilitates higher stocking rates while preventing woody plant encroachment or the loss of grass cover. I also predicted that farms with relatively high stocking rates and herds dominated by grazers will exhibit higher fractions of woody plant and bare ground cover with variable effects on NDVI.

Methods

Survey questionnaire

Questionnaire surveys have previously been used in rangeland science to assess vegetation responses to various grazing management practices (Stinner *et al.* 1997; Archer 2004; de Villiers *et al.* 2014; Roche *et al.* 2015; Becker *et al.* 2017). I distributed an online questionnaire survey (see Appendix S6 in supporting information) via the SurveyMonkey website (www.surveymonkey.com) to a range of extensive commercial livestock farmers within South Africa between 2016 and 2017 (Fig. 6.1). The University of Cape Town provided ethical clearance (certificate no. FSREC 16 – 2017). I employed the use of national farmers' associations to disseminate the survey and encouraged respondents to forward the survey link to other farmers in their respective districts. Each participant signed an online form consenting to the survey. I did not aim to survey a spread of ages nor to approach a particular gender ratio due to an apparent gender bias in livestock farming. Online surveys comprised semi-structured questions including Likert items, and closed- and open-ended questions with scales and indices, and follow-up interviews with selected farmers were conducted face-to-face. Participants were excluded if their farms were not managed consistently under a particular grazing management for more than 5 years or if they did not farm with livestock including cattle, sheep and/or goats where >75% of their diets constituted natural vegetation.

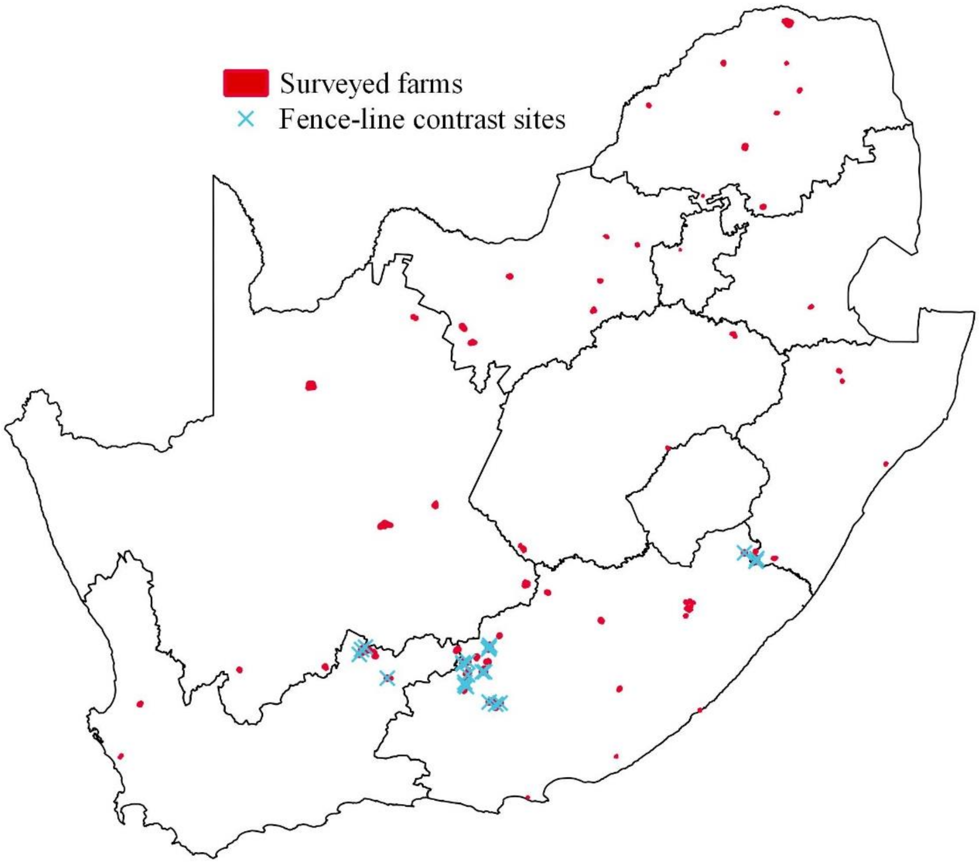


Figure 6.1 Distribution of the 48 farms that participated in the online questionnaire survey (farm boundaries in red) and the subset of those (14) that were visited for the fence-line contrast study (blue crosses).

To capture the complexity of management decisions that constitute a grazing system, I asked farmers to score their alignment with a range of established grazing management systems (Table 6.1) using a Likert-scale (Brooke 1996). I assessed these scores using a principle components analysis (PCA) to distil a composite index of grazing management. To calibrate and interpret the PCA result, I asked specific questions regarding camp number, camp size, rotation frequency, and grazing densities. A further set of questions (Table S6.1), focussed on HPG, were used to quantify the extent to which a farm was aligned with the core principles of HPG. I derived these questions from a combination of the Holistic Management Adoption Index devised by de Villiers *et al.* (2014) and principles highlighted in the book by Savory & Butterfield (2016) on Holistic Management.

Table 6.1 Description of grazing management systems with which farmers were asked to align themselves in the questionnaire survey.

System	Acronym	Description	Suggested rotationality	Reference
Continuous grazing	CG	Access to all grazing areas for at least a full season. Particularly common in communal rangelands and wildlife areas.	Very low	De V. Booysen 1967; Tainton 1999
Low density grazing	LDG	Can be considered very similar to continuous grazing. Might incorporate season-long grazing where half of the farm is rested for an entire growing season.	Low	De V. Booysen 1967; Fynn 2012
Four-camp rotation	FCG	Farm divided into four camps. One is rested while others are grazed at varying levels of intensity. Rested camp is burnt before the next growing season. Camps are then rotated.	Medium	Venter & Drewes 1969
Time-controlled grazing	TCG	Names used interchangeably to refer to the practice of rotational grazing management. Grazing area divided into multiple paddocks to create reoccurring periods of grazing and rest. Generally managed according to a fixed rotation plan, however does not exclude adaptive approaches.	High	Merrill 1954; Tainton 1999; Briske *et al.* 2008
Short-duration grazing	SDG		High	
High density grazing	HDG		High	
Holistic planned grazing	HPG	A proactive and adaptive management framework, which operates within a defined holistic management context. Often associated with the use of rotational grazing and high animal densities.	Very high	Savory 1983
Ultra-high density grazing	UHDG	A variant of rotational grazing with higher stocking densities (more camp divisions and shorter grazing durations) of hundreds or thousands of animals per hectare. Often associated with HPG.	Very high	McCosker 2000

To calculate farm stocking rates (LSU ha^{-1} yr^{-1}) I used the respondent's reported farm size (ha) and total large stock units (LSU). Relative stocking rates were calculated as the percentage difference between the farm stocking rates and those recommended by the South African Department of Agriculture, Forestry and Fisheries (Avenant 2016). Grazing densities (LSU ha^{-1} d^{-1}) were quantified as the average herd size (LSU) per average camp size (ha) per average occupancy (d). To quantify the functional type of herbivory, I defined a grazer index as the percentage of total farm LSUs constituted by grazer LSUs. Cattle were considered as grazers, sheep as mixed-feeders, and goats as browsers. A few farms stocked a diversity of wild herbivores (game) in very low numbers (on average 2% of total farm LSUs), the exact composition of which was often unknown. Due to the low numbers and diversity of species, I excluded game counts from the grazer index calculation.

Remote sensing of fence-line contrasts

Vegetation cover in managed rangelands can be influenced by a range of environmental variables besides management practice, such as soil, vegetation type, and climate (Wessels *et al.* 2012). Thus, testing hypotheses about the effect of rangeland management on vegetation change at regional scales requires disentangling the relative influence of management and environmental variables. Comparisons of management practices across farm fence-lines overcome this problem by controlling for major environmental variables (Kilpatrick *et al.* 2015). I selected farms with strong grazing management contrasts as candidates for the fence-line contrast study using the responses from the online questionnaire survey. Farms that reported grazing management most strongly aligned to HPG or with very high grazing densities (highly rotational) were selected for this study. The rationale behind this was that these farms were likely to have more extreme management differences to their neighbours and if grazing management has any effect on vegetation, it would be at these fence-line contrasts I was most likely to observe that effect.

During May 2018 I visited the selected farms and retrieved the GPS location of fence-lines (Fig. 6.1) bordering neighbours willing to participate in the study. For each fence-line I sampled remotely-sensed vegetation variables (see below) at eight paired points lying 60 m apart and 60 m from the fence (Fig. S6.1) according to the cross-fence comparison methodology outlined in Kilpatrick *et al.* (2015). These distances were chosen to control for landscape-scale variations in topography, soil, landcover and vegetation type. The change in each management (explanatory) variable across a fence-line was expressed as a relative percentage difference, $\Delta = \frac{(a-b)}{a} \times 100$ where a was the farm with highest grazing density and b was the farm with lowest grazing density, where a high percentage indicated higher density grazing in the farms of interest. To quantify the effect of the management difference on the vegetation response variables I calculated the Hedge's g (Brockwell & Gordon 2001) effect size and 95% confidence interval for each fence-line contrast as well as the combination of all fence-line contrasts using the 'effsize' package in R (Torchiano 2017).

To measure vegetation response variables, I performed a satellite remote sensing analysis using the Google Earth Engine cloud computing platform (Gorelick *et al.* 2017). All vegetation response variables were derived from composites of all imagery between Jan 2016 and Jan 2018. Sampling over a time period reduced the risk, often encountered when using single-date scene acquisitions, of biasing sampling by detecting anomalous events (e.g. livestock grazed a camp prior to satellite image capture). The satellite datasets used included the Landsat 8 Operational Land Imager (OLI), Sentinel-2 MutiSpectral Instrument, Sentinel-1 Synthetic Aperture Radar (SAR) C-band Level-1 Ground Range Detected, and Phased Array type L-band SAR (PALSAR) collections. Landsat 8 scenes were masked for clouds using the 'pixel_qa' band and Sentinel-2 scenes were filtered for those with 'CLOUDY_PIXEL_PERCENTAGE' scores of <15. Radar data, insensitive to cloud cover, included the Sentinel-1 image collection and PALSAR annual composites, pre-processed by Google Earth Engine, for 2016 and 2017.

Spectral unmixing techniques (Bateson *et al.* 2000) were used to derive fractional bare ground cover (Fig. S6.1) over South Africa using imagery from Sentinel-2 and -1. Spectral mixing models are based on the understanding that each pixel contains a mixture of information from several spectrally distinct surface components or 'endmembers'. Using a 0.5 x 0.5° sampling grid over South Africa, I defined polygons in each grid cell characterising pure bare ground and pure vegetation through visual interpretation of very-high resolution satellite imagery in Google Earth. In order to produce a balanced sample, polygon size was restricted to between 0.01 km^2 and 1 km^2. Sentinel-2 data included all bands along with the NDVI. Sentinel-1 single co-polarisation, vertical transmit/vertical receive (VV) and dual-band cross-polarisation, vertical transmit/horizontal receive (VH) bands were used. I obtained the mean reflectance value for all bands and indices over all digitised polygons. Given that vegetation displays phenological cycles, I also included the standard deviation in NDVI and VV over time to help distinguish vegetation from bare ground. These values were used as endmembers in a mixing model to discriminate pixel fractions of bare ground and vegetation at fence-lines contrast sites.

I employed a Random Forest (RF) regression model to quantify fractional woody plant cover (Fig. S6.1). RF is a machine-learning supervised classification method often used in remote sensing analyses because it avoids overfitting and can incorporate non-parametric data (Belgiu & Drăguţ 2016). I used techniques outlined in Venter *et al.* (2018) except with the addition of Sentinel-1, -2, and PALSAR data as explanatory variables in the RF model. Briefly, training data were derived from visual interpretation of fractional woody vegetation cover at 4000 randomly scattered 30 x 30 m sampling quadrats, aligning with the Landsat pixel grid. I then extracted reflectance metrics for all satellite data time stacks (2016 to 2018). From Sentinel-2 and Landsat 8 collections I extracted temporal reflectance data for visible, near infrared, and shortwave infrared bands, as well as three vegetation indices, namely NDVI, soil-adjusted vegetation index, and enhanced vegetation index. The ratio of VV to VH was calculated for Sentinel-1 imagery. I then calculated the minimum, maximum and selected percentile values (10, 25, 50, 75 and 90% percentiles) and the mean reflectance values for observations between selected percentiles (10-25%, 25-50%, 50-75%, 75-90%, and 25-75%). Similar time-series metrics have been successfully used in forest cover mapping using Landsat data (Broich *et al.* 2011; Potapov *et al.* 2012; Hansen *et al.* 2013). To further assist in differentiating between woody and herbaceous cover, which have different phenological metrics (Helman *et al.* 2015), I derived the variance and range in vegetation indices.

Fractional grass/herbaceous plant cover was simply taken to be the remaining fraction of each pixel once woody and bare ground cover were accounted for. In addition to this, I derived the median NDVI for each fence-line sampling point (Fig. S6.1). NDVI has been widely used as an indicator of vegetation productivity (Svoray *et al.* 2013; Ali *et al.* 2016). Fire activity has an important, often contrasting, influence on vegetation relative to herbivory (Venter *et al.* 2017). Although I included only fence-lines with camps that farmers reported had not been burned in the previous 10 years, I verified this using the MODIS (MCD45A1.051) burned area monthly product at 500 m resolution (Roy *et al.* 2008).

Statistical tests of significance

The effect of management differences across fence-lines on the Henge's g effect sizes in vegetation response variables were assessed using multiple linear regression in R (RCoreTeam 2016). Vegetation response variables were regressed on fence-line differences in stocking rate, grazing density, and grazer index using the 'car' package (Fox & Weisberg 2018). Analysis of variance was run on the linear regression models to assess overall significance of explanatory variables when accounting for the effect of other variables. Proportional, and non-normal variables were logit- and log-transformed, respectively, if the assumptions of linear regression were violated. Wilcoxon signed-rank tests were used to test if paired vegetation responses were significantly different across fence-lines.

Results

I received over 100 survey responses, some of which were disqualified, being from farms younger than 5 years old or farming animals other than cattle, sheep or goats on natural vegetation. After excluding ineligible farms, I retained a final sample of 48 farms covering a total surface area of 1322 km^2 spread out across all 9 provinces within South Africa (Fig. 6.1). Farms had been managed consistently for 15 ± 0.8 years (mean ± standard error), covered 61 ± 23 km^2 and were spread across five biomes and a large mean annual precipitation gradient (150 to 850 mm). Most farms (60%) stocked a mix of cattle, sheep and goats, while 40% stocked cattle only.

The PCA of farmer's Likert-scale scores for alignment with various grazing management practices revealed a strong horizontal separation between highly rotational (HPG, SDG, HDG) and less rotational (CG, FCG, LDG) approaches (Fig. 6.2A). The PC1 axis explained 37% of the variance and was correlated with log grazing density ($p < 0.0001$, $R^2 = 0.47$, Fig. 6.2B) and HPG alignment score ($p < 0.0001$, $R^2 = 0.4$, Fig. 6.2C). On-farm stocking rates were on average 59 ± 12% (mean ± standard error) higher than those recommended by government (Fig. 6.2D). There was no linear relationship between farm management practice (PC1) and their ability to increase stocking rates ($F_{(1,46)} = 0.276$, $p = 0.677$) but quantile regressions showed that 95% of farms at extremes of continuous or highly rotational grazing (far left and right of x-axis in Fig 6.2D) were only able to moderately exceed recommended stocking rates. Farms with moderate rotational management were able to stock up to double the recommended stocking rates although 95th percentiles reveal that this is highly variable between farms (Fig. 6.2D).

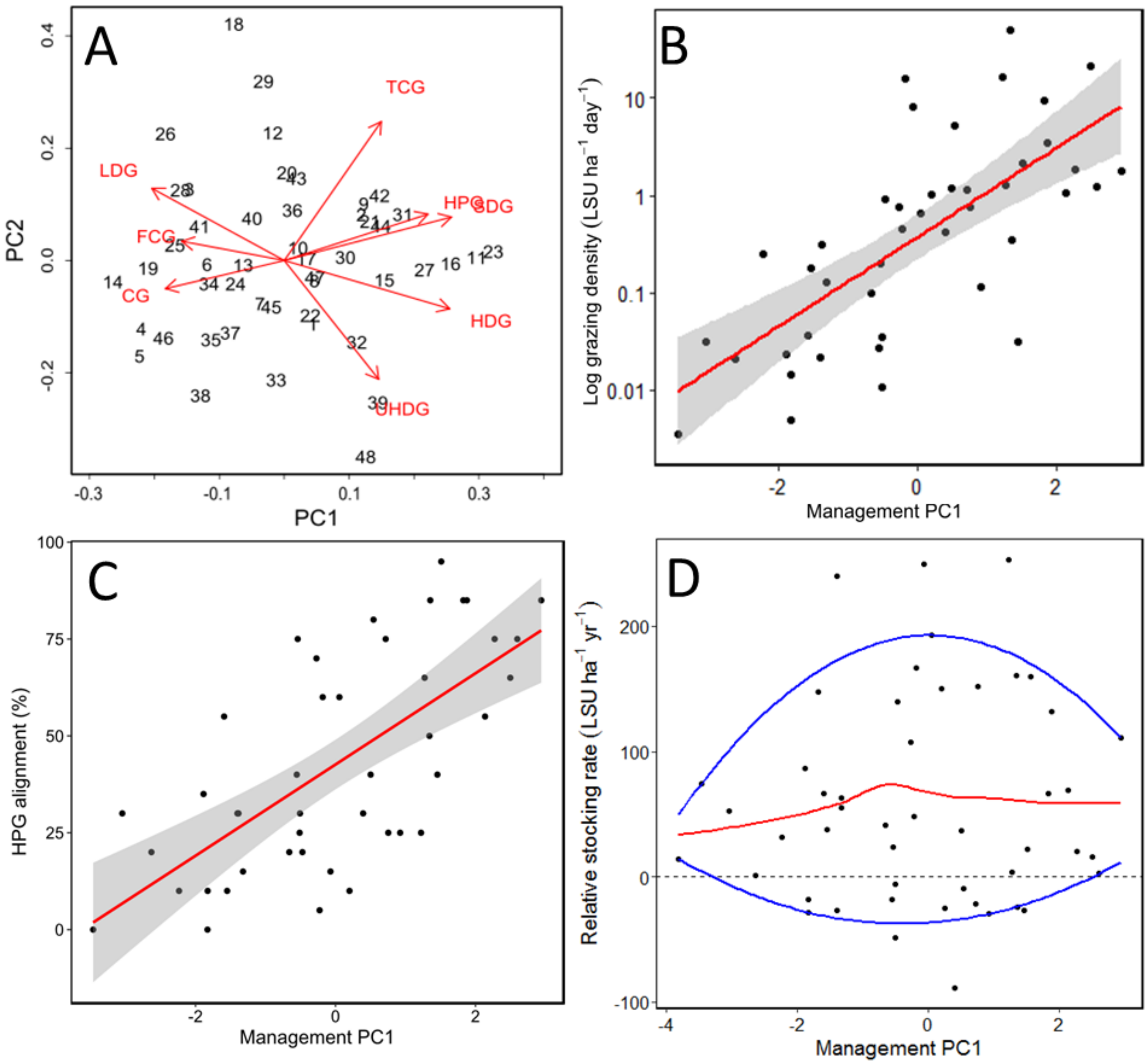


Figure 6.2 Principle components analysis biplot (A) representing the multivariate interactions between farmer alignment scores for various management practices (see Table 6.1 for acronym definitions). The relative proximity of management practices on the plot space are an indication of similarity. The direction and length of the arrows are an indication of the extent to which management practices align with the composite variable (PC1 or PC2). Here, management practices display a strong horizontal separation, along the first principle component. According to management definitions (Table 6.1), I propose that the composite variable PC1 quantifies the intensity of grazing rotation. Indeed, this index correlates significantly with the log-transformed grazing densities (number of LSUs per subunit of fenced area at any point in time on a farm, B), and the percentage alignment (Table S6.1) with holistic planned grazing (C). Linear regression lines with 95% confidence intervals are fitted in B and C. The relative percentage difference between farm and government recommended stocking rate is related to PC1 with 5th, 95th (blue) and 50th (red) quantile regression lines (D).

I visited 14 farms selected for having high grazing densities (high PC1 scores, Fig. 6.2) and identified 23 fence-lines bordering neighbours with contrasting management (Fig. 6.1). Participating farms implemented a wide range of stocking rates and grazing densities, with cattle constituting on average 41.3 ± 33.6% of farm herds (Table 6.2). Farms were dominated by grass and bare ground cover, with woody plants constituting 8.5 ± 13% of fractional ground cover (Table 6.2). There were large percentage relative fence-line differences (x-axis values in Fig. 6.3) in grazing density (85 ± 5%) and moderate differences in stocking rate (30 ± 7%) and livestock grazer index (55 ± 16%). The effect of fence-line management (Hedge's g) on fractional bare ground, woody plant cover, grass cover, and NDVI were non-significant at 74, 91, 83, 78% of the fence-lines, respectively (see red points in Fig. 6.3). Significant effect sizes (see blue points in Fig. 6.3) were a balance of both positive and negative effects (variation along the y-axis) and were related to a range of grazing density differences (delta), and both positive and negative delta stocking rate and grazer index (variation along the x-axis). For example, two fence-line contrasts with low (34%) and high (99.8%) relative differences in grazing density (see point i and ii in Fig. 6.3) both had significant positive effects on bare ground cover and negative effects on grass cover. The farm with the higher grazing density at fence-line i also had lower stocking rates and a herd composed of much fewer grazers compared to its neighbour, while the farm with the higher grazing density at fence-line ii had a much higher stocking rate and very low grazer component compared to its neighbour (Fig. 6.3). This variation in response was observed for all management variables and vegetation responses. Thus, the overall vegetation effect sizes were unrelated to fence-line differences in stocking rate, grazing density or grazer index (Table 6.3) as indicated by the non-significant overall Hedge's g effect sizes (see grey bands in Fig. 6.3).

Table 6.2 Summary statistics for farm management variables and remotely-sensed vegetation response variables measured on all farms in the fence-line contrast study. Raw variable units are reported to assist in the interpretation of results reported as effect sizes and relativised fence-line comparisons in Fig. 6.3. Data means ± standard error (SE), minimum and maximum values are reported. A farm's grazer index is calculated as the percentage grazer LSUs contribute to the sum of browser and grazer LSUs.

Attribute measured	Mean ± SE	Min	Max
Management explanatory variables:			
Grazing density (LSU ha^{-1} day^{-1})	1.45 ± 4.46	0.0003	30
Stocking rate (LSU ha^{-1} yr^{-1})	0.14 ± 0.16	0.001	0.59
Grazer index	41.3 ± 33.6	0	100
Vegetation response variables:			
Bare ground cover (%)	40.7 ± 15.9	0	96.2
Woody plant cover (%)	8.5 ± 13	0	74.5
Grass cover (%)	50.8 ± 15.8	3.8	89.3
NDVI	0.15 ± 0.06	0.07	0.34

NDVI is the normalised difference vegetation index.

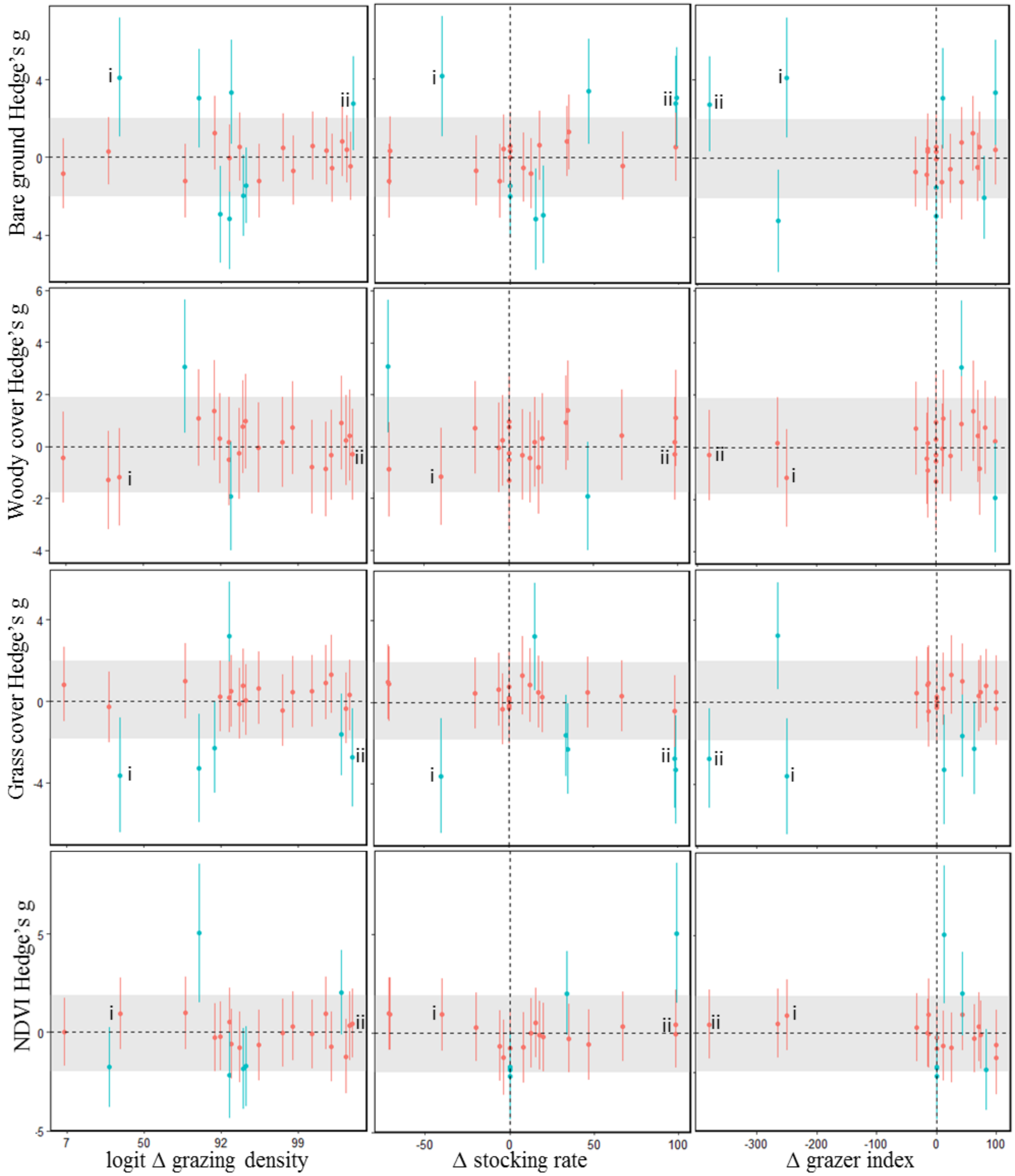


Figure 6.3. The effect of grazing density, stocking rate, and grazer index differences (panel columns), across fence-line contrasts, on remotely-sensed vegetation response variables (panel rows). Cross-fence comparisons of response variables were expressed using the Hedge's g effect size (points ± 95% confidence intervals), which quantifies, for each fence-line contrast, the magnitude of difference between the farm with highest grazing density (a) and its neighbour (b). The change in each management (explanatory) variable across a

fence-line was expressed as a relative percentage difference, $\Delta = \frac{(a-b)}{a} \times 100$. The Δ grazing density was plotted on a logit scale to better view the data spread. Positive x-axis values reflect that the farm with the higher grazing density in the fence-line contrast pair had higher stocking rates and grazer index scores relative to their neighbour. The overall effect size confidence interval across all fence-line contrasts is depicted by the grey band. A farm's grazer index is calculated as the percentage grazer LSUs contribute to the sum of browser and grazer LSUs. Wilcoxen signed-rank tests were used to identify significant ($p < 0.05$) and non-significant fence-line effects, coloured blue and red, respectively. None of the overall effect sizes were significantly different to zero. Letters i and ii indicate specific fence-line contrasts used for discussion purposes.

Table 6.3 The effect of grazing density, stocking rate, and grazer index differences across fence-line contrasts on remotely sensed vegetation response variables. Statistical results of linear regression models are reported. Cross-fence comparisons of response variables were expressed using the Hedge's g effect size which quantifies, for each fence-line contrast, the magnitude of difference between the farm with highest grazing density (a) and its neighbour (b). The change in each management (explanatory) variable across a fence-line was expressed as $\Delta = \frac{(a-b)}{a} \times 100$. A farm's grazer index is calculated as the percentage grazer LSUs contribute to the sum of browser and grazer LSUs.

	F	*df*	*p*
Bare ground cover ~			
Δ Grazing density	1.13	1	0.301
Δ Stocking rate	2.045	1	0.169
Δ Grazer index	0.196	1	0.663
Woody cover ~			
Δ Grazing density	1.674	1	0.211
Δ Stocking rate	0.064	1	0.803
Δ Grazer index	0.319	1	0.582
Grass cover ~			
Δ Grazing density	1.507	1	0.235
Δ Stocking rate	3.315	1	0.084
Δ Grazer index	0.487	1	0.494
NDVI ~			
Δ Grazing density	0.057	1	0.815
Δ Stocking rate	1.61	1	0.22
Δ Grazer index	0.452	1	0.51

Significant *p* values at $p < 0.05$ indicated with *

Discussion

The fence-line contrast study presented here overcomes the limitations inherent in farm-scale experimental trials including restricted temporal and spatial extents and the inability to accurately mimic the complexity of adaptive rotational grazing approaches such as HPG. This regional-scale analysis provides support for multiple farm-scale experimental studies where most of these found no evidence for a rotational grazing effect on vegetation characteristics (Briske *et al.* 2008; Hawkins 2017). Specifically, I found that across a range of fence-line management contrasts, most farms with a high level of rotational grazing and thus high grazing densities had vegetation NDVI, fractional bare ground, woody plant and grass cover that were similar to that of their respective neighbours. The lack of vegetation differences is especially meaningful in an agricultural context given that grazing densities were substantially different (on average 85% different, ranging between 0.0003 and 30 LSU ha^{-1} d^{-1}) across fence-lines. Further, using government recommended stocking rates as reference, I found that the implementation of high or low grazing density extremes did not alter the ability for farmers to elevate relative stocking rates, while practitioners using a moderate grazing density tended to be able to support higher stocking rates. Thus, either the livestock behavioural mechanisms claimed to induce vegetation responses under high density rotational grazing are not present or there is some critical level of grazing density that farms are not reaching to achieve necessary animal impact on vegetation change. These alternative explanations are discussed in turn in the following paragraphs.

