

Fire and herbivory in the Serengeti-Mara

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Declaration

I hereby declare that this work has been originally produced by myself for this thesis and it has not been submitted for the award of a higher degree to any other institution. Inputs from co-authors and acknowledged throughout.

James Ronald Probert, Liverpool, September 2018

Abstract

Savannahs are consumer controlled systems where fire and herbivory maintain plant biomass below the level that is predicted by rainfall and temperature. Savannahs are globally important biomes, covering around 20% of our planet's terrestrial surface and providing economic and cultural value, carbon sequestration, ecosystem services, and habitat for many unique species. Whilst both fire and herbivory consume plant biomass they vary in their mechanism, timing, geographic extent, frequency, and selectivity. Studying fire, herbivory and their effects can be challenging because both are multifaceted phenomena. They also interact and capable of both facilitating and inhibiting one another. However, understanding the patterns in fire and herbivory and the differences in how flora and fauna respond is vital to the successful management of savannah systems. Here we use both satellite data and field experiments to quantify the fire regime of the Serengeti-Mara ecosystem of southern Kenya and northern Tanzania and compare the effects of fire and herbivory on the ecology of the system. We describe the spatiotemporal patterns in the components of the Serengeti-Mara's fire regime and show that rainfall is the primary driver of the variability we observe. We also observe a striking decline in the area burnt and the number of fires and attribute this to increasing livestock density. We use the high intensity and short duration of grazing by the wildebeest migration as an analogue to fire and compare the effects of the two disturbances on vegetation, resident mammalian herbivores, and invertebrates. We show that there are similar effects on grass structure but only fire increased grass quality and there were contrasting effects on forb communities. These differences in vegetation cascade to affect the distribution of resident mammalian herbivores. Long grass areas attracted bulk grazers such as zebra and buffalo whilst short grass areas were attractive to selective grazers such as wildebeest and Thompson's gazelle. Not all of the species that were more abundant in short grass areas were attracted to high quality grazing, indicating that some species may select short grass areas for anti-predator rather than resource benefits. Finally, we show that fire and herbivory have contrasting direct and indirect effects on invertebrates, with responses varying based on taxa and ecological niche. Our results have important implications for the management of the Serengeti-Mara and our understanding of savannahs.

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Chapter 1

General introduction



Cover illustration:

Clockwise from the left – inflorescence of *Bothriochloa insculpta* (Hochst. ex A.Rich.), fire on Sasakwa Hill, Tanzania, and wildebeest (*Connochaetes taurinus* Burchell) on Sabora Plains, Tanzania. ©James Probert

The ecosystems uncertain

In 1975 Robert Whittaker attempted to predict the distribution of the world's biomes using temperature and rainfall (Whittaker, 1975). However, large parts of the world did not fit his predictions and Whittaker called these areas the "ecosystems uncertain". These areas defied Whittaker's predictions because vegetation structure in these systems is not constrained by the availability of resources, but rather by frequent consumption by fire and herbivores (Bond, 2005). Today, we would recognise the ecosystems uncertain as savannahs and grasslands.

Savannahs are defined by a continuous layer of C₄ grasses and may have tree cover varying from 0-80% (Ratnam et al. 2011, Sankaran et al. 2005). They cover around 20% of the Earth's terrestrial surface and are a particularly prominent biome in tropical regions (Bond and Parr, 2010). Savannahs are home to assemblages of unique species and are also of significant economic and cultural value to human populations (Bond & Parr, 2010; Grace et al. 2006; Scholes & Archer, 1997).

Frequent disturbance by fire and herbivory is a feature of savannah systems (Bond, 2005; Bond & Keeley, 2005). Both disturbances consume vegetation, but they vary in their extent, frequency, timing, selectivity, effect on vegetation, and the degree to which they can be manipulated by humans (Anderson et al. 2007; Hempson & Archibald, 2016). They also interact, both facilitating and inhibiting one another. Fires alter how herbivores use the landscape and alter herbivory as a result. In turn, herbivores can remove vegetation that would otherwise burn and thereby modify or prevent fire spread across the landscape (Archibald et al. 2005; Archibald & Bond, 2004). These interactions can create alternate stable states, with long grass areas which burn frequently but have low herbivory, and short grass areas which are attractive to herbivores but too short to burn (Archibald, 2008; Bond & Parr, 2010; Hempson et al. 2015).

Concerning fire

At its most fundamental, fire is a chemical reaction which rapidly oxidises a fuel source resulting in the release of heat, light, and various gaseous products (Pyne, 2001). This simple definition belies the role that fire has played shaping the geography and climate of our planet (Williams et al. 2004; Bond, 2005), its importance as an evolutionary driver (Bond & Midgley, 1995), a complex suite of ecological interactions (Bowman et al. 2009), and its role in human evolutionary development and culture (Gowlett, 2016). Fire is intrinsically linked to life as we know it; an inescapable by-product of the oxygen and carbohydrates created by photosynthesis (Pausas & Keeley, 2009).

An individual fire can be described using discrete characteristics or behaviours: its location, size, intensity, when it occurred, and how long since the last fire at the same location (Gill, 1975). Combined with the frequency of fires and the total area burnt, the long-term patterns in these characteristics at a particular location are called the fire regime (Bond and Keeley, 2005). At geological timescales fire regimes are most influenced by levels of atmospheric oxygen. The minimum required for fire to occur is 13% but in the Guadalupian epoch atmospheric oxygen was as high as 30%, when even wet vegetation would burn, and fire would have been more widespread and frequent than it is today (Scott & Glasspool, 2006). At broad spatial scales variation in fire regimes is determined by climate (Balfour and Howison, 2002), vegetation (Archibald *et al.* 2009), herbivory (Archibald *et al.* 2010a) and topography (Wood *et al.* 2011), whilst at finer scales heterogeneity in vegetation and topography, and increasingly human activity, can alter fire regimes (Archibald, 2010a, 2010b, 2013; Smit *et al.* 2013).

The manipulation of fire by organic life

Fire thrived on our planet long before the arrival of hominids, and hominids were almost certainly not the first to manipulate it for their own benefit. Many species are attracted by the feeding opportunities of burning or recently burnt areas (Pruetz & Hertzog, 2017; Pyne, 2001). Chimpanzees, human's closest extant relatives, have shown the ability to conceptualise, understand and predict the behaviour of fires in the wild and captive chimps

have even demonstrated the ability to manage fire to some extent (Brink, 1957; Pruetz & LaDuke, 2010). In Australia “firehawk” raptors have gone a step further by picking up burning sticks and dropping them in unburnt patches to facilitate fire spread (Bonta et al. 2017). It has also been suggested that plants themselves manipulate fire, increasing the likelihood of fire through flammable structures and compounds, in order to “self-immolate” and exclude less fire tolerant competitors (Bond & Midgley, 1995; Pyne, 2001; Bowman et al. 2014).

Regardless of whether they were the first, the taming of fire by early hominids marked a profound moment for both the evolutionary history of our species and the natural history of our planet. The earliest widespread and widely accepted archaeological evidence of fire use by *Homo sapiens* and their ancestors comes from Africa around 1.4 mya (Berna et al. 2012; Brain and Sillen, 1988; James, 1989; Weiner et al. 1998) with more controversial claims of fire use up to 1.9 mya (Moeller-Gorman, 2008; Wrangham et al. 1999). This archaeological evidence comes in the form of hearths, the preserved remains of fire pits used for extended periods. Hearths reflect relatively advanced fire use and it is likely that our ancestor’s first experiments in controlling and manipulating fire occurred many millions of years before visible signs appear in the archaeological record (Roebroek and Villa, 2001).

Our ancestor’s first interactions would have been with naturally occurring fire and would therefore have been more likely to occur in fire rich environments, such as African savannahs (Gowlett & Wrangham, 2013; Roebroek & Villa, 2001). Even with their first experiments our ancestors would have modified their habitat’s fire regime: by increasing the number of ignitions, facilitating fire spread, changing the season and locations where fire occurred (Bowman et al. 2011; Frazer, 1930). This manipulation of our planet’s fire regimes became truly significant around 12,000 years ago and today has reached the point where the majority of fires are started by humans (Archibald et al. 2012; Power et al. 2008). Humans also impact fire regimes indirectly, reducing large mammal populations (Dirzo et al. 2014) or introducing livestock (Andela et al. 2017), thereby modifying the amount of vegetation consumed by animals versus fire (Dublin, 1995; Hempson et al. 2017), introducing invasive plant species which are more or less flammable than native species (Brooks et al. 2004), and modifying climatic conditions (IPCC, 2007).

Fire's influence on evolution and ecology

Fire has therefore been a periodic, natural disturbance across most of our planet's terrestrial surface and, as life has influenced fire, so fire has influenced life (Bond, 2005). The patterns this has caused are visible at a range of evolutionary and geographic scales. Many plant species show adaptations which reveal fire's role as both a direct and indirect selective force (Bond & Midgley, 1995; Pausas & Schwilk, 2012). Traits such as thicker bark protect plants from fire-induced mortality, whilst adaptations such as smoke or heat-triggered germination, post-fire flowering, and post-fire resprouting allow them to take advantage of reduced competition in burnt areas (Dixon et al. 1995; Brown & van Staden, 1997; Schwilk & Ackerly, 2001). Individual plants are also able to alter their phenotype in response to fire, modifying seed traits and growth form across gradients of fire frequency (Higgins, 2007; Gomez-Gonzalez et al. 2011). Animals also respond to fire, the smell of smoke and the sound of fire prompt various taxa to seek out refuge (Whelan 1995; Scesny & Robbins 2006), whilst others will take advantage of the feeding opportunities provided by burnt areas (McNaughton, 1976). Fire dependency can be observed in certain beetles which preferentially lay their eggs in burnt wood and have evolved smoke detectors in their antennae which allow them to find these areas (Shultz et al. 1999), and also in birds which are obligate nesters in burnt trees (Collard, 2015; Pausas & Parr; 2018).

The role of herbivores in savannahs

Mammalian herbivores have a long association with savannahs and may have been the reason for their expansion around 10 mya (Jacobs et al. 1999; Charles-Dominique et al. 2016). It is for this reason that we will focus on large mammals, although it should be noted that invertebrates can also be important herbivores (Davies et al. 2016). Africa contains a greater diversity of large mammalian herbivores than any other continent, with 30 species found in the savannahs of East Africa (duToit & Cumming. 1999). These species are important consumers of plant biomass and affect vegetation structure and composition (Augustine and McNaughton, 1998; Sankaran et al. 2008).

In the same way that individual fires can be described using a number of discrete characteristics, so mammalian herbivores can be defined based on their morphology and physiology. Herbivores which feed primarily on grass (monocots) are classified as grazers, and those which feed primarily on woody plants or forbs (dicots) as browsers. Some species are strictly grazers, some browsers and others mixed feeders (Shipley, 1999). Within this classification exist foregut ruminants, which require high quality food, and hindgut ruminants, which eat larger quantities of poor quality food. There is a correlation between body size and gut physiology, smaller herbivores are often foregut ruminants (Hoffman, 1989). Different herbivore types exert top-down controls on vegetation in different ways, for example browsers can severely impact seedling recruitment (Sankaran et al. 2008), whilst grazers can exclude fire by creating areas which are too short to burn (Archibald et al. 2005). A further important distinction is the contrast between resident and migratory herbivores. Migrations typically occur to take advantage of seasonally available high-quality food or avoid predators and have been observed in 24 species of mammalian herbivore worldwide (Fryxell & Sinclair, 1988; Harris et al. 2009). Migratory herbivores tend to be more abundant than resident herbivores and can rapidly consume large volumes of vegetation (Sinclair et al. 2007). Migratory herbivores can also provide a very large pulse of nutrients, increase primary productivity, compete with resident herbivores, and spread disease (Holdo et al. 2009; Holdo et al. 2011).

The uncertain future of savannahs

Savannahs are being affected by changes in both fire and herbivory. There has been a global decline in the area burnt, particularly in savannahs, driven by expanding and increasing human populations (Andela et al. 2017). Large mammalian herbivores have been disproportionately affected by population declines and extinctions, and migrations are particularly vulnerable to disruption (Harris et al. 2009; Dirzo et al. 2014; Ripple et al. 2015). Extirpated herbivores may be replaced by livestock, which have substantially different functional traits and effects on vegetation (Hempson et al. 2015). Climate change is causing shifts in rainfall patterns, temperature, and atmospheric CO₂, affecting fire and herbivores both directly and indirectly (IPCC, 2007). Fluctuations in the balance between fire and herbivory may have substantial impacts on the ecology of savannah systems, causing shifts

to stable states dominated either by fire or herbivory (Bond, 2005; Hempson & Archibald, 2016). Such shifts would likely have undesirable consequences on the vegetation structure, biodiversity, and ecosystem function (Lehmann et al. 2011; Parr et al. 2011; Archibald et al. 2013).

The Serengeti-Mara

The Serengeti-Mara ecosystem is possibly the most iconic savannah in the world. It is broadly defined by the limits of the annual migration of blue wildebeest (*Connochaetes taurinus*, Burchell, 1823), zebra (*Equus quagga*, Boddaert, 1785) and Thompson's gazelles (*Eudorcas thomsonii*, Gunther, 1884) between southern Kenya and northern Tanzania (McNaughton, 1983; Watson, 1967). The movement of these herbivores is limited by physical and habitat boundaries including Lake Victoria to the west, the Loita Hills and Ngorongoro highlands to the east and Lake Eyasi to the south, but also increasingly by the expansion of human settlements (McNaughton, 1982, 1983; Sinclair, 1979).

The Ngorongoro Highlands influence the two main bottom up drivers of the Serengeti: rainfall and soil nutrients. Ash from the eruptions of *Keremasi* and, more recently, *Ol Doinyo Lengai* has created rich volcanic soils in the south east. Soil fertility gradually declines to the north and west with soils in these areas largely consisting of alluvial deposits from old lake beds (Dawson, 1962; Holdo et al. 2009; Pickering, 1968; Ruess & McNaughton, 1987). A rain shadow cast by the Ngorongoro Highlands and evaporation from Lake Victoria create a contrasting spatial gradient in rainfall. Mean annual rainfall varies from 350mm in the south east to 1400mm in the north west (Norton-Griffiths et al. 1975). Rainfall in the Serengeti is also highly seasonal with a wet season from October to May and a dry season from June to September. A shorter dry season sometimes occurs in January or February, but this does not happen every year. Both spatial and temporal patterns in rainfall have significant effects on the ecosystem. In the south east the growing season is less than 90 days per year whereas in the north west the growing season continues for almost the entire year (McNaughton, 1985). Fires are predominantly confined to the dry seasons but higher rainfall during the wet season creates more grass biomass and therefore larger, more intense fires and a greater total area burned during the following dry season (McNaughton,

1992). Heavier rainfall in the north west also allows grass biomass to recover sufficiently for fires to occur twice per year (Sinclair et al. 2009).

The ecosystem encompasses several protected areas: Serengeti National Park, Maasai Mara National Reserve, Grumeti, Ikorongo and Maswa Game Reserves, Ngorongoro Conservation Area, Mwiba Wildlife Reserve and Loliondo Game Controlled Area. In many cases each protected area can be further subdivided into a number of concessions and land use zones. Management approaches and resources in these protected areas vary widely but fire is consistently used as a management tool in all of them.

Challenges in savannah ecology

The contrast between the global distribution of savannahs, their large spatial extent, and the temporal scale over which processes can occur, versus the short duration and limited geographic area of many studies often creates problems for savannah ecologists. An uneven distribution of study plots can result in spatial autocorrelation, where values from points closer together are more likely to be similar due to chance alone than points further away (Legendre, 1993; Tobler, 1970). This problems can be controlled for in models, but studies sometimes lack sufficient data points to do this. The level of spatial autocorrelation may also provide useful insights into the processes and mechanisms structuring a dataset and it is possible to examine the level of spatial autocorrelation using Moran's I and variograms (Legendre, 1993). In addition to spatial autocorrelation, the placement of plots to study an event such as a fire often results in pseudo-replication, where data points are not truly independent of each other, and logistical constraints may not allow before-after-control-impact studies, making it difficult to differentiate between correlation and causation. These weaknesses in experimental design must be considered when interpreting many ecological studies (Legendre et al. 2004).

Thesis outline

In this thesis I seek to understand some of the complex interactions between fire and herbivory, the biotic and abiotic factors which influence them, the role that they play in

shaping the Serengeti-Mara, and the degree to which the ecosystem's land managers can manipulate them. Chapter 2 describes in detail the fire regime of the Serengeti-Mara and examines the drivers of the spatiotemporal patterns we observed. Chapters 3, 4, and 5 are based on the same experimental set up and investigate different aspects of the functional differences between fire and grazing. Chapter 3 quantifies the impacts that fire and grazing by the wildebeest migration have on the vegetation of the Serengeti-Mara, Chapter 4 looks at how these vegetation characteristics influence the distribution of mammalian herbivores, and Chapter 5 examines how the impacts of fire and grazing cascade to affect invertebrate communities. Chapter 6 aims to summarise the main findings of my work, explain how these fit into our understanding of savannah ecology, and identify the key questions which emerge from this work.