Assuming rotational grazing does not change livestock behaviour so as to enhance the trampling of plant litter and dung, or reduce the overgrazing of palatable vegetation compared to continuous or low density grazing, then it is unsurprising that I have observed no effect on vegetation cover. Although few have studied the behavioural mechanisms behind claimed rotational grazing effects, those that have present mixed results. For example, studies in the USA found that rotational grazing may increase (Walker *et al.* 1989), reduce (Hepworth *et al.* 1991) or have little effect (Hart *et al.* 1993) on cattle walking or trampling behaviour. Others have found that rotational management does not influence non-selective grazing behaviour relative to other factors including the location of water points, topography or stocking rates (Launchbaugh & Howery 2005; Soder *et al.* 2009; Bailey & Brown 2011). A recent experimental trial in a mesic grassland of South Africa showed that HPG, apart from reducing the ability of cattle to select for patches of forage with high NDVI at the landscape-scale, did not alter the majority of cattle behaviours (Venter *et al.* 2019). At the same trial, cattle under low density season-long grazing were able to repeatedly graze palatable forage patches, thereby reinforcing NDVI heterogeneity but reducing bare ground cover, although this effect was limited to nutrient-rich soils with high clay contents and water retention capacities (Chapter 5). Thus, perhaps the large variation in grazing management effects on vegetation responses across fence-lines reported here (Fig. 6.3) might be due to fence-line differences in soil characteristics unrelated to grazing management. Indeed, while fence-line comparisons isolate management effects on vegetation from that of climate, they remain vulnerable to small-scale variation in topography and soil type (Kilpatrick *et al.* 2015). Both soil chemical and hydrological variables can be extremely variable over spatial scales <5 m (Beckett 1971; Schlesinger *et al.* 1996), and thus experimental trials that attempt to control for these confounding abiotic variables are valuable.

Experimental trials that have shown no effect of rotational grazing on vegetation or animal responses (see references in Hawkins 2017) have been criticised for implementing grazing densities that are of insufficient magnitude to bring about enhanced productivity (Venter *et al.* 2019). I find it unlikely that there is some critical threshold of grazing density that none of the farms in this study have reached given that the respondents were strongly self-aligned with some of the most extreme forms of rotational grazing practices including HDG, HPG and UHDG. Further, an accredited HM trainer (Lambrechts, J. *pers comm* 2016) affirmed that grazing densities of ca. 30-40 LSU ha^{-1} d^{-1} do constitute high density grazing in mesic grasslands. Given that the majority of fence-line contrast farms were located in the transition zone between the Nama Karoo and Grassland biomes (Fig. 6.1), and are thus relatively less productive than mesic grasslands, the upper grazing densities of 30 LSU ha^{-1} d^{-1} (Table 6.2) reported by farmers here indeed constitute high density grazing. The fence-line with the most extreme difference in grazing density (fence-line ii in Fig. 6.3), revealed that although the farm with higher grazing densities afforded double the stocking rate of its neighbour, it had significantly greater bare ground cover and less grass cover. Evidence like this brings into question HPG claims that it can afford the doubling of farm stocking rates through enhanced primary production (Savory 1983; Butterfield *et al.* 2006). The relationship between relative stocking rate and rotational grazing index (Fig. 6.2D) indicates that if a threshold exists, it may be found at moderate and not extreme grazing densities. Given that the range of possibilities for enhancing stocking rates (gap between 95% quantile regression lines in Fig. 6.2D) is much smaller at very low or high levels of rotational grazing management, there might be the greatest potential to enhance stocking rates at moderate levels of rotational management although one would also have to consider the effects on vegetation responses.

Another critique made of experimental studies investigating rotational grazing management is that they do not capture the adaptive and proactive nature of decision making that give practices like HPG the edge over conventional low density grazing systems. Indeed, advocates of HPG claim that it is distinct from rotational grazing management systems (Savory & Butterfield 2016) while rangeland scientists consider rotational grazing to be a core tenant of HPG (Briske *et al.* 2011; Hawkins 2017). I found that farmers who aligned themselves strongly with HPG were also strongly aligned with other forms of high density rotational grazing (Fig. 6.2).

A potential benefit of rotational grazing practices, assuming it prevents the competitive release of woody plants through overgrazing of palatable grasses, might include the suppression of woody plant encroachment. Given that woody plant encroachment is widespread across Africa (Venter *et al.* 2018) and can have negative consequences for rangeland grazing capacities (Archer *et al.* 2017), any tools available to combat it are worthy of investigation. Almost all of the fence-line contrasts in grazing density had no effect on woody plant cover (Fig. 6.3) suggesting rotational grazing management is not a sufficient tool to mitigate woody plant encroachment. Increasing stocking rate and shifting livestock functional composition to include more browsers also appeared to have no effect on woody plant cover. This is surprising given that increasing browser densities combined with increasing fire frequencies is suggested as a tool to mitigate woody plant encroachment (O'Connor *et al.* 2014; Venter *et al.* 2018). The lack of response in woody plant cover might be because fence-line contrasts were largely limited to the arid rangelands of South Africa (Fig. 6.1) where farmers reported fires being almost completely absent. Thus, aspects of grazing management might have a stronger influence on woody vegetation in more mesic savannas, where fire plays a larger role in rangeland management (Archibald & Hempson 2016), although this would require further research to confirm.

Stocking rate, as noted by many studies on rotational grazing effects, is more important than grazing system in inducing vegetation change (Hawkins 2017). A long-held principle in rangeland management is to maintain farm livestock populations below the ecological carrying capacity, often defined by the forage availability during the non-growing season (Illius & O’connor 1999). I found that fence-line contrasts in stocking rate were unrelated to vegetation response variables (Table 6.3) despite the fact that most farm stocking rates were marginally higher (59%) than those recommended by government (Fig. 6.2D). Further, fence-line contrasts in stocking rate were only 30% different, compared to the 85 and 55% difference observed for grazing density and grazer index, respectively. Thus, perhaps if there were greater contrasts in fence-line stocking rate differences, (i.e. more farms with either very high or very low relative stocking rates), one would then begin to detect changes in vegetation responses.

Conclusion

These results confirm global reviews of experimental trials showing rotational grazing management has little effect on plant or animal production. Although some fence-line management differences did produce significant contrasts in vegetation cover, the direction of this change was not regionally consistent. Similarly, although striking anecdotal evidence exists and is often used in the advocacy for high density grazing management, it is seldom replicated on other farms and fails to emerge under experimental manipulation where confounding variables such as soil type are controlled for. Indeed, the effect of local variation in topography and soil characteristics might be stronger determinants of fence-line variation in vegetation cover than grazing management. Nevertheless, farms implementing moderate rather than extremely high or low grazing densities appear to sustain slightly higher stocking rates without apparent declines in vegetation cover. Thus, I suggest that continued advocacy for extreme forms of rotational grazing management is unfounded, particularly given that there was no added benefit for reducing woody plant encroachment.

Chapter 7: General Discussion and Synthesis

Seasonal movement patterns of wild ungulates such as the bison in the American prairies (Frank *et al.* 1998) or the "trekbokken" (i.e. springbuck) in the South African arid savannas (Rowland 1937) have been mimicked for centuries by traditional pastoralists practising transhumance (Lamprey 1983). Pastoralists managed the migration of their livestock within large herds, responding to both seasonal and stochastic variation in resource (primarily water) availability, permitting alternating periods of defoliation and recovery for vegetation (Smith 1899). The success at mimicking the migratory pattern of wild herbivores enjoyed by early cattlemen in America was hampered by the fences erected by settlers which prevented open range herds from "drifting with the storms" (Vass 1926). Likewise, "trek farmers" in South Africa, accustomed to moving livestock seasonally between "sourveld" unpalatable savannas and "sweetveld" relatively palatable savannas became restricted by fencing and thus the early farm-scale rotational grazing systems were pioneered (Sampson 1913). Since then, many forms of rotational grazing have been developed, none of which have produced consistent benefits for vegetation or animal productivity when exposed to experimental testing (Briske *et al.* 2008). Nevertheless, forms of rotational grazing remain practiced and advocated particularly under the banner of holistic planned grazing (HPG) within a Holistic Management approach (HM, Savory 1983; Savory & Butterfield 2016). Thus, there has been a recent resurgence in the debate and controversy over the efficacy of high density rotational grazing (Briske *et al.* 2011; Briske *et al.* 2014b) and policy endorsements thereof (Sherren *et al.* 2012; Briske *et al.* 2014a; Sherren & Kent 2017), most recently in South Africa (Hawkins *et al.* 2017).

Paralleled to the restriction of herbivore mobility by fencing, humans have drastically altered both the intensity and form of herbivory over Africa (Hempson *et al.* 2017). The loss of large herbivores during the late Pleistocene and Holocene was concomitant with human expansion across the globe (Gill *et al.* 2009). Over recent centuries colonial hunting has decimated the remaining indigenous herbivore populations in Africa (Spinage 1973) and the net result has been a decline in total herbivore biomass across Africa since the pre-colonial era, ca. 1 kya (Hempson *et al.* 2017). The vegetation in African ecosystem has evolved with a diverse set of herbivore functional guilds (Hempson *et al.* 2015a) including large browsers (e.g. kudu), water-dependent grazers (e.g. wildebeest), non-ruminants (e.g. elephant), and smaller-bodied mixed diet (e.g. impala) and non-social (e.g. duiker) browsers. With the advent of livestock agriculture, this diversity has been simplified through the dominance of extensive cattle farming (Robinson *et al.* 2014) and the consequent inflation of the role that water-dependent grazers have in rangeland ecosystems. The loss of herbivores in African savannas has arguably led to an increased prevalence of fire (Chapter 2; Venter *et al.* 2017) because fire and herbivores are in competition for vegetation biomass as a resource (Archibald & Hempson 2016). Indeed, recent paleoecological evidence suggests fire prevalence increased with human expansion across the globe (Thevenon *et al.* 2010; Leys *et al.* 2018), and although fire activity has been reduced over recent decades (Andela *et al.* 2017), the profligate use of fire to remove biomass may not be appropriate for vegetation that has coevolved with herbivore pressures comparatively higher than what they are currently. Further, the management of fire in rangelands has possibly reduced fire intensity due to burning practices that take place during seasons that reduce the risk of run-away fires, and thus promote low-intensity burns with significant consequences for vegetation (Govender *et al.* 2006).

Altering the pattern, type and quantity of herbivory (Fig. 7.1) within African rangelands may change vegetation composition and structure with implications for rangeland productivity and ultimately global carbon cycling and climate change. To elucidate these interactions, I have integrated evidence from a grazing management trial that measured animal behavioural mechanisms, a national fence-line contrast study that captured long-term and landscape-scale management effects on vegetation, and a continental analysis of the interactive effect of herbivory, fire and climatic drivers on vegetation structure. The evidence derived from these diverse approaches (Fig. 7.1) largely refuted my initial hypothesis (Chapter 1) that concentrating herbivores over space and moving them adaptively, primarily through forms of high density rotational grazing management, will reduce the overgrazing of palatable vegetation, increase vegetation cover and thereby enhance rangeland productivity (Chapter 4; Venter *et al.* 2019). Apart from manipulating herbivory patterns through rotational grazing, I found partial evidence to support my more general hypothesis (Chapter 1) that local scale disturbances including herbivory and fire are significant determinants of vegetation structure, heterogeneity, and productivity in African rangelands. Specifically, areas with low browser densities and reductions in fire extent have facilitated enhanced rates of woody plant encroachment (Chapter 3; Venter *et al.* 2018).

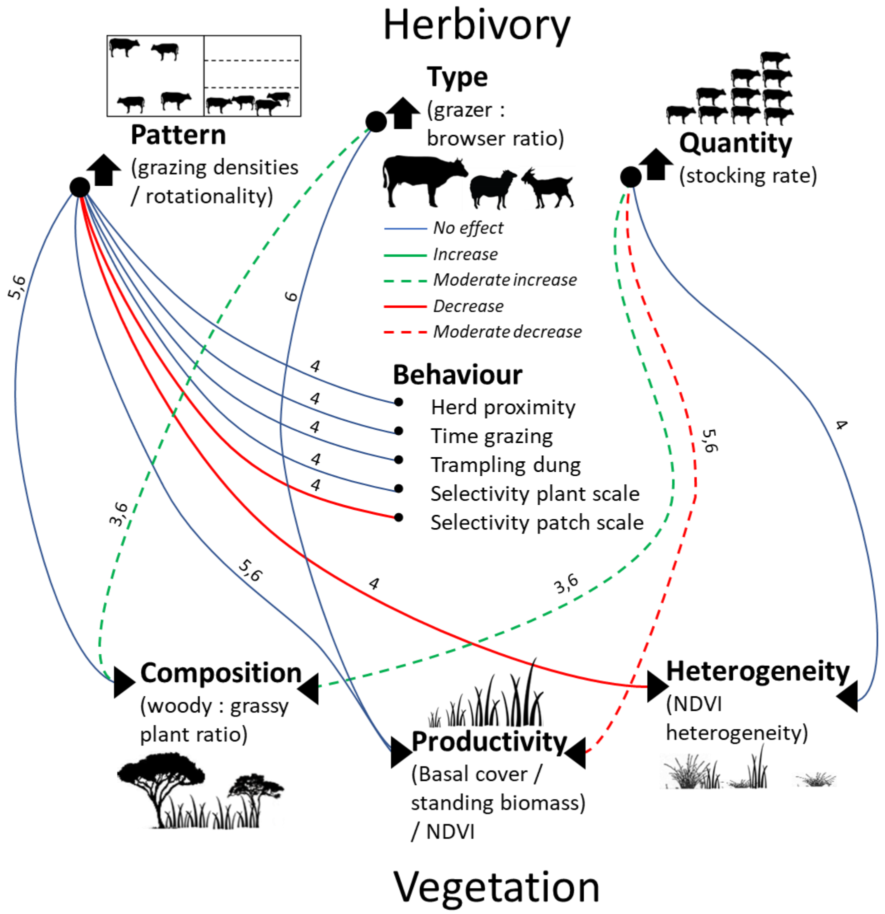


Figure 7.1 A schematic summary of my thesis findings. Lines connecting herbivory and vegetation attributes indicate relationships that were tested with numbers indicating the thesis chapters that document the result. The primary aspect of herbivory tested was the effect of altering the pattern of herbivory through rotational, high density grazing (Chapter 4). A national farm survey and fence-line contrast study of grazing management approaches complimented this (Chapter 6). The quantity and functional composition of herbivory were tested using continental estimates of browser-grazer densities (Chapter 3), experimental defoliation of plants at varying intensities (Chapter 5), and a national farm survey which quantified livestock type and stocking rate differences across fence-line contrasts (Chapter 6). Vegetation attributes measured included productivity, composition and heterogeneity. A range of animal behaviours were measured as mechanistic links in the causal chain between herbivore management and vegetation response (Chapter 4). Where separate chapters gave conflicting evidence for relationships, I have used dashed lines. For example, the continental remote sensing analysis in Chapter 3 found that areas with elevated grazer numbers increased in woody plant cover whereas the fence-line contrast study in Chapter 6 showed that increasing grazer:browser ratios had no effect on woody plant cover.

The controversy over forms of high density rotational grazing, including HPG, persist partly because previous experimental studies (see studies in Hawkins 2017) have (1) been limited in extent to small-scale grazing trials which fail to account for long-term landscape-scale vegetation changes (Teague *et al.* 2013), (2) failed to test the animal behavioural mechanisms assumed to bring about vegetation changes (Hawkins 2017), and (3) made little reference to the influence of other ecosystem disturbances such as fire and herbivory by native ungulates which are of particular relevance in African rangelands. Nevertheless, even where farms have practiced HPG and rotational management for decades, vegetation cover and structure remain similar to that of neighbours with relatively low density grazing management (Chapter 6). This is largely because rotating animals using fencing does not appear to prevent them from targeting palatable species at the plant scale (Chapter 4; Kirby *et al.* 1986; Kreuter & Tainton 1988; Morris & Tainton 1996; Venter *et al.* 2019) and thus the overgrazing and subsequent mortality of plants is predicted to be similar regardless of grazing management. Indeed, any systematic movement of livestock with fencing by managers, particularly in response to resource availability and the inherent palatability of vegetation patches, may theoretically be implemented by free-ranging livestock themselves (Spedding 1971). However, because animal movements are strongly determined by the spatio-temporal distribution of limiting resources including water and soil nutrients (Launchbaugh & Howery 2005; Soder *et al.* 2009; Bailey & Brown 2011), in rangelands where limiting resources and topography are heterogenous, it may be expected that implementing rotational grazing will cause significantly more homogenous movement patterns than those of free-ranging livestock. In a mesic grassland of South Africa, cattle under HPG were restricted from selecting for patches of high vegetation NDVI at the landscape scale, and this prevented the reinforcement of vegetation heterogeneity (Chapter 4; Venter *et al.* 2019). Theoretically, this effect might scale with increasing rangeland resource heterogeneity, particularly in areas with topographic barriers to animal movement that might be overcome using herding or fencing.

Concentrating livestock using fencing or herding under rotational grazing management might not result in farm-level changes in productivity (Chapter 4; Briske *et al.* 2008; Hawkins 2017; Venter *et al.* 2019), however it may have potential as a restoration tool. Season-long grazing (SLG) allowed cattle to concentrate on and repeatedly graze green vegetation patches thereby reducing bare ground cover and increasing NDVI on nutrient rich soils (Chapter 5). Although this frequent re-grazing by cattle occurred in the absence of human intervention under SLG, it could be enforced using herding, fencing or patch burning techniques. In savannas, where soil nutrients and moisture are abundant, and grass species composition facilitates it, frequent grazing can initiate grazing lawns which increase basal plant cover and produce forage of higher nutrient concentrations than the matrix surrounding the grazing lawn (Hempson *et al.* 2015b). Small fires and associated patches of nutrient rich regrowth have been used to attract and concentrate herbivores in rangelands (Fuhlendorf *et al.* 2009) and conservation reserves (Donaldson *et al.* 2017) to initiate grazing lawns. In traditional African pastoral systems, where livestock are corralled into small areas at night the import of nutrients via dung, together with repeated grazing, has potential to enhance grass cover (Porensky & Veblen 2015) and mitigate woody plant encroachment (Veblen 2013). Recent evidence suggests corralling by ancient pastoralists has resulted in nutrient hotspots that persist for millennia (Marshall *et al.* 2018). Like pastoral corralling, targeted grazing has been adopted in commercial rangelands to manage woody plant encroachment, exotic weed invasions and to reduce flammable biomass loads (Rinella & Bellows 2016; Briske 2017). Although targeted fires can be used to achieve the same management goals, the use of herbivory has the added benefit of producing meat and reducing the loss of carbon into the atmosphere with negative consequences for climate change (Venter *et al.* 2017).

Rangeland systems are significant regulators of global climate change given that they currently occupy 36% of the global land area (Fig. 1.1, Chapter 1) and the livestock occupied by them are responsible for between 12 (Westhoek *et al.* 2011) and 18% (O'Mara 2011) of anthropogenic greenhouse gas (GHG) emissions. Compared to vegetable protein, the production of beef protein produces 100 times more GHG emissions and requires 50 times more land, although this does not include extensive grasslands where the conversion to cropland is often impractical (Herrero *et al.* 2016). Advocates of HPG argue that livestock can be managed to mitigate climate change through enhancing vegetation root growth and consequent carbon sequestration (Savory 2013). These claims have been widely refuted by the scientific literature (Briske *et al.* 2013) and are particularly unlikely given findings that vegetation production is unaffected by grazing management (Chapter 5, Fig. 7.1). The consensus of the broader scientific literature holds that, apart from a move to vegetarian diets, the primary mechanism proposed to mitigate GHG emissions from livestock is through improving the efficiency of converting feed to meat (Herrero *et al.* 2013). Based on this logic, studies using life cycle analyses of beef production show that intensive feedlot systems produce fewer GHS emissions compared to extensive pasture-based systems, although these analyses often stop at the farm gate and do not account for GHG emissions from land use conversion (e.g. deforestation) to produce feed crops (Gerssen-Gondelach *et al.* 2017). Livestock are predicted to consume less grass in the future (Havlík *et al.* 2014) due to the transition from extensive grassland- and pasture-based diets to mixed and intensive feedlot-based farming, particularly in sub-Saharan Africa which currently has low feed efficiencies and high emission intensities (McDermott *et al.* 2010). Consequently, there might be a reduction in livestock numbers within grasslands and savannas which may increase the risk of woody plant encroachment depending on the magnitude and type of livestock removal.

Under most global warming scenarios, the climate in Africa is expected to warm significantly, resulting in longer dry spells and more severe rainfall events (Weber *et al.* 2018). The role of temperature in driving regional woody plant encroachment has been unclear (O'Connor *et al.* 2014; Brandt *et al.* 2017), yet I have found that continental increases in temperature are correlated with increases in woody plant cover (Chapter 3; Venter *et al.* 2018). Counter to the narrative that atmospheric CO_2 is the primary global determinant of woody plant cover change (Bond & Midgley 2012), I found evidence to suggest that incorporating fire and introducing moderate grazer and elevated browser densities can be of continental, if not global significance in mitigating future woody plant encroachment in savannas. Apart from the increased temperature, climate change is predicted to increase rainfall variability and seasonality (Cooper *et al.* 2008). This will introduce higher levels of stochasticity in vegetation and forage resources for livestock which highlights the importance of nonequilibrium (Wiens 1984) and resilience theories (Briske 2017) as conceptual frameworks for managing rangelands in the future. Nonequilibrium theory holds that vegetation change is driven primarily by temporal variations in climate and secondarily by herbivory. Indeed, fence-line grazing management contrasts in South Africa exposed to decades of equivalent rainfall and temperature, but different stocking rates did not significantly differ in woody or grass vegetation cover or NDVI (Chapter 6, Fig. 7.1). Adapting to rainfall and vegetation stochasticity under climate change scenarios might involve enhancing the resilience of rangeland ecosystems to perturbation through diversifying livestock functional guilds and implementing heterogenous grazing patterns. Enforcing vegetation heterogeneity in rangelands may increase biodiversity (Fuhlendorf *et al.* 2009), and biodiversity can enhance ecosystem stability at moderate levels (Pennekamp *et al.* 2018).

The findings presented in my thesis have management implications that, although not necessarily generalizable to all rangelands in Africa, align with the bulk of rangeland ecology literature and are thus important for practitioners and policy makers. My findings support the idea that stocking rate should remain the guiding principle in rangeland management, although varying grazing pressure over space and time in response to variations in soil nutrients and rainfall is important. In contrast to management decisions on varying stocking rate in response to resource availability, decisions about whether to adopt rotational versus continuous management appear less important. Managers who aim to homogenize grazing at the landscape scale, presumably to homogenize vegetation structure, can adopt rotational grazing management while being aware of the high input costs and lack of response in animal productivity. Managers in mesic grasslands who wish to enhance vegetation heterogeneity and initiate grazing lawns can implement SLG on nutrient rich soils with grass species that can switch to low-growth forms. At regional and continental scales, managing the magnitude and type of herbivory appears more important than implementing forms of farm-scale rotational grazing, unless policy makers could achieve the unlikely vision of reinstating herbivore migratory routes and transhumance by removing farm fences or expanding communal grazing areas to incorporate the spatial extent of seasonal resource fluctuations. Global trends toward industrial livestock farming should be approached with consideration for the potential unintended consequences that removing herbivores from African rangelands might have on other ecosystem services supported under alternative woody or grassy stable states. Similarly, global reforestation initiatives should account for woody plant encroachment in carbon balance calculations before advocating tree planting as a carbon offset, particularly in areas, currently considered ‘deforested’ by humans, that were in fact deforested by large herbivores such as elephants in the past. Perhaps the ‘defaunation’ taking place in the Anthropocene should indeed be elevated to a status equivalent to that of ‘deforestation’ (Dirzo *et al.* 2014). My thesis mounts evidence across multiple spatial and temporal scales to suggest that, in the face of population growth and global climate change, herbivory is a powerful tool for land managers in rangelands.

References

Acocks, J. (1966) Non-selective grazing as a means of veld reclamation, *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 1(1): 33-39.

Ainsworth, E.A. & Long, S.P. (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2, *New Phytologist*, 165(2): 351-372.

Ainsworth, E.A., Leaky, A.D.B., Ort, D.R. & Long, S.P. (2008) FACE-ing the facts: inconsistencies and interdependence among field, chamber and modeling studies of elevated [CO_2] impacts on crop yield and food supply, *New Phytologist*, 179: 5-9.

Ali, I., Cawkwell, F., Dwyer, E., Barrett, B. & Green, S. (2016) Satellite remote sensing of grasslands: from observation to management—a review, *Journal of Plant Ecology*, 9(6): 649–671.

Alvarenga, F.A.P., Borges, I., Palkovič, L., Rodina, J., Oddy, V.H. & Dobos, R.C. (2016) Using a three-axis accelerometer to identify and classify sheep behaviour at pasture, *Applied Animal Behaviour Science*, 181: 91-99.

Andela, N., Morton, D., Giglio, L., Chen, Y., van der Werf, G., Kasibhatla, P., DeFries, R., Collatz, G., et al. (2017) A human-driven decline in global burned area, *Science*, 356(6345): 1356-1362.

Anderson, D. (1988) Seasonal stocking of tobosa managed under continuous and rotation grazing, *Journal of Range Management*, 41(1): 78-83.

Anderson, T.M., Ritchie, M.E., Mayemba, E., Eby, S., Grace, J.B. & McNaughton, S.J. (2007) Forage nutritive quality in the Serengeti ecosystem: the roles of fire and herbivory, *American Naturalist*, 170(3): 343-357.

Anderson, T.M., Kumordzi, B.B., Fokkema, W., Fox, H.V. & Olff, H. (2013) Distinct physiological responses underlie defoliation tolerance in African lawn and bunch grasses, *International Journal of Plant Sciences*, 174(5): 769-778.

Anderson, V.J. & Briske, D.D. (1995) Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance?, *Ecological Applications*, 5(4): 1014-1024.

Andrew, M.H. (1988) Grazing impact in relation to livestock watering points, *Trends in Ecology & Evolution*, 3(12): 336-339.

Archer, E.R. (2004) Beyond the “climate versus grazing” impasse: using remote sensing to investigate the effects of grazing system choice on vegetation cover in the eastern Karoo, *Journal of Arid Environments*, 57(3): 381-408.

Archer, S.R., Andersen, E.M., Predick, K.I., Schwinning, S., Steidl, R.J. & Woods, S.R. (2017) Woody Plant Encroachment: Causes and Consequences, in: Briske, D. D., ed., *Rangeland Systems: Processes, Management and Challenges.*, Switzerland: Springer International Publishing, 25-84.

Archibald, S., Bond, W., Stock, W. & Fairbanks, D. (2005) Shaping the landscape: fire–grazer interactions in an African savanna, *Ecological Applications*, 15(1): 96-109.

Archibald, S., Staver, A.C. & Levin, S.A. (2012) Evolution of human-driven fire regimes in Africa, *Proceedings of the National Academy of Sciences*, 109(3): 847-852.

Archibald, S. & Hempson, G.P. (2016) Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa, *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 371(1703): 20150309.

Aryal, S., Maraseni, T.N. & Cockfield, G. (2014) Sustainability of transhumance grazing systems under socio-economic threats in Langtang, Nepal, *Journal of Mountain Science*, 11(4): 1023-1034.

Ash, A.J. & Smith, D.S. (1996) Evaluating stocking rate impacts in rangelands: animals don't practice what we preach, *The Rangeland Journal*, 18(2): 216-243.

Asner, G.P., Levick, S.R., Kennedy-Bowdoin, T., Knapp, D.E., Emerson, R., Jacobson, J., Colgan, M.S. & Martin, R.E. (2009) Large-scale impacts of herbivores on the structural diversity of African savannas, *Proceedings of the National Academy of Sciences, U.S.A*, 106(12): 4947-4952.

Augustine, D.J. & McNaughton, S.J. (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland, *Journal of Applied Ecology*, 41(1): 45-58.

Augustine, D. J. & McNaughton, S. J. (2006). Interactive Effects of Ungulate Herbivores, Soil Fertility, and Variable Rainfall on Ecosystem Processes in a Semi-arid Savanna. *Ecosystems*, 9(8), 1242–1256.

Augustine, D.J., Veblen, K.E., Goheen, J.R., Riginos, C. & Young, T.P. (2011) Pathways for positive cattle–wildlife interactions in semiarid rangelands, *Smithsonian Contributions to Zoology*, 632: 55-71.

Avenant, P. (2016) *Grazing Capacity map of South Africa 2016* [online database], available: https://www.firestop.co.za/FPA%20Docs/Grazing%20Capacity%202016%20Metadata.pdf [accessed June 2017].

Avery, D.J. & Lacey, H.J. (1968) Changes in the Growth-regulator Content of Plum Infested with Fruit Tree Red Spider Mite, Panonychus ulmi (Koch), *Journal of Experimental Botany*, 19(4): 760-769.

Baddeley, A., Rubak, E. & Turner, R. (2015) *Spatial point patterns: methodology and applications with R*, New York: CRC Press.

Badgery, W., Millar, G., Michalk, D., Cranney, P. & Broadfoot, K. (2017) The intensity of grazing management influences lamb production from native grassland, *Animal Production Science*, 57(9): 1837-1848.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. & Sims, P.L. (1996) Mechanisms that result in large herbivore grazing distribution patterns, *Journal of Range Management*, 49(5): 386-400.

Bailey, D.W. & Brown, J.R. (2011) Rotational Grazing Systems and Livestock Grazing Behavior in Shrub-Dominated Semi-Arid and Arid Rangelands, *Rangeland Ecology & Management*, 64(1): 1-9.

Baker, J.N. & Hunt, O.J. (1961) Effects of Clipping Treatments and Clonal Differences on Water Requirement of Grasses, *Journal of Range Management*, 14(4): 216-219.

Bardgett, R.D. & Wardle, D.A. (2003) Herbivore-mediated linkages between aboveground and belowground communities, *Ecology*, 84(9): 2258-2268.

Barnes, D.L. (1990) A survey of grazed and ungrazed grassland in the south-eastern Transvaal highveld 1. Palatability composition and grazing capacity, *Journal of the Grassland Society of Southern Africa*, 7(4): 217-222.

Barnes, M.K., Norton, B.E., Maeno, M. & Malechek, J.C. (2008) Paddock size and stocking density affect spatial heterogeneity of grazing, *Rangeland Ecology & Management*, 61(4): 380-388.

Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L. & Shabel, A.B. (2004) Assessing the causes of Late Pleistocene extinctions on the continents, *Science*, 306(5693): 70-75.

Bastin, J.-F., Berrahmouni, N., Grainger, A., Maniatis, D., Mollicone, D., Moore, R., Patriarca, C., Picard, N., et al. (2017) The extent of forest in dryland biomes, *Science*, 356(6338): 635-638.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) *Fitting linear mixed-effects models using lme4*.

Bateson, C.A., Asner, G.P. & Wessman, C.A. (2000) Endmember bundles: A new approach to incorporating endmember variability into spectral mixture analysis, *IEEE Transactions on Geoscience and Remote Sensing*, 38(2): 1083-1094.

Baumgartner, S.A., Treydte, A.C., Grant, C.C. & van Rooyen, J. (2015) Can diverse herbivore communities increase landscape heterogeneity? Comparing wild and domestic herbivore assemblages in a South African savanna, *Perspectives in Plant Ecology, Evolution and Systematics*, 17(1): 34-43.

Becker, W., Kreuter, U., Atkinson, S. & Teague, R. (2017) Whole-Ranch Unit Analysis of Multipaddock Grazing on Rangeland Sustainability in North Central Texas, *Rangeland Ecology & Management*, 70(4): 448-455.

Beckett, P. (1971) Soil variability: a review, *Soils and fertilizers*, 34(1): 1-15.

Beeri, O., Phillips, R., Hendrickson, J., Frank, A.B. & Kronberg, S. (2007) Estimating forage quantity and quality using aerial hyperspectral imagery for northern mixed-grass prairie, *Remote Sensing of Environment*, 110(2): 216-225.

Behnke, R.H. (1994) Rethinking range ecology: implications for rangeland management in Africa, *Range ecology at disequilibrium*: 1-30.

Belgiu, M. & Drăguţ, L. (2016) Random forest in remote sensing: A review of applications and future directions, *ISPRS Journal of Photogrammetry and Remote Sensing*, 114: 24-31.

Bell, R.H. (1982) The effect of soil nutrient availability on community structure in African ecosystems, in: Huntley, B. and BH, W., eds., *Ecology of tropical savannas*, New York: Springer, 193-216.

Belsky, A.J. (1986) Does Herbivory Benefit Plants? A Review of the Evidence, *The American Naturalist*, 127(6): 870-892.

Berg, R.T. & Butterfield, R.M. (1976) *New concepts of cattle growth*, Sydney, Australia: Sydney University Press.

Besag, J. (1977) Contribution to the discussion of Dr Ripley's paper, *Journal of the Royal Statistical Society Series*, B39: 193-195.

Beuchner, H. & Dawkins, H. (1961) Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda, *Ecology*, 42(4): 752-766.

Bird, M. & Cali, J. (1998) A million-year record of fire in sub-Saharan Africa, *Nature*, 394(6695): 767-769.

Blanco, L., Aguilera, M., Paruelo, J. & Biurrun, F. (2008) Grazing effect on NDVI across an aridity gradient in Argentina, *Journal of Arid Environments*, 72(5): 764-776.

Bond, W.J. & Midgley, G.F. (2000) A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas, *Global Change Biology*, 6(8): 865-869.

Bond, W.J. & Midgley, J.J. (2001) Ecology of sprouting in woody plants: the persistence niche, *Trends in ecology & evolution*, 16(1): 45-51.

Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems, *Trends in Ecology & Evolution*, 20(7): 387-394.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire, *New Phytologist*, 165(2): 525-538.

Bond, W.J. & Midgley, G.F. (2012) Carbon dioxide and the uneasy interactions of trees and savannah grasses, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1588): 601-612.

Bond, W.J. & Van Wilgen, B.W. (2012) *Fire and plants*, Springer Science & Business Media.

Booth, D.T. & Tueller, P.T. (2003) Rangeland Monitoring Using Remote Sensing, *Arid Land Research and Management*, 17(4): 455-467.

Bork, E.W., Broadbent, T.S. & Willms, W.D. (2017) Intermittent Growing Season Defoliation Variably Impacts Accumulated Herbage Productivity in Mixed Grass Prairie, *Rangeland Ecology & Management*, 70(3): 307-315.

Botha, J. & Fouche, P. (2000) An assessment of land degradation in the Northern Province from satellite remote sensing and community perception, *South African Geographical Journal*, 82(2): 70-79.

Bowman, D.M., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'antonio, C.M., DeFries, R., Johnston, F.H., et al. (2011) The human dimension of fire regimes on Earth, *Journal of Biogeography*, 38(12): 2223-2236.

Brandt, M., Rasmussen, K., Peñuelas, J., Tian, F., Schurgers, G., Verger, A., Mertz, O., Palmer, J.R., et al. (2017) Human population growth offsets climate-driven increase in woody vegetation in sub-Saharan Africa, *Nature Ecology & Evolution*, 1: 1-6.

Bransby, D.I. & Tainton, N.M. (1977) The disc pasture meter : Possible applications in grazing management, *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 12(1): 115-118.

Breiman, L. (2001) Random forests, *Machine Learning*, 45(1): 5-32.

Briske, D. (1996) Strategies of plant survival in grazed systems: a functional interpretation, *The Ecology and Management of Grazing Systems*: 37-67.

Briske, D., Sayre, N.F., Huntsinger, L., Fernandez-Gimenez, M., Budd, B. & Derner, J. (2011) Origin, persistence, and resolution of the rotational grazing debate: integrating human dimensions into rangeland research, *Rangeland Ecology & Management*, 64(4): 325-334.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. (2003) Vegetation dynamics on rangelands: a critique of the current paradigms, *Journal of Applied Ecology*, 40(4): 601-614.

Briske, D.D., Derner, J., Brown, J., Fuhlendorf, S., Teague, W., Havstad, K., Gillen, R.L., Ash, A.J., et al. (2008) Rotational grazing on rangelands: reconciliation of perception and experimental evidence, *Rangeland Ecology & Management*, 61(1): 3-17.

Briske, D.D., Bestelmeyer, B.T., Brown, J.R., Fuhlendorf, S.D. & Polley, H.W. (2013) The Savory Method can not green deserts or reverse climate change: a response to the Allan Savory TED video, *Rangelands*, 35(5): 72-74.

Briske, D.D., Ash, A.J., Derner, J.D. & Huntsinger, L. (2014a) Commentary: A critical assessment of the policy endorsement for holistic management, *Agricultural systems*, 125: 50-53.

Briske, D.D., Bestelmeyer, B.T. & Brown, J.R. (2014b) Savory's unsubstantiated claims should not be confused with multipaddock grazing, *Rangelands*, 36(1): 39-42.

Briske, D.D. (2017) Rangeland Systems: Foundation for a Conceptual Framework, in: *Rangeland Systems*, Switzerland: Springer, 1-21.

Briske, D.D., Illius, A.W. & Anderies, J.M. (2017) Nonequilibrium Ecology and Resilience Theory, in: Briske, D. D., ed., *Rangeland Systems: Processes, Management and Challenges*, Switzerland: Springer International Publishing, 197-227.

Brockett, G. (1983) The effect of defoliation on the persistence of Elionurus muticus (Spreng.) Kunth in the Highland Sourveld of Natal, *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 18(1): 81-83.

Brockwell, S.E. & Gordon, I.R. (2001) A comparison of statistical methods for meta-analysis, *Statistics in Medicine*, 20(6): 825-840.

Broich, M., Hansen, M.C., Potapov, P., Adusei, B., Lindquist, E. & Stehman, S.V. (2011) Time-series analysis of multi-resolution optical imagery for quantifying forest cover loss in Sumatra and Kalimantan, Indonesia, *International Journal of Applied Earth Observation and Geoinformation*, 13(2): 277-291.

Brooke, J. (1996) SUS-A quick and dirty usability scale, *Usability evaluation in industry*, 189(194): 4-7.

Brunson, M.W. & Burritt, E.A. (2009) Behavioral Factors in Rotational Grazing Systems, *Rangelands*, 31(5): 20-25.

Bryant, J.P., Chapin III, F.S. & Klein, D.R. (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory, *Oikos*: 357-368.

Buitenwerf, R., Bond, W.J., Stevens, N. & Trollope, W.S.W. (2012) Increased tree densities in South African savannas: >50 years of data suggests CO_2 as a driver, *Global Change Biology*, 18(2): 675-684.

Burney, D.A. & Flannery, T.F. (2005) Fifty millennia of catastrophic extinctions after human contact, *Trends in Ecology & Evolution*, 20(7): 395-401.

Bustamante, M., Medina, E., Asner, G., Nardoto, G. & Garcia-Montiel, D. (2006) Nitrogen cycling in tropical and temperate savannas, in: *Nitrogen Cycling in the Americas: Natural and Anthropogenic Influences and Controls*, Dordrecht: Springer, 209-237.

Butterfield, J., Bingham, S. & Savory, A. (2006) *Holistic Management handbook: healthy land, healthy profits*, Washington, DC: Island Press.

Byrnes, R.C., Eastburn, D.J., Tate, K.W. & Roche, L.M. (2018) A Global Meta-Analysis of Grazing Impacts on Soil Health Indicators, *Journal of Environmental Quality*, 7(4): 758-765.

Campbell, H., Gao, L., Bidder, O., Hunter, J. & Franklin, C. (2013) Creating a behavioural classification module for acceleration data: Using a captive surrogate for difficult to observe species, *The Journal of Experimental Biology*, 216: 4501-4506.

Carter, J., Jones, A., O'Brien, M., Ratner, J. & Wuerthner, G. (2014) Holistic Management: Misinformation on the Science of Grazed Ecosystems, *International Journal of Biodiversity*, 2014: 163431.

Chapin, F.S. & McNaughton, S.J. (1989) Lack of compensatory growth under phosphorus deficiency in grazing-adapted grasses from the Serengeti Plains, *Oecologia*, 79(4): 551-557.

Charles-Dominique, T., Davies, T.J., Hempson, G.P., Bezeng, B.S., Daru, B.H., Kabongo, R.M., Maurin, O., Muasya, A.M., et al. (2016) Spiny plants, mammal browsers, and the origin of African savannas, *Proceedings of the National Academy of Sciences, U.S.A*, 113(38): E5572-E5579.

Charles, B., Ring, I., Nicholson, R.A. & Launchbaugh, J.L. (1985) Vegetational traits of patch-grazed rangeland in west-central Kansas, *Journal of Range Management*, 38(1): 51-55.

Chen, J., Chen, J., Liao, A., Cao, X., Chen, L., Chen, X., He, C., Han, G., et al. (2015) Global land cover mapping at 30 m resolution: A POK-based operational approach, *ISPRS Journal of Photogrammetry and Remote Sensing*, 103: 7-27.

Chen, Y., Randerson, J.T., van der Werf, G.R., Morton, D.C., Mu, M. & Kasibhatla, P.S. (2010) Nitrogen deposition in tropical forests from savanna and deforestation fires, *Global Change Biology*, 16(7): 2024-2038.

Christensen Jr, N.L. (1997) Managing for heterogeneity and complexity on dynamic landscapes, in: Pickett, S., Ostfeld, R., Schachak, M. and Likens, G., eds., *The Ecological Basis of Conservation*, New York: Springer, 167-186.

CIESIN (2005) 'Gridded Population of the World, Version 4 (GPWv4): Population Density Grid', [online], available: http://sedac.ciesin.columbia.edu/data/collection/gpw-v4 [accessed 12 July 2016].

Coetsee, C., February, E.C. & Bond, W.J. (2008) Nitrogen availability is not affected by frequent fire in a South African savanna, *Journal of Tropical Ecology*, 24(6): 647-654.

Cooper, P.J.M., Dimes, J., Rao, K.P.C., Shapiro, B., Shiferaw, B. & Twomlow, S. (2008) Coping better with current climatic variability in the rain-fed farming systems of sub-Saharan Africa: An essential first step in adapting to future climate change?, *Agriculture, Ecosystems & Environment*, 126(1): 24-35.

Cordova, F., Wallace, J.D. & Pieper, R.D. (1978) Forage intake by grazing livestock: a review, *Journal of Range Management*: 430-438.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., et al. (1997) The value of the world's ecosystem services and natural capital, *Nature*, 387: 253-260.

Coughenour, M.B. (1991) Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems, *Journal of Range Management*, 44(6): 530-542.

Cowling, R.M. (2000) Challenges to the "new" rangeland science, *Trends in Ecology & Evolution*, 15(8): 303-304.

Cox, F., Badgery, W.B., Kemp, D.R. & Krebs, G. (2017) Seasonal diet selection by ewes grazing within contrasting grazing systems, *Animal Production Science*, 57(9): 1824-1836.

Craine, J.M., Angerer, J.P., Elmore, A. & Fierer, N. (2016) Continental-Scale Patterns Reveal Potential for Warming-Induced Shifts in Cattle Diet, *PloS one*, 11(8): e0161511.

Cramer, M. & Mazel, A. (2007) The past distribution of giraffe in KwaZulu-Natal, *South African Journal of Wildlife Research*, 37(2): 197-201.

Cramer, M.D., Power, S.C., Belev, A., Gillson, L., Bond, W.J., Hoffman, M.T. & Hedin, L.O. (2018) Are forest-shrubland mosaics of the Cape Floristic Region an example of alternate stable states?, *Ecography*, 42: 1-13.

Crider, F.J. (1955) *Root-growth stoppage resulting from defoliation of grass*, US Department of Agriculture.

Cromsigt, J.P.G.M. & Olff, H. (2008) Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes, *Oikos*, 117(10): 1444-1452.

Danckwerts, J. & Gordon, A. (1990) Partitioning, storage and remobilization of 14C assimilated by Themeda triandra Forssk, *Journal of the Grassland Society of Southern Africa*, 7(2): 97-105.

Dantas, V.d.L., Hirota, M., Oliveira, R.S. & Pausas, J.G. (2016) Disturbance maintains alternative biome states, *Ecology Letters*, 19(1): 12-19.

Daskin, J.H., Stalmans, M. & Pringle, R.M. (2016) Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines, *Journal of Ecology*, 104(1): 79-89.

Davies, D.K., Ilavajhala, S., Wong, M.M. & Justice, C.O. (2009) Fire information for resource management system: archiving and distributing MODIS active fire data, *IEEE Transactions on Geoscience and Remote Sensing*, 47(1): 72-79.

Davis, O.K. (1987) Spores of the dung fungus Sporormiella: increased abundance in historic sediments and before Pleistocene megafaunal extinction, *Quaternary Research*, 28(2): 290-294.

Davis, O.K. & Shafer, D.S. (2006) *Sporormiella* fungal spores, a palynological means of detecting herbivore density, *Palaeogeography, Palaeoclimatology, & Palaeoecology*, 237(1): 40-50.

Dawson, L.A., Thornton, B., Pratt, S.M. & Paterson, E. (2004) Morphological and topological responses of roots to defoliation and nitrogen supply in Lolium perenne and Festuca ovina, *New Phytologist*, 161(3): 811-818.

De'Ath, G. (2007) Boosted trees for ecological modeling and prediction, *Ecology*, 88(1): 243-251.

De V. Booysen, P. (1967) Grazing and grazing management terminology in Southern Africa, *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 2(1): 45-57.

de Villiers, A.C., Esler, K.J. & Knight, A.T. (2014) Social processes promoting the adaptive capacity of rangeland managers to achieve resilience in the Karoo, South Africa, *Journal of Environmental Management*, 146: 276-283.

DeBano, L.F. & Conrad, C.E. (1978) The effect of fire on nutrients in a chaparral ecosystem, *Ecology*, 59(3): 489-497.

Del-Val, E.K. & Crawley, M.J. (2005) Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight British grassland species, *Journal of Ecology*, 93(5): 1005-1016.

Denevan, W.M. (1992) The pristine myth: the landscape of the Americas in 1492, *Annals of the Association of American Geographers*, 82(3): 369-385.

Derner, J.D., Gillen, R.L., McCollum, F.T. & Tate, K.W. (1994) Little bluestem tiller defoliation patterns under continuous and rotational grazing, *Journal of Range Management*, 47(3): 220-225.

Derner, J.D., Hart, R.H., Smith, M.A. & Waggoner, J.W. (2008) Long-term cattle gain responses to stocking rate and grazing systems in northern mixed-grass prairie, *Livestock Science*, 117(1): 60-69.

Detling, J.K., Dyer, M.I. & Winn, D.T. (1979) Net photosynthesis, root respiration, and regrowth of Bouteloua gracilis following simulated grazing, *Oecologia*, 41(2): 127-134.

Devine, A.P., McDonald, R.A., Quaife, T. & Maclean, I.M. (2017) Determinants of woody encroachment and cover in African savannas, *Oecologia*, 183(4): 939-951.

di Virgilio, A. & Morales, J.M. (2016) Towards evenly distributed grazing patterns: including social context in sheep management strategies, *PeerJ*, 4: e2152.

Diamond, J. (2002) Evolution, consequences and future of plant and animal domestication, *Nature*, 418(6898): 700-707.

Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., et al. (2007) Plant trait responses to grazing–a global synthesis, *Global Change Biology*, 13(2): 313-341.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the Anthropocene, *Science*, 345(6195): 401-406.

Donaldson, J.E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z. & Parr, C.L. (2017) Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns, *Journal of Applied Ecology*, 25: 225-235.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance, *Ecography*, 36(1): 27-46.

Dowling, P., Kemp, D., Ball, P., Langford, C., Michalk, D., Millar, G., Simpson, P. & Thompson, R. (2005) Effect of continuous and time-control grazing on grassland components in south-eastern Australia, *Animal Production Science*, 45(4): 369-382.

Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., et al. (2012) Sentinel-2: ESA's Optical High-Resolution Mission for GMES Operational Services, *Remote Sensing of Environment*, 120: 25-36.

Du Toit, G.v.N., Snyman, H. & Malan, P. (2009) Physical impact of grazing by sheep on soil parameters in the Nama Karoo subshrub/grass rangeland of South Africa, *Journal of Arid Environments*, 73(9): 804-810.

Du Toit, J.T. (1995) Determinants of the composition and distribution of wildlife communities in southern Africa, *Ambio*, (24): 2-6.

Du Toit, J.T. & Cumming, D.H. (1999) Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism, *Biodiversity and Conservation*, 8(12): 1643-1661.

Dublin, H.T., Sinclair, A.R. & McGlade, J. (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands, *The Journal of Animal Ecology*, 59(3): 1147-1164.

Dunn, J.H. & Engel, R.E. (1971) Effect of Defoliation and Root-Pruning on Early Root Growth from Merion Kentucky Bluegrass Sods and Seedlings, *Agronomy Journal*, 63(5): 659-663.

Dyksterhuis, E.J. (1949) Condition and Management of Range Land Based on Quantitative Ecology, *Journal of Range Management*, 2(3): 104-115.

East, R. (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals, *African Journal of Ecology*, 22(4): 245-270.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees, *Journal of Animal Ecology*, 77(4): 802-813.

Ellis, J.E. & Swift, D.M. (1988) Stability of African pastoral ecosystems: alternate paradigms and implications for development, *Rangeland Ecology & Management/Journal of Range Management Archives*, 41(6): 450-459.

Ellison, L. (1960) Influence of grazing on plant succession of rangelands, *The Botanical Review*, 26(1): 1-78.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., et al. (2011) Trophic Downgrading of Planet Earth, *Science*, 333(6040): 301-306.

FAO (2001) *Global forest resources assessment 2000*, Rome: Food and Agriculture Organization of the United Nations.

FAO (2010) *Land degradation assessment in drylands (LADA): assessing the status causes and impact of land degradation*, Rome: Food and Agriculture Organization of the United Nations.

FAO (2014) *FAOSTAT* [online], Permanent meadows and pastures, available: http://faostat3.fao.org/ [accessed 2018/08/29].

Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., et al. (2007) The shuttle radar topography mission, *Reviews of Geophysics*, 45(2): 1-33.

Fassnacht, F., Hartig, F., Latifi, H., Berger, C., Hernández, J., Corvalán, P. & Koch, B. (2014) Importance of sample size, data type and prediction method for remote sensing-based estimations of aboveground forest biomass, *Remote Sensing of Environment*, 154: 102-114.

Fensholt, R., Langanke, T., Rasmussen, K., Reenberg, A., Prince, S.D., Tucker, C., Scholes, R.J., Le, Q.B., et al. (2012) Greenness in semi-arid areas across the globe 1981–2007—an Earth Observing Satellite based analysis of trends and drivers, *Remote Sensing of Environment*, 121: 144-158.

Fernández, R.J. (2002) Do humans create deserts?, *Trends in Ecology & Evolution*, 17(1): 6-7.

Ferraro, D.O. & Oesterheld, M. (2002) Effect of defoliation on grass growth. A quantitative review, *Oikos*, 98(1): 125-133.

Fisher, R.A. (1921) Some remarks on the methods formulated in a recent article on “the quantitative analysis of plant growth, *Annals of Applied Biology*, 7(4): 367-372.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., et al. (2005) Global consequences of land use, *Science*, 309(5734): 570-574.

Foran, B.D., Tainton, N.M. & Booysen, P.d.V. (1978) The development of a method for assessing veld condition in three grassveld types in natal, *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 13(1): 27-33.

Fox, J. & Weisberg, S. (2018) *An R Companion to Applied Regression*, Thousand Oaks, CA: Sage.

Frank, D.A. & Groffman, P.M. (1998) Ungulate vs. landscape control of soil c and n processes in grasslands of yellowstone national park, *Ecology*, 79(7): 2229-2241.

Frank, D.A., McNaughton, S.J. & Tracy, B.F. (1998) The ecology of the earth's grazing ecosystems, *Bioscience*, 48(7): 513-521.

Fraser, J.G. (1922) *Episodes in My Life.*, Cape Town: Juta & Co. Ltd.

Friedl, M.A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A. & Huang, X. (2010) MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets, *Remote Sensing of Environment*, 114(1): 168-182.

Friedman, J.H. & Meulman, J.J. (2003) Multiple additive regression trees with application in epidemiology, *Statistics in Medicine*, 22(9): 1365-1381.

Friedman J.H. & Popescu B.E. (2005). Predictive Learning via Rule Ensembles. Section 8.1

Fuhlendorf, S.D. & Engle, D.M. (2001) Restoring heterogeneity on Rangelands: ecosystem -management based on evolutionary grazing patterns, *Bioscience*, 51(8): 625-632.

Fuhlendorf, S.D., Engle, D.M., Kerby, J. & Hamilton, R. (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing, *Conservation Biology*, 23(3): 588-598.

Fuhlendorf, S.D., Fynn, R.W., McGranahan, D.A. & Twidwell, D. (2017) Heterogeneity as the Basis for Rangeland Management, in: Briske, D., ed., *Rangeland Systems*, Cham: Springer, 169-196.

Fulkerson, W. & Donaghy, D. (2001) Plant-soluble carbohydrate reserves and senescence-key criteria for developing an effective grazing management system for ryegrass-based pastures: a review, *Animal Production Science*, 41(2): 261-275.

Fuls, E. (1992) Ecosystem modification created by patch-overgrazing in semi-arid grassland, *Journal of Arid Environments*, 23(1): 59-69.

Funk, C.C., Peterson, P.J., Landsfeld, M.F., Pedreros, D.H., Verdin, J.P., Rowland, J.D., Romero, B.E., Husak, G.J., et al. (2014) *A quasi-global precipitation time series for drought monitoring*, online: US Geological Survey.

Fynn, R.W. & O'Connor, T.G. (2005) Determinants of community organization of a South African mesic grassland, *Journal of Vegetation Science*, 16(1): 93-102.

Fynn, R.W., Augustine, D.J., Peel, M.J. & Garine-Wichatitsky, M. (2016) REVIEW: Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife–livestock coexistence, *Journal of Applied Ecology*, 53(2): 388-397.

Fynn, R.W.S., Morris, C.D. & Kirkman, K.P. (2005) Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance, *Journal of Ecology*, 93(2): 384-394.

Fynn, R.W.S. (2012) Functional Resource Heterogeneity Increases Livestock and Rangeland Productivity, *Rangeland Ecology & Management*, 65(4): 319-329.

Georgiadis, N.J., Ruess, R.W., McNaughton, S.J. & Western, D. (1989) Ecological conditions that determine when grazing stimulates grass production, *Oecologia*, 81(3): 316-322.

Gerssen-Gondelach, S.J., Lauwerijssen, R.B.G., Havlík, P., Herrero, M., Valin, H., Faaij, A.P.C. & Wicke, B. (2017) Intensification pathways for beef and dairy cattle production systems: Impacts on GHG emissions, land occupation and land use change, *Agriculture, Ecosystems & Environment*, 240: 135-147.

Gifford, R. & Marshall, C. (1973) Photosynthesis and Assimilate Distribution in Lolium Multiflorum Lam. Following Differential Tiller Defoliation, *Australian Journal of Biological Sciences*, 26(3): 517-526.

Gilbert, M., Nicolas, G., Cinardi, G., Van Boeckel, T.P., Vanwambeke, S.O., Wint, G.R.W. & Robinson, T.P. (2018) Global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010, *Scientific Data*, 5: 180227.

Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B. & Robinson, G.S. (2009) Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America, *Science*, 326(5956): 1100-1103.

Gillen, R.L., McCollum III, F.T., Tate, K.W. & Hodges, M.E. (1998) Tallgrass prairie response to grazing system and stocking rate, *Journal of Range Management*, 51(2): 139-146.

Gillson, L. & Hoffman, M.T. (2007) Rangeland Ecology in a Changing World, *Science*, 315(5808): 53-54.

Global Savory Network. (2015) *What is Holistic Planned Grazing?* [online], available: https://www.savory.global/wp-content/uploads/2017/02/about-holistic-planned-grazing.pdf [accessed November 2018].

Gómez, C., White, J.C. & Wulder, M.A. (2016) Optical remotely sensed time series data for land cover classification: A review, *ISPRS Journal of Photogrammetry and Remote Sensing*, 116: 55-72.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D. & Moore, R. (2017) Google Earth Engine: Planetary-scale geospatial analysis for everyone, *Remote Sensing of Environment*, 202: 18-27.

Govender, N., Trollope, W. S. & 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*(4), 748-758.

Greenwood, K. & McKenzie, B. (2001) Grazing effects on soil physical properties and the consequences for pastures: a review, *Australian Journal of Experimental Agriculture*, 41(8): 1231-1250.

Griffith, D.M., Lehmann, C.E.R., Strömberg, C.A.E., Parr, C.L., Pennington, R.T., Sankaran, M., Ratnam, J., Still, C.J., et al. (2017) Comment on "The extent of forest in dryland biomes", *Science*, 358(6365).

Gunderson, L.H. (2000) Ecological Resilience—In Theory and Application, *Annual Review of Ecology and Systematics*, 31(1): 425-439.

Hamilton III, E.W., Giovannini, M.S., Moses, S.A., Coleman, J.S. & McNaughton, S.J. (1998) Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: compensation requires a critical [N], *Oecologia*, 116(3): 407-418.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S., et al. (2013) High-resolution global maps of 21st-century forest cover change, *Science*, 342(6160): 850-853.

Harper, J.L. (1989) The value of a leaf, *Oecologia*, 80(1): 53-58.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., et al. (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology, *PeerJ*, 6: e4794.

Hart, R., Bissio, J., Samuel, M. & Waggoner Jr, J. (1993) Grazing systems, pasture size, and cattle grazing behavior, distribution and gains, *Journal of Range Management*, 46(1): 81-87.

Hartnett, D.C., Potgieter, A.F. & Wilson, G.W. (2004) Fire effects on mycorrhizal symbiosis and root system architecture in southern African savanna grasses, *African Journal of Ecology*, 42(4): 328-337.

Hartshorn, A.S., Coetsee, C. & Chadwick, O.A. (2009) Pyromineralization of soil phosphorus in a South African savanna, *Chemical Geology*, 267(1): 24-31.

Havlík, P., Valin, H., Herrero, M., Obersteiner, M., Schmid, E., Rufino, M.C., Mosnier, A., Thornton, P.K., et al. (2014) Climate change mitigation through livestock system transitions, *Proceedings of the National Academy of Sciences*, 111(10): 201308044.

Hawkes, C.V. & Sullivan, J.J. (2001) The impact of herbivory on plants in different resource conditions: a meta-analysis, *Ecology*, 82(7): 2045-2058.

Hawkins, H.-J. (2017) A global assessment of Holistic Planned Grazing™ compared with season-long, continuous grazing: meta-analysis findings, *African Journal of Range & Forage Science*, 34(2): 65-75.

Hawkins, H.-J., Short, A. & Kirkman, K.P. (2017) Does Holistic Planned Grazing™ work on native rangelands?, *African Journal of Range & Forage Science*, 34(2): 59-63.

Haynes, R.J. & Naidu, R. (1998) Influence of lime, fertilizer and manure applications on soil organic matter content and soil physical conditions: a review, *Nutrient Cycling in Agroecosystems*, 51(2): 123-137.

Heady, H. & Child, R.D. (1999) *Rangeland ecology and management*, United States: Westview Press.

Heady, H.F. (1961) Continuous vs. Specialized Grazing Systems: A Review and Application to the California Annual Type, *Journal of Range Management*, 14(4): 182-193.

Heitschmidt, R. & Taylor Jr, C.A. (1991) Livestock production, in: Heitschmidt, R. and Stuth, J., eds., *Grazing management: an ecological perspective*, Portland, OR, USA: Timber Press, 161-177.

Helman, D., Lensky, I.M., Tessler, N. & Osem, Y. (2015) A phenology-based method for monitoring woody and herbaceous vegetation in Mediterranean forests from NDVI time series, *Remote Sensing*, 7(9): 12314-12335.

Hempson, G.P., Archibald, S. & Bond, W.J. (2015a) A continent-wide assessment of the form and intensity of large mammal herbivory in Africa, *Science*, 350(6264): 1056-1061.

Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., Kruger, L.M., Moxley, C., et al. (2015b) Ecology of grazing lawns in Africa, *Biological Reviews*, 90(3): 979-994.