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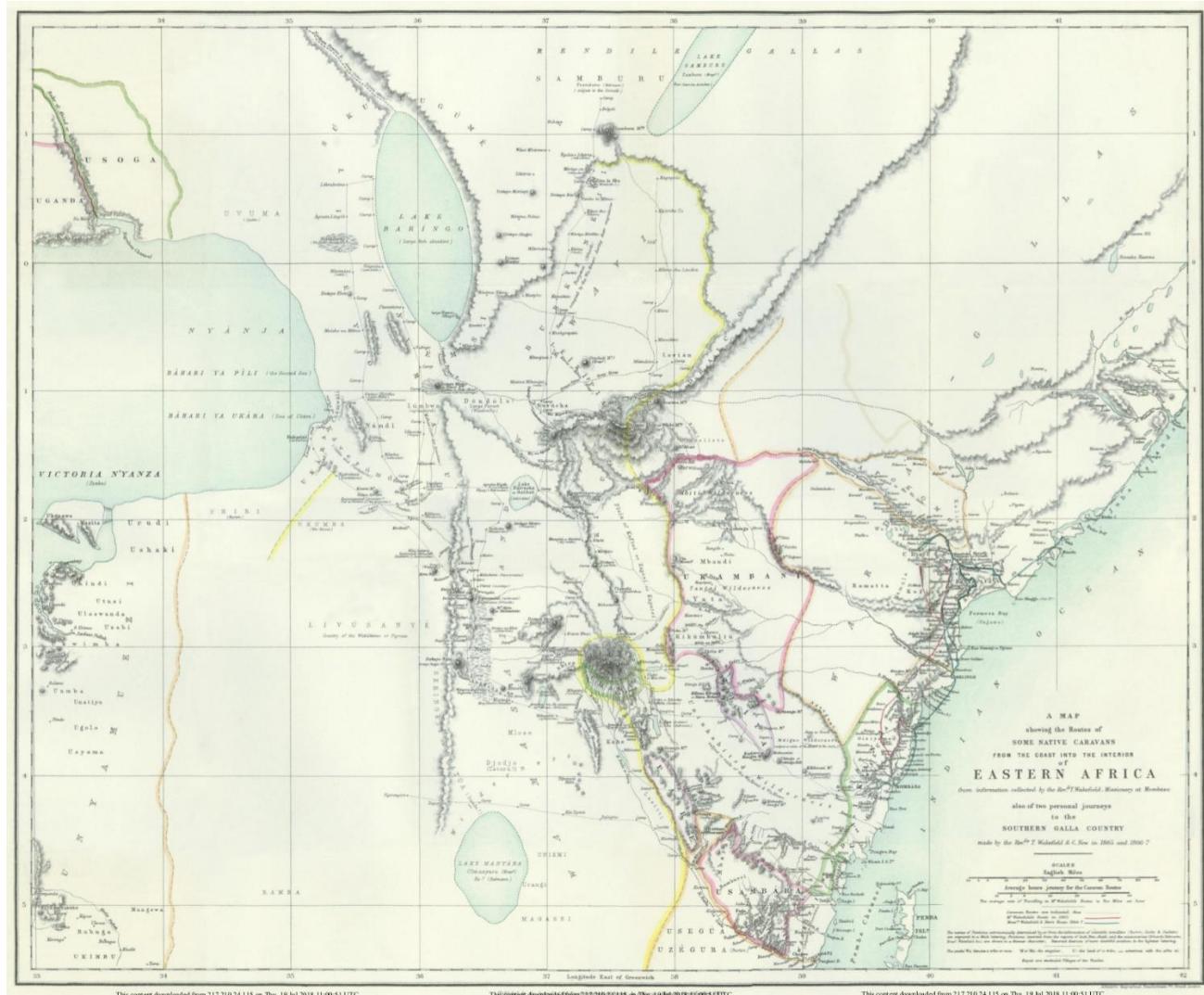
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Chapter 2

Human activities disrupt fire regimes in the wider Serengeti-Mara ecosystem



Cover illustration:

The Wakefield Map, the earliest known map featuring the Serengeti (or rather “Seringeti”, 3.5°S, 36.2°W). Modified from *Routes of Native Caravans from the Coast to the Interior of Eastern Africa, Chiefly from Information Given by Sádi Bin Ahédi, a Native of a District near Gázi, in Udigo, a Little North of Zanzibar* (Wakefield et al. 1870)

ABSTRACT

1. Fire is a key driver in savannah systems, where it is widely used as a management tool. Yet growing human populations may be altering savanna fire regimes with consequences for ecosystem functioning and composition. Here we undertake a novel analysis describing the spatial patterns of fire regimes across the Serengeti-Mara ecosystem, document striking temporal changes, and investigate the factors underlying these patterns.
2. We used MODIS active fire and burned area products from 2001-2014 to identify individual fires, and summarised four attributes for each fire: size, ignition date, time since last fire, and radiative power. Using satellite imagery, we estimated the rate of change in the density of livestock *bomas*, as a proxy for livestock density. We used these data to model drivers of spatial and temporal variation in our four individual fire attributes, and two aggregate measures: the total number of fires and the total area burned.
3. We found that fires in the Serengeti-Mara show high spatial variability, with a conspicuous east-west split (following the prevailing gradient in mean annual precipitation) in both the number of fires and the ignition date. The immediate effect of rainfall (monthly rainfall) is to decrease fire size and intensity. In the long term, the main driver is rainfall in the previous two wet seasons, which increases standing grass biomass and therefore fuel loads.
4. Our study highlights dramatic changes in the Serengeti-Mara fire regime over time, with a reduction in the total number of fires and the total area burned. We suggest increasing livestock numbers are driving this decline, presumably by inhibiting fire spread. Locally, different management practices are also altering the fire regime in the Serengeti-Mara's protected areas.
5. Although fire plays a crucial role in modulating spatial heterogeneity and biodiversity in the savannahs of the Serengeti-Mara ecosystem, some areas now experience

virtually no fire. Consequently, we caution that healthy savannah ecosystem functioning is likely to have been compromised. Managers need to monitor and manage fire as a key driver for maintaining the integrity of the ecosystem.

Key words: Fire regime, savannah, management, overgrazing, conservation, protected areas, Serengeti

INTRODUCTION

Fire has been a natural ecological process for millions of years (Bond, 2005; Bowman et al. 2009), and is a key ecological and evolutionary driver in many ecosystems (Bond & Keeley, 2005). Fire influences the distribution of biomes (Bond et al. 2004, 2005), carbon sequestration (Williams et al. 2004), nutrient exchange (Frost & Robertson, 1987) and vegetation structure (Govender et al. 2006). In many flammable ecosystems, burning is widely used, formally and informally, as a land management tool both inside and outside protected areas (Parr et al. 2004). Understanding the spatiotemporal patterns exhibited by fire, the factors driving fire occurrence, and the extent to which fire behaviour can be manipulated is therefore essential for the successful management of fire-prone ecosystems, particularly given increasing human pressures and climate change (Bowman et al. 2009).

Understanding how fires shape the ecology of a system requires an understanding of the multidimensionality of fire. Individual fires can be characterised by their size, season, return period and intensity (Gill, 1975). The long-term patterns in these attributes at a particular location comprise the fire regime (Bond & Keeley, 2005), which is determined by both broad- and fine-scale environmental factors, including climate (Balfour & Howison, 2001), vegetation (Archibald et al. 2009), herbivory (Archibald et al. 2010a) and topography (Wood et al. 2011). At large spatial scales fire regimes are driven by environmental factors, but at finer scales human activities also influence burning (Archibald, 2010a, 2010b, 2013; Smit et al. 2013). Humans increase the number of ignition events, and broaden the times of year when ignitions happen, but also inhibit fire spread by fragmenting landscapes and reducing fuel load through livestock grazing (Archibald et al. 2010b, 2013; Frost, 1999; Guyette et al. 2002). Diverse socio-economic, cultural, political and environmental conditions result in great variability in the motives behind anthropogenic burning, in the practice of how burns are applied, and in the effects realised on fire regimes (Laris, 2002; Le Page et al. 2010; Bowman et al. 2011). Determining how people influence fire regimes is especially important given increasing human population pressures and associated land use changes in savannahs (Archibald et al. 2010b).

Savannah ecosystems cover approximately half of the African continent (Parr et al. 2014), including many protected areas. Fire is one of the most common (and in some cases only) management tools used in African protected areas (Beale et al. 2018). Despite this, there is widespread debate concerning the practice of fire management across the continent with approaches ranging from complete fire suppression (e.g. in Kenya), burning to control woody encroachment (e.g. in Gabon), and “burning for biodiversity” (e.g. in South Africa), where patchiness in fire attributes is considered to increase biodiversity (Beale et al. 2018; Parr & Brockett, 1999). One study of a 45-year interval in Kruger National Park, South Africa found that variation in the area burnt was dependent on rainfall and not on management objectives, although managers were able to influence when in the year fires occurred (van Wilgen et al. 2004; Smit et al. 2013). However, the context-dependent nature of fire and its effects means that this finding may not be globally applicable. Many studies focus on a single variable to describe a fire regime, span a limited temporal range, or do not include changes at regional scales and among management units (although see Buthelezi et al. 2016; Tarimo et al. 2015). There is therefore a need for studies that document fire regimes and their drivers more widely and cover other African regions (Archibald et al. 2009; Beale et al. 2018; van Wilgen et al. 2004).

The Serengeti-Mara ecosystem of southern Kenya and northern Tanzania is one of the largest transboundary protected area complexes in the world, covering around 33,000 km². This savannah system burns frequently, and the importance of fire for the ecology of the ecosystem is well documented (e.g. Dublin, 1995; Holdo et al. 2009). The ecosystem is characterised by contrasting spatial gradients in rainfall and soil nutrients and comprises multiple management units with different fire management strategies (Jager, 1982). Consequently, there is scope for great variability in the drivers of fire across the ecosystem. There have been substantial historical changes to the fire regime of the Serengeti-Mara that have been attributed to the recovery of the wildebeest (*Connochaetes taurinus* Burchell, 1823) population from rinderpest (Sinclair et al. 2007). During the mid-nineteenth century, the rapidly increasing wildebeest population consumed large quantities of grass biomass leading to reductions in the total area burned each year, with subsequent changes in the ecology of the system, most notably enhanced tree recruitment and woody cover (Dublin, 1995). Whilst the wildebeest population has stabilised in abundance at 1.3 million animals

during the past decades (Hopcraft et al. 2015), burgeoning human populations surrounding the ecosystem's protected areas continue to alter land use (Estes et al. 2012), rainfall has increased across the broader region (Ogutu et al. 2006) and there have been changes in the management of some protected areas (Sinclair et al. 2008).

Here we present the first study to use Earth Observation Satellite products to comprehensively describe the fire regime of the broader Serengeti-Mara ecosystem and investigate its spatiotemporal drivers. We examine how six characteristics of the Serengeti-Mara's fire regime (fire size, ignition date, time since last fire, radiative power, total number of fires, and the total area burned) vary through space and time, both across the ecosystem and within its component management units, and investigate which factors drive these spatiotemporal patterns. Specifically, our objectives are to: 1) characterise spatiotemporal variation in fire regimes across the wider Serengeti-Mara ecosystem over a 14-year period (2001-2014), and 2) determine the biotic and abiotic factors driving these patterns (rainfall, soil type, elevation, slope, management type, primary productivity and livestock density). We predicted that the combination of strong environmental gradients and differences in management approaches would result in high levels of variability in the observed patterns of fire across the Serengeti-Mara. We anticipated that rainfall would be the primary driver of these patterns, but that human activities, particularly livestock grazing, may have a detectable influence on certain aspects of the fire regime.

METHODS

Study Area

We defined our study area (Fig. 1) as the protected areas of the Serengeti-Mara system and included a 5 km buffer zone around the Maasai Mara National Reserve, Serengeti National Park (SNP), Grumeti Game Reserve, Maswa Game Reserve and Mwiba Wildlife Reserve to allow management within protected areas to be compared with the *de facto* land management that takes place in the absence of protected areas. The buffer zone did not extend around Loliondo Game Controlled Area and Ngorongoro Conservation Area, as these protected areas contain settlements within their boundaries. The resulting region covered 36,305 km², of which 91.5% (33,232 km²) is encompassed by protected areas. For the purposes of this analysis, each of the seven protected areas and the 5 km buffer zone were counted as a discrete management unit. Grumeti and Ikorongo Game Reserves were combined (hereafter ‘Grumeti Game Reserve’) as both are managed by the same organisation. Fire management approaches differ between protected areas: the Maasai Mara follows a policy of active fire suppression; managers in Grumeti, SNP, and Maswa actively burn, for a variety of reasons and with varying levels of control; whilst managers in NCA and Loliondo adopt a more localised approach with most fires being lit by communal agro-pastoralists.

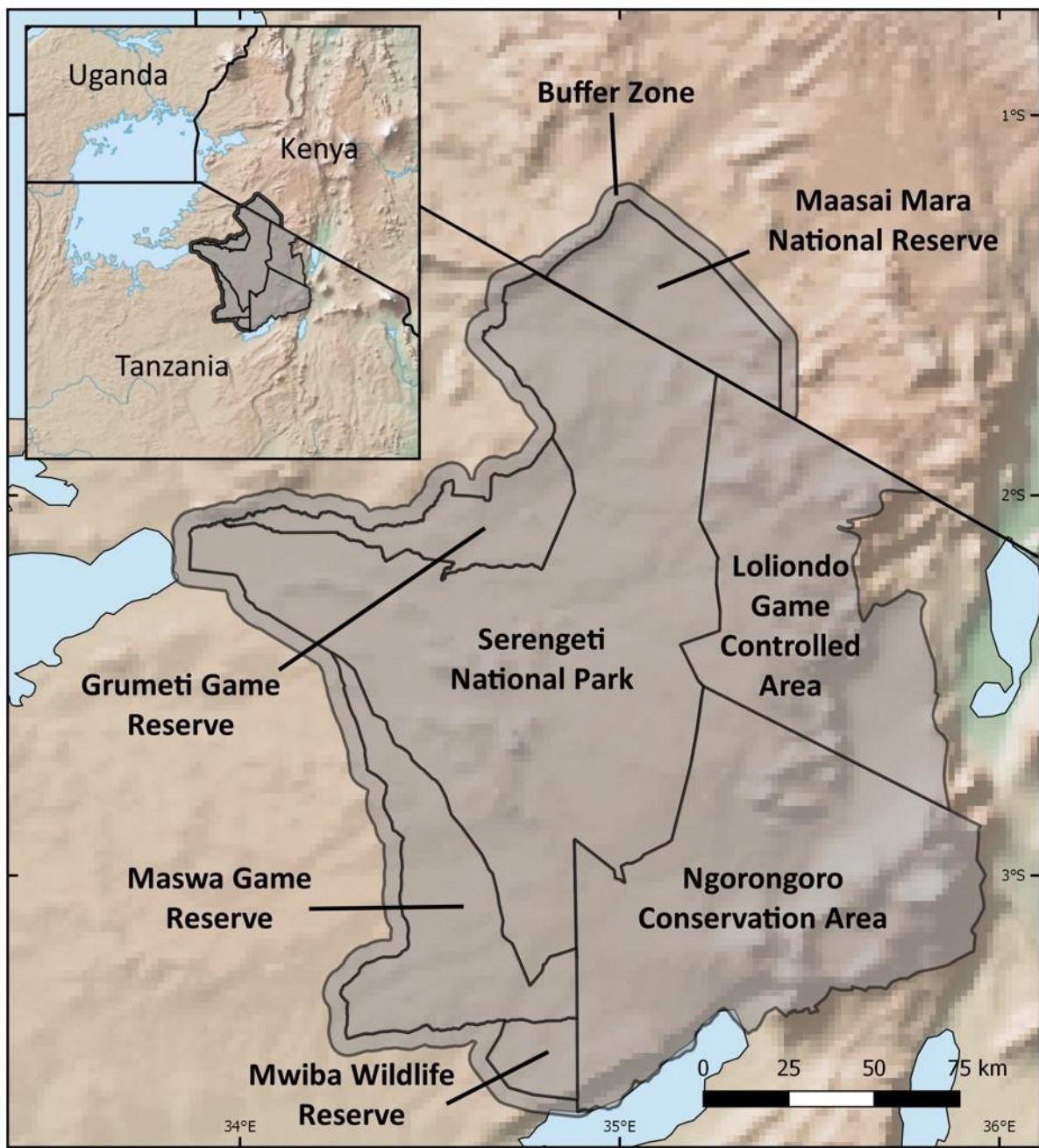


Figure 1: Map of the study area with the management units labelled and inset a map of East Africa showing the location of the study area. The base map is of elevation (made with Natural Earth) with protected areas shown in grey.

Data sources

Soil type

Soil type can be used as a proxy for nutrients and texture; these play an important role in determining vegetation structure and species composition that affect fire (Anderson & Talbot, 1965). Soil data were downloaded from the FAO/UNESCO Digital Soil Map of the World (Fischer et al. 2008) and a soil type for each fire was extracted from the “dominant soil” field.

Elevation and slope

Topography can either facilitate or hinder the spread of fire and affect attributes such as radiative power (Pyne, 1996). We used the NASA ASTER Global Digital Elevation Map (Meyer, 2011) to extract elevation and slope values for each fire.

Primary productivity

Fuel load is one of the key factors determining the attributes of a fire and is the medium through which drivers such as rainfall, soil type and herbivory influence fire. Net primary productivity (NPP) is a useful measure of the local rate of accumulation of grass biomass (Running et al. 2004). Rasters of annual NPP were downloaded from the Land Processes Distributed Active Archive Centre using Echo Reverb in the form of MODIS-1 km NPP MOD173 and rasters of monthly gross primary productivity were downloaded from the Numerical Terradynamic Simulation Group at the University of Montana (MOD17 A2) (Running & Zhao, 2015).

Livestock density

It is illegal to graze livestock within game reserves and national parks in Tanzania, but in practice this is difficult to enforce and encroachment along borders occurs. Reliable data on livestock distribution across our study area were not available and we therefore used the

density of active *bomas* as a proxy for livestock density. *Bomas* are livestock enclosures, generally constructed of thorny scrub. The “scar” left by a *boma* can persist for decades after the *boma* has been abandoned (Veblen, 2013), and for this reason we defined an active *boma* using two criteria: 1) a clear contrast between the colour of the substrate within the *boma* and the colour of the substrate surrounding it, and 2) an unbroken fence surrounding the *boma*. Each *boma* may comprise multiple internal “cells”, either to separate cattle, goats and sheep, or to accommodate the livestock of an extended family. Where this was the case we counted the structure as a single *boma* rather than counting each cell individually. We used Google Earth (2017) to identify areas where two or more satellite images from different years overlapped. By counting the number of active bomas in each satellite image in the area of overlap we could estimate the change in *boma* density through time.

Rainfall

Rainfall data from 1960-2006 were available as monthly rainfall surfaces. More recent rainfall data were not available. These surfaces were interpolated from rainfall data collected at 61 rainfall gauges across the Serengeti-Mara (Holdo et al. 2009). The effect of rainfall on fire differs depending on the temporal scale considered. The immediate effect of rainfall is to increase atmospheric and vegetative moisture and thereby make fires smaller and cooler whilst the longer-term effect of rainfall is to increase grass biomass and thereby increase fire size and intensity. We therefore extracted values for rainfall during the month of the fire (monthly rainfall) and accumulated rainfall from the two rainfall years prior to the date of the fire (cumulative rainfall) (van Wilgen et al. 2004).