Hempson, G.P., Archibald, S. & Bond, W.J. (2017) The consequences of replacing wildlife with livestock in Africa, *Scientific Reports*, 7: 17196.

Hengl, T., de Jesus, J.M., MacMillan, R.A., Batjes, N.H., Heuvelink, G.B., Ribeiro, E., Samuel-Rosa, A., Kempen, B., et al. (2014) SoilGrids1km—global soil information based on automated mapping, *PLoS One*, 9(8): e105992.

Hepworth, K., Test, P., Hart, R., Waggoner Jr, J. & Smith, M. (1991) Grazing systems, stocking rates, and cattle behavior in southeastern Wyoming, *Journal of Range Management*, 44(3): 259-262.

Herrero, M., Havlík, P., Valin, H., Notenbaert, A., Rufino, M.C., Thornton, P.K., Blümmel, M., Weiss, F., et al. (2013) Biomass use, production, feed efficiencies, and greenhouse gas emissions from global livestock systems, *Proceedings of the National Academy of Sciences*, 110(52): 20888-20893.

Herrero, M., Henderson, B., Havlík, P., Thornton, P.K., Conant, R.T., Smith, P., Wirsenius, S., Hristov, A.N., et al. (2016) Greenhouse gas mitigation potentials in the livestock sector, *Nature Climate Change*, 6: 452.

Hickman, K.R., Hartnett, D.C., Cochran, R.C. & Owensby, C.E. (2004) Grazing management effects on plant species diversity in tallgrass prairie, *Journal of Range Management*, 57(1): 58-65.

Higgins, S.I., Bond, W.J., February, E.C., Bronn, A., Euston-Brown, D.I., Enslin, B., Govender, N., Rademan, L., et al. (2007) Effects of four decades of fire manipulation on woody vegetation structure in savanna, *Ecology*, 88(5): 1119-1125.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas, *International Journal of Climatology*, 25(15): 1965-1978.

Hilbert, D.W., Swift, D.M., Detling, J.K. & Dyer, M.I. (1981) Relative growth rates and the grazing optimization hypothesis, *Oecologia*, 51(1): 14-18.

Hilker, T., Natsagdorj, E., Waring, R.H., Lyapustin, A. & Wang, Y. (2014) Satellite observed widespread decline in Mongolian grasslands largely due to overgrazing, *Global Change Biology*, 20(2): 418-428.

Hirota, M., Holmgren, M., Van Nes, E.H. & Scheffer, M. (2011) Global resilience of tropical forest and savanna to critical transitions, *Science*, 334(6053): 232-235.

Hobbs, N.T., Schimel, D.S., Owensby, C.E. & Ojima, D.S. (1991) Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets, *Ecology*, 72(4): 1374-1382.

Hobbs, N.T. (1996) Modification of ecosystems by ungulates, *The Journal of Wildlife Management*: 695-713.

Hodgkinson, K. (1974) Influence of Partial Defoliation on Photosynthesis, Photorespiration and Transpiration by Lucerne Leaves of Different Ages, *Functional Plant Biology*, 1(4): 561-578.

Hoffman, M. & Cowling, R. (2003) 'Nature's method of grazing': Non-Selective Grazing (NSG) as a means of veld reclamation in South Africa, *South African Journal of Botany*, 69(1): 92-98.

Hoffmann, W.A., Bazzaz, F.A., Chatterton, N.J., Harrison, P.A. & Jackson, R.B. (2000) Elevated CO_2 enhances resprouting of a tropical savanna tree, *Oecologia*, 123(3): 312-317.

Holdo, R.M., Mack, M.C. & Arnold, S.G. (2012) Tree canopies explain fire effects on soil nitrogen, phosphorus and carbon in a savanna ecosystem, *Journal of Vegetation Science*, 23(2): 352-360.

Holechek, J.L., Pieper, R.D. & Herbel, C.H. (1989) *Range management. Principles and practices*, Englewood Cliffs, USA: Prentice-Hall.

Holland, E.A., Parton, W.J., Detling, J.K. & Coppock, D.L. (1992) Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow, *American Naturalist*, 140(4): 685-706.

Holling, C.S. (1973) Resilience and Stability of Ecological Systems, *Annual Review of Ecology and Systematics*, 4(1): 1-23.

Huete, A.R. (1988) A soil-adjusted vegetation index (SAVI), *Remote Sensing of Environment*, 25(3): 295-309.

Huffman, G.J., Adler, R.F., Bolvin, D.T. & Nelkin, E.J. (2010) The TRMM multi-satellite precipitation analysis (TMPA), in: *Satellite rainfall applications for surface hydrology*Springer, 3-22.

Illius, A. & O'connor, T. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems, *Ecological Applications*, 9(3): 798-813.

Illius, A.W. & O'Connor, T.G. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems, *Ecological Applications*, 9(3): 798-813.

Illius, A.W. & O'Connor, T.G. (2000) Resource heterogeneity and ungulate population dynamics, *Oikos*, 89(2): 283-294.

Iqbal, N., Masood, A. & Khan, N.A. (2012) Analyzing the significance of defoliation in growth, photosynthetic compensation and source-sink relations, *Photosynthetica*, 50(2): 161-170.

Jacobs, J. (1974) Quantitative measurement of food selection, *Oecologia*, 14(4): 413-417.

Jakoby, O., Quaas, M.F., Müller, B., Baumgärtner, S. & Frank, K. (2014) How do individual farmers' objectives influence the evaluation of rangeland management strategies under a variable climate?, *Journal of Applied Ecology*, 51(2): 483-493.

Jeltsch, F., Milton, S.J., Dean, W.R.J. & Rooyen, N. (1997) Simulated pattern formation around artificial waterholes in the semi-arid Kalahari, *Journal of Vegetation Science*, 8(2): 177-188.

Jones, C.G. & Hartley, S.E. (1999) A protein competition model of phenolic allocation, *Oikos*, 86(1): 27-44.

Juffe-Bignoli, D., Burgess, N., Bingham, H., Belle, E., De Lima, M., Deguignet, M., Bertzky, B., Milam, A., et al. (2014) *Protected planet report 2014*, Cambridge, UK.

Justice, C., Giglio, L., Korontzi, S., Owens, J., Morisette, J., Roy, D., Descloitres, J., Alleaume, S., et al. (2002) The MODIS fire products, *Remote Sensing of Environment*, 83(1): 244-262.

Kauffman, J.B., Cummings, D. & Ward, D. (1994) Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado, *Journal of Ecology*, 82(3): 519-531.

Kellner, K. & Bosch, O. (1992) Influence of patch formation in determining the stocking rate for southern African grasslands, *Journal of Arid Environments*, 22(1): 99-105.

Kgope, B.S., Bond, W.J. & Midgley, G.F. (2010) Growth responses of African savanna trees implicate atmospheric [CO_2] as a driver of past and current changes in savanna tree cover, *Austral Ecology*, 35: 451-463.

Kilpatrick, A.D., Lewis, M.M. & Ostendorf, B. (2015) Rangeland Condition Monitoring: A New Approach Using Cross-Fence Comparisons of Remotely Sensed Vegetation, *PloS one*, 10(11): e0142742.

Kirby, D. & Webb, H. (1989) Cattle Diets on Rotation and Seasonlong Grazing Treatments, *North Dakota Farm Research*, 46(6): 14-17.

Kirby, D.R., Pessin, M.F. & Clambey, G.K. (1986) Disappearance of forage under short duration and seasonlong grazing, *Journal of Range Management*, 39(6): 496-500.

Koch, P.L. & Barnosky, A.D. (2006) Late Quaternary extinctions: state of the debate, *Annual Review of Ecology, Evolution, and Systematics*, 37: 215-250.

Koide, R. & Kabir, Z. (2000) Extraradical hyphae of the mycorrhizal fungus *Glomus intraradices* can hydrolyse organic phosphate, *New Phytologist*, 148(3): 511-517.

Körner, C. (2006) Plant CO_2 responses: an issue of definition, time and resource supply, *New Phytologist*, 172(3): 393-411.

Krawchuk, M.A. & Moritz, M.A. (2011) Constraints on global fire activity vary across a resource gradient, *Ecology*, 92(1): 121-132.

Krebs, J.R. & Davies, N.B. (2009) *Behavioural ecology: an evolutionary approach*, Oxford, UK: Blackwell Publishing.

Kreuter, U.P. & Tainton, N.M. (1988) The effect of continuous and rotational grazing of sourveld on the selection of plant fractions by simmentaler heifers, *Journal of the Grassland Society of Southern Africa*, 5(2): 68-71.

Krumins, J.A., Krumins, V., Forgoston, E., Billings, L. & van der Putten, W.H. (2015) Herbivory and stoichiometric feedbacks to primary production, *PloS One*, 10(6): e0129775.

Laca, E.A. (2009) New approaches and tools for grazing management, *Rangeland Ecology & Management*, 62(5): 407-417.

Lamoot, I., Meert, C. & Hoffmann, M. (2005) Habitat use of ponies and cattle foraging together in a coastal dune area, *Biological Conservation*, 122(4): 523-536.

Lamprey, H. (1983) Pastoralism yesterday and today: the over-grazing problem, in: F, B., ed., *Tropical savannas, Ecosystems of the World*, Amsterdam: Elsevier, 643-667.

Launchbaugh, K.L. & Howery, L.D. (2005) Understanding Landscape Use Patterns of Livestock as a Consequence of Foraging Behavior, *Rangeland Ecology & Management*, 58(2): 99-108.

Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA, *Canadian Journal of Zoology*, 79(8): 1401-1409.

LeBauer, D.S. & Treseder, K.K. (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed, *Ecology*, 89(2): 371-379.

Lee, J.M., Sathish, P., Donaghy, D.J. & Roche, J.R. (2011) Impact of defoliation severity on photosynthesis, carbon metabolism and transport gene expression in perennial ryegrass, *Functional Plant Biology*, 38(10): 808-817.

Lehmann, C.E., Archibald, S.A., Hoffmann, W.A. & Bond, W.J. (2011) Deciphering the distribution of the savanna biome, *New Phytologist*, 191(1): 197-209.

Lehmann, C.E., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., et al. (2014) Savanna vegetation-fire-climate relationships differ among continents, *Science*, 343(6170): 548-552.

Levy, E.B. & Madden, E.A. (1933) The point method of pasture analysis., *New Zealand Journal of Agriculture*, 46: 267 - 279.

Leys, B.A., Marlon, J.R., Umbanhowar, C. & Vannière, B. (2018) Global fire history of grassland biomes, *Ecology and Evolution*, 8(17): 8831-8852.

Liaw, A. & Wiener, M. (2002) Classification and regression by randomForest, *R news*, 2(3): 18-22.

Liedloff, A.C., Coughenour, M.B., Ludwig, J.A. & Dyer, R. (2001) Modelling the trade-off between fire and grazing in a tropical savanna landscape, northern Australia, *Environment International*, 27(2): 173-180.

Limb, R.F., Fuhlendorf, S.D., Engle, D.M., Weir, J.R., Elmore, R.D. & Bidwell, T.G. (2011) Pyric–herbivory and cattle performance in grassland ecosystems, *Rangeland Ecology & Management*, 64(6): 659-663.

Liu, H.Q. & Huete, A. (1995) A feedback based modification of the NDVI to minimize canopy background and atmospheric noise, *IEEE Transactions on Geoscience and Remote Sensing*, 33(2): 457-465.

Lu, X., Wang, L. & McCabe, M.F. (2016) Elevated CO 2 as a driver of global dryland greening, *Scientific Reports*, 6: 20716.

Machado, R.A.R., Ferrieri, A.P., Robert, C.A.M., Glauser, G., Kallenbach, M., Baldwin, I.T. & Erb, M. (2013) Leaf-herbivore attack reduces carbon reserves and regrowth from the roots via jasmonate and auxin signaling, *New Phytologist*, 200(4): 1234-1246.

Makarewicz, C. & Tuross, N. (2012) Finding Fodder and Tracking Transhumance: Isotopic Detection of Goat Domestication Processes in the Near East, *Current Anthropology*, 53(4): 495-505.

Mann, C. & Sherren, K. (2018) Holistic Management and Adaptive Grazing: A Trainers' View, *Sustainability*, 10: 1-19.

Marlon, J.R., Bartlein, P.J., Daniau, A.-L., Harrison, S.P., Maezumi, S.Y., Power, M.J., Tinner, W. & Vanniére, B. (2013) Global biomass burning: a synthesis and review of Holocene paleofire records and their controls, *Quaternary Science Reviews*, 65: 5-25.

Marshall, F., Reid, R.E.B., Goldstein, S., Storozum, M., Wreschnig, A., Hu, L., Kiura, P., Shahack-Gross, R., et al. (2018) Ancient herders enriched and restructured African grasslands, *Nature*, 561(387-390).

Martin, P.S. (1966) Africa and Pleistocene overkill, *Nature*, 212(5060): 339-342.

Maschinski, J. & Whitham, T.G. (1989) The Continuum of Plant Responses to Herbivory: The Influence of Plant Association, Nutrient Availability, and Timing, *The American Naturalist*, 134(1): 1-19.

McCollum III, F.T., Gillen, R.L., Karges, B.R. & Hodges, M.E. (1999) Stocker cattle response to grazing management in tallgrass prairie, *Journal of Range Management*, 52(2): 120-126.

McCormick, A.J., Cramer, M.D. & Watt, D.A. (2006) Sink strength regulates photosynthesis in sugarcane, *New Phytologist*, 171(4): 759-770.

McCosker, T. (2000) Cell Grazing—the first 10 years in Australia, *Tropical Grasslands*, 34: 207-218.

McDermott, J.J., Staal, S.J., Freeman, H.A., Herrero, M. & Van de Steeg, J.A. (2010) Sustaining intensification of smallholder livestock systems in the tropics, *Livestock Science*, 130(1): 95-109.

McNaughton, S. (1979) Grazing as an Optimization Process: Grass-Ungulate Relationships in the Serengeti, *The American Naturalist*, 113(5): 691-703.

McNaughton, S. (1983) Compensatory plant growth as a response to herbivory, *Oikos*: 329-336.

McNaughton, S. (1984) Grazing lawns: animals in herds, plant form, and coevolution, *American Naturalist*, 124(6): 863-886.

McNaughton, S. (1985) Ecology of a grazing ecosystem: the Serengeti, *Ecological Monographs*, 55(3): 259-294.

McNaughton, S., Ruess, R. & Seagle, S. (1988) Large mammals and process dynamics in African ecosystems, *Bioscience*, 38(11): 794-800.

McNaughton, S.J. & Chapin, F.S. (1985) Effects of Phosphorus Nutrition and Defoliation on C4 Graminoids from the Serengeti Plains, *Ecology*, 66(5): 1617-1629.

McNaughton, S.J. (1993) Grasses and Grazers, Science and Management, *Ecological Applications*, 3(1): 17-20.

McNaughton, S.J., Banyikwa, F.F. & McNaughton, M.M. (1998) Root biomass and productivity in a grazing ecosystem: The Serengeti, *Ecology*, 79(2): 587-592.

Merrill, L.B. (1954) A variation of deferred rotation grazing for use under southwest range conditions, *Journal of Range Management*, 7(4): 152-154.

Milton, S.J. (2004) Grasses as invasive alien plants in South Africa : working for water, *South African Journal of Science*, 100(1): 69-75.

Molvar, E.M. & Bowyer, R.T. (1994) Costs and Benefits of Group Living in a Recently Social Ungulate: The Alaskan Moose, *Journal of Mammalogy*, 75(3): 621-630.

Morokong, T. (2016) *Sustainable options in communal beef cattle grazing systems in the Matatiele local municipality of the Eastern Cape, South Africa*, unpublished thesis (MSc), Stellenbosch University.

Morris, C. & Tainton, N. (1996) Long-term effects of different rotational grazing schedules on the productivity and floristic composition of Tall Grassveld in KwaZulu-Natal, *African Journal of Range & Forage Science*, 13(1): 24-28.

Morris, C.D. (2016) Is the grazing tolerance of mesic decreaser and increaser grasses altered by soil nutrients and competition?, *African Journal of Range & Forage Science*, 33(4): 235-245.

Mouillot, F. & Field, C.B. (2005) Fire history and the global carbon budget: a 1× 1 fire history reconstruction for the 20th century, *Global Change Biology*, 11(3): 398-420.

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

Munyati, C. & Makgale, D. (2009) Multitemporal Landsat TM imagery analysis for mapping and quantifying degraded rangeland in the Bahurutshe communal grazing lands, South Africa, *International Journal of Remote Sensing*, 30(14): 3649-3668.

Musemwa, L., Mushunje, A., Chimonyo, M. & Mapiye, C. (2010) Low cattle market off-take rates in communal production systems of South Africa: Causes and mitigation strategies, *Journal of Sustainable Development in Africa*, 12(5): 209-226.

O'Connor, T.G., Puttick, J.R. & Hoffman, M.T. (2014) Bush encroachment in southern Africa: changes and causes, *African Journal of Range & Forage Science*, 31(2): 67-88.

O'Reagain, P. & Turner, J. (1992) An evaluation of the empirical basis for grazing management recommendations for rangeland in southern Africa, *Journal of the Grassland Society of Southern Africa*, 9(1): 38-49.

O'Mara, F.P. (2011) The significance of livestock as a contributor to global greenhouse gas emissions today and in the near future, *Animal Feed Science and Technology*, 166-167: 7-15.

Odadi, W.O. & Rubenstein, D.I. (2015) Herd Size-Dependent Effects of Restricted Foraging Time Allowance on Cattle Behavior, Nutrition, and Performance, *Rangeland Ecology & Management*, 68(4): 341-348.

Odadi, W.O., Riginos, C. & Rubenstein, D.I. (2018) Tightly Bunched Herding Improves Cattle Performance in African Savanna Rangeland, *Rangeland Ecology & Management*, 71(4): 481-491.

Oliver, J.E. (1980) Monthly precipitation distribution: a comparative index, *The Professional Geographer*, 32(3): 300-309.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V., Underwood, E.C., D'amico, J.A., Itoua, I., et al. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity, *Bioscience*, 51(11): 933-938.

Olson, K.C. & Malechek, J.C. (1988) Heifer nutrition and growth on short duration grazed crested wheatgrass, *Journal of Range Management*, 41(2): 259-263.

Oosthuizen, I.B. & Snyman, H.A. (2003) Impact of water stress on growth reserves and re-growth of Themeda triandra (Forssk) following defoliation, *African Journal of Range & Forage Science*, 20(1): 41-45.

Opperman, D., Roberts, B. & RENS-BURG, W.V. (1970) The influence of defoliation on the root weights, stubble weights and growth reserves of 3 perennial veld grasses, *Agricultural Science of Southern Africa*, 2(2): 51-9.

Oswalt, D.L., Bertrand, A.R. & Teel, M.R. (1959) Influence of Nitrogen Fertilization and Clipping on Grass Roots1, *Soil Science Society of America Journal*, 23: 228-230.

Owen-Smith, N. (1987) Pleistocene extinctions: the pivotal role of megaherbivores, *Paleobiology*, 13(03): 351-362.

Palmer, A.R. & Fortescue, A. (2004) Remote sensing and change detection in rangelands, *African Journal of Range and Forage Science*, 21(2): 123-128.

Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing Effects of Native and Exotic Herbivores on Plant Invasions, *Science*, 311(5766): 1459-1461.

Paul, M.J. & Foyer, C.H. (2001) Sink regulation of photosynthesis, *Journal of Experimental Botany*, 52(360): 1383-1400.

Pellegrini, A.F., Hedin, L.O., Staver, A.C. & Govender, N. (2015) Fire alters ecosystem carbon and nutrients but not plant nutrient stoichiometry or composition in tropical savanna, *Ecology*, 96(5): 1275-1285.

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., Fronhofer, E.A., Ganesanandamoorthy, P., et al. (2018) Biodiversity increases and decreases ecosystem stability, *Nature*, 563: 109-112.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change, *Trends in Ecology & Evolution*, 20(9): 503-510.

PlanetTeam (2017) *Planet Application Program Interface: In Space for Life on Earth* [online], available: https://api.planet.com [accessed June 2018].

Porensky, L.M. & Veblen, K.E. (2015) Generation of Ecosystem Hotspots Using Short-Term Cattle Corrals in an African Savanna, *Rangeland Ecology & Management*, 68(2): 131-141.

Potapov, P.V., Turubanova, S.A., Hansen, M.C., Adusei, B., Broich, M., Altstatt, A., Mane, L. & Justice, C.O. (2012) Quantifying forest cover loss in Democratic Republic of the Congo, 2000–2010, with Landsat ETM+ data, *Remote Sensing of Environment*, 122: 106-116.

Poulter, B., Frank, D., Ciais, P., Myneni, R.B., Andela, N., Bi, J., Broquet, G., Canadell, J.G., et al. (2014) Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle, *Nature*, 509(7502): 600-603.

Power, M.J., Marlon, J., Ortiz, N., Bartlein, P.J., Harrison, S.P., Mayle, F.E., Ballouche, A., Bradshaw, R.H., et al. (2008) Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data, *Climate Dynamics*, 30(7-8): 887-907.

Probo, M., Lonati, M., Pittarello, M., Bailey, D.W., Garbarino, M., Gorlier, A. & Lombardi, G. (2014) Implementation of a rotational grazing system with large paddocks changes the distribution of grazing cattle in the south-western Italian Alps, *The rangeland journal*, 36(5): 445-458.

QGIS (2014) 'Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project'.

Ralphs, M.H., Kothmann, M.M. & Taylor, C.A. (1990) Vegetation response to increased stocking rates in short-duration grazing, *Journal of Range Management*, 43(2): 104-108.

R Core Team (2016) 'R: A language and environment for statistical computing', Vienna, Austria: R Foundation for Statistical Computing.

Reed, M.S., Stringer, L.C., Dougill, A.J., Perkins, J.S., Atlhopheng, J.R., Mulale, K. & Favretto, N. (2015) Reorienting land degradation towards sustainable land management: Linking sustainable livelihoods with ecosystem services in rangeland systems, *Journal of Environmental Management*, 151: 472-485.

Resende, J.C.F., Markewitz, D., Klink, C.A., da Cunha Bustamante, M.M. & Davidson, E.A. (2011) Phosphorus cycling in a small watershed in the Brazilian Cerrado: impacts of frequent burning, *Biogeochemistry*, 105(1-3): 105-118.

Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B., Mortimore, M., Batterbury, S.P., Downing, T.E., Dowlatabadi, H., et al. (2007) Global desertification: building a science for dryland development, *Science*, 316(5826): 847-851.

Richards, J. & Caldwell, M. (1985) Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with Agropyron species, *Journal of Applied Ecology*: 907-920.

Riley, S.J. (1999) Index that quantifies topographic heterogeneity, *Intermountain Journal of sciences*, 5(1-4): 23-27.

Rinella, M.J. & Bellows, S.E. (2016) Evidence-Targeted Grazing Benefits to Invaded Rangelands Can Increase over Extended Time Frames, *Rangeland Ecology & Management*, 69(3): 169-172.

Ripley, B.D. (1976) The second-order analysis of stationary point processes, *Journal of Applied Probability*, 13(2): 255-266.

Ripple, W.J., Larsen, E.J., Renkin, R.A. & Smith, D.W. (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range, *Biological Conservation*, 102(3): 227-234.

Robinson, G.S., Pigott Burney, L. & Burney, D.A. (2005) Landscape paleoecology and megafaunal extinction in southeastern New York State, *Ecological Monographs*, 75(3): 295-315.

Robinson, T.P., Wint, G.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aietti, L., et al. (2014) Mapping the global distribution of livestock, *PloS one*, 9(5): e96084.

Roche, L.M., Cutts, B.B., Derner, J.D., Lubell, M.N. & Tate, K.W. (2015) On-Ranch Grazing Strategies: Context for the Rotational Grazing Dilemma, *Rangeland Ecology & Management*, 68(3): 248-256.

Rodell, M., Houser, P., Jambor, U., Gottschalck, J., Mitchell, K., Meng, C., Arsenault, K., Cosgrove, B., et al. (2004) The global land data assimilation system, *Bulletin of the American Meteorological Society*, 85(3): 381-394.

Roques, K., O'connor, T. & Watkinson, A. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence, *Journal of Applied Ecology*, 38(2): 268-280.

Rosenzweig, M.L. (2003) *Win-win ecology: how the earth's species can survive in the midst of human enterprise*, Oxford University Press on Demand.

Rowland, J.W. (1937) *Grazing management*, Union of South Africa.

Roy, D.P., Boschetti, L., Justice, C.O. & Ju, J. (2008) The collection 5 MODIS burned area product—Global evaluation by comparison with the MODIS active fire product, *Remote Sensing of Environment*, 112(9): 3690-3707.

Roy, D.P., Kovalskyy, V., Zhang, H.K., Vermote, E.F., Yan, L., Kumar, S.S. & Egorov, A. (2016) Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity, *Remote Sensing of Environment*, 185: 57-70.

Rule, S., Brook, B.W., Haberle, S.G., Turney, C.S., Kershaw, A.P. & Johnson, C.N. (2012) The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia, *Science*, 335(6075): 1483-1486.

Ryle, G.J.A. & Powell, C.E. (1975) Defoliation and Regrowth in the Graminaceous Plant: The Role of Current Assimilate, *Annals of Botany*, 39(2): 297-310.

Sala, O.E., Yahdjian, L., Havstad, K. & Aguiar, M.R. (2017) Rangeland Ecosystem Services: Nature’s Supply and Humans’ Demand, in: Briske, D. D., ed., *Rangeland Systems: Processes, Management and Challenges*, Cham: Springer International Publishing, 467-489.

Sampson, A.W. (1913) *Range improvement by deferred and rotation grazing*, 34, USA: United States Department of Agriculture.

Sampson, A.W. (1951) A Symposium on Rotation Grazing in North America, *Journal of Range Management*, 4(1): 19-24.

Samuels, I., Cupido, C., Swarts, M.B., Palmer, A.R. & Paulse, J.W. (2016) Feeding ecology of four livestock species under different management in a semi-arid pastoral system in South Africa, *African Journal of Range & Forage Science*, 33(1): 1-9.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., & Ardo, J. (2005). Determinants of woody cover in African savannas. *Nature*, *438*(7069): 846.

Sankaran, M., Ratnam, J. & Hanan, N. (2008) Woody cover in African savannas: the role of resources, fire and herbivory, *Global Ecology and Biogeography*, 17(2): 236-245.

Sankaran, M., Augustine, D.J. & Ratnam, J. (2013) Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna, *Journal of Ecology*, 101(6): 1389-1399.

Savory, A. (1978) A holistic approach to ranch management using short duration grazing., in: Hyder, D., ed., *Proceedings of the 1st International Rangeland Congress*, Denver, Colorado: Peerless Printing, 555-557.

Savory, A. (1983) The Savory grazing method or holistic resource management, *Rangelands*, 5(4): 155-159.

Savory, A. (2013) *How to fight desertification and fight climate change* [online], available: http://www.ted.com [accessed 25 November].

Savory, A. & Butterfield, J. (2016) *Holistic Management: A Commonsense Revolution to Restore Our Environment*, Washinton, DC: Island Press.

Scasta, J.D., Duchardt, C., Engle, D.M., Miller, J.R., Debinski, D.M. & Harr, R.N. (2016) Constraints to restoring fire and grazing ecological processes to optimize grassland vegetation structural diversity, *Ecological Engineering*, 95: 865-875.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E. & Cross, A.F. (1996) On the Spatial Pattern of Soil Nutrients in Desert Ecosystems, *Ecology*, 77(2): 364-374.

Scholes, R., Kendall, J. & Justice, C. (1996) The quantity of biomass burned in southern Africa, *Journal of Geophysical Research: Atmospheres*, 101(D19): 23667-23676.

Schwilk, D.W. (2015) Dimensions of plant flammability, *New Phytologist*, 206(2): 486-488.

Sexton, J.O., Song, X.-P., Feng, M., Noojipady, P., Anand, A., Huang, C., Kim, D.-H., Collins, K.M., et al. (2013) Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with lidar-based estimates of error, *International Journal of Digital Earth*, 6(5): 427-448.

Sherren, K., Fischer, J. & Fazey, I. (2012) Managing the grazing landscape: Insights for agricultural adaptation from a mid-drought photo-elicitation study in the Australian sheep-wheat belt, *Agricultural systems*, 106(1): 72-83.

Sherren, K. & Kent, C. (2017) Who's afraid of Allan Savory? Scientometric polarization on Holistic Management as competing understandings, *Renewable Agriculture and Food Systems*, 06/07: 1-16.

Sinclair, A.R.E. & Fryxell, J.M. (1985) The Sahel of Africa: ecology of a disaster, *Canadian Journal of Zoology*, 63(5): 987-994.

Singh, R., Raghubanshi, A. & Singh, J.S. (1991) Nitrogen-mineralization in dry tropical savanna: effects of burning and grazing, *Soil Biology and Biochemistry*, 23(3): 269-273.

Sitters, J. & Venterink, H.O. (2015) The need for a novel integrative theory on feedbacks between herbivores, plants and soil nutrient cycling, *Plant and Soil*, 1(396): 421-426.

Skead, C.J., Boshoff, A., Kerley, G.I.H. & Lloyd, P. (2007) *Historical incidence of the larger land mammals in the broader Eastern Cape*, Port Elizabeth, South Africa: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Skovlin, J. (1987) Southern Africa's experience with intensive short duration grazing, *Rangelands*: 162-167.

Skowno, A.L., Thompson, M.W., Hiestermann, J., Ripley, B., West, A.G. & Bond, W.J. (2016) Woodland expansion in South African grassy biomes based on satellite observations (1990–2013): general patterns and potential drivers, *Global Change Biology*: 1-12.

Smith, E.F. & Owensby, C.E. (1978) Intensive-early stocking and season-long stocking of Kansas Flint Hills range, *Journal of Range Management*, 31(1): 14-17.

Smith, J.G. (1899) *Grazing problems in the Southwest and how to meet them*, US Department of Agriculture, Division of Agrostology.

Snyman, H.A., Ingram, L.J. & Kirkman, K.P. (2013) Themeda triandra: a keystone grass species, *African Journal of Range & Forage Science*, 30(3): 99-125.

Soder, K.J., Gregorini, P., Scaglia, G. & Rook, A.J. (2009) Dietary Selection by Domestic Grazing Ruminants in Temperate Pastures: Current State of Knowledge, Methodologies, and Future Direction, *Rangeland Ecology & Management*, 62(5): 389-398.

Spasojevic, M.J., Aicher, R.J., Koch, G.R., Marquardt, E.S., Mirotchnick, N., Troxler, T.G. & Collins, S.L. (2010) Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits, *Ecology*, 91(6): 1651-1659.

Spedding, C.R.W. (1971) Grassland ecology, *The Journal of Agricultural Science*, 76: 567-572.

Spinage, C. (2012) *African ecology: benchmarks and historical perspectives*, New York: Springer Science & Business Media.

Spinage, C.A. (1973) A review of ivory exploitation and elephant population trends in Africa, *African Journal of Ecology*, 11(3-4): 281-289.

Staver, A.C., Bond, W.J., Stock, W.D., Van Rensburg, S.J. & Waldram, M.S. (2009) Browsing and fire interact to suppress tree density in an African savanna, *Ecological Applications*, 19(7): 1909-1919.

Staver, A.C., Archibald, S. & Levin, S.A. (2011) The global extent and determinants of savanna and forest as alternative biome states, *Science*, 334(6053): 230-232.

Staver, A.C., Bond, W.J., Cramer, M.D. & Wakeling, J.L. (2012) Top-down determinants of niche structure and adaptation among African Acacias, *Ecology Letters*, 15(7): 673-679.

Stevens, N., Seal, C.E., Archibald, S. & Bond, W. (2014) Increasing temperatures can improve seedling establishment in arid-adapted savanna trees, *Oecologia*, 175(3): 1029-1040.

Stevens, N., Erasmus, B., Archibald, S. & Bond, W. (2016) Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock?, *Philosophical Transactions of the Royal Society of London B: Biological Science*, 371(1703): 20150437.

Stevens, N., Lehmann, C.E., Murphy, B.P. & Durigan, G. (2017) Savanna woody encroachment is widespread across three continents, *Global Change Biology*, 23(1): 235-244.

Stinner, D.H., Stinner, B.R. & Martsolf, E. (1997) Biodiversity as an organizing principle in agroecosystem management: case studies of holistic resource management practitioners in the USA, *Agriculture, Ecosystems & Environment*, 62(2): 199-213.

Svenning, J.-C., Pedersen, P.B., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D.M., Sandel, B., et al. (2016) Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research, *Proceedings of the National Academy of Sciences*, 113(4): 898-906.

Svoray, T., Perevolotsky, A. & Atkinson, P.M. (2013) Ecological sustainability in rangelands: the contribution of remote sensing, *International Journal of Remote Sensing*, 34(17): 6216-6242.

Tainton, N., De V. Booysen, P. & Scott, J. (1970) Response of tall grassveld to different intensities, seasons and frequencies of clipping, *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 5(1): 32-41.

Tainton, N.M., Edwards, P.J. & Mentis, M.T. (1980) A revised method for assessing veld condition, *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 15(1): 37-42.

Tainton, N.M. (1999) *Veld Management in South Africa*, University of Natal press.

Teague, R., Provenza, F., Kreuter, U., Steffens, T. & Barnes, M. (2013) Multi-paddock grazing on rangelands: why the perceptual dichotomy between research results and rancher experience?, *Journal of Environmental Management*, 128: 699-717.

Teague, W., Dowhower, S. & Waggoner, J. (2004) Drought and grazing patch dynamics under different grazing management, *Journal of Arid Environments*, 58(1): 97-117.

Teague, W., Dowhower, S., Baker, S., Haile, N., DeLaune, P. & Conover, D. (2011) Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie, *Agriculture, Ecosystems & Environment*, 141(3): 310-322.

Texeira, J. (2009) 'AIRS/Aqua L3 8-day CO_2 in the free troposphere (AIRS-only) 2.5 degrees x 2 degrees V005', [online], available: https://disc.gsfc.nasa.gov/datasets/AIRS3C2M_V005/summary [accessed 20/09/2017].

Thevenon, F., Williamson, D., Vincens, A., Taieb, M., Merdaci, O., Decobert, M. & Buchet, G. (2003) A late-Holocene charcoal record from Lake Masoko, SW Tanzania: climatic and anthropologic implications, *The Holocene*, 13(5): 785-792.

Thevenon, F., Williamson, D., Bard, E., Anselmetti, F.S., Beaufort, L. & Cachier, H. (2010) Combining charcoal and elemental black carbon analysis in sedimentary archives: Implications for past fire regimes, the pyrogenic carbon cycle, and the human–climate interactions, *Global and Planetary Change*, 72(4): 381-389.

Thorne, J.H. & Koller, H.R. (1974) Influence of Assimilate Demand on Photosynthesis, Diffusive Resistances, Translocation, and Carbohydrate Levels of Soybean Leaves, *Plant Physiology*, 54(2): 201-207.

Thurow, T.L. (1991) Hydrology and erosion, in: *Grazing Management: An Ecological Perspective.* , Portland, Oregon: Timber Press, 141-160.

Tiedeman, J. (1986) *Short duration grazing: proceedings of the short duration grazing and current issues in grazing management shortcourse, 21–23 January 1986*, Kennewick, Washington: Pullman: Washington University.

Tiffin, P. (2000) Mechanisms of tolerance to herbivore damage:what do we know?, *Evolutionary Ecology*, 14(4): 523-536.

Tilman, D. & Clark, M. (2014) Global diets link environmental sustainability and human health, *Nature*, 515(7528): 518.

Torchiano, M. (2017) effsize: Efficient effect size computation, *R package version 0.7*, 4.

Tucker, C.J. (1979) Red and photographic infrared linear combinations for monitoring vegetation, *Remote Sensing of Environment*, 8(2): 127-150.

Ungar, E.D. & Noy-Meir, I. (1988) Herbage Intake in Relation to Availability and Sward Structure: Grazing Processes and Optimal Foraging, *Journal of Applied Ecology*, 25(3): 1045-1062.

Van de Vijver, C.A., Poot, P. & Prins, H.H. (1999) Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna, *Plant and Soil*, 214(1): 173-185.

Van Langevelde, F., Van De Vijver, C.A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., et al. (2003) Effects of fire and herbivory on the stability of savanna ecosystems, *Ecology*, 84(2): 337-350.

Van Poollen, H.W. & Lacey, J.R. (1979) Herbage Response to Grazing Systems and Stocking Intensities, *Journal of Range Management*, 32(4): 250-253.

van Wilgen, B.W., Trollope, W.S., Biggs, H.C., Potgieter, A.L. & Brockett, B.H. (2003) Fire as a driver of ecosystem variability, in: du Toit, J. T., Rogers, K. H. and Biggs, H. C., eds., *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, Washington, DC: Island Press, 149-170.

van Wilgen, B.W., Govender, N., Smit, I.P. & MacFadyen, S. (2014) The ongoing development of a pragmatic and adaptive fire management policy in a large African savanna protected area, *Journal of Environmental Management*, 132: 358-368.

van Wilgen, B.W. & Wannenburgh, A. (2016) Co-facilitating invasive species control, water conservation and poverty relief: achievements and challenges in South Africa's Working for Water programme, *Current Opinion in Environmental Sustainability*, 19: 7-17.

Vass, A.F. (1926) *Range and ranch studies in Wyoming*14Wyoming Agriculture Experiment Station.

Veblen, K.E. (2013) Impacts of traditional livestock corrals on woody plant communities in an East African savanna, *The Rangeland Journal*, 35(3): 349-353.

Venter, A. & Drewes, R. (1969) A flexible system of management for sourveld in Natal, *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 4(1): 104-107.

Venter, Z.S. (2017) *Holistic planned grazing and the herd effect* [online], available: https://www.youtube.com/watch?v=xlqnG-Wjhls&t=1s%20[accessed November 2018].

Venter, Z.S., Hawkins, H.-J. & Cramer, M.D. (2017) Implications of historical interactions between herbivory and fire for rangeland management in African savannas, *Ecosphere*, 8(10): 1-14.

Venter, Z.S., Cramer, M.D. & Hawkins, H.J. (2018) Drivers of woody plant encroachment over Africa, *Nature Communications*, 9(1): 2272.

Venter, Z.S., Hawkins, H.-J. & Cramer, M.D. (2019) Cattle don't care: Animal behaviour is similar regardless of grazing management in grasslands, *Agriculture, Ecosystems & Environment*, 272: 175-187.

Vesk, P.A. & Westoby, M. (2001) Predicting plant species' responses to grazing, *Journal of Applied Ecology*, 38(5): 897-909.

Vetter, S. (2005) Rangelands at equilibrium and non-equilibrium: recent developments in the debate, *Journal of Arid Environments*, 62(2): 321-341.

Voisin, A. (1988) *Grass productivity*, Washington, DC: Island Press.

Volesky, J.D. (1994) Tiller defoliation patterns under frontal, continuous, and rotation grazing, *Journal of Range Management*, 47(3): 215-219.

Voosen, P. (2016) Anthropocene pinned to postwar period, *Science*, 353(6302): 852-853.

Walker, J.W. & Heitschmidt, R.K. (1986) Effect of Various Grazing Systems on Type and Density of Cattle Trails, *Journal of Range Management*, 39(5): 428-431.

Walker, J.W., Heitschmidt, R.K. & Dowhower, S.L. (1989) Some effects of a rotational grazing treatment on cattle preference for plant communities, *Journal of Range Management*, 42(3): 143-148.

WallisDeVries, M.F., Laca, E.A. & Demment, M.W. (1999) The importance of scale of patchiness for selectivity in grazing herbivores, *Oecologia*, 121(3): 355-363.

Wardlaw, I.F. (1990) Tansley Review No. 27 The control of carbon partitioning in plants, *New Phytologist*, 116(3): 341-381.

Warren, S., Thurow, T., Blackburn, W. & Garza, N. (1986) The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics, *Journal of Range Management*, 39(6): 491-495.

Weber, T., Haensler, A., Rechid, D., Pfeifer, S., Eggert, B. & Jacob, D. (2018) Analyzing Regional Climate Change in Africa in a 1.5, 2, and 3°C Global Warming World, *Earth's Future*, 6(4): 643-655.

Wessels, K., Prince, S., Frost, P. & Van Zyl, D. (2004) Assessing the effects of human-induced land degradation in the former homelands of northern South Africa with a 1 km AVHRR NDVI time-series, *Remote Sensing of Environment*, 91(1): 47-67.

Wessels, K.J., Van Den Bergh, F. & Scholes, R. (2012) Limits to detectability of land degradation by trend analysis of vegetation index data, *Remote Sensing of Environment*, 125: 10-22.

Westhoek, H., Rood, T., van den Berg, M., Janse, J., Nijdam, D., Reudink, M., Stehfest, E., Lesschen, J., et al. (2011) *The protein puzzle: the consumption and production of meat, dairy and fish in the European Union*Netherlands Environmental Assessment Agency.

Westoby, M., Walker, B. & Noy-Meir, I. (1989) Opportunistic management for rangelands not at equilibrium, *Journal of Range Management*, 42(4): 266-274.

White, A.C., Rogers, A., Rees, M. & Osborne, C.P. (2016) How can we make plants grow faster? A source–sink perspective on growth rate, *Journal of Experimental Botany*, 67(1): 31-45.

White, F. (1983) *Vegetation of Africa – A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*, Paris: Unesco.

Wiegand, K., Ward, D., Saltz, D. & Ezcurra, E. (2005) Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer, *Journal of Vegetation Science*, 16(3): 311-320.

Wiegand, T. & Moloney, K.A. (2004) Rings, circles, and null-models for point pattern analysis in ecology, *Oikos*, 104(2): 209-229.

Wiens, J.A. (1984) On understanding a nonequilibrium world: myth and reality in community patterns and processes, *Ecological communities: conceptual issues and the evidence*: 439-458.

Willms, W.D., Smoliak, S. & Dormaar, J.F. (1990) Vegetation response to time-controlled grazing on mixed and fescue prairie, *Journal of Range Management*: 513-517.

Wilson, J.B. (1988) A Review of Evidence on the Control of Shoot: Root Ratio, in Relation to Models, *Annals of Botany*, 61(4): 433-449.

Wise, M.J. & Abrahamson, W.G. (2005) Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory, *Oikos*, 109(3): 417-428.

Wise, M.J. & Warren G. Abrahamson (2007) Effects of Resource Availability on Tolerance of Herbivory: A Review and Assessment of Three Opposing Models, *The American Naturalist*, 169(4): 443-454.

Woodcock, C.E., Allen, R., Anderson, M., Belward, A., Bindschadler, R., Cohen, W., Gao, F., Goward, S.N., et al. (2008) Free access to Landsat imagery, *Science*, 320(5879): 1011.

Worthington, D. (1984) The Charter Estate grazing trial: Animal production and management, *Zimbabwe Journal of Agricultural Research*, 81: 41-48.

Yahdjian, L., Sala, O.E. & Havstad, K.M. (2015) Rangeland ecosystem services: shifting focus from supply to reconciling supply and demand, *Frontiers in Ecology and the Environment*, 13(1): 44-51.

Zhai, P., Zhang, X., Wan, H. & Pan, X. (2005) Trends in total precipitation and frequency of daily precipitation extremes over China, *Journal of Climate*, 18(7): 1096-1108.

Zhao, W., Chen, S.-P. & Lin, G.-H. (2008) Compensatory growth responses to clipping defoliation in Leymus chinensis (Poaceae) under nutrient addition and water deficiency conditions, *Plant Ecology*, 196(1): 85-99.

Zhou, G., Zhou, X., He, Y., Shao, J., Hu, Z., Liu, R., Zhou, H. & Hosseini-Bai, S. (2016) Grazing intensity significantly affects belowground carbon and nitrogen cycling in grassland ecosystems: a meta-analysis, *Global Change Biology*, 23: 1167-1179.

Zhu, Z., Piao, S., Myneni, R.B., Huang, M., Zeng, Z., Canadell, J.G., Ciais, P., Sitch, S., et al. (2016) Greening of the Earth and its drivers, *Nature climate change*, 6(8): 791-795.

Supporting Information

Appendix S3

Table S3.1 Woody plant cover statistics for African countries derived from data presented in Fig. 3.1. The average trend (slope of the linear regression between 1986 and 2016) of the area undergoing significant gains and losses in woody cover should be interpreted relative to the total percentage woody cover, average trend and unmasked area (Fig. S3.1) for each country.

Country	Total			Gain		Loss	
	Woody cover (%)	Trend (% yr^{-1})	Unmasked area (km^2)	Area (km^2)	Trend (% yr^{-1})	Area (km^2)	Trend (% yr^{-1})
Angola	53	0.7	1023879	247131	0.8	28905	-0.6
Benin	42	0.6	63464	6929	0.6	374	-0.5
Botswana	28	0.8	618648	291435	0.8	6549	-0.3
Burkina Faso	19	0.4	105059	24446	0.4	2280	-0.4
Burundi	62	0.1	7100	546	0.5	405	-0.4
Cameroon	57	1.1	199047	27175	1.1	808	-0.7
Central African Republic	60	1.4	535743	221859	1.3	3600	-0.4
Chad	20	0.4	504490	59107	0.7	36507	-0.3
Congo	60	-0.3	71747	2359	0.6	5931	-0.7
Congo DRC	62	1.0	805462	195762	1.1	27197	-0.7
Eritrea	11	0.0	63511	14375	0.2	5082	-0.5
Ethiopia	34	0.4	851864	199166	0.6	34544	-0.5
Gabon	73	0.2	19744	243	0.5	89	-0.5
Gambia	39	0.5	1115	197	0.6	8	-0.6
Ghana	44	0.1	112289	4714	0.9	4156	-0.8
Guinea	58	0.5	219488	20913	0.7	4539	-0.6
Guinea-Bissau	60	0.8	20890	2924	0.9	183	-0.6
Ivory Coast	61	0.5	155198	16654	0.8	4746	-0.7
Kenya	32	-0.1	477358	37970	0.4	32216	-0.7
Lesotho	37	0.5	34873	15330	0.5	287	-0.5
Liberia	77	0.8	35788	4699	0.8	20	-0.5
Madagascar	44	-0.6	492315	28858	0.5	76792	-1.0
Malawi	50	0.5	83995	25878	0.6	2730	-0.6
Mali	19	0.5	256609	48260	0.5	4149	-0.2
Mauritania	4	0.3	6760	2104	0.2	43	-0.2
Mozambique	60	0.3	747550	116220	0.7	53230	-0.6
Namibia	19	0.5	886784	254625	0.5	9884	-0.2
Niger	2	-0.1	207426	15690	0.2	36477	-0.2
Nigeria	44	0.8	279679	37073	0.9	3036	-0.5

Table S3.1 Cont.

Country	Total			Gain		Loss	
	Woody cover (%)	Trend (% yr^{-1})	Unmasked area (km^2)	Area (km^2)	Trend (% yr^{-1})	Area (km^2)	Trend (% yr^{-1})
Niger	2	-0.1	207426	15690	0.2	36477	-0.2
Nigeria	44	0.8	279679	37073	0.9	3036	-0.5
Rwanda	65	0.0	3557	275	0.5	414	-0.4
Senegal	27	0.6	55462	8735	0.7	763	-0.4
Sierra Leone	69	0.3	49381	4563	0.7	2112	-0.6
Somalia	21	-0.1	544493	39083	0.4	79199	-0.4
South Africa	28	0.4	1214440	478366	0.5	31016	-0.4
South Sudan	43	1.2	518436	120047	1.1	3039	-0.6
Sudan	14	0.1	596673	53714	0.5	48360	-0.3
Swaziland	58	0.7	15672	5515	0.7	428	-0.5
Tanzania	55	0.6	700997	175749	0.8	32055	-0.6
Togo	47	0.6	27772	2407	0.8	476	-0.6
Uganda	57	1.1	63329	19481	1.1	764	-0.4
Zambia	57	0.5	676749	148146	0.7	26399	-0.6
Zimbabwe	46	0.7	399737	146043	0.7	4638	-0.6

Table S3.2 Internal and external random forest (RF) regression validation accuracies for predicting fractional woody cover using time-series metrics derived from Landsat satellites. Internal accuracies are evaluated by the proportion of variance in the response variable explained (PVE) as well as the mean of square residuals (MSR) produced from cross-validation between in-bag and out-of-bag samples. External accuracies are evaluated by predicting against a testing dataset withheld during model construction. The adjusted R^2 of the linear regression between observed and predicted woody cover is presented.

	Internal		External
RF model	PVE	MSR	Adjusted R^2
Landsat 5 TM	0.935	0.152	0.915
Landsat 7 ETM+	0.917	0.161	0.924
Landsat 8 OLI	0.93	0.134	0.925

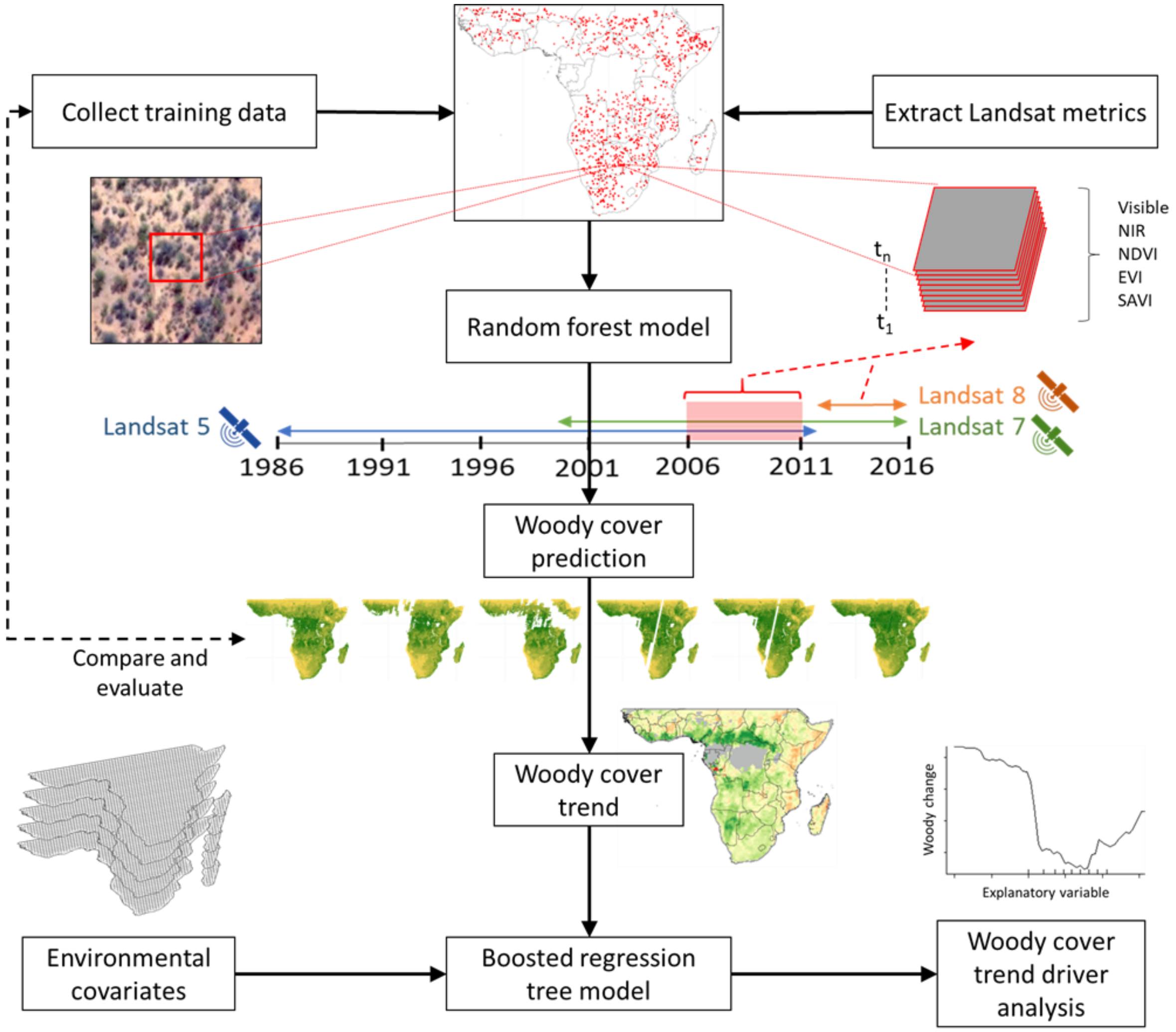


Figure S3.1 Data processing flow for woody cover prediction and environmental covariate analysis. Aerial photograph: Google, DigitalGlobe. Maps constructed in Google Earth Engine (Gorelick *et al.* 2017).

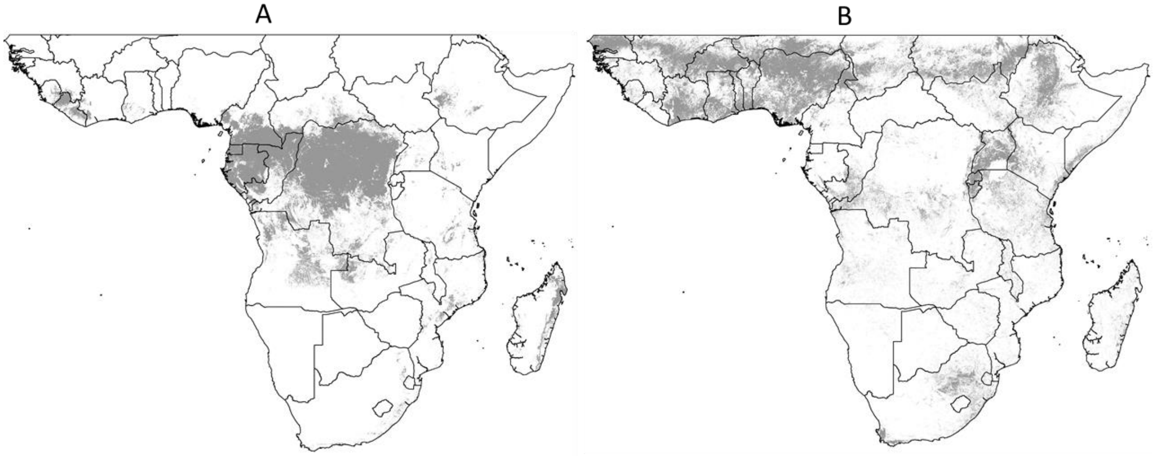


Figure S3.2 Data masks, represented in grey, include Landsat-derived forest and forestry cover (A), MODIS-derived urban, water, wetland, cropland, and natural-cropland mosaics (B). Maps constructed in Google Earth Engine (Gorelick *et al.* 2017).

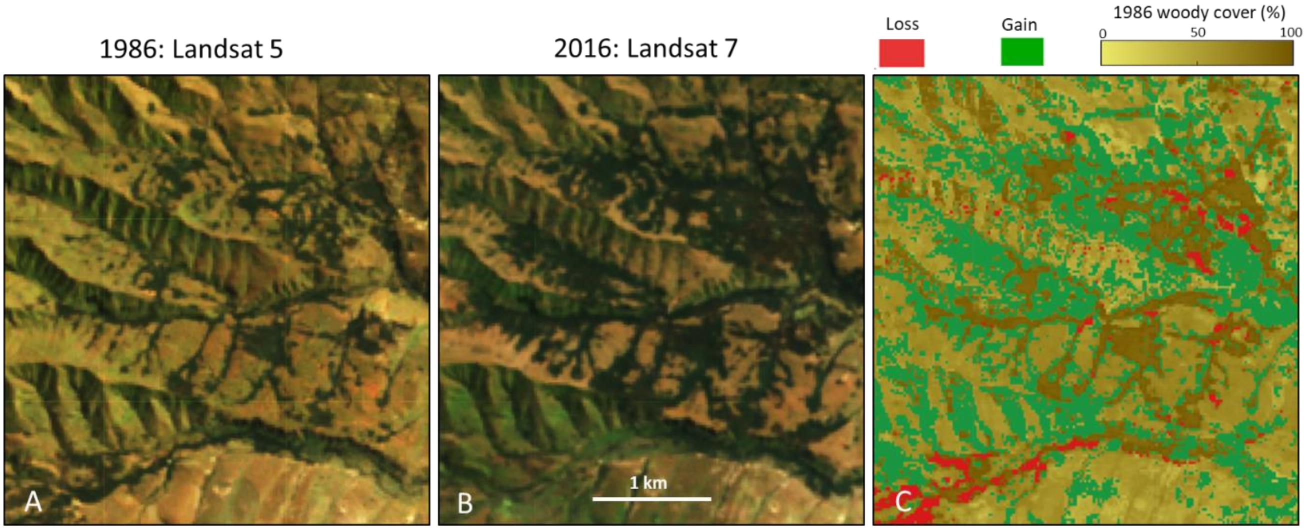


Figure S3.3 Landscape-scale example of fractional woody plant cover change. Landsat true-colour composites of Mariazell Mission in the Eastern Cape of South Africa are shown for comparison over time (A, B). Gain and loss represent areas with >50% change (C). This communal rangeland has been invaded by the exotic *Acacia mearnsii*, however, bush clearing efforts, initiated by the Working for Water Programme, and implemented through Conservation South Africa with the aim of rehabilitation of grazing capacity, are evident in red. Landsat-5 and -7 images courtesy of the U.S. Geological Survey.

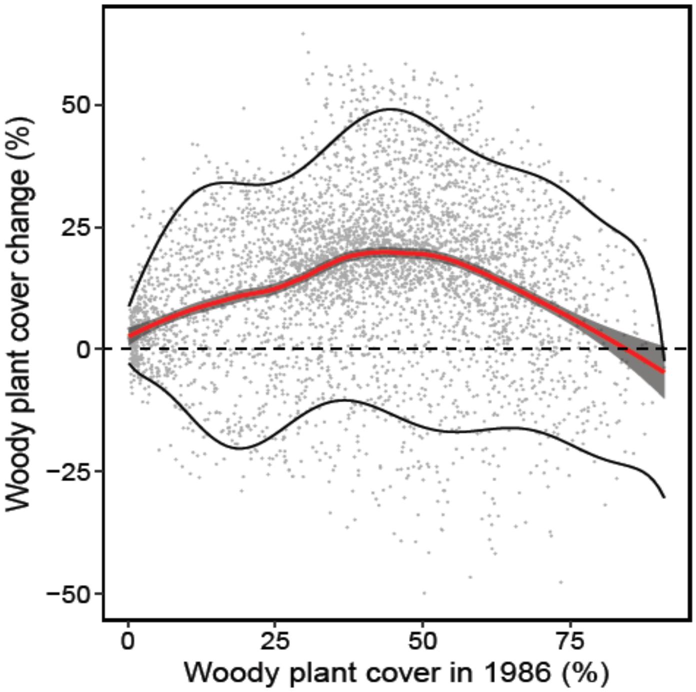


Figure S3.4 Woody plant cover change relative to the initial fractional cover in 1986 for each 0.5° grid cell over sub-Saharan Africa. A loess regression line (red), its 95% confidence intervals (grey ribbon), and the 5th and 95th quantile regression lines (black) are indicated.