Fire data

The MODIS (moderate resolution imaging spectroradiometer) Active Fire (MCD14ML) and Burned Area products (MCD45A1) were obtained from the Land Processes Distributed Active Archive Centre at 500 m² resolution for the period January 2001 – December 2014. We combined the products to create a dataset of individual fires, their locations and associated fire attributes. Details were presented by Hempson et al. (2018), but in

summary: individual fires were identified using a flood-fill algorithm (Archibald et al. 2009) with any spatially contiguous pixels that burned within five days of each other treated as a single fire. We calculated the centroid of each fire to represent it as a single point in space and to this point we added individual fire attributes calculated from both MODIS products: fire size, ignition date (season), mean time since last fire (frequency) and radiative power (intensity).

Fire size was calculated as the number of pixels covered by an individual fire in the Burned Area Product. The date of ignition was calculated as the earliest date within a fire and was split into the calendar year (2001-2014), the “rainfall year”, and a value from 0-366 where 0 = 1st January and 366 = 31st December. A rainfall year was considered to run from October (the start of the short rainy season) to September and is more ecologically meaningful than a calendar year as it contains a full seasonal cycle. The time since the last fire at a given location was calculated by taking the mean value for all the pixels that had burned before a given fire. Because a pixel had to burn twice before a ‘time since last fire’ value could be calculated, fires early in the dataset are more likely to lack a value for the time since last fire. This adds an element of temporal bias and means that we expect the time since last fire to increase as a function of time. Also, the maximum time since last fire is constrained by the length of our dataset. Finally, the maximum radiative power (MW/km²) for any pixel within a fire was taken as a measure of fire intensity. Not all fires had an associated fire radiative power value due to differences in the detection probabilities of active fires versus burn scars (Krawchuk & Moritz, 2014). Fire radiative power data are only available if a fire was burning at the time of the satellite overpass, and burn scars are not always detected if they are small (<250 x 250m) or underneath tree canopies. Small fires are least likely to have a value for fire radiative power, which biases our dataset towards larger and potentially hotter fires. Although missing data in both FRP and FRI variables add known biases, they do not add spatial bias, only additional noise.

Analysis

Spatial drivers of fire

To examine the spatial drivers of fire in the Serengeti-Mara we used a recently developed Bayesian conditional autoregressive modelling approach using an integrated nested Laplace approximation (INLA). This spatially-explicit approach allows us to account for spatial autocorrelation of predictor variables. INLA provides a computationally efficient framework for approximating posterior parameter estimates (Rue et al. 2009; Lindgren et al, 2011) while conditional autoregressive models have been found to perform well when compared to spatial regression models (Beale et al. 2010). We fitted a stochastic partial differential equation (SPDE) model for each of our four fire attributes, explaining the attribute as a function of rainfall, slope, elevation, management unit, soil type, year, monthly GPP, annual NPP, and boma density. To account for correlations between fire attributes, we included them as covariates in our models. We centred and scaled covariates to have a mean of zero and standard deviation of one and used vague priors. We split rainfall into two separate covariates: rainfall during the month of the fire (monthly rainfall) and rainfall from the start of the previous rainfall year until the date of the fire (cumulative rainfall). We included all covariates as linear effects except cumulative rainfall which was both a linear and quadratic effect, as it was unclear where the Serengeti-Mara fell on the intermediate fire-aridity curve (Pausas & Bradstock, 2007). As INLA is a Bayesian technique, we assessed the support for the influence of each covariate through 95% credible intervals. All analyses were carried out in R version 3.2.3 (R Core Team, 2015) using the R-INLA package (Martins et al. 2013).

Temporal drivers of fire

We assessed the temporal trends in six characteristics of the fire regime of the Serengeti-Mara during our study period: each of our four individual fire attributes (size, ignition date, time since last fire and radiative power), and two aggregate fire attributes (the total number of fires and the total area burned). We used Pearson's product-moment correlations to assess trends across the ecosystem as a whole and conducted a spatially-explicit analysis which calculated the rate of change in each characteristic of the fire regime across 1000 36

km^2 pixels to investigate spatial variation in these temporal trends. For each characteristic, we aggregated the values for all the fires in each year of our study into a separate raster and used generalised linear models (GLMs) to estimate the rate of change in each pixel over the period 2001-2014. We also used the GLM that estimated the rate of change in the area burned to predict a baseline area burnt for each pixel in 2001.

We processed the raw *boma* count data to generate a raster of the rate of change in *boma* density across our study area. To do this we fitted a GLM to the raw count data using individual areas of overlap as the unit of analysis to estimate the rate of change in *boma* density over time. As we had an *a priori* assumption that management would affect the rate of change in *boma* density, we interpolated the rate of change in *boma* density from within protected areas and from the 5 km buffer zone separately. We used regression kriging, a method of weighting values by distance, with management unit as an auxiliary variable, to predict the rate of change in *boma* density within protected areas and universal kriging to interpolate the rate of change in *boma* density within the 5 km buffer zone (Cressie, 1993). We then combined these to create a single raster of the rate of change in *boma* density across our study area. Finally, we created rasters of mean annual rainfall from 2001-2006 and used a GLM to estimate the rate of change in mean annual rainfall in each pixel.

To explain the rate of change in the total area burned we fitted a GLM using the rate of change in *boma* density, management unit, the mean and rate of change in mean annual rainfall, and the baseline area burned in each pixel as predictors. The baseline area burned determines the capacity for the burned area of a pixel to change while the mean annual rainfall determines the resilience of a pixel to any changes in the mean annual rainfall or *boma* density. We anticipated that including interactions between these covariates would improve our model. From a full model containing all predictors we fit a reduced model using single term deletions and log likelihood ratio tests. We performed a *post-hoc* Tukey's honestly significant difference (HSD) test to compare levels within our management covariate, used diagnostic plots to assess whether the residuals met the assumptions of all GLMs, and tested our Poisson GLM for overdispersion. A table of the error structures, link functions and data transformations used for all GLMs can be found in Supplementary

Material Table 1. Finally, we used Pearson's product-moment correlations to assess whether significant covariates were impacting the area burnt by reducing the number of fires or by reducing fire size.

RESULTS

Spatial patterns

We recorded 13,635 individual fires across our study site between 2001 and 2014. The median area burnt annually was 8,211.1 km² (22.6% of our study area), although the area burnt differed considerably between protected areas and the buffer zone. In the buffer zone the median area burnt annually was 116 km² (3.2%) whilst within protected areas the median area burnt annually was 8,001 km² (24.1%). Most fires in the Serengeti-Mara were small: 37.2% occupied only a single 500 x 500 m pixel (0.25km²), 78.4% occupied no more than 20 pixels (5 km²), whilst the largest fire (in SNP) occupied 9,263 pixels (2316 km²) (Fig. 2a). Fire occurrence throughout the year was bimodal, with fire seasons broadly matching the two dry seasons (Fig. 2b). Time since fire varied widely with a maximum of 13.1 years and a minimum 0.25 years. However, 10,383 km² (28.6%) remained unburnt for the entire duration of the study, indicating the maximum time since last fire is greater than the 14-year study duration. Overall, 21.7% of fires occurred within one year of a previous fire, 57.6% within two years of a previous fire and 70.8% within three years of a previous fire, although some areas burnt twice within three months (Fig. 2c). Due to limitations in the MODIS active fire product (see Methods) only 2,869 fires (21%) had an associated value for radiative power. Of these, 2,869 fires 99.2% had a radiative power of less than 50 MW/km² (Fig. 2d), which is comparable to the intensities of fires across southern Africa reported by Archibald et al. (2010a).

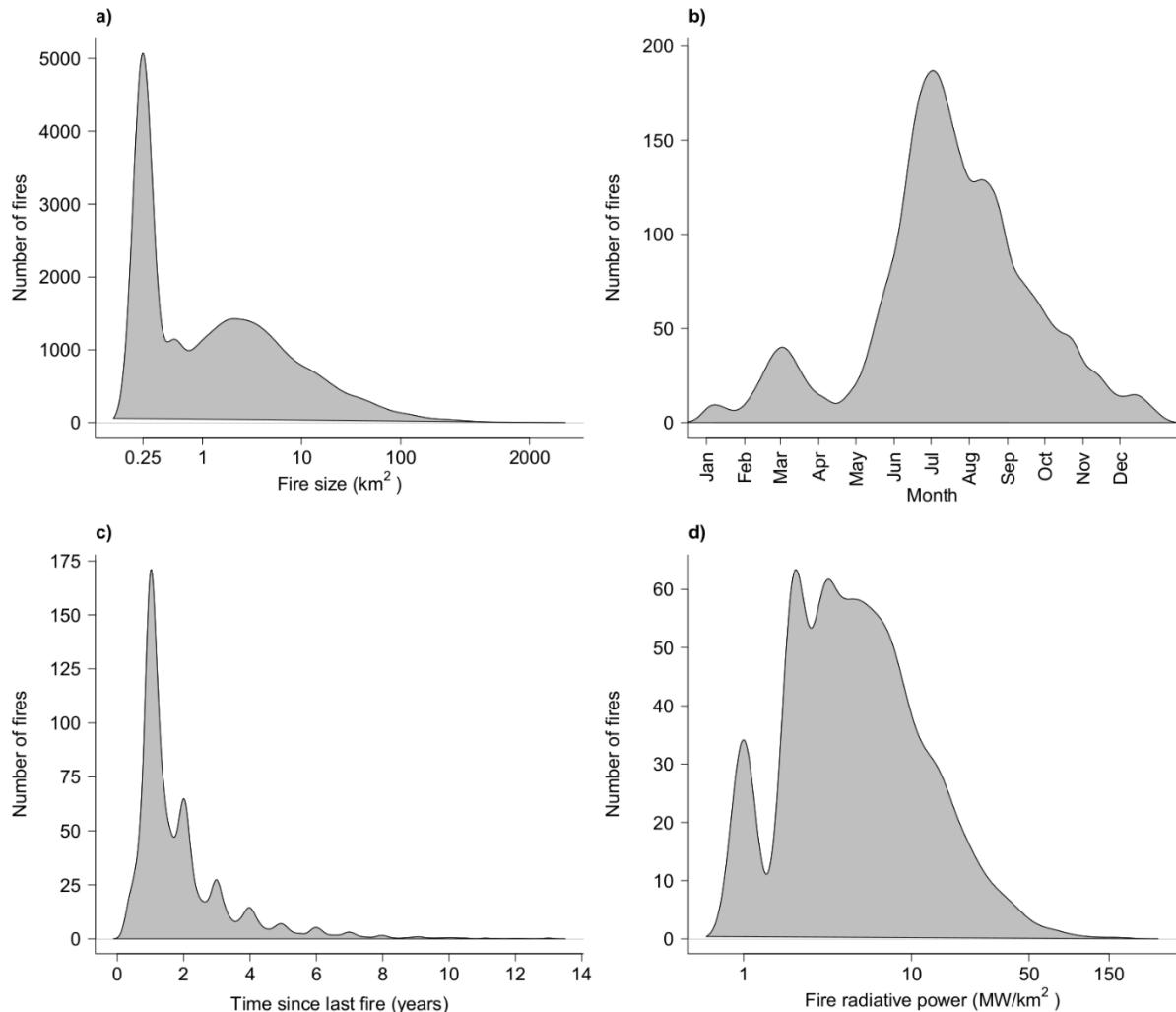


Figure 2: The distribution of fire traits: a) fire size, b) ignition date, c) time since last fire, and d) fire radiative power.

There was a clear east-west split in the occurrence of fires, with most fires occurring in the west (Fig. 3a). The number of fires was particularly high in the SNP, with few fires occurring in the Maasai Mara, Loliondo Game Reserve and the Ngorongoro Conservation Area, although Ngorongoro Crater is visually distinguishable (Fig. 3a). There was also an east-west split in the seasonality of fires, with fires across Mwiba, Maswa, SNP and Grumeti concentrated in the long dry season (June-August) and fires in the NCA, Loliondo and to some extent the Maasai Mara occurring at the start of the short rains (September-December) (Fig. 3c). Large fires ($>50 \text{ km}^2$) were most common in the Maasai Mara, but also occurred throughout the ecosystem (Fig. 3b). The Maasai Mara and NCA had longer times since last fire than the rest of the region, although the short-grass plains are also clearly

distinct from the surrounding landscape (Fig. 3d). Fires were most intense in the north-west (Fig. 3e). There were also patterns in the variability in each fire trait, with ignition date showing higher variability in the north-west (Supplementary Material Fig. 1c). There were pronounced differences in the number of fires and the area burned across management units. Whilst the absolute area burnt and number of fires are a function of the area of each management unit, when area was controlled for, management units in the west (SNP, Grumeti, Maswa and Mwiba) had a greater proportional area burned and number of fires (Supplementary Material Fig. 2).

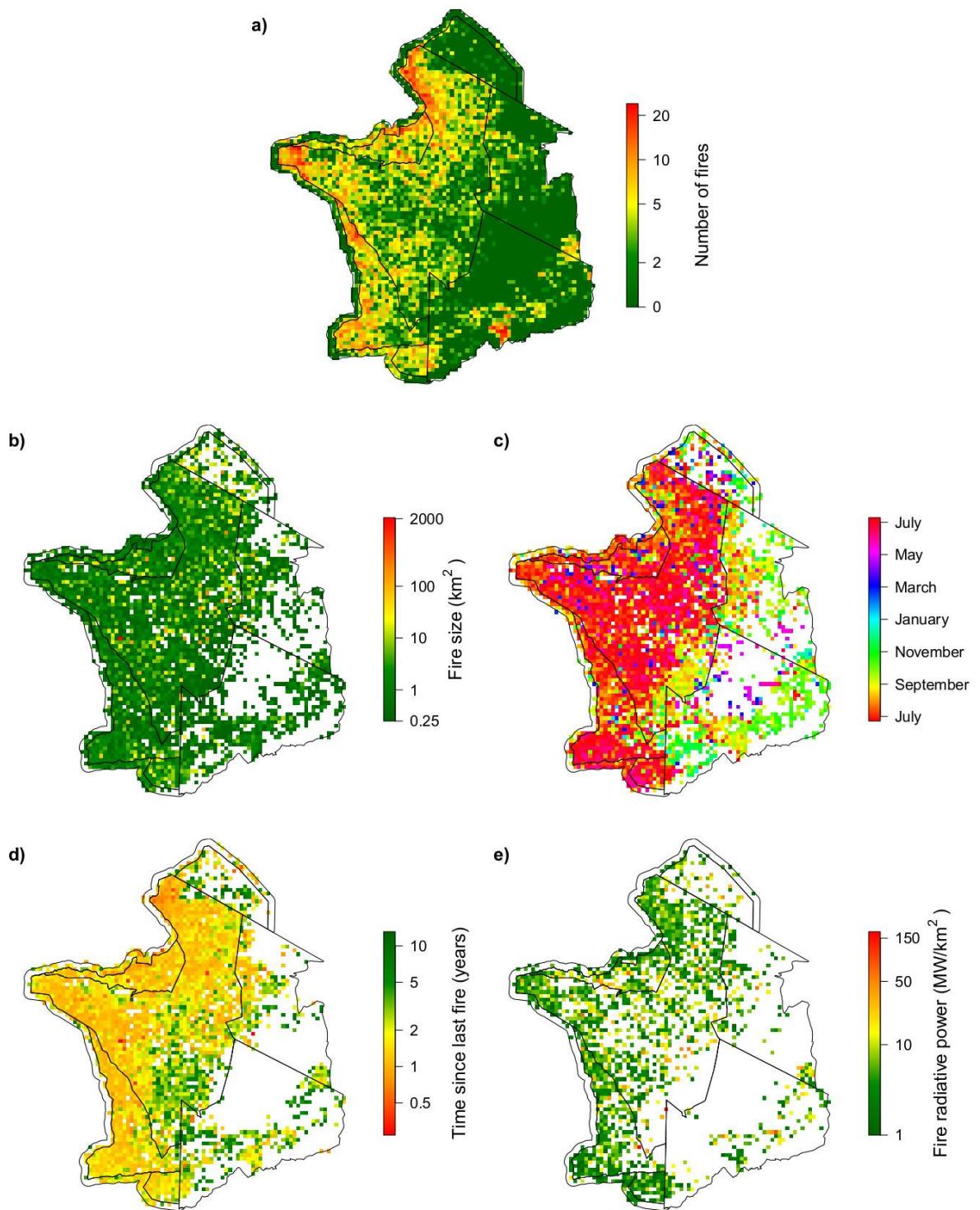


Figure 3: Spatial fire patterns between January 2001–December 2014: a) number of fires; note fires are much rarer in the Maasai Mara than in other areas focusing primarily on photographic tourism, b) the median fire size, c) the median ignition date, note the east-west split, d) the median time since last fire; note the short grass plain in south-eastern SNP and the difference between the Maasai Mara and northern SNP, and e) the median fire radiative power.

Temporal trends

The number of fires varied from 474 to 1,456 per year and the area burned between 2,819 and 13,017 km² (7.8-35.9%) of the study area each year. The largest 10% of fires accounted for 61.8-87.2% (median 77.5%) of the area burnt each year. There was a strong positive correlation between the total number of fires and the total area burned each year ($p < 0.001$, $r^2 = 0.82$, $df = 12$), no correlation between the median fire size of the largest 10% of fires and the area burned annually ($p = 0.63$, $r^2 = 0.02$, $df = 12$), and no correlation between the median fire size of the largest 10% of fires and the total number of fires annually ($p = 0.70$, $r^2 = 0.01$, $df = 12$).

Across the Serengeti-Mara ecosystem as a whole, there was a 40% decline in the total number of fires annually ($p = 0.03$, $r^2 = 0.33$, $df = 12$) (Fig. 4a) between 2001 and 2014, with a corresponding 39% decrease in the area burning annually ($p = 0.07$, $r^2 = 0.25$, $df = 12$) (Fig. 4b). Median fire size of the largest 10% of fires ($p = 0.58$, $r^2 = 0.03$, $df = 12$) (Fig. 4c) and radiative power ($p = 0.97$, $r^2 = 0.0001$, $df = 12$) (Fig. 4f) did not change over this period, but fires burned earlier in the year ($p = 0.004$, $r^2 = 0.5$, $df = 12$) (Fig. 4d). The reported increase in time since last fire ($p = 0.009$, $r^2 = 0.44$, $df = 12$) (Fig. 4e) is likely an artefact of our methods, because the maximum time since last fire increases with study duration.