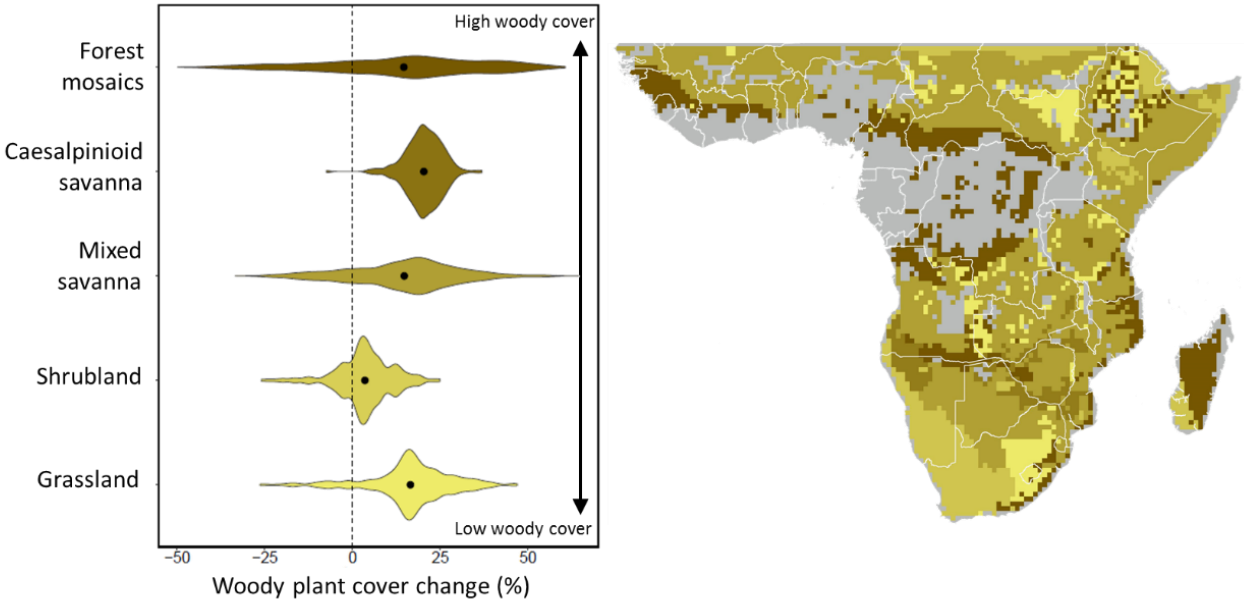


Figure S3.5 Violin plot distributions of woody cover trends for different vegetation types (left). Vegetation types, plotted spatially for reference (right), are based on those defined by White (1983), and are ordered and coloured categorically by increasing fractional woody cover. Grey areas were masked from the analysis and represent urban, wetland, cropland, and forest (areas >40% cover by trees >5 m). Maps constructed in Google Earth Engine (Gorelick *et al.* 2017).

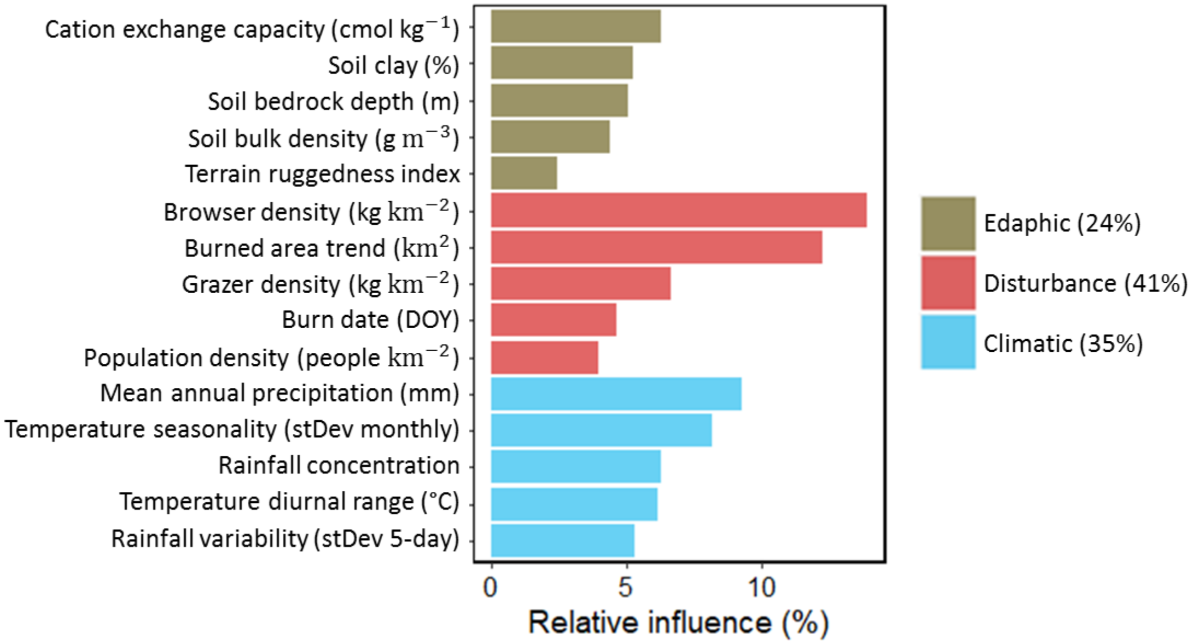


Figure S3.6 The percentage contribution of the five most important facilitator variables (edaphic, disturbance, and climatic temporal means) as predictors employed in the final boosted regression tree model explaining the spatial variation in woody plant cover change. Summed contributions are indicated in the colour key. The model was able to explain 75% of the total deviance in woody cover change.

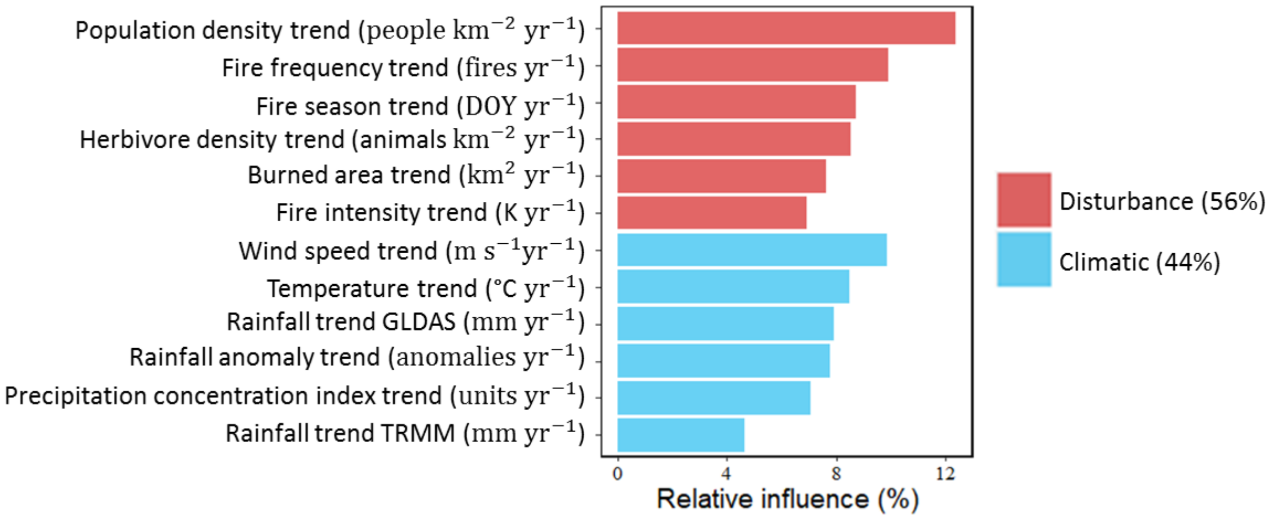


Figure S3.7 The percentage contribution of the most important driver variables (climatic and disturbance trends) as predictors employed in the final boosted regression tree model explaining the spatial variation in woody plant cover change. Summed contributions are indicated in the colour key. The model was able to explain 51% of the total deviance in woody cover change.

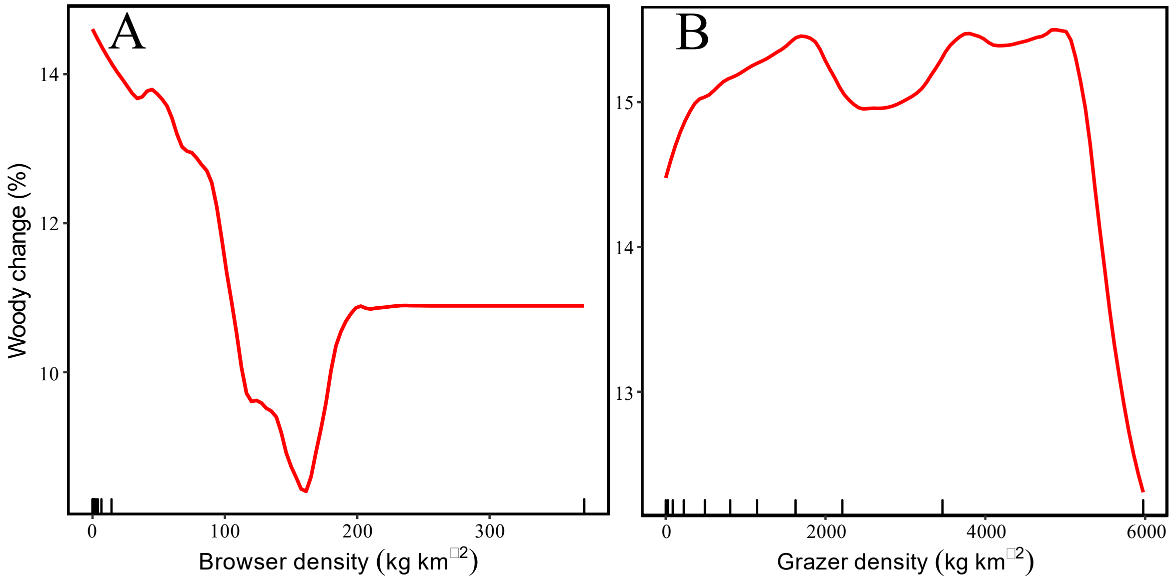


Figure S3.8 Boosted regression tree partial dependence of fractional woody cover change on browser (A) and grazer (B) densities when accounting for the average effect of all explanatory variables. These contributed 8.6 and 5.6% to the final model combining drivers and facilitator variables which explained 78% of the deviance in woody cover change. The red line is the smoothed representation of the response, with fitted values (model predictions based on the original data) for each 0.5° grid cell over sub-Saharan Africa. The trend of the line, rather than the actual values, describes the nature of the dependence between response and explanatory variables. Small bats on the x-axis represent data deciles.

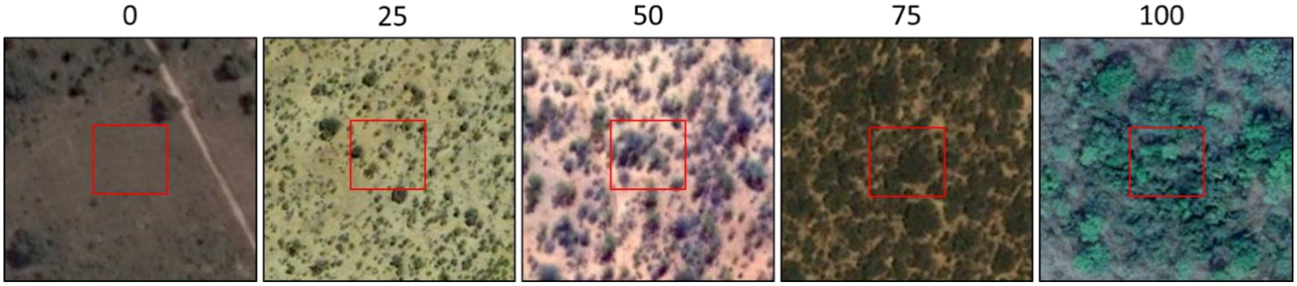


Figure S3.9 Google Earth image examples for each fractional woody plant cover (%) category with 30 x 30 m sampling quadrat overlaid in red. Aerial photographs: Google, DigitalGlobe.

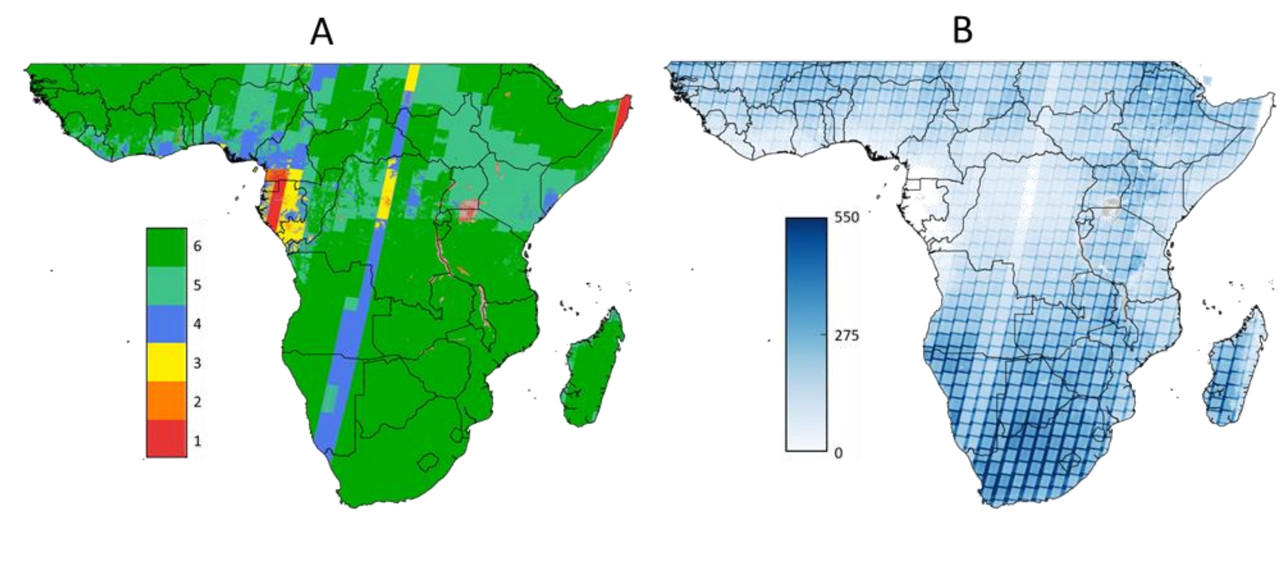


Figure S3.10 Quality layers for fractional woody cover change prediction. Number of epochal time-points available for linear regression (A). Total number of cloud-free Landsat pixels between 1986 and 2016 (B). Maps constructed in Google Earth Engine (Gorelick *et al.* 2017).

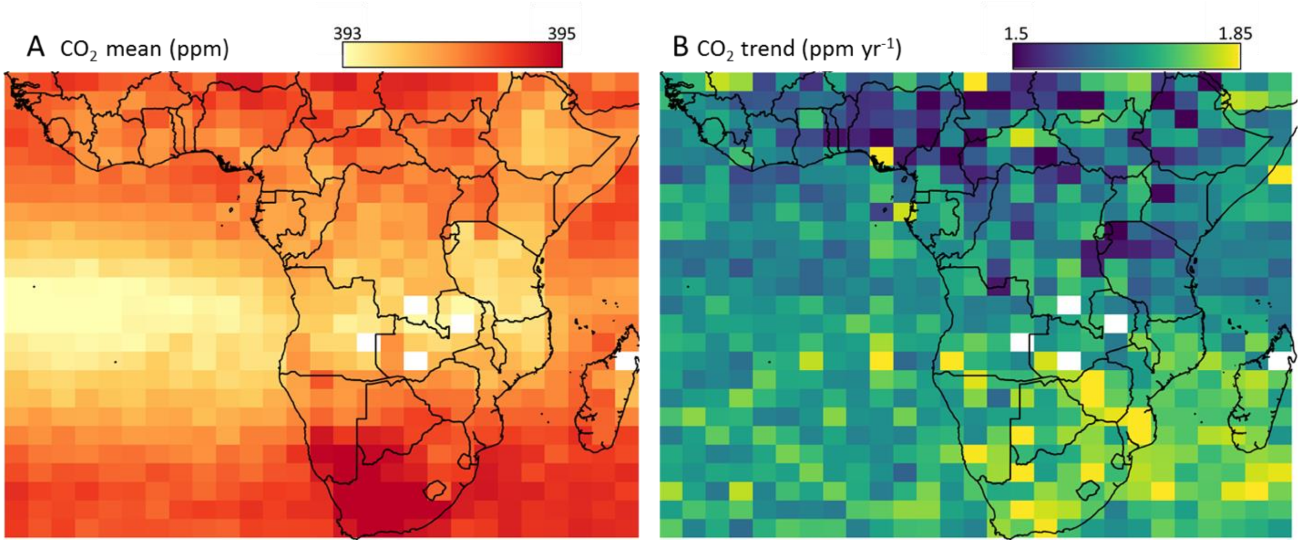


Figure S3.11 Mean (A) and trend (B) in mid-troposphere atmospheric CO_2 concentrations (parts per million) for the period 2009-2017. The ranges of the spatial variation in CO_2 means and trends were 2 ppm and 0.35 ppm yr^{-1}, respectively.

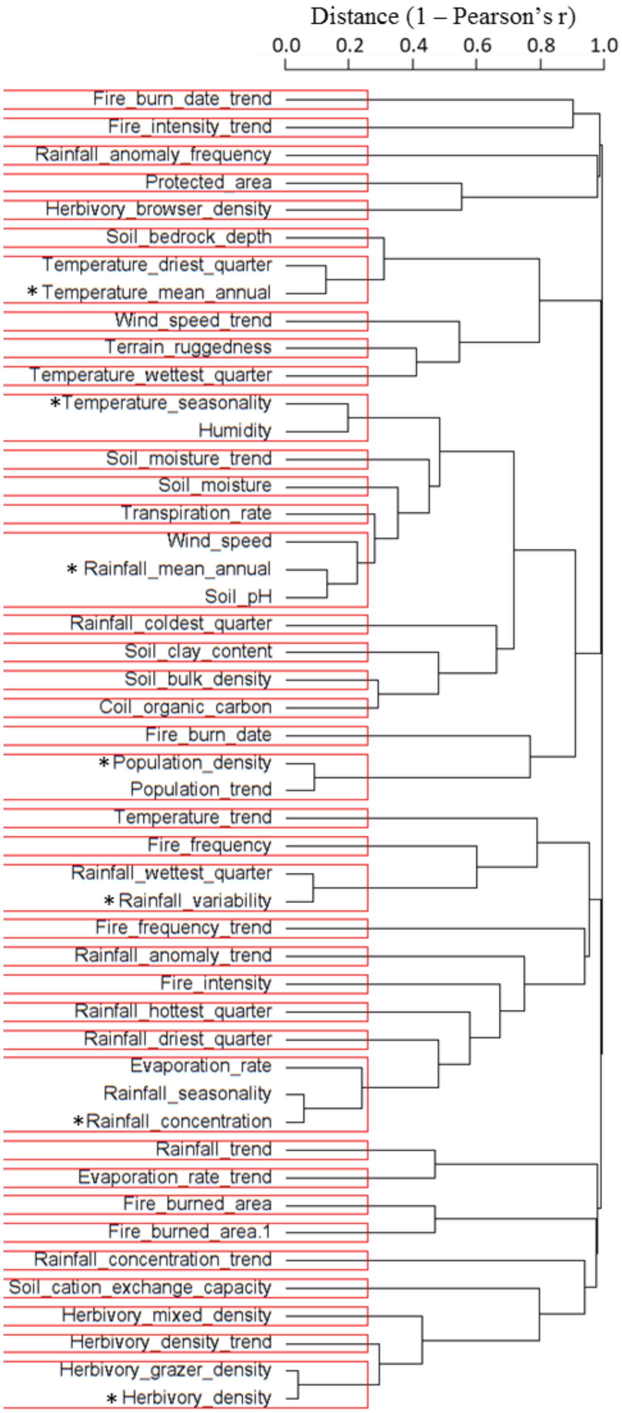


Figure S3.12 Collinearity plot of explanatory variables used in the boosted regression tree model. Groups of variables that are collinear (Pearson's r of > 0.7) are delineated in red. Within collinear groups, one variable (identified with an asterisk) was selected prior to model fitting.

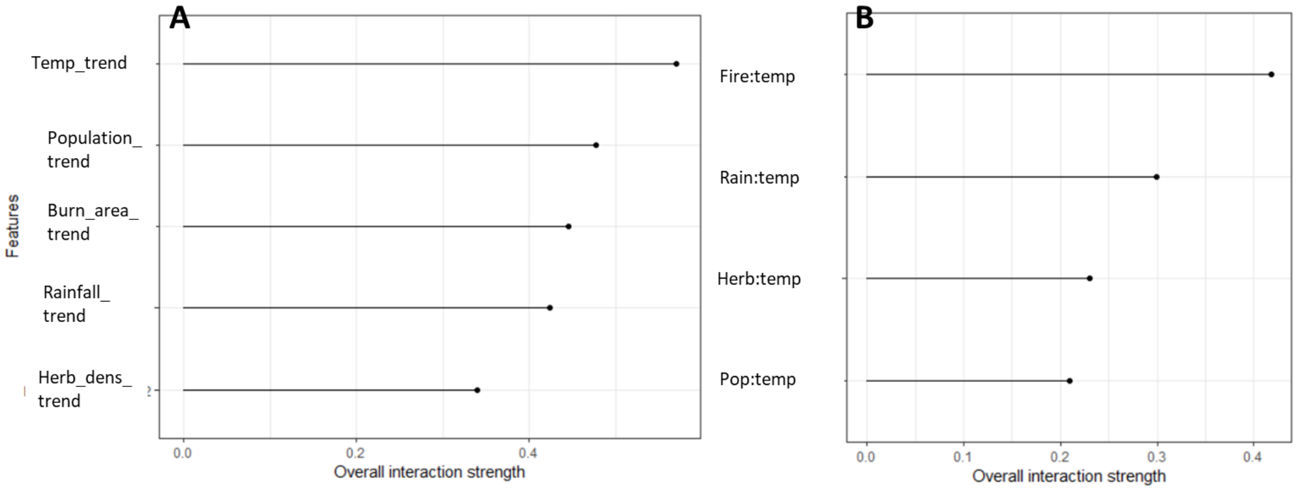


Figure S3.13. Strength of average interactive effects for trend explanatory variables in the boosted regression tree model explaining the trend in woody plant cover (A). The interaction strength is calculated using Friedman’s H-statistic (Friedman & Propescu 2005). The strength of two-way interactions between trends in burned area and other explanatory variables shows that herbivore-fire interactions rank lower than interactions between fire-rainfall and fire-temperature (B).

Appendix S4

Table S4.1 Baseline vegetation and soil characteristics measured before the initiation of the Merino Walk experimental grazing trial in December 2015. All sampling was performed at regularly spaced (90 m apart) sampling points over the farm. Standing biomass was measured using a disc pasture meter and calibrated using oven dried clippings of vegetation foliage. The normalised difference vegetation index (NDVI), NDVI heterogeneity, and percentage bare ground were measured using satellite imagery captured during 2015. Five soil cores were taken at each sampling location, bulked, air dried, sieved to 2 mm and sent to a lab for total soil nutrient analysis. Treatment means for season-long (SLG), four-camp (FCG) and holistic planned grazing (HPG) are presented ± standard error, along with the results from an ANOVA of a linear mixed models.

Attribute	SLG			FCG			HPG			χ^2	*df*	*p*
Standing biomass (kg ha^{-1})	605.2^{b}	±	17.97	1021.7^{a}	±	36.26	922.3^{a}	±	19.94	10.51	2	0.005*
NDVI	0.453	±	0.027	0.457	±	0.003	0.46	±	0.003	1.462	2	0.481
NDVI heterogeneity	0.012^{ab}	±	0.0003	0.015^{b}	±	0.0012	0.023^{a}	±	0.0018	6.224	2	0.045*
Bare ground (%)	0.05	±	0.0027	0.042	±	0.004	0.053	±	0.002	4.39	2	0.111
Soil N (%)	0.11	±	0.0035	0.137	±	0.0018	0.109	±	0.001	0.89	2	0.642
Soil P (%)	0.0375	±	0.0024	0.043	±	0.0004	0.042	±	0.0004	0.61	2	0.736
Soil K (%)	0.97^{b}	±	0.012	1.063^{ab}	±	0.005	1.094^{b}	±	0.007	6.17	2	0.046*

Significance is indicated at $p < 0.05$* and $p < 0.001$**. For direct treatment effects, significant differences are indicated with letters.

Table S4.2 Error matrix for the random forest model built with triaxial accelerometer data to classify cattle behaviour. The confusion matrix shows the number of reference epochs (5 s each) that were classified as grazing, resting or walking. Accuracy assessment includes the user's (positive predictive value), producer's (negative predictive value) and overall accuracies.

		Reference data			
		Resting	Grazing	Walking	**Total**
Classified	Resting	211	5	7	223
	Grazing	4	139	10	153
	Walking	4	8	61	73
	Total	219	152	78	
	User's Acc.	94.60%	90.80%	83.60%	
	Producer's Acc.	96.30%	91.50%	95.50%	
	Overall Acc.	91.50%			

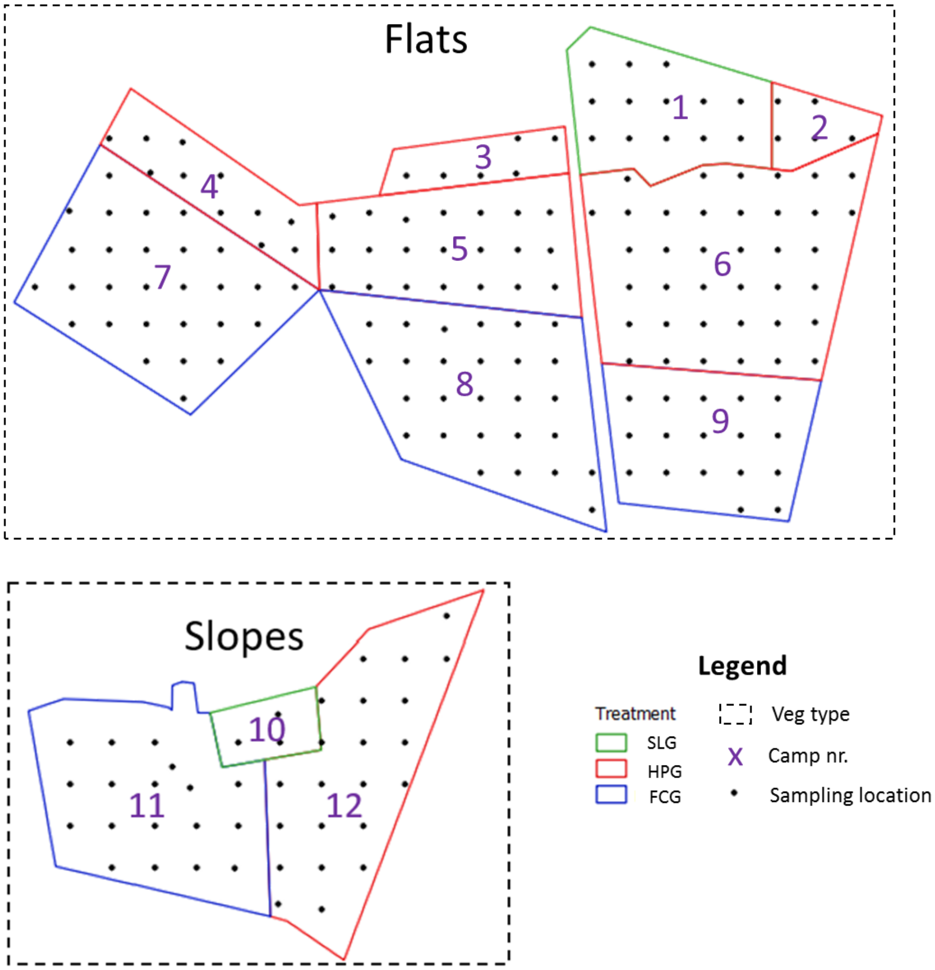


Figure S4.1 Merino Walk experimental trial layout for three grazing management treatments, season-long grazing (SLG), four-camp grazing (FCG), and holistic planned grazing (HPG). Dung and plant bite-mark sampling locations are indicated with black points. Camps, and when dealing with repeated measures, sampling point, were assigned to random effects in linear mixed-effects models.

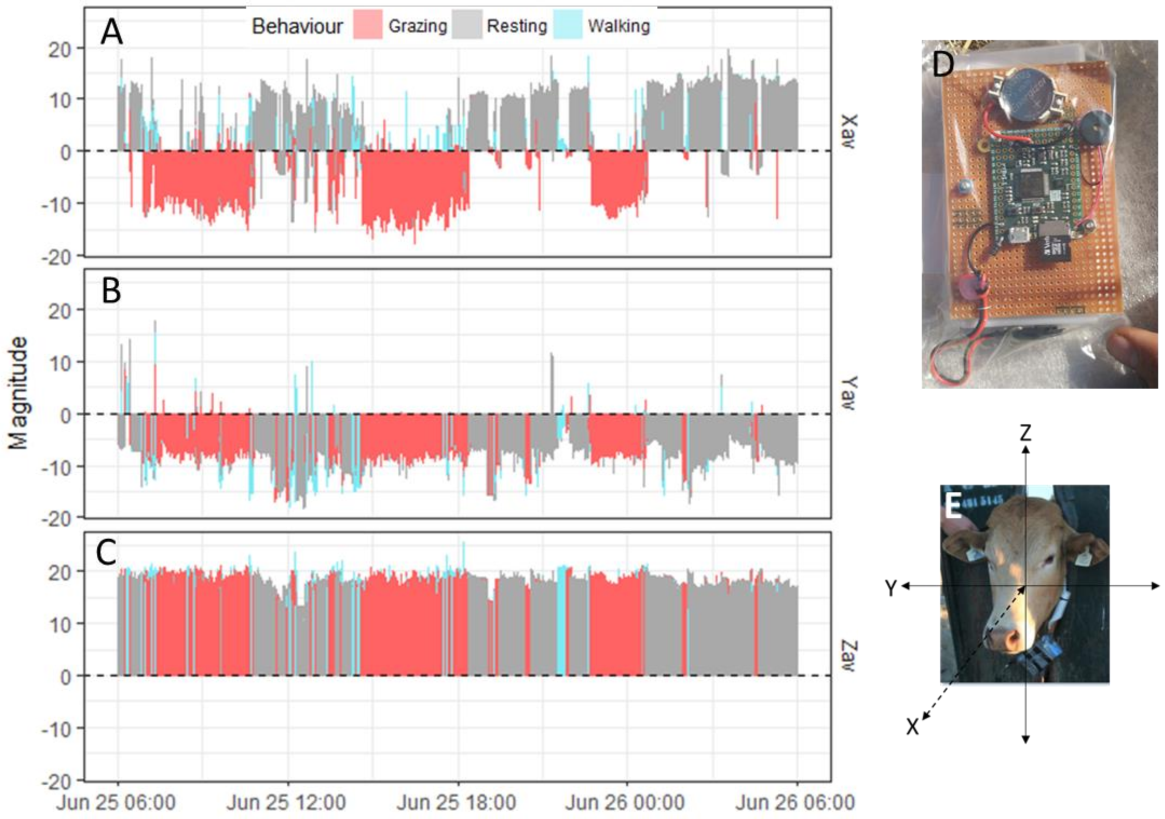


Figure S4.2 X-, Y- and Z-axis accelerometer readings (A, B and C) over the period of a randomly-selected 24-hr day for one steer. Triaxial accelerometers (larger box in D), fitted on steers along with GPS trackers (white box in D), measured movement in three directions. The movement magnitudes, averaged every 5 s, were used in combination with synchronous field observations to train a machine learning algorithm able to predict grazing, resting and walking behaviour. This figure reports the average values which at a glance do not appear to strongly differentiate behavioural states. That is why a set of 44 composite variables derived from raw X-, Y- and Z-axis readings were used in a Random Forest model which was able to predict behavioural state with an overall accuracy of 91.5%.