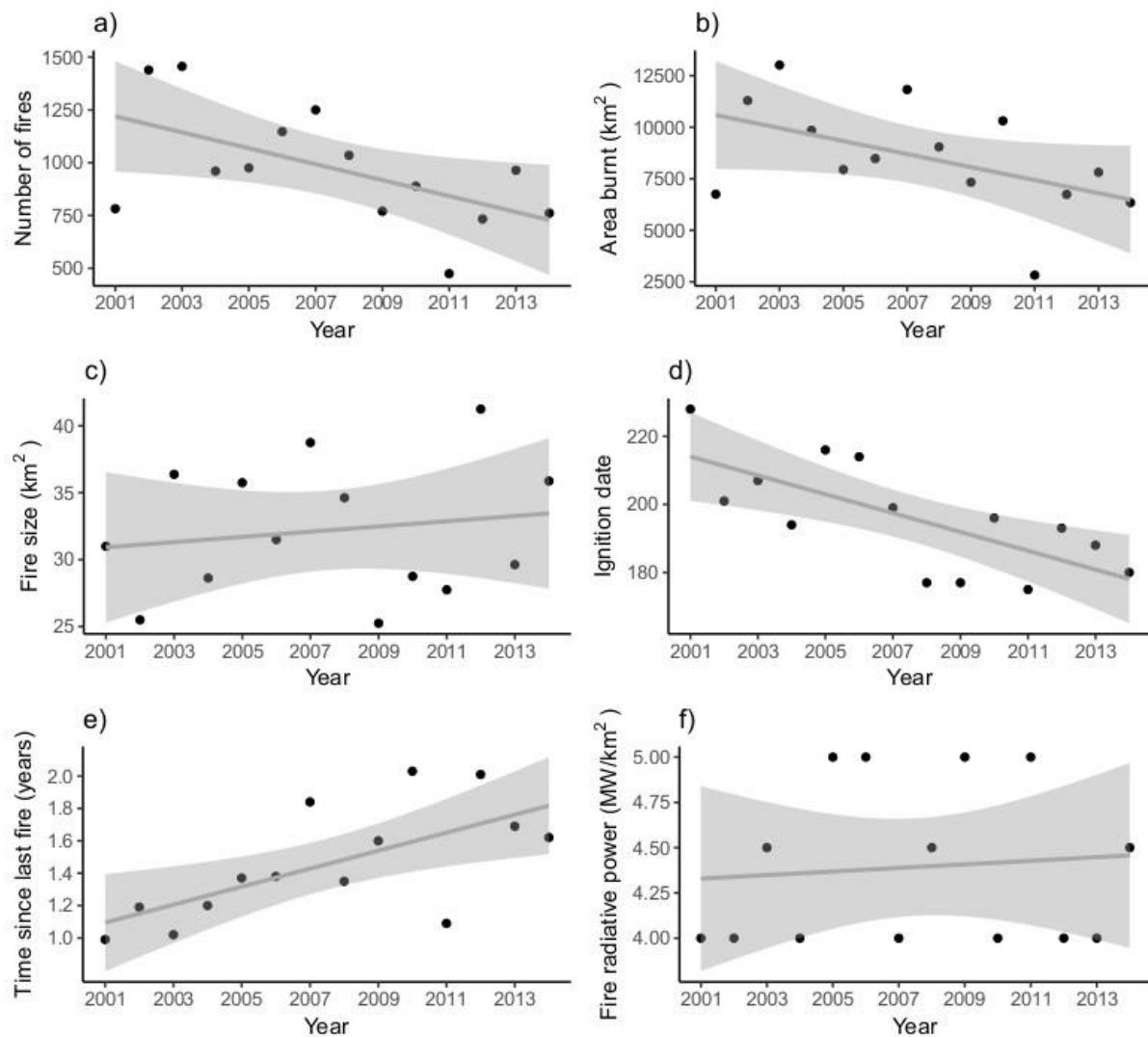


Figure 4: Temporal trends in fire across the Serengeti-Mara: a) the total number of fires, b) the total area burnt, c) the median fire size, d) the median ignition date, e) the median time since last fire, f) the median fire radiative power.

The observed temporal trends differed among management units. The overall decrease in total area burned across the Serengeti-Mara was driven by significant reductions in Loliondo, Maasai Mara and the buffer zone (Fig. 5a). However, the decline in number of fires occurred more widely, with only SNP and Maswa showing no change. There was also variation in the temporal trends of our four fire attributes across management units. Whilst fire size did not decline across the ecosystem as a whole, there were significant declines in fire size in Ngorongoro and in the buffer zone. Time since last fire increased significantly in

all management units except Maswa, and fire radiative power increased significantly in Mwiba (Supplementary Material Fig. 3).

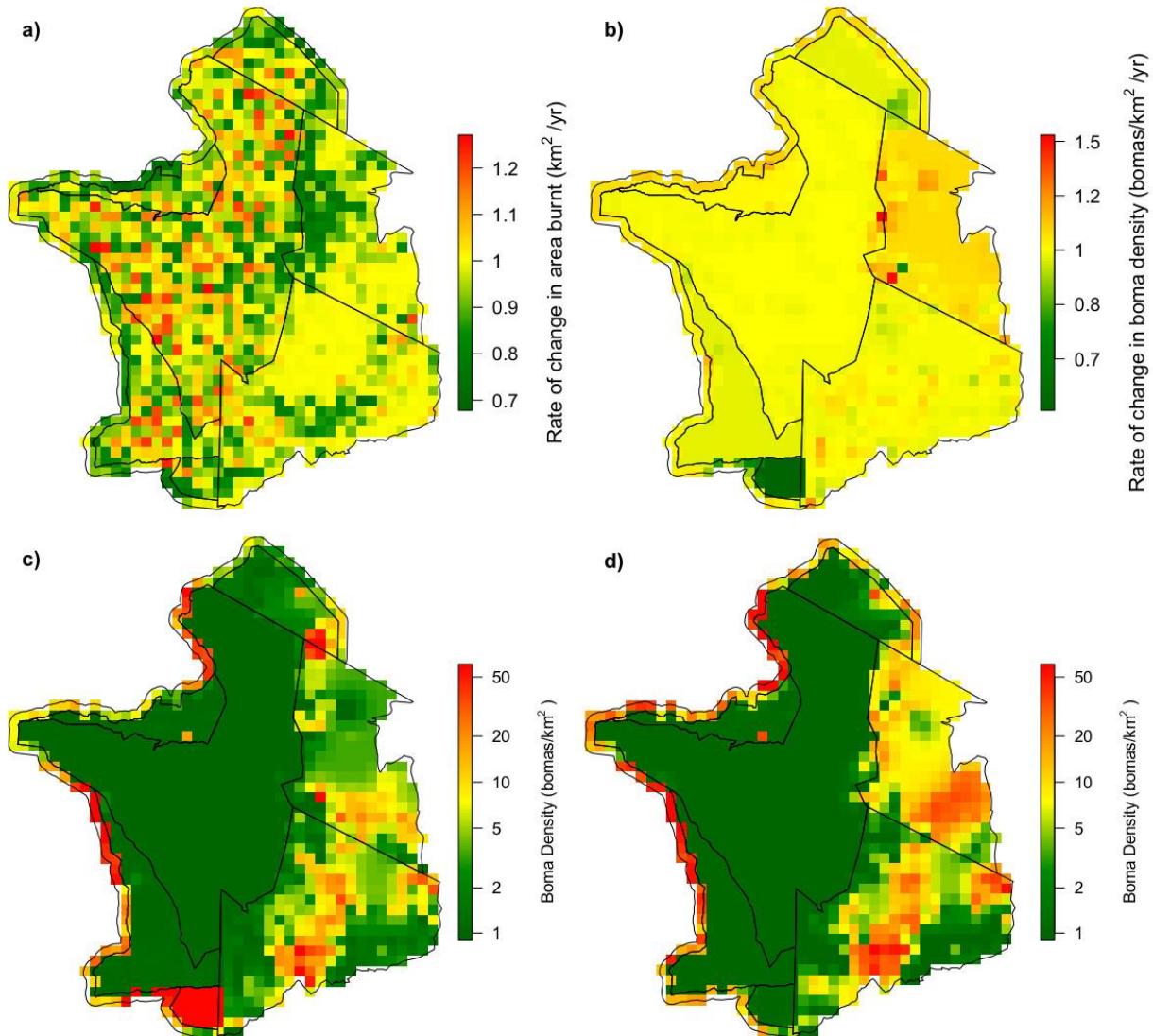


Figure 5: a) The rate of change in the area burnt (km^2/yr), b) the rate of change in the boma density ($\text{bomas}/\text{km}^2/\text{yr}$), c) predicted boma density in 2001, and d) predicted boma density in 2014. Note active removal of bomas from Mwiba occurred from 2006.

Spatial drivers of fire

Our INLA models suggest that both monthly and cumulative rainfall play an important role in driving the behaviour of individual fires in the Serengeti-Mara. The results supported a link between higher monthly rainfall and smaller fires, monthly NPP (which is linked to

monthly rainfall and fuel moisture) with smaller and cooler fires, and also suggested higher monthly rainfall shifted fires later into the year (Supplementary Material Fig. 4). The effect of cumulative rainfall was non-linear. Both high and low cumulative rainfall resulted in fires occurring later in the year and also in shorter times since last fire (Fig. 6). Our models also suggested that fires were smaller in areas with high boma density, and detected some known methodological issues with MODIS data, such as suggesting that larger fires had higher fire radiative power, and that time since last fire increased with year (Supplementary Material Fig. 4).

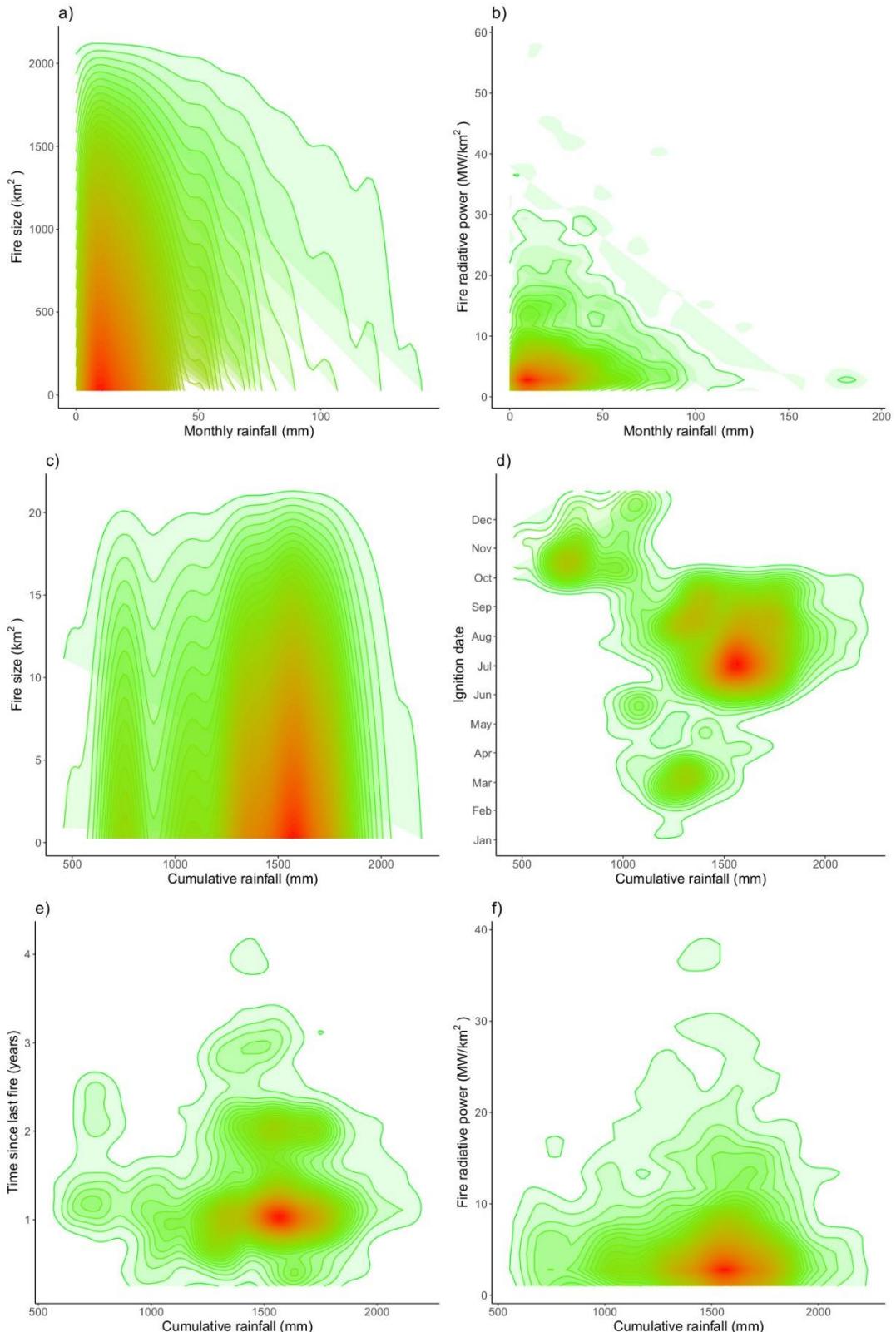


Figure 6: The relationship between monthly rainfall and, a) fire size and b) fire radiative power, and between cumulative rainfall and, c) fire size, d) ignition date, e) time since last fire and f) fire radiative power. Warmer colours indicate space where the highest density of fires occur.

Temporal drivers of fire

We identified 27,145 km² (74.7% of our study area) where two or more satellite images from different years overlapped. Within these areas we recorded 55,940 *bomas* in satellite images dating from 2001 to 2017. The highest boma density for an area of overlap in a single year was 56.4 *bomas/km²*, whilst large areas contained no bomas throughout the study period. The trends in boma density over time differed widely across the ecosystem with boma density in some pixels increasing at a rate of 1.53 *bomas/km²/yr* and in others decreasing by 0.55 *bomas/km²/yr* (Fig. 5b, c, d).

Our model estimated that an increase of 0.01 *bomas/km²/year* was associated with a 10% decline in the area burned in each cell per year. A post-hoc Tukey's test found no difference in the relationship between area burnt and boma density between Grumeti, SNP and Maswa and no difference between NCA, Loliondo and the buffer zone (Fig. 7). The rate of change in the area burnt in a pixel was strongly positively correlated with both the rate of change in fire size ($p < 0.001$, $r^2 = 0.66$, $df = 1066$) and the rate of change in the number of fires ($p < 0.001$, $r^2 = 0.42$, $df = 1066$). Model selection removed only a single term from our model explaining the rate of change in boma density (the interaction between the rate of change in mean annual rainfall and the baseline area burnt ($df = 1$, $\chi^2 = 0.0047$, $p = 0.268$)). The rate of change in boma density, rate of change in mean annual rainfall, management unit, the baseline area burnt and mean annual rainfall were all significant predictors of the rate of change in the area burnt (Supplementary Material Table 2).

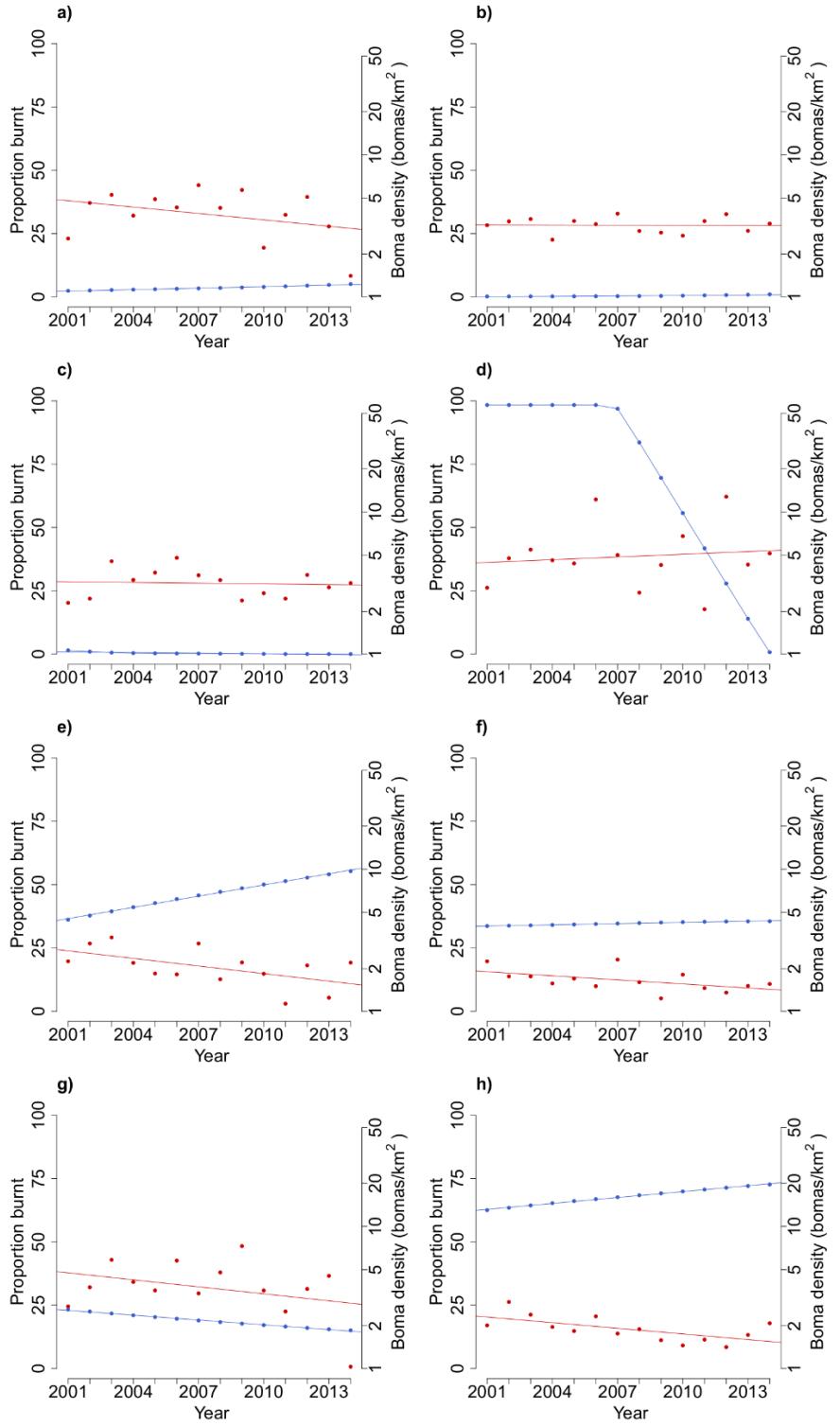


Figure 7: The proportion burnt each year (red) and the predicted boma density each year (blue) for: a) Grumeti, b) SNP, c) Maswa, d) Mwiba, e) Loliondo, f) Ngorongoro, g) Maasai Mara and h) the 5 km buffer zone. Note the contrasting patterns between d) Mwiba (where boma density is decreasing and the area burnt increasing), e) Loliondo (where boma density is increasing and the area burnt is decreasing) and b) SNP (where boma density and area burnt are stable).

DISCUSSION

Our study provides the first comprehensive spatial and temporal assessment of fire regimes across the wider Serengeti-Mara ecosystem. High spatial variability in the characteristics of individual fires across the Serengeti-Mara was primarily driven by differences in rainfall. Strikingly, we found that fire declined over time, to virtually zero in some areas. This was principally driven by human activities: both an increase in livestock density, and variable fire management objectives and practices throughout the Serengeti-Mara ecosystem. We observed contrasting spatial patterns in the temporal trends in different areas of the system that would have been obscured by a larger-scale analysis, emphasising that fire studies need to be spatially explicit at the relevant scale. While the response to rainfall was expected (Archibald et al. 2009), the effect of fire management found here differs from previous studies (e.g. van Wilgen et al. 2004). Our results raise concerns over the long-term functioning of the Serengeti-Mara as a savannah system (Andela et al. 2017; Sinclair et al. 2007; Hempson et al. 2017).

Our study showed that rainfall is the primary driver of the behaviour of individual fires in the Serengeti-Mara. The principal effect of the Serengeti-Mara's bimodal rainfall pattern was to create corresponding bimodal fire seasons with fewer fires occurring in wetter months. Higher monthly rainfall reduced both the size and radiative power of fires occurring in those months, presumably due to the dampening effect of green vegetation on fire. Fires occurred later in areas of both high and low cumulative rainfall. Whilst this result may initially seem contradictory, we suggest that high rainfall areas remain wetter for longer, resulting in fires occurring later into the long dry season, whilst low rainfall areas remain dry for longer, resulting in fires occurring for longer at the end of the long dry season. Our findings concur with other African studies that concluded that by modifying grass growth rates (Sinclair, 1975), cumulative rainfall is primarily responsible for fire size, intensity and return interval (although our study did not make explicit links between rainfall and primary productivity), whilst rainfall immediately preceding the date of a fire increases fuel moisture, decreasing fire size and intensity and resulting in fewer fires in wet periods (Govender et al. 2006; van Wilgen et al. 2004).

We proposed several possible drivers of changes in the Serengeti-Mara's fire regime: changes in rainfall, management regimes, and increased wildebeest numbers. Rainfall increased across most of the ecosystem during the study period and, as expected, this increase had a significant positive effect on the total area burnt (Van Wilgen et al. 2004). Although managers may indirectly affect the fire regime (e.g. by fragmenting the landscape through roads/fire breaks or by modifying herbivore distribution through construction of artificial water points) (Beale et al. 2013), it is unlikely that direct fire management practices could be responsible for such large decreases in the area burnt. Van Wilgen et al. (2004) examined different fire management approaches in Kruger National Park over a 45 year period and found that total area burnt was a function of rainfall and was entirely independent of fire management policy, although other characteristics of the fire regime could be influenced (e.g. season of fire). It therefore seems unlikely that managers in the Serengeti-Mara should be able to significantly influence the area burnt by pursuing specific burning objectives.

In the 1960s and 1970s the Serengeti-Mara's wildebeest increased in abundance roughly six-fold, resulting in a reduction in the area burnt through their consumption of grass biomass (Dublin, 1995). The wildebeest population has since stabilised (Hopcraft et al. 2015), so it is unlikely wildebeest account for the reduction in the area burnt observed in this study. It is possible, however, that localised changes in the distribution of wild grazers mediate the fire regime at finer scales (Kimuyu et al. 2014). The organisations managing Grumeti, Maswa and Mwiba have all changed within our study period, representing both changes in management approaches to burning and the intensity of management interventions.

Grumeti has seen a fourfold increase in the biomass of resident wild herbivores between 2003 and 2015 including a tenfold increase in its buffalo population (Goodman & Mbise, 2016). This increase is not possible by reproduction alone and must therefore be caused by immigration into Grumeti from other areas of the Serengeti-Mara, indicating that local increases and decreases in wild herbivores are taking place. However, in Grumeti there was no significant change in any of the six characteristics of the fire regime we examined, suggesting that either an increase in wild herbivores was having no effect, perhaps because the area's high rainfall offsets any impact, or the effect was being offset by other management actions, such as the exclusion of cattle encroachment.

Whilst the change in the area burnt did not appear to be linked to changes in rainfall, wild herbivores or fire management policy, livestock density (and associated grazing) was strongly implicated as the key factor driving the decline in the area burnt over our study period. By consuming grass biomass livestock reduce the available fuel, limiting the ability of fires to spread to the point where they are not large enough to be detected by MODIS (Archibald et al. 2009; Donaldson et al. 2017), and highlighting the importance of fuel loads over ignitions in savannah systems (Archibald et al. 2010b, 2013; Frost, 1999). Our analysis found the relationship between *boma* density and the area burnt was different in management units which excluded all livestock (SNP, Grumeti and Maswa) and in management units which permitted livestock (NCA, Loliondo and the buffer zone). This suggests that management decisions and actions related to livestock may represent the largest effect land managers can have on fire regimes. Previous studies in the Serengeti-Mara observed a decline in the area burnt as wild herbivore numbers increased (Dublin, 1975), but it is significant that the decline we observed took place within the Serengeti-Mara's protected areas and was caused by year round grazing by increasing populations of relatively sedentary livestock, rather than seasonal grazing by migratory wild herbivores. Our findings also contrast previous studies which found that land cover change was restricted primarily to the Kenyan portion of the Serengeti-Mara (Homewood et al. 2001).

Overgrazing is frequently identified as a cause of degradation in savannah and grassland ecosystems (Brauch & Spring, 2011; Oldeman et al. 1990), resulting in reduced biodiversity (Alkemade et al. 2013), increased soil erosion (Kosmas et al. 2015), decreased soil carbon storage (Dlamini et al. 2016), bush encroachment (Coetzee et al. 2007) and desertification (Homewood and Rodgers, 1987). We observed the modification of the fire regime as a result of increasing grazing pressure from livestock (Hempson et al. 2015; 2017). In the buffer zone and parts of Ngorongoro and Loliondo the area burnt has been reduced to virtually zero. This exclusion of fire represents a substantial shift in the dominant driver of spatial heterogeneity in these areas, a shift which is likely to be outside the range of variation that evolved within this system (Gillson & Duffin, 2007), and which may surpass critical ecological thresholds (Gillson & Ekblom, 2009), leading to a change in stable state (Eby et al. 2017). Fire plays an important role in governing the structure and function of the

Serengeti-Mara (Anderson et al. 2012; Holdo et al. 2009) and its exclusion could lead to an increase in bush encroachment (O'Connor et al. 2014), the displacement of wild herbivore species (Madhusudan, 2004), and a shift in the grass community from palatable to unpalatable species (Smith et al. 2013). This will simultaneously limit productivity in terms of pastoralism and tourism; the two principal means of income generation in the region. Existing livestock densities in some areas may be too high for savannahs to persist in their current state, and there is therefore an urgent need to re-evaluate the status and management of these areas to ensure the success of both conservation objectives and the socioeconomic prosperity of the Serengeti-Mara's human population.

CONCLUSIONS

This is the first study to document the spatial and temporal fire patterns and drivers across the wider Serengeti-Mara ecosystem. Whilst some patterns were expected, we did not anticipate such a large decline in the area burnt in some areas of the system. Our findings are consistent with studies reporting a global decline in the area burnt, particularly in savannahs, and raising concerns about the impact this decline has on the ecology of these ecosystems (Andela et al. 2017). The suppression of fire is likely to result in changes in the structure, function, and biodiversity of some areas of the Serengeti-Mara which may not be compatible with the objectives of the stakeholders involved in these areas (Trollope et al. 2002). For instance, a possible consequence of a decline in the area burnt is the increase in understorey tree and bush recruitment recently documented in the Serengeti-Mara (Holdo et al. 2014; O'Connor et al. 2014). Given the 40% and 39% decline in the number of fires and the area burnt respectively, our results suggest that some areas of the Serengeti-Mara may already have been substantially modified and the widespread decreasing trend in these aspects of the fire regime indicates other areas require close monitoring to achieve the desired management outputs. If periodic burning is a management goal, then our results suggest that altering the suppressive effects of intense grazing by resident livestock will result in more fires and larger areas burnt. Our findings underscore the importance of managers monitoring fire and using the information they gather to inform future management decisions.

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SUPPLEMENTARY MATERIAL

Table 1: The error structures, link functions and data transformations for all GLMs.

	Model	Error structure	Link function	Data transformation
Preliminary models	Change in fire size	Gaussian	Identity	Log
	Change in ignition date	Gaussian	Identity	Log
	Change in time since last fire	Gaussian	Identity	Log
	Change in radiative power	Gaussian	Identity	Log
	Change in number of fires	Gaussian	Identity	Log
	Change in area burnt	Gamma	Log	-
	Change in boma density	Poisson	Log	-
	Change in mean annual rainfall	Gaussian	Identity	-
	Final Model	Gaussian	Identity	-

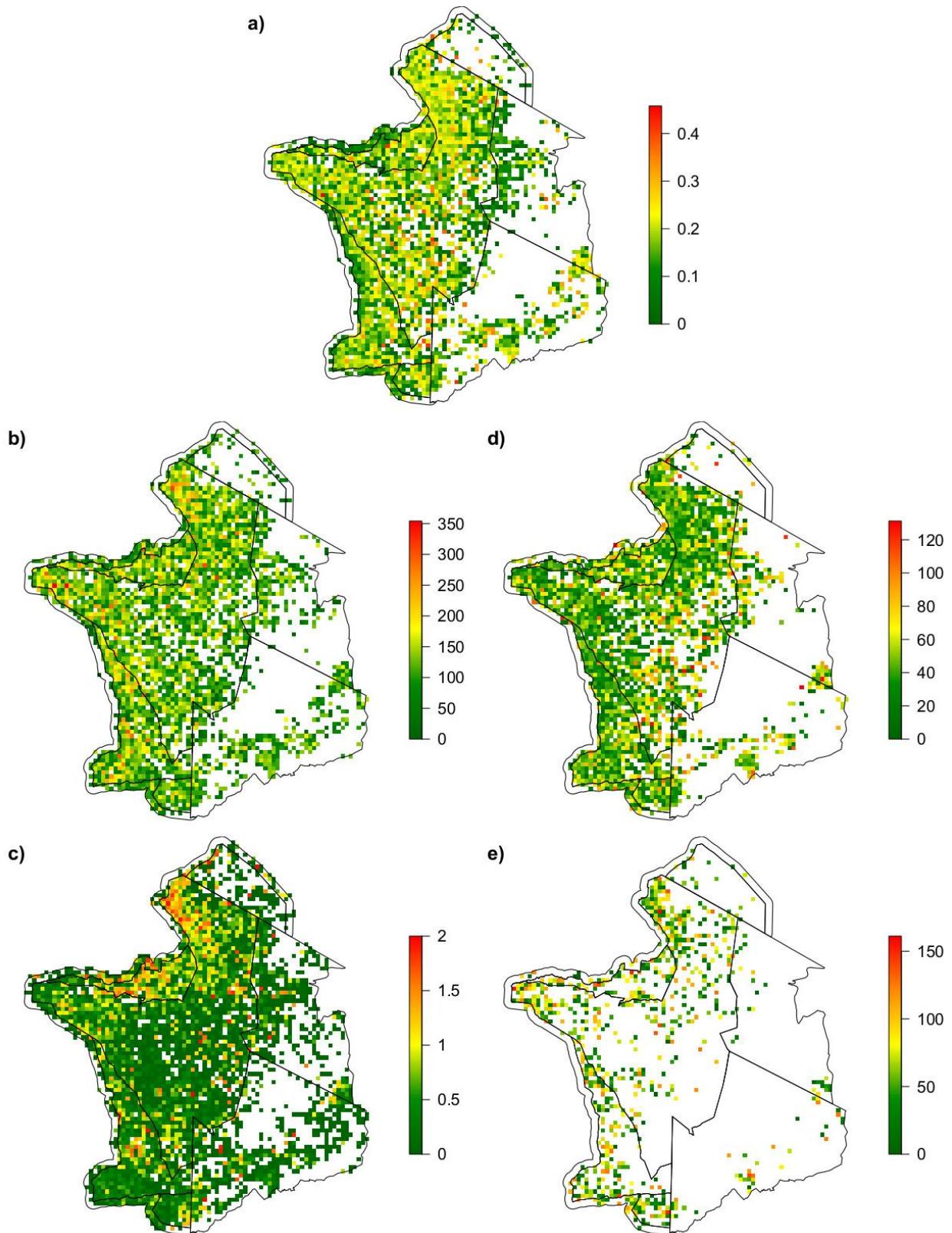


Figure 1: Variability (measured by the coefficient of variation) in: a) the number of fires, b) fire size, c) ignition date, d) time since last fire, and e) fire radiative power. Note ignition date is more variable in the north-west. Variability is measured by the coefficient of variation except for ignition date, for which the angular variance was used.

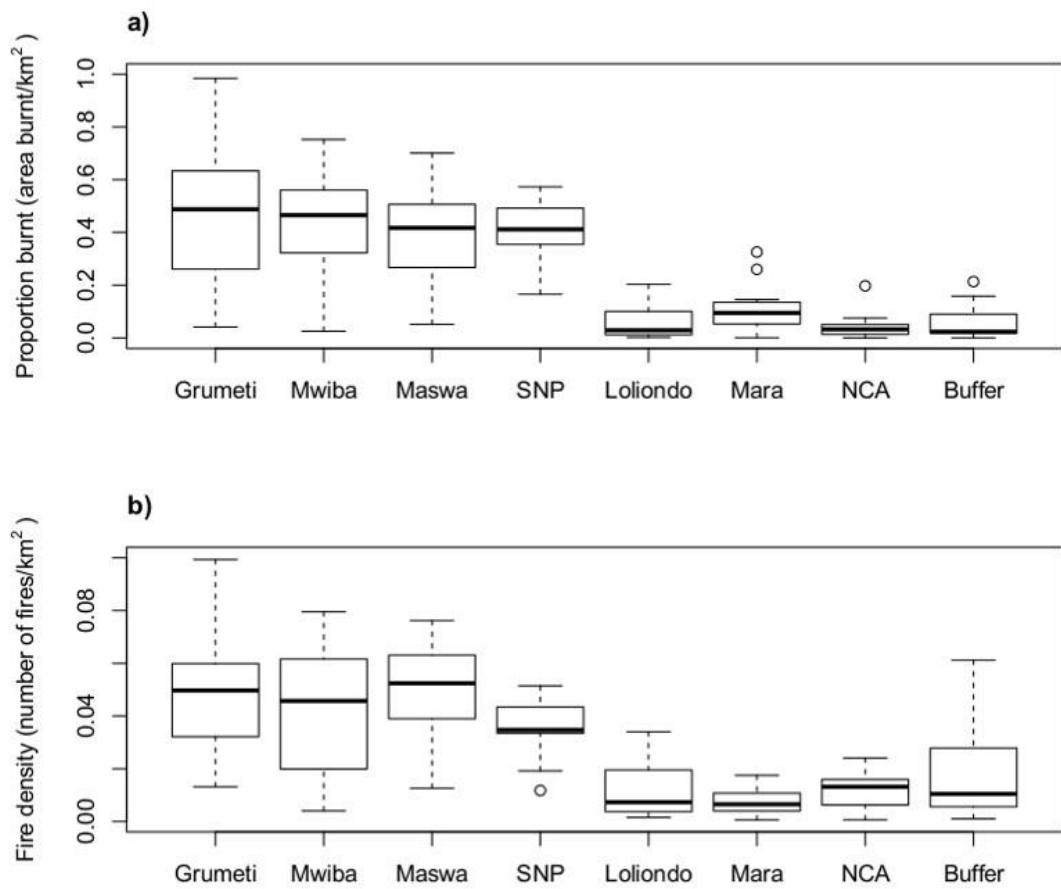


Figure 2: a) The proportion burnt and b) the number of fires per km² in each management unit during our study period.

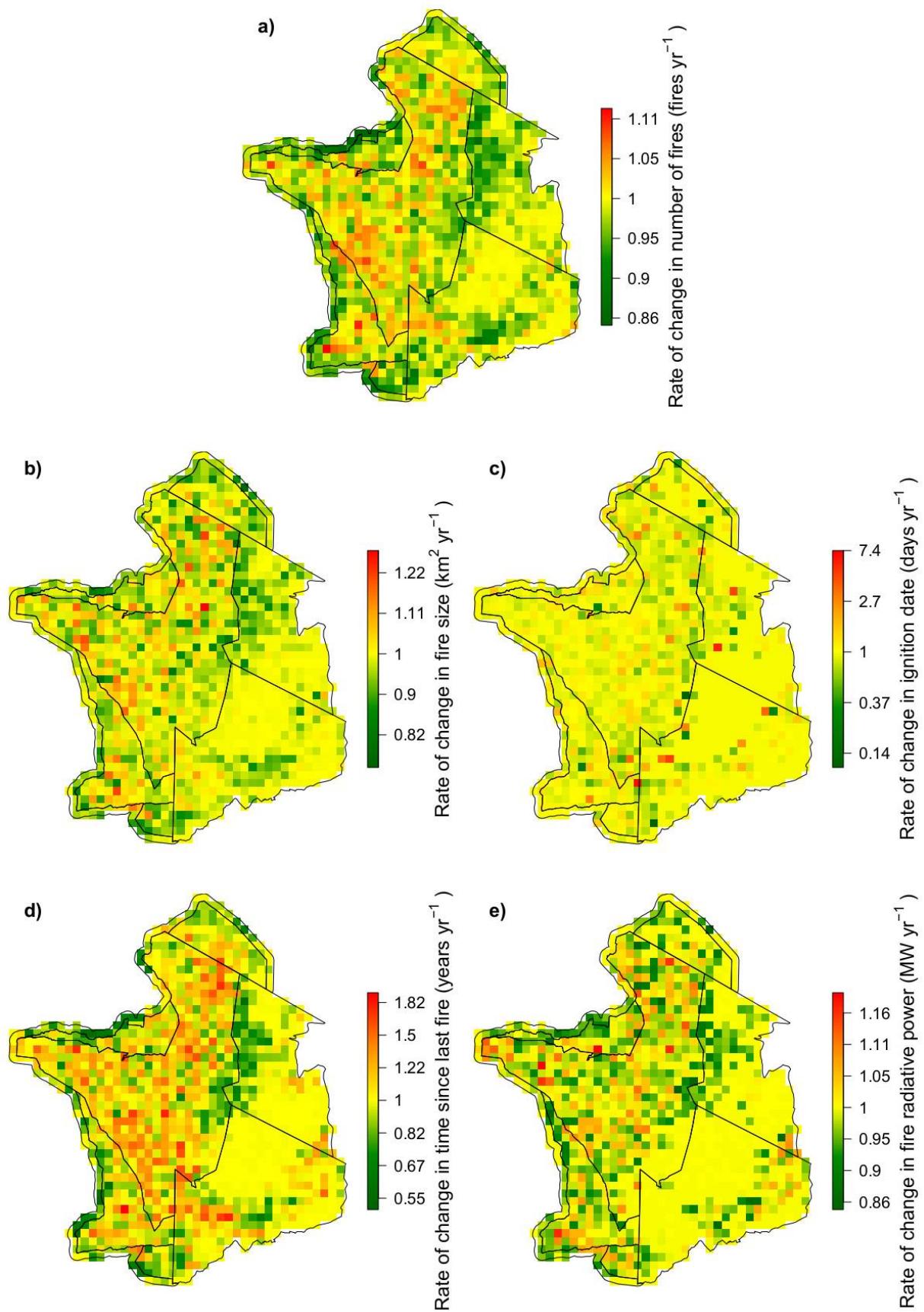


Figure 3: The rate of change in: a) the number of fires, b) median fire size, c) median ignition date, d) median time since last fire, and e) median fire radiative power.