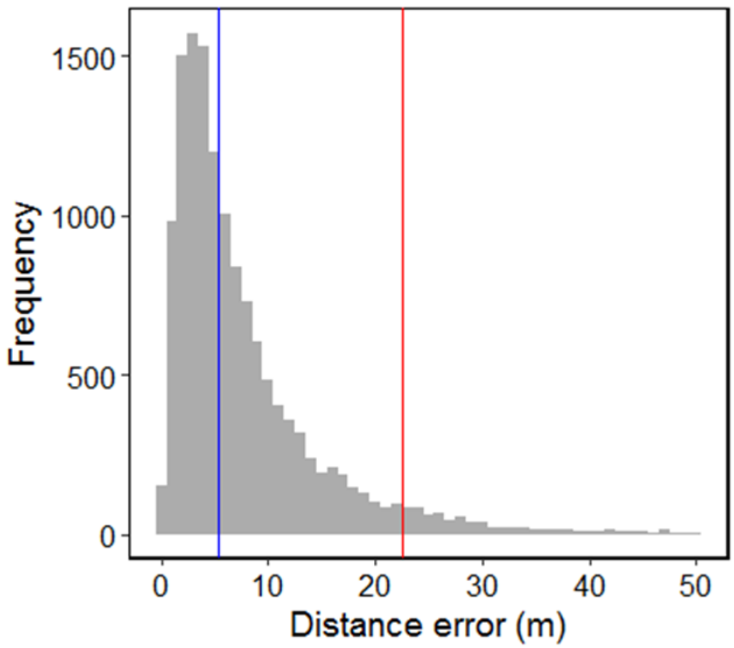
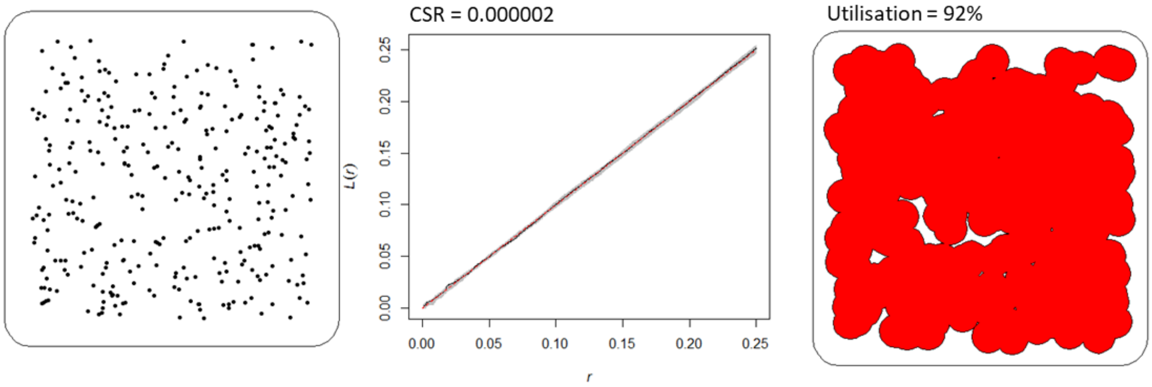


Figure S4.3 Frequency histogram of GPS point error from three devices tested over three weeks. Blue and red vertical lines represent the 50th and 95th percentiles, respectively.

(A) Random distribution



(B) Clustered distribution

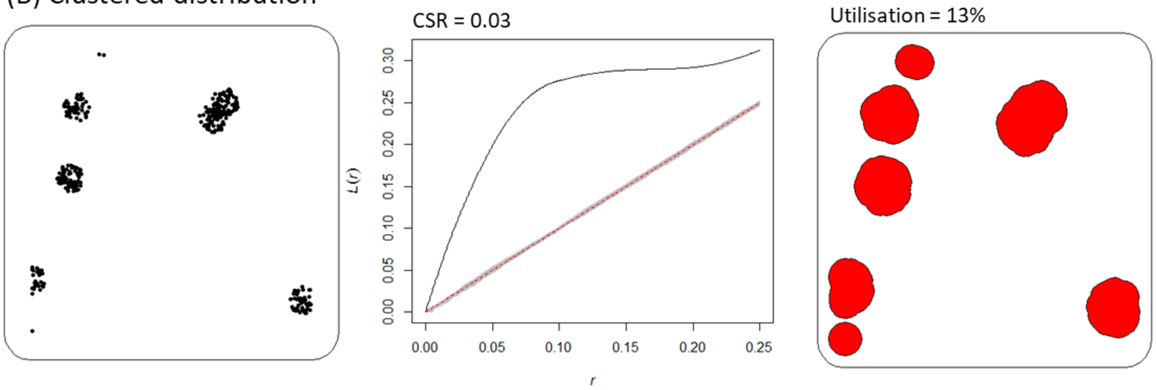


Figure S4.4 Theoretical GPS point distributions (left panel) for cattle in a square camp. A completely random distribution (a) indicates grazing homogeneity while a clustered distribution (b) indicates grazing selectivity. The measure of complete spatial randomness (CSR – centre panel) is derived from a transformed Ripley's K function (L(r)). The dotted red line represents the relationship between L(r) over spatial distances (r) for a completely random stationary Poisson process. The grey ribbons are 95% confidence bands. The black line is the observed L(r) and the CSR is calculated as the area between this line and the upper confidence interval on the Poisson process line. The spatial utilisation (right panel) is calculated by buffering each point by a hypothetical cattle utilisation footprint (highlighted in red). More clustering of cattle GPS locations will produce a lower spatial forage utilisation relative to randomly distributed GPS locations.

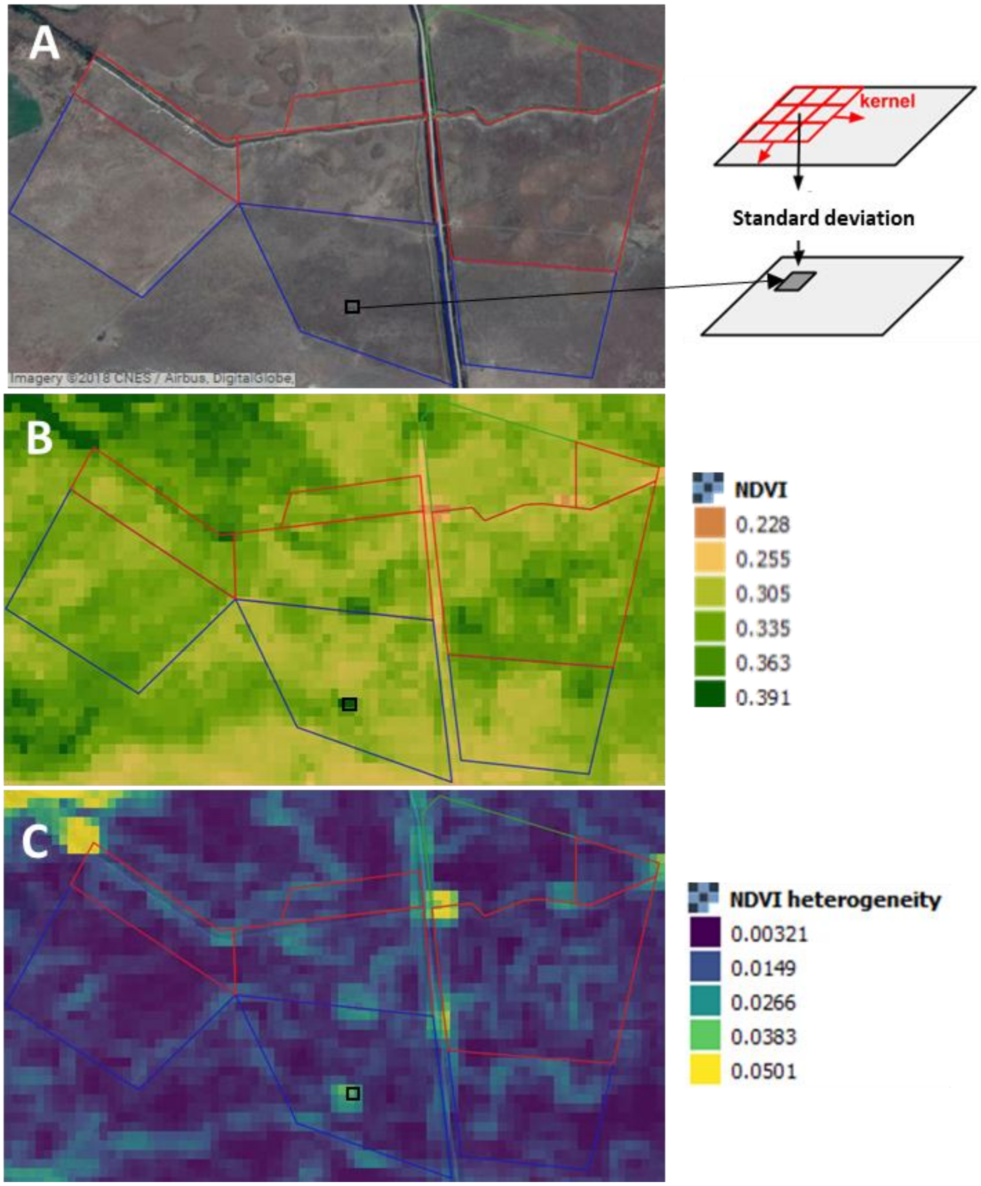


Figure S4.5 The process of calculating vegetation spatial heterogeneity. A Google Earth satellite image (A) of the farm camps gives little information about how heterogeneous vegetation is over space. For each pixel, I calculated the normalised difference vegetation index (NDVI, B), a good proxy for forage biomass and quality, I quantified heterogeneity (C) by assigning each pixel with the standard deviation in its eight neighbouring pixels.

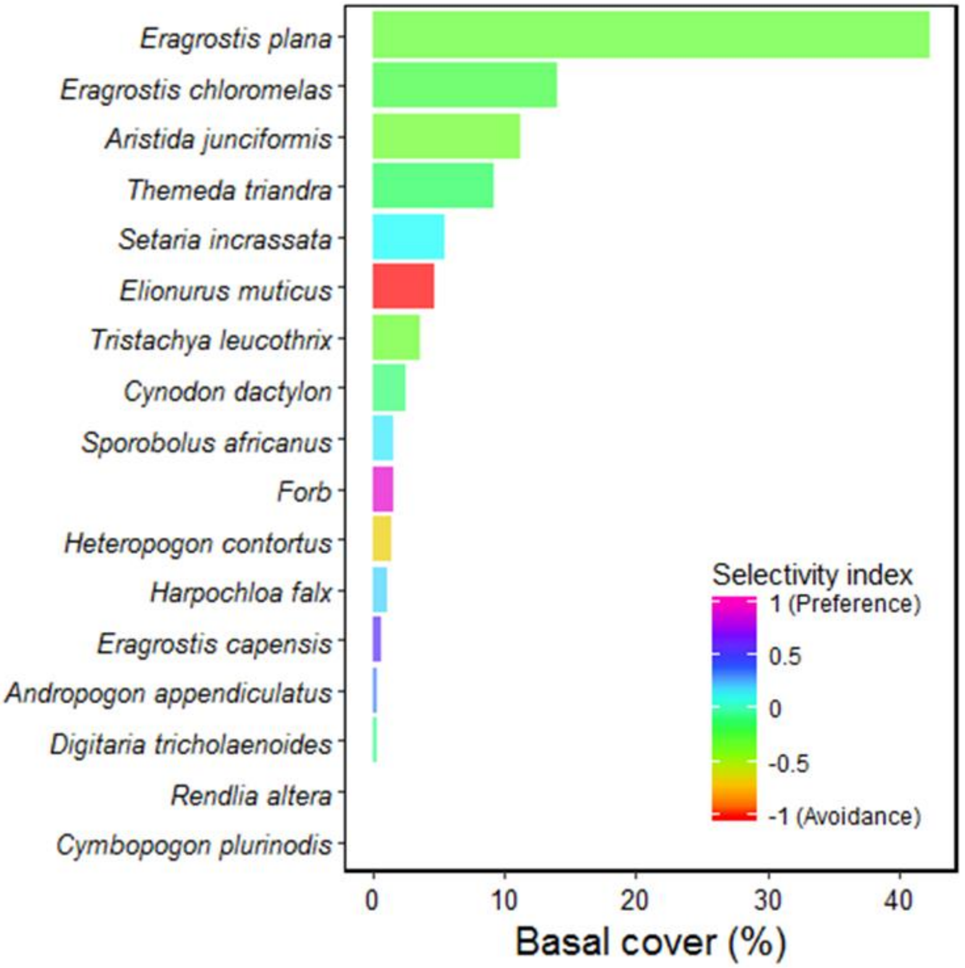


Figure S4.6 Relative abundance of forage taxa recorded over the study period with a Levy bridge point-intercept method. Taxa are ranked in order of abundance and are coloured based on their selectivity index. The selectivity index scores are an average of those calculated from bite mark and faecal DNA sampling. The score ranges from -1 to 1 indicating species that were positively and negatively selected for.

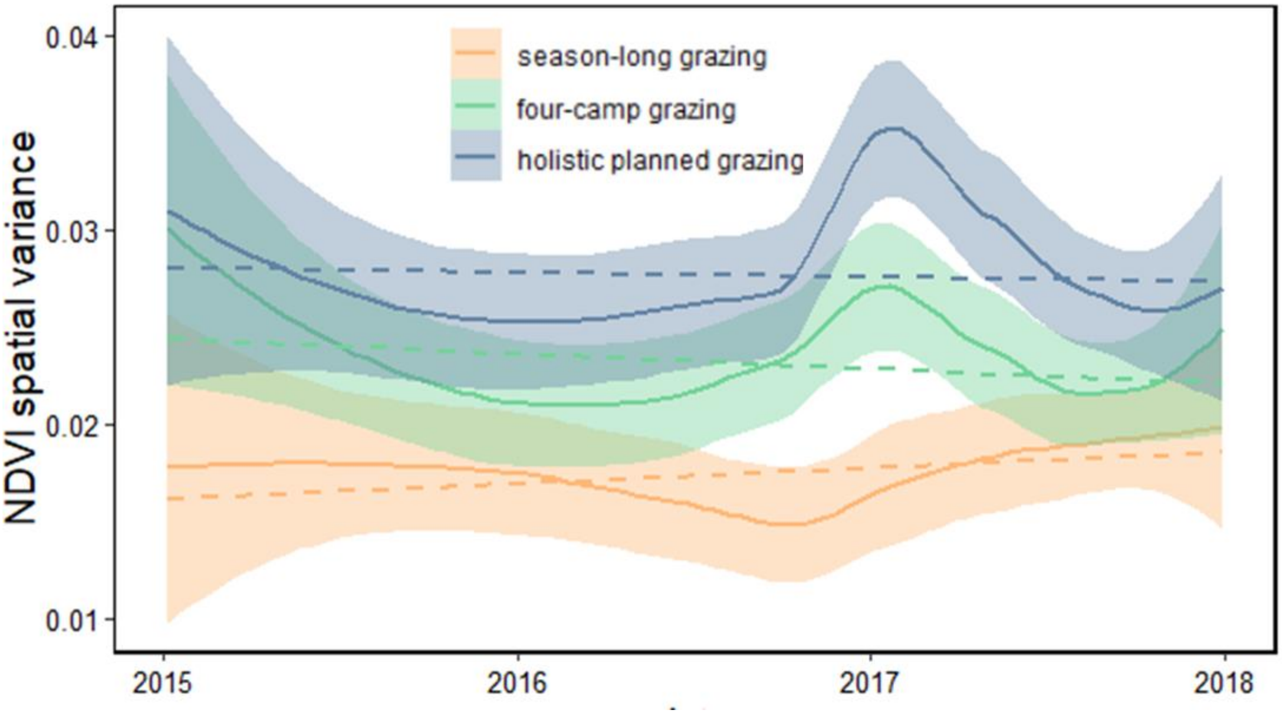


Figure S4.7 Trend in NDVI variance (standard deviation in NDVI pixels per grazing camp) over the Merino Walk experimental farm management treatments between 2015 and 218. Loess regression lines and 95% confidence interval ribbons are plotted (solid lines and ribbons) along with linear regression lines (dashed lines). The variance (measure of heterogeneity) reported here differs to that in Fig. 4.3 in that this is calculated at the camp scale (ca. 20 ha in area) and not for the pixel neighbourhood scale (ca. 1 ha in area).

Appendix S5

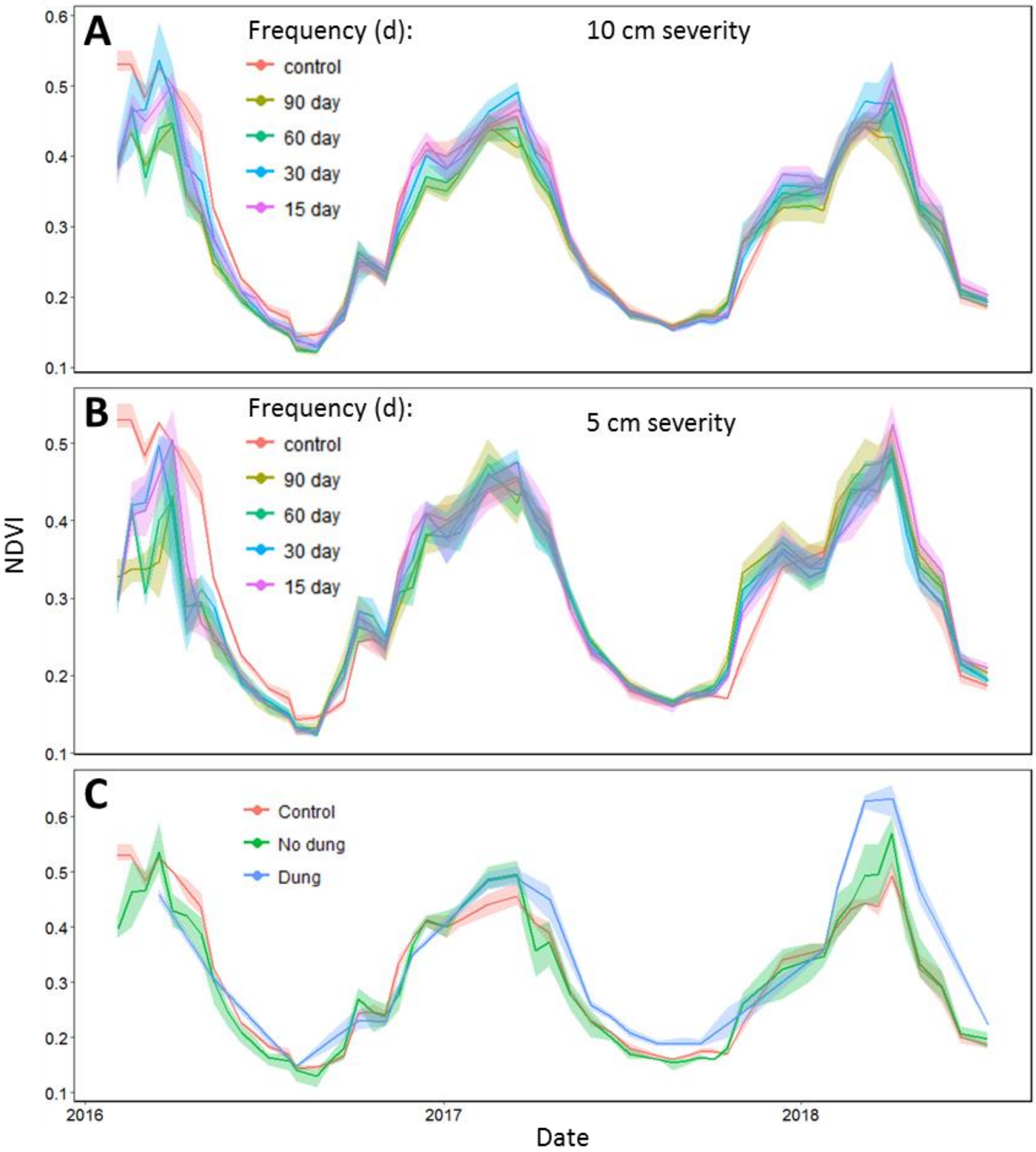


Figure S5.1 Vegetation greenness, as measured by the normalised difference vegetation index (NDVI), recorded every two weeks for the experimental plots located on the Merino Walk (Goedehoop section) experimental farm. Responses to two levels of clipping severity and four levels of frequency (A and B), and dung application with 60 d defoliation at 10 cm severity (C) are compared to an unclipped control (red). Plot lines and colour ribbons represent treatment means (n = 3) and 95% confidence intervals, respectively. NDVI peaks during the growing season between Nov and Apr.

Appendix S6

Table S6.1 Questions directed at identifying a respondent's alignment with holistic planned grazing. Respondents were able to choose one answer per question and scores were assigned post-response. The holistic planned grazing alignment score was calculated as a percentage of the total possible score of 7.

Question	**Potential answer with scoring**				**Potential score**
Do you consider your farm to be under Holistic Management or Holistic Planned Grazing as coined by Allan Savory?	Yes (1)	No (0)	Partly (0.5)	Unsure (0.5)	1
Have you had formal Holistic Planned Grazing training?	Yes (1)	No (0)	Partly (0.5)		1
Have you set a Holistic goal for your farm?	Yes (1)	No (0)	Partly (0.5)		1
Do you plan grazing using a Holistic Panned Grazing chart?	Yes (1)	No (0)	Partly (0.5)		1
Do you draw up a grazing chart/plan for the growing season and non-growing season separately?	Yes (1)	No (0)			1
Do you leave any camps to rest for an entire growing season?	Yes (1)	No (0)			1
Do you perform daily monitoring of grass off-take and re-growth and adjust your grazing plan accordingly?	Yes, daily (1)	Yes, at least weekly (0.5)	No (0)		1
			Total potential score		**7**

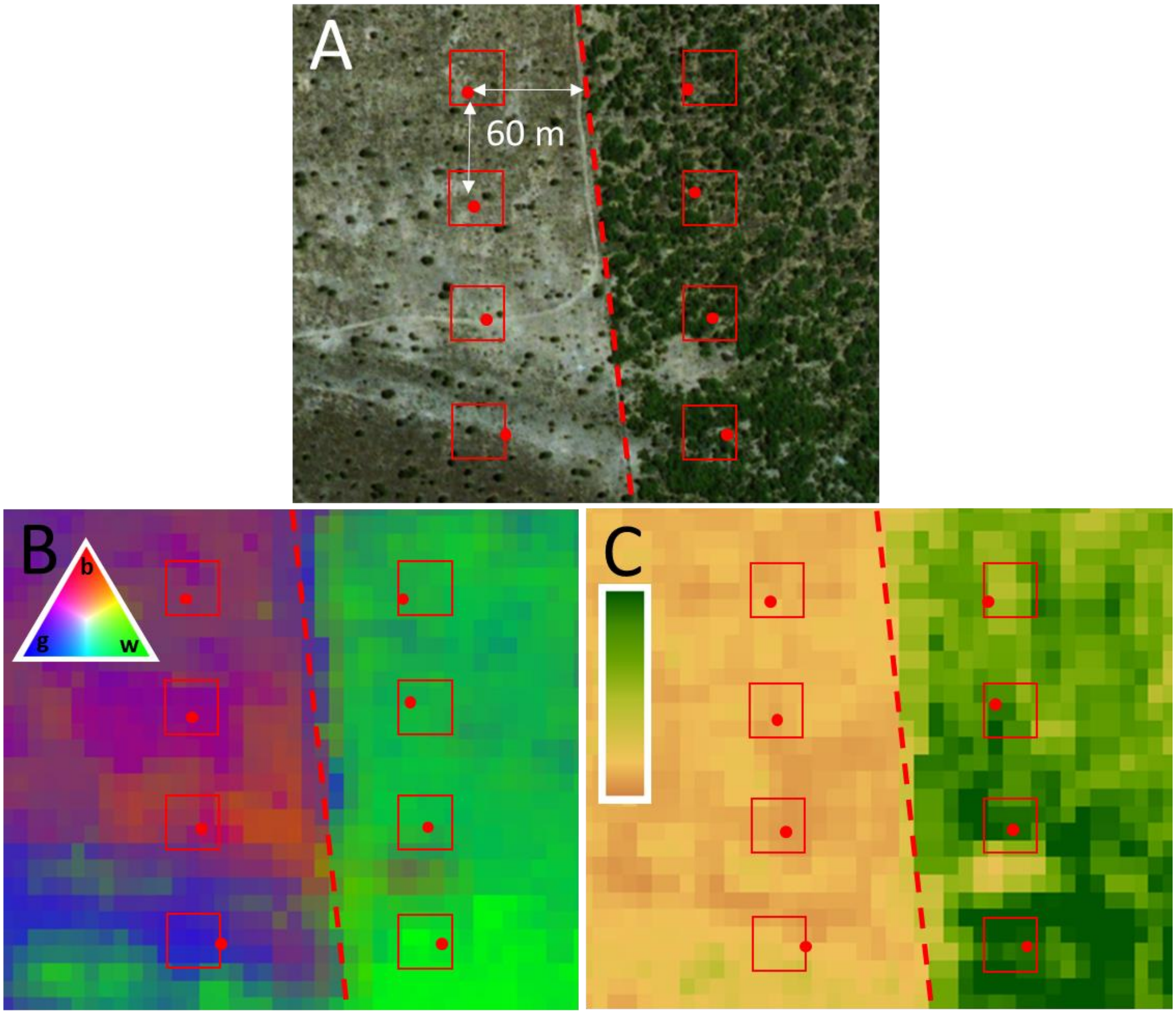
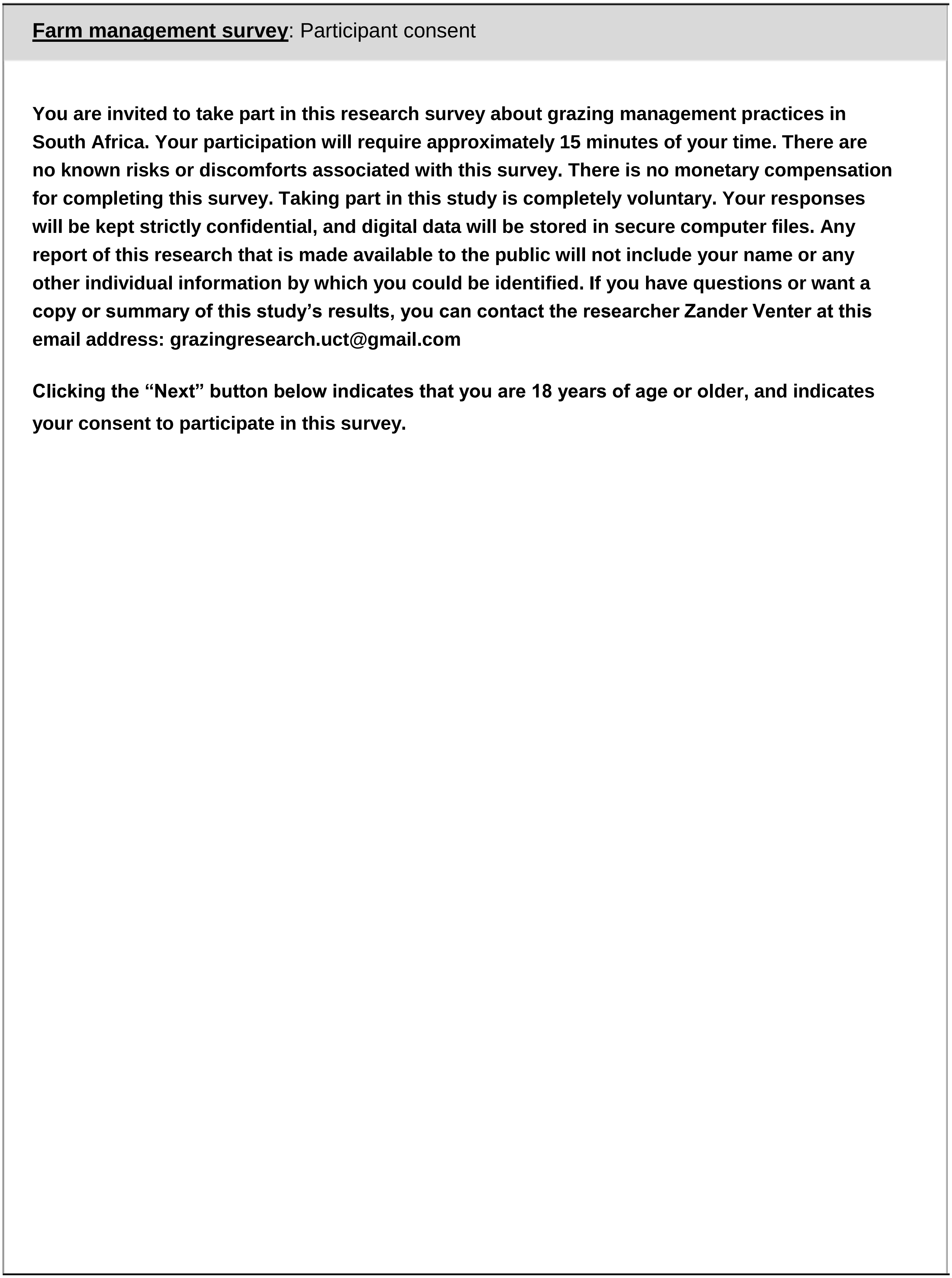


Figure S6.1 An example of a fence-line (dashed line) contrast with sampling points and 30 x 30 m quadrats (red points and boxes) at which remotely-sensed vegetation response variables were derived. A very high-resolution aerial photograph (A) shows contrasting woody vegetation cover across the fence-line. Spectral unmixing combined with machine learning techniques were used to derive pixel (10 x 10 m) fractions of bare ground (b), grass (g), and woody (w) cover (B). Sentinel-2 normalised difference vegetation index, a commonly used measure of vegetation greenness, was also derived (C).