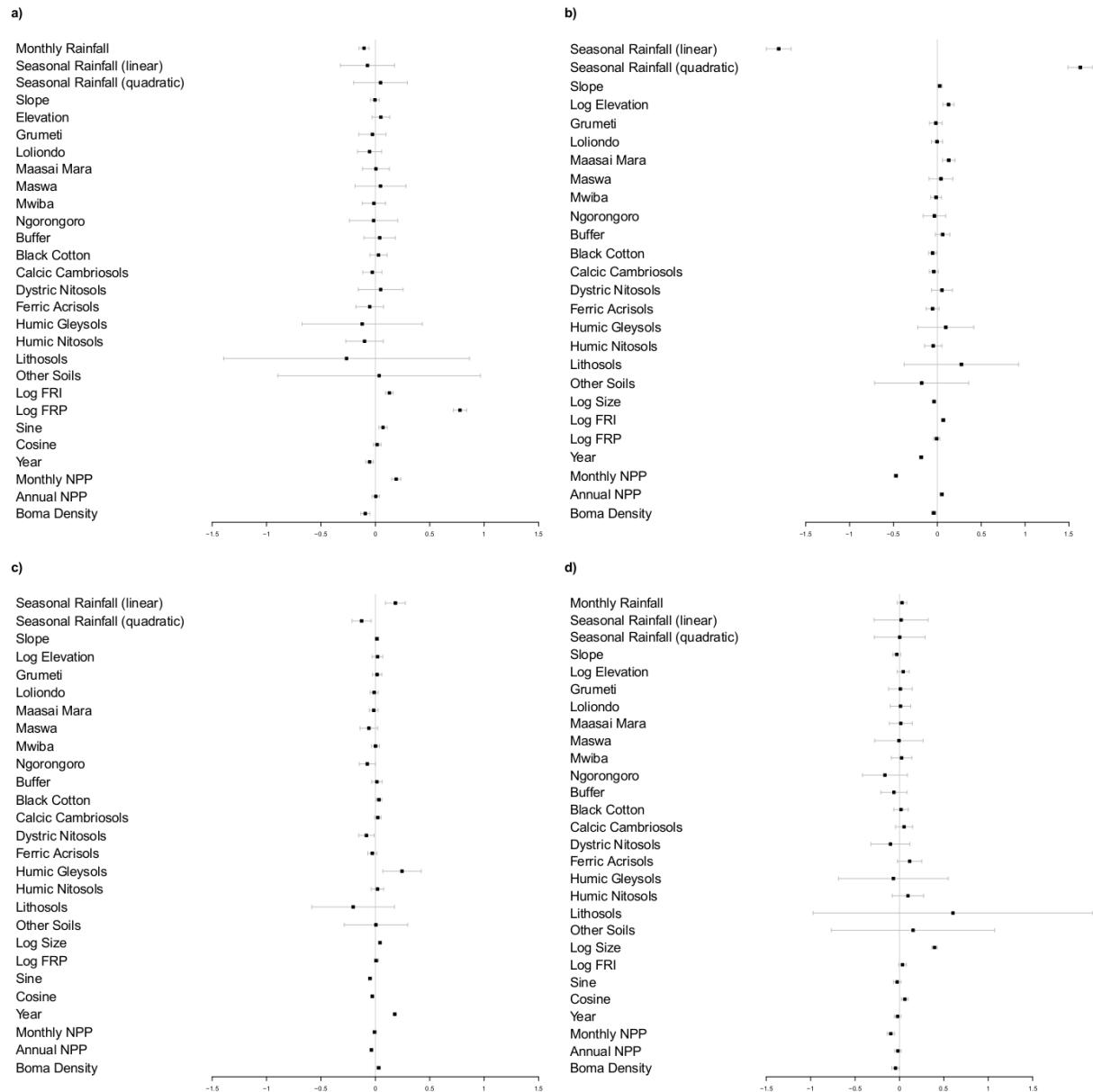


Figure 4: The 95% credible intervals for each fire trait from the INLA models: a) fire size, b) ignition date, c) time since last fire, and d) fire radiative power.

Table 2: The results of our GLM on the rate of change in the area burnt.

Variable	Df	Deviance	Residual Df	Residual deviance	Pr(>Chi)	Significance
NULL	-	-	1067	1067	-	-
Change in boma density	1	50.46	1066	1016.54	<0.001	***
Change in mean annual rainfall	1	1.34	1065	1015.20	0.05	.
Management	6	42.73	1059	972.47	<0.001	***
Baseline area burnt	1	569.59	1058	402.89	<0.001	***
Mean annual rainfall	1	24.83	1057	378.06	<0.001	***
Change in boma density:baseline area burnt	1	0.08	1056	377.98	0.64	
Change in boma density:mean annual rainfall	1	6.77	1055	371.21	<0.001	***
Change in mean annual rainfall:mean annual rainfall	1	1.36	1054	369.85	0.049	

Chapter 3

Same same but different: Fire and grazing have contrasting functional effects on African savannah vegetation



Cover illustration:

Sporobolus ioclados (Trin.) Nees a common grass species in the Serengeti-Mara. Modified from *Illustrationes floriae atlanticae, seu icones plantarum novarum* (Cosson & Barratte, 1882).

ABSTRACT

1. Fire and grazing are important consumers of plant biomass in many ecosystems. It has been suggested that fire may be viewed as a generalist herbivore, but this has not been quantified and the degree to which these two consumers may be considered functionally equivalent is unknown.
2. Using a large-scale experimental approach, we quantified the impacts of fire and grazing by the wildebeest migration on six measures of savannah vegetation over a six-month period: grass biomass, grass patchiness, grass quality, forb abundance, forb species richness and forb community composition.
3. We found that fire and grazing had similar effects on grass structure, but that these similarities were superficial as they had distinct differing effects on grass quality and on forb community composition.
4. Our results highlight the importance of maintaining both fire and herbivory as consumers in savannah systems and suggest that the extirpation of large mammals across much of the world as well as fire suppression can have had significant impacts on savannah floral diversity.

Keywords: Fire, grazing, herbivores, wildebeest, savannah, consumers, Serengeti, forb

INTRODUCTION

Opposing schools of thought exist concerning the primary factor determining the distribution of biomes globally. The green world hypothesis states that climate is the primary driver, that by constraining plant growth, climate sets an upper limit on the plant biomass of a region (Hairston et al. 1960). Certainly, it is possible to make broad predictions concerning plant biomass and habitat structure based on available sunlight, moisture and temperature, however, large areas of the world do not conform to these predictions (Polis, 1990; Whitaker, 1975). In many areas, consumers, such as herbivores and fire, maintain plant biomass at a level far below the potential predicted by climate (Bond et al. 2005, Bond & Keeley, 2005). There are parallels between fire and herbivory, and it has been suggested that fire can be viewed as a generalist herbivore (e.g. Bond & Keeley, 2005), yet the distinction between the ecology of brown worlds (herbivore controlled) and black worlds (fire controlled), and whether these two consumers can be considered functionally equivalent, is not clear.

Savannahs are one example of a consumer-controlled biome. They cover as much as 20% of the Earth's land surface and are a dominant terrestrial biome in tropical regions, providing significant economic and cultural value, carbon storage capacity, and habitat for diverse assemblages of unique species (Bond & Parr, 2010; Grace et al. 2006; Scholes & Archer, 1997). They are principally defined by a continuous layer of C₄ grasses, but vegetation structure can vary from open grasslands to areas with as much as 80% tree cover (Ratnam et al. 2011; Sankaran et al. 2005). Fires are most frequent in tall grass savannahs with low herbivory, whilst grazers are most abundant in short grass areas where there is not enough biomass for regular fires (Archibald et al. 2005). Both fire and herbivory remove low-quality moribund grass, allowing a flush of nutritious regrowth which is highly attractive to grazers (McNaughton, 1976). Positive feedback mechanisms can maintain areas in either short or long grass states (Archibald & Bond 2003; Donaldson et al. 2018), and specialisation in plant traits suggests many species have adapted to frequent disturbance by fire and herbivory (Diaz et al. 2004; Keeley et al. 2011; Ripley et al. 2015). Changes in fire and herbivory can have important consequences for the ecology of savannah systems (Parr et al. 2011), including rapid shifts in vegetation structure and turnover in plant communities (Archibald

et al. 2013; Lehmann et al. 2011). Both fire and herbivores can be important disturbances within the same ecosystems and both consume biomass, but they do so through contrasting mechanisms, and vary in their selectivity for certain species, effect on woody cover, and differ in their frequency, geographic extent and the degree to which they can be manipulated or controlled by land managers (Anderson et al. 2007). The degree to which the short-term effects of these two consumers can be viewed as functionally equivalent has not been quantified and the implications of fire suppression, herbivore extirpation and habitat conversion on consumer-controlled biomes remains unclear.

Much of our understanding of how fire and herbivory interact to influence savannah vegetation is derived from southern African systems (e.g. Donaldson et al. 2018; Hempson et al. 2014 Trollope et al. 2014). However, in the Serengeti-Mara ecosystem of Southern Kenya and Northern Tanzania, the annual migration of approximately 1.4 million wildebeest (*Connochaetes taurinus* Burchell, 1823) represents a level of disturbance not seen in systems with primarily resident grazers (Hopcraft et al. 2013). The migration exerts intense grazing pressure over a relatively brief period and may also provide significant nutrient inputs through the deposition of dung and urine (McNaughton, 1979, 1984). In this way the wildebeest migration acts much like a fire, rapidly removing large quantities of biomass and simultaneously providing significant post-disturbance nutrient inputs. This pattern of grazing may also be more typical of grazing in African savannahs before mega-herbivory across the continent was disrupted by human influence (Owen Smith, 1988). If the effects of grazing by the wildebeest migration are analogous to those of fire it would suggest that under certain circumstances the distinction between brown and black worlds is less obvious than previously thought and may have important practical implications for managing savannahs in the Anthropocene. From a conservation perspective, it is important to understand the consequences if the wildebeest migration were to be disrupted, decline or collapse, or if fire regimes are altered by increasing human pressures, the uncertain impacts of climate change, or programmes such as REDD+ (Reducing Emissions from Deforestation and Forest Degradation) which may promote fire suppression (Bond & Parr, 2010; Parr & Chown, 2003).

Using a large-scale experiment, we examined to what extent fire and grazing by the wildebeest migration have functionally similar effects on savannah vegetation. Specifically, we examined the short-term effects of early dry season fires and grazing by the wildebeest migration in the Western Corridor region of the Serengeti-Mara ecosystem over a six-month period. We focused on six measures of savannah vegetation: grass biomass, grass patchiness, grass quality, forb abundance, forb species richness and forb community composition. We anticipated that fire and wildebeest grazing will both reduce grass biomass, but that greater selectivity and the input of dung and urine will result in a patchier distribution of this biomass and higher grass quality in wildebeest grazed areas. Forbs (non-graminoid herbaceous flowering plants) are understudied in savannah ecology and yet are abundant in natural savannahs, representing a large portion of savannah diversity (Zaloumis & Bond, 2011), and, due to competition with grass, are one of the guilds likely to be most responsive to changes in biomass (Bond & Keeley, 2005). We therefore predicted that the direct and indirect effects of fire and wildebeest grazing will result in similar forb abundance, species richness and community composition.

METHODS

Study area

Our study was carried out in Grumeti Game Reserve (417 km^2) and Ikona Wildlife Management Area (242 km^2) (2.0185° S , 34.2199° E). These protected areas are located in the Western corridor region of the Serengeti-Mara ecosystem in Northern Tanzania and are bounded by non-protected village lands to the north and west, Serengeti National Park to the south, and Ikorongo Game Reserve to the east (Fig. 1). They form part of the buffer zone between Serengeti National Park and local communities and neither protected area allows human settlements or grazing within their boundaries.

Whilst the Serengeti-Mara system contains a wide range of environmental conditions and habitat types our study site experiences only a limited subset of these. Mean annual rainfall is at the upper end of the range for the ecosystem, varying between 800 and 1400 mm per year, and occurs in two distinct rainy seasons (Norton-Griffiths et al. 1975). The soil is predominantly composed of alluvial deposits from old lake beds but there is granitic rock beneath this which becomes more prominent on ridges and hills (Jaeger, 1982). Woody cover is high for the Serengeti-Mara. *Terminalia* woodlands can be found on the ridges and hills whilst lower areas tend towards open plains dominated by *Themeda triandra* with occasional *Acacias* and *Balanites*, and riverine forest can also be found along the Grumeti River (Sinclair, 1979). The high rainfall in the Western Corridor results in more fires than other areas of the Serengeti-Mara and it is one of the few places in the ecosystem which can burn twice in a single year (Chapter 2). The wildebeest migration typically arrives in the Western Corridor at the start of the long dry season (May) and has continued its journey north to the Maasai Mara by July or August. However, the movement of the migration is highly variable and difficult to predict (Hopcraft et al. 2015).

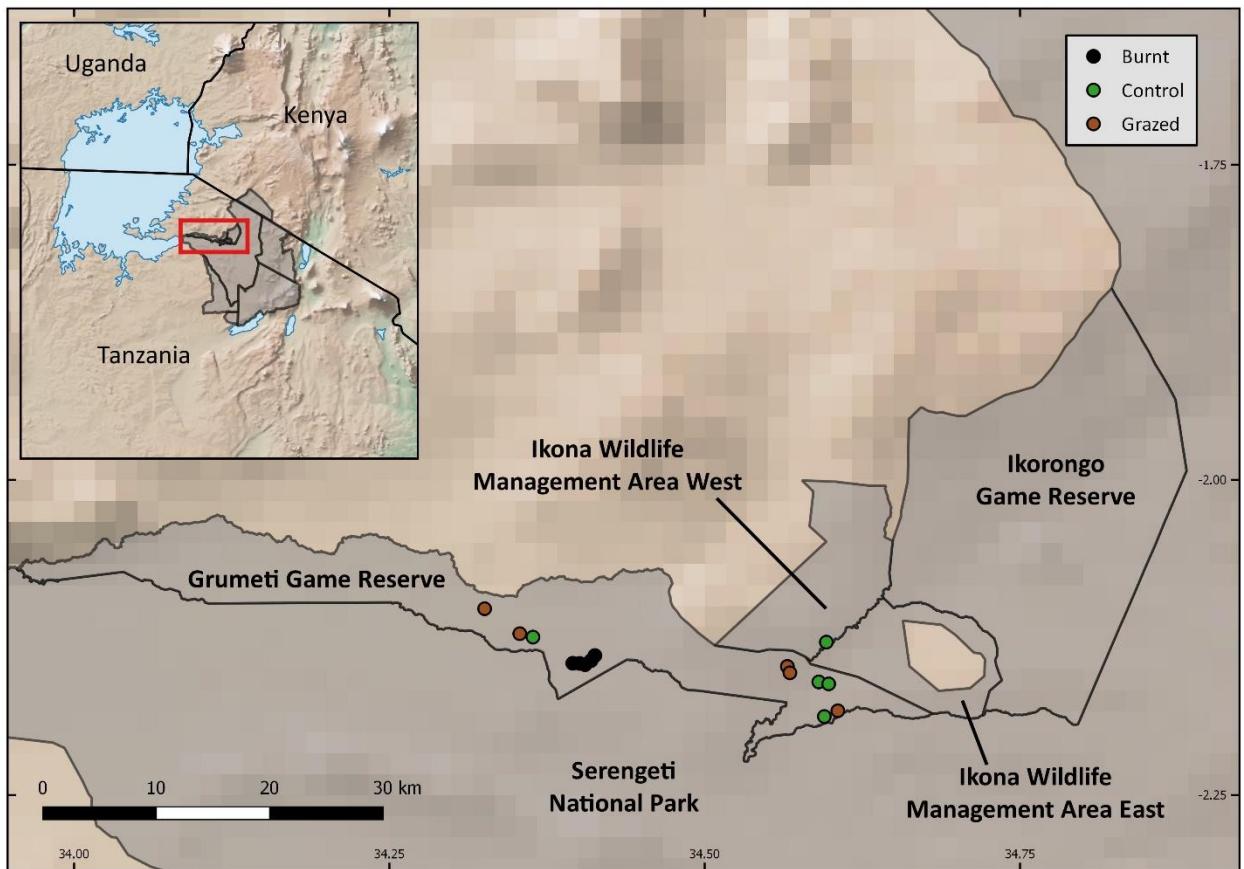


Figure 1: Map of study area with the location of survey plots. Burnt plots are black, wildebeest plots brown and control plots green. The base map is of elevation (made with Natural Earth) with protected areas shown in grey.