Farm management survey: Participant consent

You are invited to take part in this research survey about grazing management practices in South Africa. Your participation will require approximately 15 minutes of your time. There are no known risks or discomforts associated with this survey. There is no monetary compensation for completing this survey. Taking part in this study is completely voluntary. Your responses will be kept strictly confidential, and digital data will be stored in secure computer files. Any report of this research that is made available to the public will not include your name or any other individual information by which you could be identified. If you have questions or want a copy or summary of this study's results, you can contact the researcher Zander Venter at this email address: grazingresearch.uct@gmail.com

Clicking the "Next" button below indicates that you are 18 years of age or older, and indicates your consent to participate in this survey.

Should you complete this survey?

This survey is focussed on cattle, sheep and/or goat farming on veld (natural vegetation). This excludes dairy, pig and chicken production where animal diet is based on external feed and/or pasture. Please answer these two questions to see if you qualify for the survey.

* 1. What livestock do you farm commercially?

☐ Cattle

☐ Sheep

☐ Goats

☐ None of the above

Other (please specify)

* 2. What is the main source of food for your livestock? i.e. which of the following constitute >75% of your livestock's diet?

○ Veld (natural vegetation)

○ Pasture

○ Feed

Other (please specify)

General Farm Information

3. What is your full name?

4. If you would like to be informed of the results from this study, please give us your preferred**contact number** and **email address**.

* 5. Please enter the **name and number** of the parent farm(s) you own as registered by the municipality:

* 6. Please name the municipal district in which your farm is located:

7. Please enter your farm address or describe the location of your farm so that we can find it from Google Earth:

8. If you are aware of them, please give your farm GPS coordinates.

9. Do you have neighbouring land with very different vegetation to yours so that it produces a fence-line contrast?

○ Yes

○ No

Other (please specify)

10. Which of the following environmental variables do you keep detailed records for on your farm?

○ Rainfall

○ Temperature

○ None of the above

Other (please specify)

11. Please indicate your **Mean Annual Precipitation** in millimetres of rainfall per year (mm/year):

Farm management: Grazing

12. What livestock breed(s) do you use for your commercial stock? Leave boxes blank if you do not farm these animals.

Cattle	
Sheep	
Goats	
Other (please specify)	

13. What are your approximate total stock numbers for your livestock? (you only need to fill in the appropriate boxes)

Cattle	
Sheep	
Goats	
Other (please specify)	

14. Do you use urea or other protein licks as a feed supplement?

○ Yes

○ No

Other (please specify)

15. What is the size of your land that is used for grazing (hectares)?

16. How long have you been in operation for?

○ 0-5 years

○ 6-10 years

○ 10-15 years

○ 15-20 years

○ >20 years

17. On a scale of 1 (no alignment) to 5 (strong alignment) please rate how your management system compares with the following grazing systems. The closer your management practices match a grazing system below, the higher you would score it. If you do not know of the grazing system please select N/A.

	1. No alignment	2. Weak alignment	3. Moderate alignment	4. Strong alignment	5. Very strong alignment	**N/A**
Continuous grazing						○
Low density grazing	○	○	○	○	○	○
Four-camp rotation						○
Holistic Planned Grazing	○	○	○	○	○	○
High density grazing						○
Ultra high density strip grazing	○	○	○	○	○	○
Time-controlled rotational grazing						○
Short duration grazing	○	○	○	○	○	○

18. If you do not align with any of the grazing systems listed in the question above, please describe your own grazing management system below.

19. For the past 10 years please select the grazing system(s) you used during each year. You may select multiple grazing systems per year, however please try and select the one that best describes your grazing management at that point in time. You may choose "Other" which refers to the system you may have described in the previous question.

	Continuous grazing	Low density grazing	Four-camp rotation	Holistic Planned Grazing	High density grazing	Ultra high density strip grazing	Time-controlled rotational grazing	Short duration grazing	Other
2016	☐	☐	☐	☐	☐	☐	☐	☐	☐
2015	☐	☐	☐	☐	☐	☐	☐	☐	☐
2014	☐	☐	☐	☐	☐	☐	☐	☐	☐
2013	☐	☐	☐	☐	☐	☐	☐	☐	☐
2012	☐	☐	☐	☐	☐	☐	☐	☐	☐
2011	☐	☐	☐	☐	☐	☐	☐	☐	☐
2010	☐	☐	☐	☐	☐	☐	☐	☐	☐
2009	☐	☐	☐	☐	☐	☐	☐	☐	☐
2008	☐	☐	☐	☐	☐	☐	☐	☐	☐
2007	☐	☐	☐	☐	☐	☐	☐	☐	☐
2006	☐	☐	☐	☐	☐	☐	☐	☐	☐

20. Do you graze different stock (e.g. sheep and cattle) together in the same herd?

○ Yes

○ No

Other (please specify)

21. How many herds/flocks do you run during the summer (excluding bulls and calving/lambing herds)?

22. How many camps/divisions/cells do you have for animals to graze?

23. What is the average size of your camps (hectares)?

24. How often (on average) do you move your stock between camps?

- ☐ Once a day
- ☐ Once a week
- ☐ Twice a week
- ☐ Once a month
- ☐ Twice a month
- ☐ Once every two months
- ☐ Once every 3 months
- ☐ Once a season
- ☐ Never

Other (please specify)

☐

25. For the past 10 years please select the average **grazing densities** (*LSU/ha*) you used per grazing camp/strip/cell. Where *grazing density* is the number of stock in a herd divided by the average camp/strip/cell size in hectares. *LSU* is defined as a 450 kg animal.

For the conversion for sheep (*SSU* to *LSU*) please see the link:
http://gadi.agric.za/software/renting/lsu_calc.php

*Note: This is different to *stocking rate* (see next question).

	<0.5 LSU.ha-1	0.5 - 1 LSU.ha-1	1 - 5 LSU.ha-1	5 - 25 LSU.ha-1	25 - 75 LSU.ha-1	75 - 150 LSU.ha-1	150 - 300 LSU.ha-1	>300 LSU.ha-1
2016	☐	☐	☐	☐	☐	☐	☐	☐
2015	☐	☐	☐	☐	☐	☐	☐	☐
2014	☐	☐	☐	☐	☐	☐	☐	☐
2013	☐	☐	☐	☐	☐	☐	☐	☐
2012	☐	☐	☐	☐	☐	☐	☐	☐
2011	☐	☐	☐	☐	☐	☐	☐	☐
2010	☐	☐	☐	☐	☐	☐	☐	☐
2009	☐	☐	☐	☐	☐	☐	☐	☐
2008	☐	☐	☐	☐	☐	☐	☐	☐
2007	☐	☐	☐	☐	☐	☐	☐	☐
2006	☐	☐	☐	☐	☐	☐	☐	☐

26. What has your **stocking rate** (LSU/ha) been for the past 10 years? Where *stocking rate* is the total number of stock divided by the total size of your farm grazing area in hectares.

	0 - 0.1 LSU.ha-1	0.1 - 0.2 LSU.ha-1	0.2 - 0.3 LSU.ha-1	0.3 - 0.4 LSU.ha-1	0.4 - 0.5 LSU.ha-1	0.5 - 0.6 LSU.ha-1	>0.6 LSU.ha-1
2016	○	○	○	○	○	○	○
2015	○	○	○	○	○	○	○
2014	○	○	○	○	○	○	○
2013	○	○	○	○	○	○	○
2012	○	○	○	○	○	○	○
2011	○	○	○	○	○	○	○
2010	○	○	○	○	○	○	○
2009	○	○	○	○	○	○	○
2008	○	○	○	○	○	○	○
2007	○	○	○	○	○	○	○
2006	○	○	○	○	○	○	○

* 27. Please follow this link to a website where you can find your farm on Google Maps and **outline your grazing areas**. Please outline the pieces of **natural veld** that are grazed according to the management practices you have listed above.

This is so that we can **exclude croplands/pasture/unused veld** from our satellite imagery

analysis. After following this link, please indicate whether you were able to complete this task?

Click here: *not compatible with Safari - please use **internet Explorer, Google Chrome or Mozilla Firefox**
http://unibase.web.za/Map.html

○ Yes

○ No

○ Other (please specify)

☐

Farm management: Fire

28. Do you use fire as a management tool (apart from burning fire breaks)?

○ Yes

○ No

Other (please specify)

29. If you use fire, why do you use it?

☐ For fire breaks

☐ Remove moribund vegetation

☐ Control bush encroachment

☐ Wildlife management

☐ Control tick loads

☐ **N/A**

Other (please specify)

30. How often do you use fire (apart from fire breaks)?

○ Once a year

○ Once every 2 years

○ Once every 3 years

○ Once every 4 years

○ Once every 5 years

○ Less often than every 5 years

○ **N/A**

Other (please specify)

31. When you do use fire, what percentage of your land do you burn (excluding fire breaks)?

○ <10%
○ 10 - 25%
○ 25 - 50%
○ 50 - 75%
○ >75%
○ **N/A**

32. What percentage of your fires are unintentional? i.e. What percentage are caused by other people or natural phenomena?

○ <10%
○ 10 - 25%
○ 25 - 50%
○ 50 - 75%
○ >75%

Farm management: Bush encroachment

33. What change in woody vegetation (bush encroachment) have you noticed over the past 10 years?

○ No change

○ Increase

○ Decrease

○ Other (please specify)

34. If you answered increase or decrease above, how much has the bush cover has increased/decreased?

○ <25%

○ 25-50%

○ 50-75%

○ >75%

○ No change

35. How much area (hectares) of bush do you remove/clear each year?

36. Which are the main plant species involved? If you can, please give the common names below.

37. What do you think the most important cause of bush encroachment is on your farm?

○ Fire

○ Grazing

○ Temperature

○ Rainfall

○ Atmospheric carbon dioxide

○ **N/A**

Other (please specify)

☐

Alignment with Holistic Planned Grazing

38. Do you consider your farm to be under Holistic Management or Holistic Planned Grazing as coined by Allan Savory?

○ Yes

○ No

○ Partly

○ Unsure

39. Have you had formal Holistic Planned Grazing training?

○ Yes

○ No

○ Partly

Other (please specify)

40. Have you set a Holistic goal for your farm?

○ Yes

○ No

○ Partly

41. Do you plan grazing using a Holistic Panned Grazing chart?

○ Yes

○ No

○ Partly

42. Do you draw up a grazing chart/plan for the growing season and non-growing season separately?

○ Yes

○ No

Other (please specify)

43. Do you leave any camps to rest for an entire growing season?

☐ No

☐ Yes, to have a drought reserve

☐ Yes, to allow grasses to regain their vigour and set seed

Other (please specify)

☐

44. How often do you leave a camp to rest for an entire growing season?

☐ Never

☐ In good years only

☐ Every year

☐ Every second year

☐ Every third year

☐ Every fourth year or less often

Other (please specify)

☐

45. Do you perform daily monitoring of grass off-take and re-growth and adjust your grazing plan accordingly?

○ No

○ Yes, at least weekly

○ Yes, daily

Other (please specify)

☐

Disqualification page

Thank you for your time, but unfortunately this survey is focused on cattle, sheep or goat farming on veld (natural vegetation). This excludes dairy, pig and chicken production where the majority of diet is sourced from external feed and/or pasture. Please forward this survey to any farmers you may know who would meet the above criteria.

FINISHED

Thank you very much for your time and effort. Your questions are valuable to us and will contribute to knowledge gaps within the livestock industry in South Africa. We will keep you up to date with the results of this study.

Finally, if you know of other farmers who could complete this survey, please send them the original email with the survey link, thanks!

Please click the DONE button below to submit your survey response.

Media Gallery

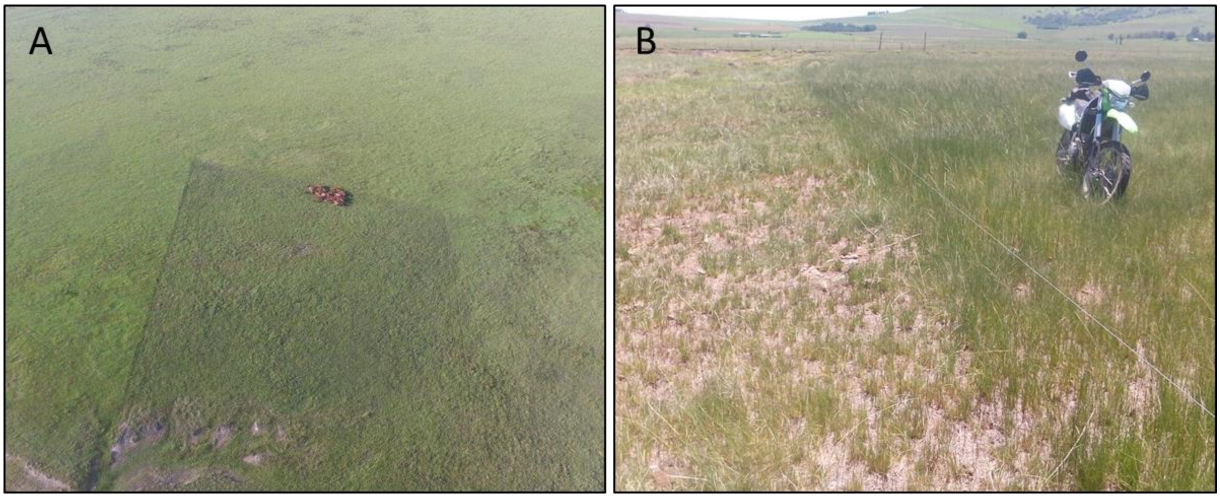


Plate 1. Forms of high density grazing often involve the use of portable electric fencing to rotate livestock grazing pressure over the farm. On the Merino Walk experimental trial, holistic planned grazing was implemented using this technique. An aerial view (A), taken from a drone, shows a grazing strip after 24 hr of grazing pressure. A large proportion of the herd are outside of the field of view. At ground level (B) the effects of high density grazing on the vegetation are clearly visible. The cattle were to be moved into the grass on which the motorbike was standing. Photographs courtesy of Gerbrand Nel.

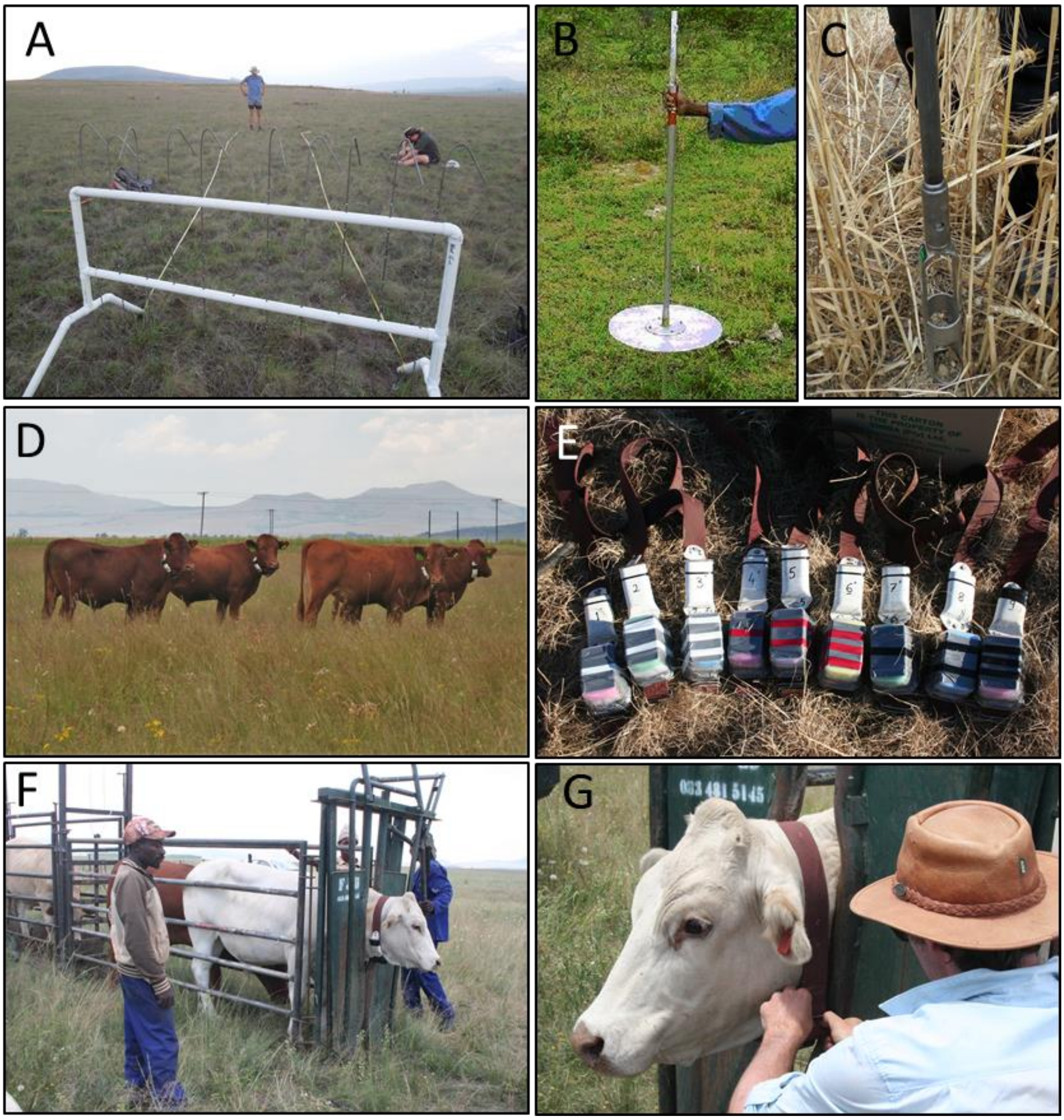


Plate 2. Photographs taken at the Merino Walk experimental grazing trial. Before the grazing trial commenced, baseline vegetation and soil sampling was performed using a levy bridge (A), disc pasture meter (B) and soil auger (C). Dung pats were counted in a 10 x 2 m belt transect (A). To monitor cattle behaviour, they were collared (D) with GPS tracking devices and triaxial accelerometers (E). Collars were deployed using a cattle race (F) and head clamp (G) commonly used on the farm to medicate or inspect livestock. Photographs courtesy of Samantha Venter.

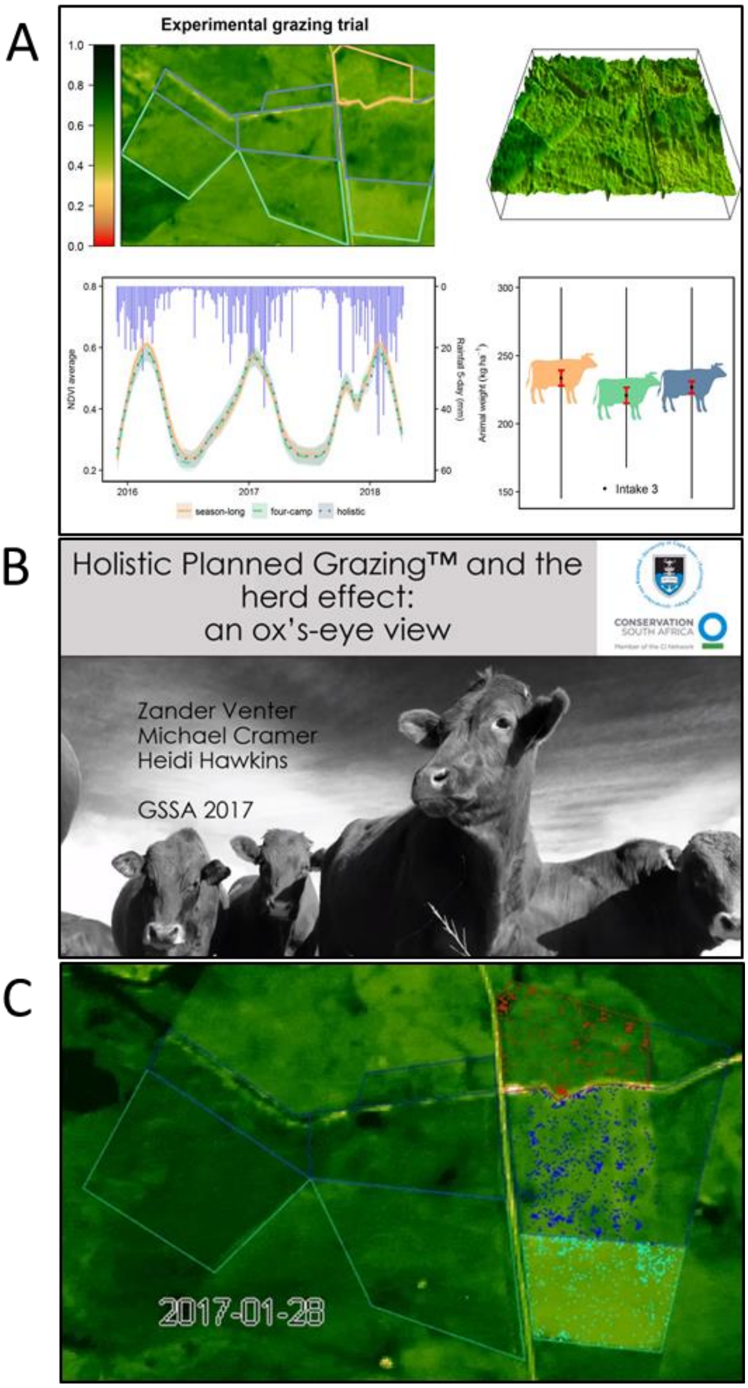


Plate 3. Videos summarising vegetation and cattle responses at the Merino Walk experimental grazing trial. A time-lapse of vegetation normalised vegetation index (NDVI) is presented in 3D, summarised on a graph with rainfall, along with synchronous cattle weights per grazing treatment are displayed in A. Mid-way through data collection for results presented in Chapter 4, I presented preliminary results at the Grassland Society of Southern Africa Congress 2017 and recorded a video of this presentation (B). Finally, a short time-lapse illustrating the effect of cattle grazing on NDVI using cattle GPS locations is presented in vide C. Click on the hyperlinks to watch the corresponding videos: A, B, C.

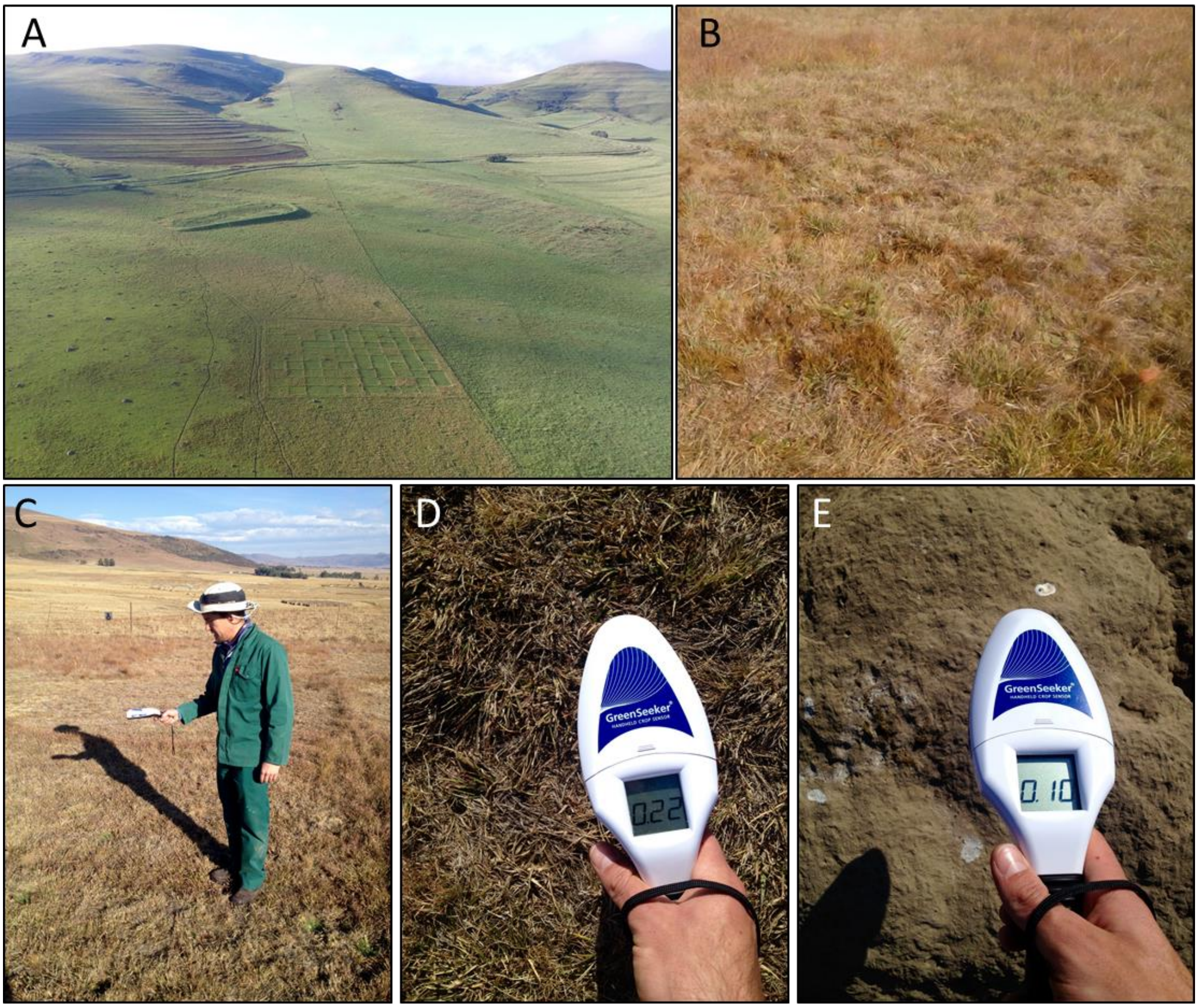


Plate 4. Photographs from an in situ field plot defoliation and dung addition experiment located on a separate piece of land on the Merino Walk experimental grazing trial. One hectare of grassland (checked square in drone aerial view in A) was allocated to the experiment which included a randomized design of various defoliation frequencies and severities as well as dung application (B). To measure vegetation normalised difference vegetation index, a handheld GreenSeeker device was used (C). Two illustrative GreenSeeker readings of grass (D) and bare ground (E) give NDVI readings of 0.22 and 0.2, respectively.

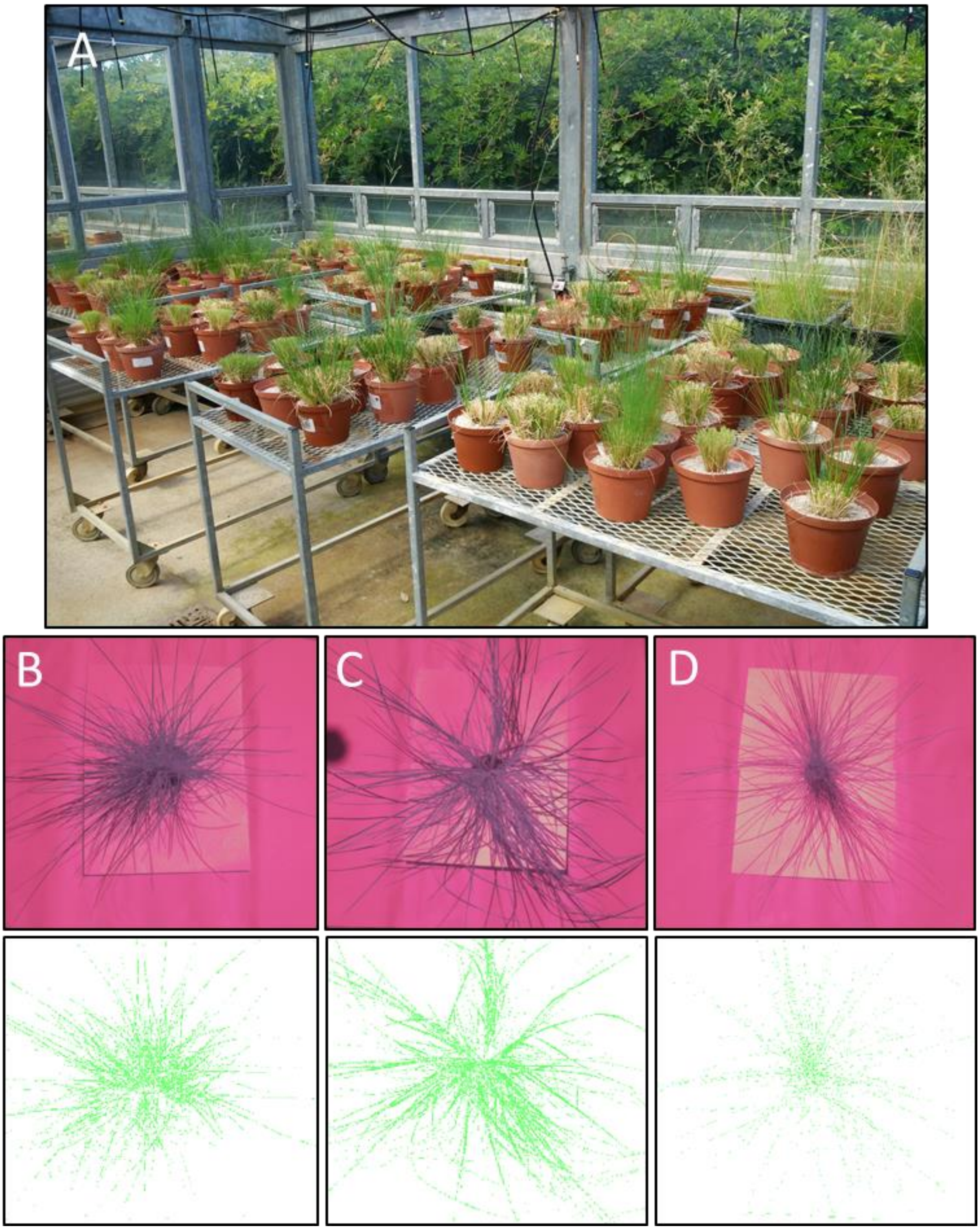


Plate 5. Photographs from my glasshouse pot experiment (A). A combination of *Themeda triandra* (B), *Eragrostis plana* (C), and *Elionurus muticus* (D) were defoliated at various frequencies and severities. Pots were placed on metal trolleys and were randomly rotated every week. To measure normalized difference vegetation index of grass foliage, a MAPIR Survey 2 camera was used. Images were processed in R to isolate leaf pixels (B, C, D).