Data collection

To determine the effects of fire and herbivory we used a post-hoc natural experimental design. We sampled 15 plots, split equally between three treatments: 1) burnt with resident herbivores, 2) unburnt but grazed by the wildebeest migration and resident herbivores or 3) unburnt and ungrazed by the wildebeest migration but with resident herbivores (control). We surveyed all plots six times between mid-August and late September 2016 and once in mid-January 2017. Plots in our burnt treatment burnt on 16th July 2016 and wildebeest arrived in Grumeti from the start of June 2016.

Each plot was 50 x 50 m (0.25 ha) with a standardised sampling protocol. Grass quantity (vegetative height, inflorescence height and biomass) was sampled every 2 m along two 50

m line transects on each plot. Grass biomass was measured using a disc pasture metre (DPM). We collected samples of new grass growth from each plot in August, September and January. These were analysed for their carbon and nitrogen (C:N) content and the ratio of carbon to nitrogen was used as a proxy for grass quality. Where possible we collected five samples of the same five grass species from each plot: *Themeda triandra* Forssk., *Digitaria macroblephara* Hack., *Cynodon nlemfuensis* Vanderyst., *Bothriochloa insculpta* Hochst. ex A.Rich. and *Panicum coloratum* Linnaeus. The five samples for each species were combined and ground into a homogenous powder for analysis. This was carried out in an elemental analyser calibrated to Acetanilide 114d from the National Institute of Standards and Technology (NIST), Maryland, USA. The forb community was sampled by counting all forbs within two 50 m x 1 m belt transects across each plot. For each individual forb we recorded the morphospecies and the presence or absence of flowers. Morphospecies were later identified to genus level where possible (see Appendix I).

Data processing

We processed our raw data to generate a single value for each response variable per survey: biomass (the quantity of grass in a plot), patchiness in grass vegetative height, inflorescence height and biomass (how this quantity of grass was distributed), C:N ratio (the quality of grass in a plot), forb abundance, forb species richness and forb community composition. To calculate the median biomass per survey, DPM readings in centimetres were converted to biomass in kilograms per hectare using a formula developed specifically for the Serengeti-Mara (Stuart Smith, pers. comm. 18/8/17):

$$\text{Biomass} = 513.9 * \text{DPM}^{0.7}$$

To quantify grass patchiness we used Moran's I to compute the strength and the scale of the autocorrelation in vegetative height, inflorescence height and biomass along each transect. The strength of the autocorrelation varies from -1 to 1, where -1 is perfectly dispersed, 0 is perfectly random and 1 is perfectly clustered. Autocorrelation scale identified the number of points along each transect which were autocorrelated. We calculated separate values for

the patchiness of vegetative height, inflorescence height and biomass because they reveal different aspects of the recovery of a plot following disturbance by either fire or wildebeest grazing. Using the C:N ratio of each of our five grass species we calculated the median C:N ratio in each survey. We calculated forb abundance as the total number of individual forbs found in each survey and the observed forb species richness as the total number of forb species found in each survey. Rarefaction curves indicated that we had undersampled the forb community in some surveys and therefore we estimated forb species richness using the Chao 1 estimator and used this for our analysis (Chao, 1984). We could not estimate forb species richness in plots where no forbs (seven surveys, 6.7%) or only one forb species (three surveys, 2.9%) had been observed, therefore forb species richness in these plots remained either zero or one.

Data analysis

We used reduced-maximum likelihood generalised linear mixed-effects models to test the relationship between our response and explanatory variables. We centered and scaled our data, and used treatment, time and an interaction between the two as fixed effects and plot as a random effect. It was not possible to equally distribute our surveys throughout our study period. Because of this, the final set of surveys would disproportionately influence our results if we included time as a continuous numeric covariate. To avoid this, we included time as an ordered factor, grouping our actual survey dates into survey sets (a set being one survey of every plot), with levels from 1-7. We used diagnostic plots to determine if we had met the assumptions of our models in terms of normally distributed residuals and homoscedasticity. Forb abundance data were subsequently logged prior to modelling to ensure our residuals met our model assumptions.

To visualise the similarity between the forb communities recorded in each of our surveys we calculated the distance between each community using the Bray-Curtis dissimilarity index and plotted the results using non-metric multidimensional scaling (NMDS). We then analysed the effects that treatment and time were having on the distance between communities using a permutational multivariate analysis of variance (PERMANOVA) (Oksanen et al. 2017), and partitioned beta diversity (the pairwise Bray-Cutis dissimilarity

between the forb communities in each survey) into nestedness and turnover (Baselga et al. 2017). We identified the forb species contributing most to the overall Bray-Curtis dissimilarity between our treatments using similarity percentages (SIMPER) (Clarke, 1993). Finally, we used indicator values (IndVal) (Dufrene & Legendre, 1997) to calculate a quantitative index of the fidelity (the proportion of the individuals of a given species that are in a treatment) and specificity (the proportion of the plots in a given treatment that contain a given species) of a species to a treatment. All analyses were carried out in R version 3.2.3 (R Core Team, 2015).

The spatial clustering of our plots made it likely our data would be affected by some degree of spatial autocorrelation. However, we considered a full GLMER with spatial random effects would be overcomplicated, given the quantity of data available. We therefore assessed the strength of the spatial autocorrelation in each response variable using empirical and fitted semi-variograms based on the residuals of each model. We also examined the fire history of each plot by extracting values for fire size, date, return interval, radiative power, and number of fires from Chapter 2 at the location of each plot and using GLMs and post-hoc ANOVAs to determine if they differed between treatments. As fire date was circular data we used a Watson-Williams test to determine if fire dates differed significantly between treatments.

RESULTS

Grass

Grass biomass varied widely across treatments with as much as 3340 kg/ha in some control plots and as little as 682 kg/ha in some burnt plots. Both wildebeest and fire significantly reduced grass biomass, with no significant difference between the biomass in these treatments, and in control plots grass biomass also declined significantly over our study period (Supplementary Material Table 1, Fig. 2).

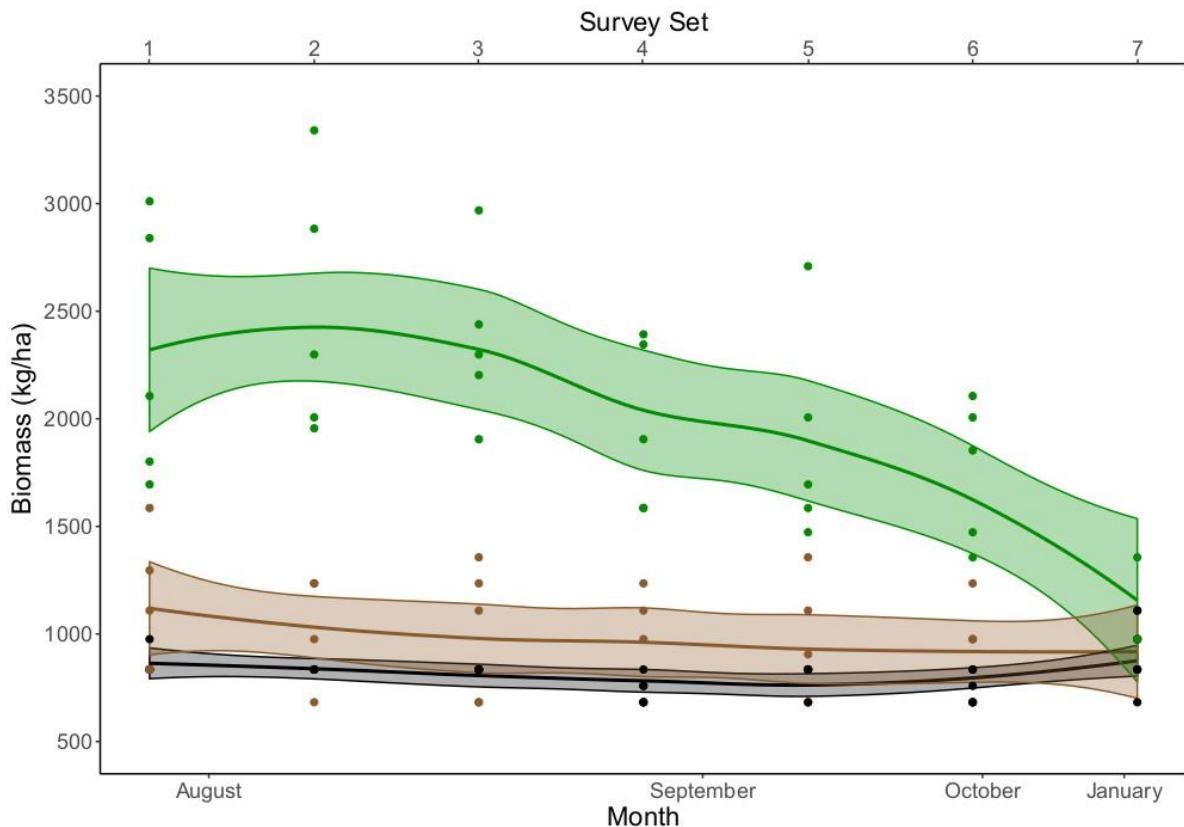


Figure 2: The temporal trends in grass biomass for each treatment. Surveys of burnt plots are shown in black, wildebeest plots in brown and control plots in green.

In addition to differences in the quantity of biomass between treatments, patchiness in the arrangement of that biomass, and how it changed over time, also differed significantly between treatments. The scale of autocorrelation in biomass differed significantly between treatments, with larger patches in control plots than in burnt and grazed plots. In addition

to this, patchiness in inflorescence height became increasingly random in burnt plots over the course of the dry season before becoming more clustered in January. Grazed plots showed the opposite trend, with autocorrelation in inflorescence height becoming more clustered over the dry season and then more random by January. Autocorrelation in inflorescence height in grazed plots became gradually more clustered throughout our study period (Supplementary Material Table 1, Fig. 3).

Grass quality was significantly affected by treatment and was consistently higher (lower C:N ratio) in burnt plots than either wildebeest or control plots (Supplementary Material Table 1). Grass quality also changed significantly over time with C:N ratios declining towards the end of the dry season (September) and then rising again by January. The magnitude of this temporal change was affected by treatment, with greater changes in grazed and control plots than in burnt plots (Supplementary Material Table 1, Fig. 4).

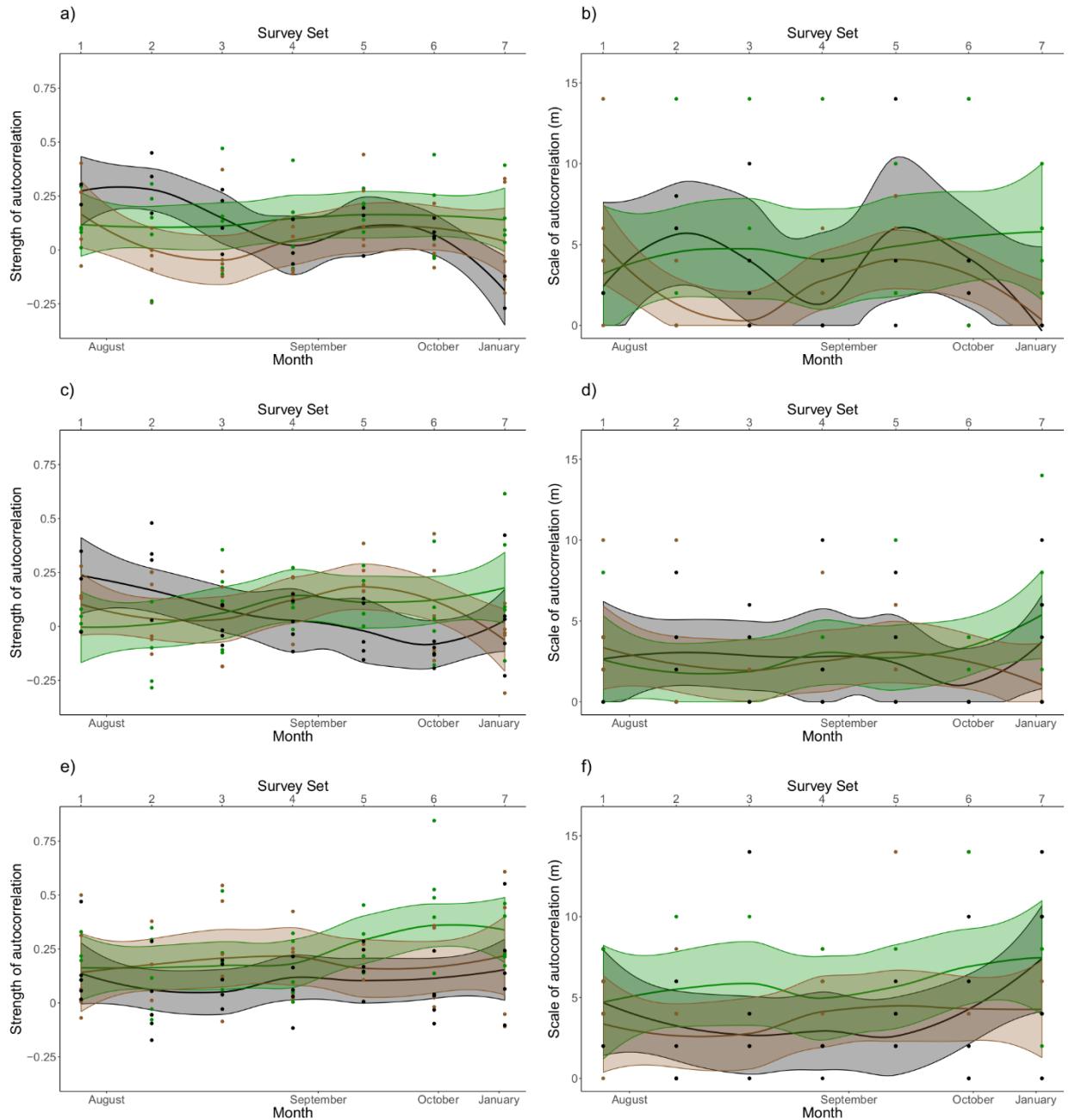


Figure 3: The temporal trends in grass patchiness for each treatment: a) strength of autocorrelation in vegetative height, b) scale of autocorrelation in vegetative height, c) strength of autocorrelation in inflorescence height, d) scale of autocorrelation in inflorescence height, e) strength of autocorrelation in biomass, f) scale of autocorrelation in biomass. Surveys of burnt plots are in black, wildebeest plots in brown and control plot in green.

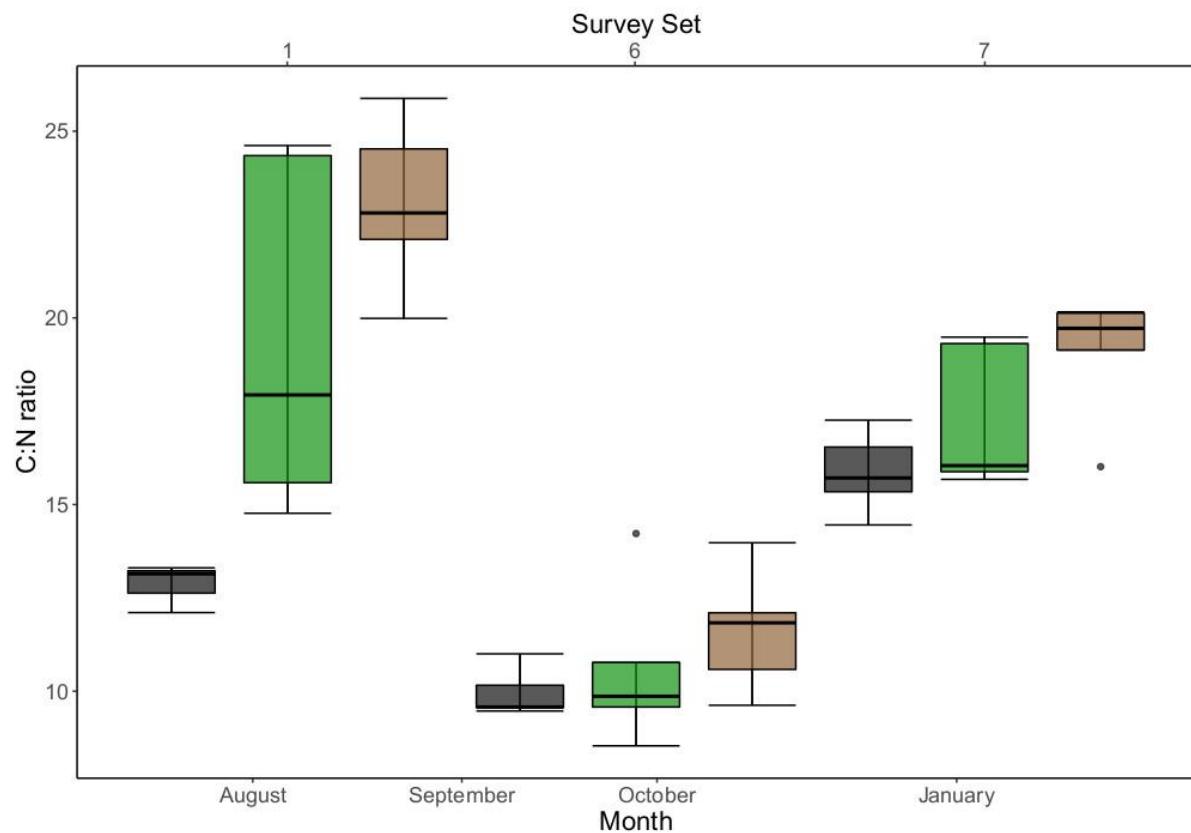


Figure 4: The temporal trends in C:N ratio for each treatment. Surveys of burnt plots are in black, wildebeest plots in brown and control plot in green. Note that a lower C:N ratio indicates more nutritious grass.

Forbs

We recorded a total of 7488 individual forb plants, comprising 111 species and morphospecies. Forb abundance and species richness were not affected by treatment but did change over time with higher forb abundance and species richness in the wet season in January (survey set 7). Treatment significantly affected how forb abundance changed over time with increases particularly apparent in grazed plots (Supplementary Material Table 1, Fig. 5).

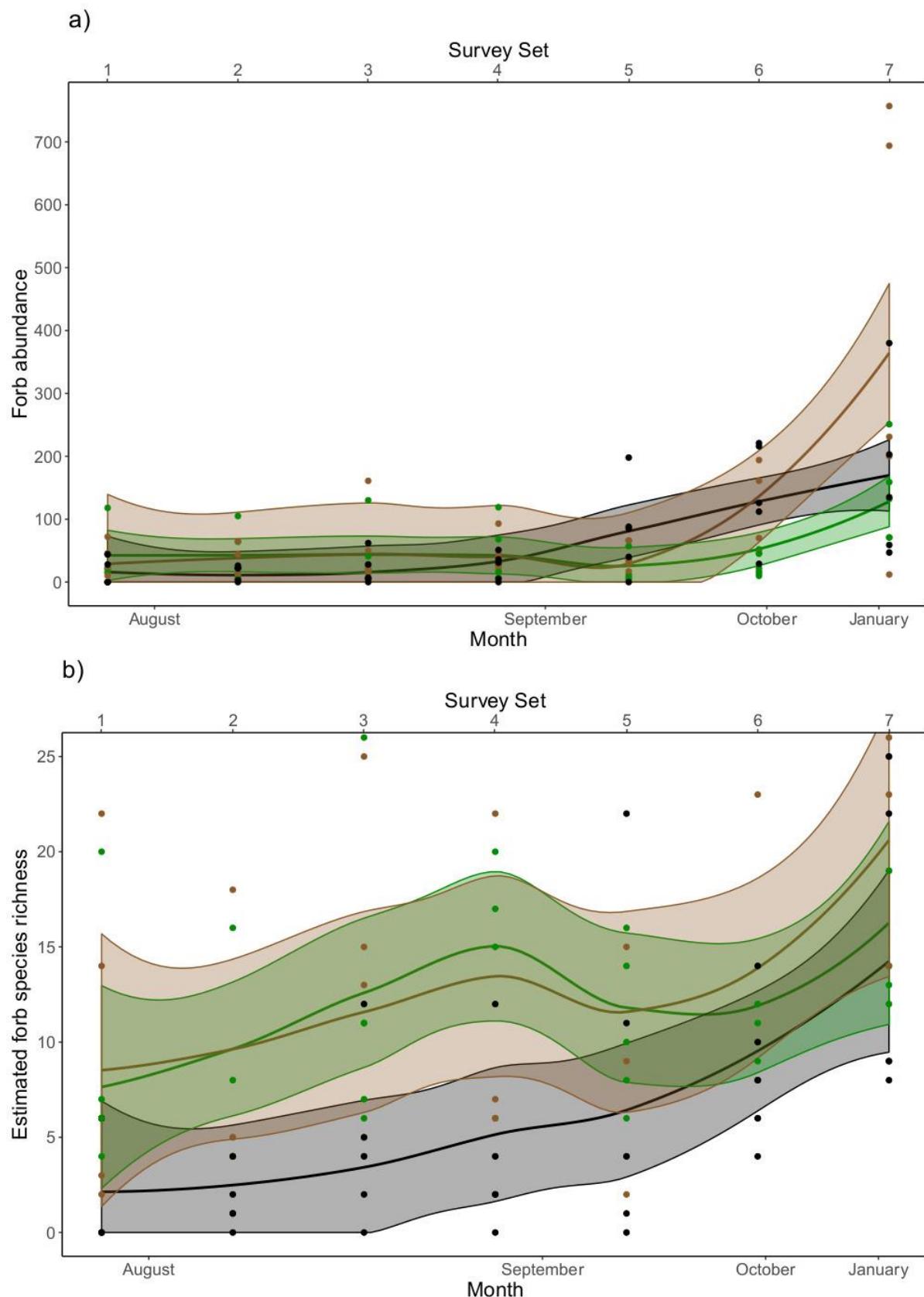


Figure 5: The temporal trends in: a) forb abundance and b) estimated forb species richness for each treatment. Surveys of burnt plots are in black, wildebeest plots in brown and control plots in green.

Treatment had a significant effect on forb community composition with forb communities in burnt plots differing significantly from forb communities in both control plots and wildebeest plots (Supplementary Material Table 2, Fig. 6). Forb communities in control plots did not differ significantly from those in wildebeest plots and were in fact nested within the forb communities in wildebeest plots. There was also a significant change over time with forb communities becoming more similar through time, regardless of treatment.

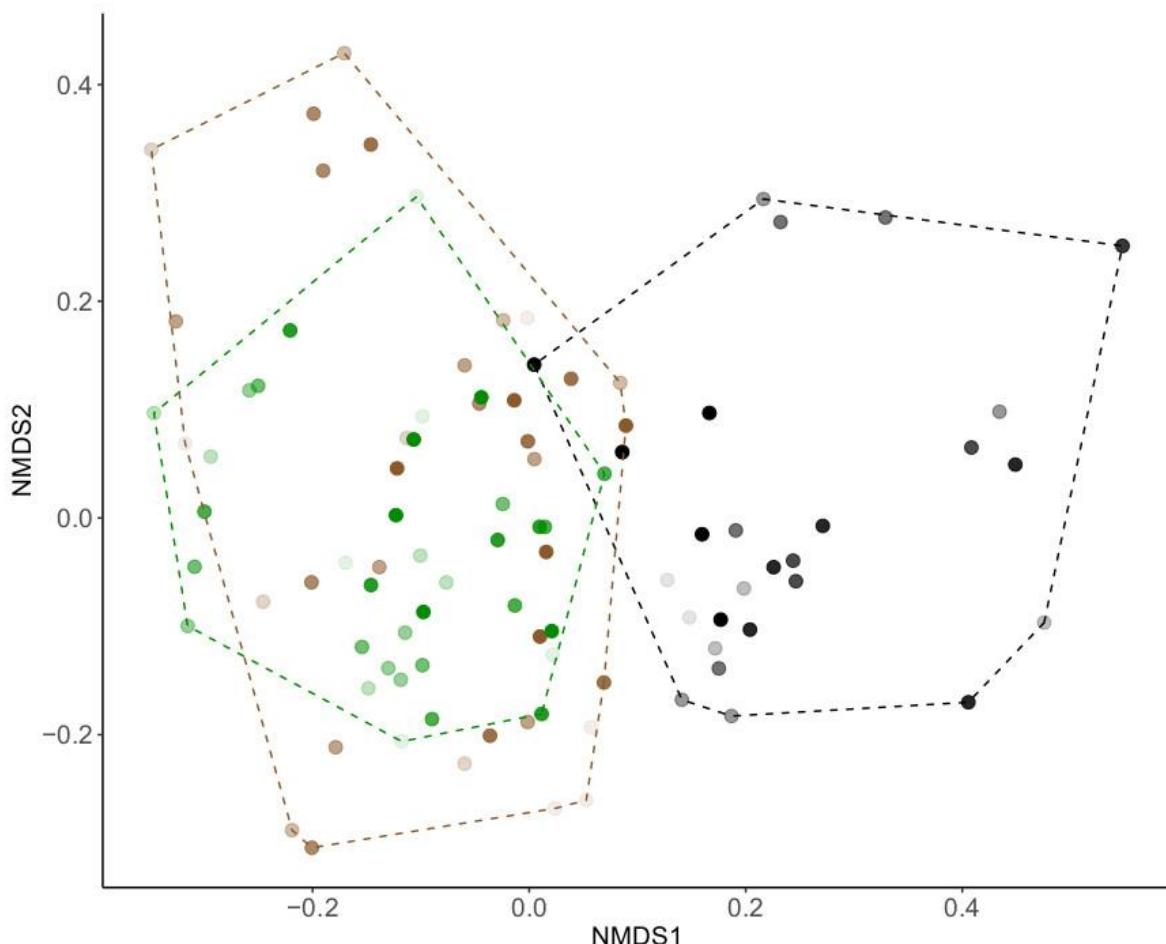


Figure 6: The similarity of the forb communities in each treatment. Surveys of burnt plots are in black, wildebeest plots in brown and control plot in green. Shading represents time: darker points are more recent surveys.

The differences between the forb communities in each treatment were explained by turnover rather than nestedness, and primarily by the most abundant forb species (Supplementary Material Table 3). The two most abundant forb species (comprising 37.9% of the individual forbs recorded) alone accounted for 26.9-30.3% of the variation between

treatments. The proportion of forbs which were flowering did not differ significantly between treatments but did change significantly over time with more forbs flowering in the wet season (January) (Supplementary Material Table 2, Fig. 7). Our IndVal analysis showed that burnt plots were characterised by *Talinum* spp., wildebeest plots by *Asteraceae* spp., and control plots by *Sida* and *Clerodendrum* spp. (Supplementary Material Table 4).

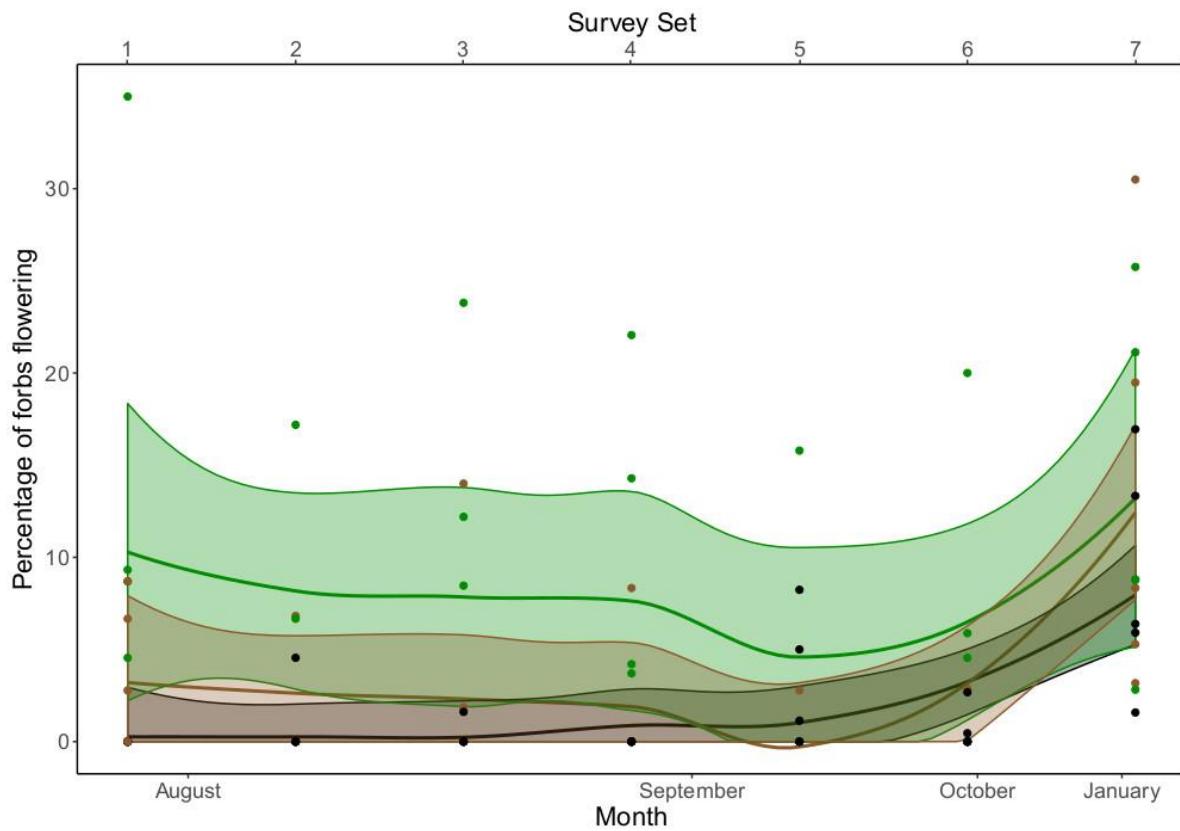


Figure 7: The temporal trends in the percentage of forbs which were flowering for each treatment. Surveys of burnt plots are in black, wildebeest plots in brown and control plots in green.

We found evidence of weak spatial autocorrelation between some of our variables (Supplementary Material Fig. 1) and no significant differences between the fire histories of our survey plots (Supplementary Material Fig. 2, Tables 5 & 6), although it was not possible to model radiative power due to insufficient data points.

DISCUSSION

Our study is the first to contrast the functional short-term effects of fire and grazing and examine to what extent fire can be considered a generalist herbivore. We have shown that while the effects of fire and wildebeest grazing appeared superficially similar, as they had similar effects on grass biomass and structure, fire had distinct effects on grass quality and on the composition of forb communities. Our findings confirm the theoretical results of Bond (2005) and highlight the unique role that fire plays as a consumer in savannah systems and its importance in maintaining heterogeneity in savannah habitats.

As predicted, both fire and grazing by the wildebeest migration had similar effects on grass structure in terms of reducing grass biomass, but there were some differences in terms of how that biomass was distributed and in grass quality. Both burning and wildebeest grazing created a pattern of short grass areas interspersed by clumps of longer grass, likely because of selective grazing preference for higher quality grass species (Archibald et al. 2005) and differences in flammability (Simpson et al. 2016), whilst in control plots grass biomass remained more uniformly distributed. There were contrasting patterns in the patchiness of inflorescence height with burnt plots showing an increasingly random pattern over the dry season and a more clustered pattern by January, and grazed plots becoming more clustered over the dry season but more random by January.

Grass quality was highest in burnt plots, followed by control plots and then grazed plots. On burnt plots the immediate (and largest) effect is likely to be caused by the input of ash and mineralisation of nutrients (Van de Vijver et al. 2009), whilst on wildebeest plots selective grazing of the highest quality grass by wildebeest would leave only poorer quality patches, overriding any signal from the input of dung and urine (Murray & Brown, 1993). However, this pattern of highest grass quality on burnt plots and lowest on grazed plots persisted for the duration of our study, despite grass quality varying with time, suggesting an additional factor may be maintaining the pattern in the long term. Heavy defoliation by either fire or grazing can result in a flush of nutritious new growth (Hempson et al. 2015). Grazers show a preference for these areas, and their grazing can maintain burnt or grazed patches in a lawn

state of higher quality than the surrounding landscape (Donaldson et al, 2018; McNaughton, 1976, 1979, 1984). This preferential grazing by resident herbivores could maintain our burnt plots in a high-quality lawn state for the duration of our study. High C:N ratios (above 20) may not be preferred by either selective or bulk grazers and may instead be consumed by other herbivores, in particular termites. The changes we observed in grass quality over time conform to expected changes in grass quality with rainfall (Shrader et al. 2006). In our first sample grass has stopped growing for the dry season and is therefore low quality, our second sample captures the flush of new, high quality, growth at the start of the wet season, and our third sample, whilst not as new and high quality as the second, is still green and of better quality than our first sample (Shrader et al. 2006).

Forbs are abundant in savannahs and display numerous adaptations to regular disturbance by fire and herbivory (Bond and Parr, 2010). They can develop large underground storage organs which allow them to resprout rapidly following a fire (Uys, 2006), are stimulated to flower by fire (Bond & Parr, 2010), and many have chemical defences to herbivores (Bews, 1925; Filgueiras, 2002). Savannah forbs are intolerant of shade and dependent upon frequent defoliation in order to persist, disappearing from savannahs where fire and grazing have been excluded (Uys et al. 2004; Overbeck et al. 2007). However, in our study, forb abundance and species richness varied with time but not with treatment, suggesting that they were primarily influenced by something other than fire or grazing, or that differences could not be detected in the dry season when few forbs were present. It is possible that rainfall explains the patterns we observed, with forb abundance and richness increasing as rainfall increased at the start of the wet season (Casillo et al. 2012). This increase was particularly rapid in grazed plots, perhaps because grazing had reduced the competition with grass, enabling forbs to take advantage of the available light and moisture (Bond & Parr, 2010).

In contrast to forb abundance and species richness, forb community composition differed significantly between treatments with burnt sites distinct from grazed and control sites. This suggests fire is promoting a suite of forb species not present in the grazed or control plots, but it is difficult to pinpoint a mechanism. Fire can affect forbs directly, with heat from combustion exerting a physiological stress not present in control or grazed plots.

However, many forb species have been shown to be tolerant to a diverse range of fire regimes, so it seems unlikely that this is the primary driver of the patterns we observed (Ulys et al. 2004). Many forbs have adapted to emerge and flower post-fire (Fig. 8) to take advantage of minimal competition from grass (Bond & Parr, 2010) but there was no difference in the proportion of individual forbs which were flowering between treatments, and few forbs in early surveys of burnt plots, suggesting there was not a large emergence of forbs post-fire. Fire can also affect forbs by modifying environmental conditions, indirectly favouring forb species with certain traits or adaptations. Fire removed standing grass biomass more completely than grazing and also removed the layer of fallen grass litter, leaving burnt plots more exposed and therefore likely to experience higher surface temperatures and lower moisture retention. In this situation species with physiological adaptations for dealing with a lack of moisture would be more competitive post-fire. Finally, browsers such as Thompson's gazelle (*Eudorcas thomsonii* Günther, 1884) may be preferentially feeding in burnt areas. By selectively browsing palatable forbs this fire-browser interaction may influence the forb community in burnt plots (Scott-Shaw & Morris, 2015).

Forb communities in control plots were nested within those in grazed plots, indicating that control areas contained a subset of the communities in grazed areas. One explanation for this could be that heavy grazing from the wildebeest migration is opening up the landscape, reducing the competition from grass and modifying the microclimate created by the presence of standing grass biomass (Bond & Parr, 2010). Grazing will also affect forbs directly through defoliation and trampling, with some species better able to survive and regenerate following these disturbances. The pattern we observed suggests that forbs are able to cope well with grazing and trampling and that the alteration of environmental conditions is shifting the competitive balance between forb species and allowing new forb species to colonise or emerge in grazed areas.



Figure 8: Forbs flowering post-burn in Ikorongo Game Reserve, Tanzania. ©James Probert

Looking beyond the Serengeti-Mara, it has been suggested that applying specific burning regimes may be able to replicate the functional effects of extirpated herbivores by concentrating resident grazers and generating grazing lawns (Archibald et al. 2005, Donaldson et al. 2018; Fuhlendorf et al. 2009). Our results suggest that this approach may provide an acceptable analogue for extirpated herbivores in terms of grass structure and quality, but that it would not replicate the effects of grazing on forb communities. Conversely, the exclusion of fire from a savannah system would likely result in the loss of fire-adapted forb species and their associated biodiversity (Parr et al. 2012). Global declines in the area burnt have been attributed to livestock grazing and it is likely these declines will become more widespread and increase in magnitude as human populations continue to grow (e.g. Andela et al. 2017; Chapter 1). Appropriate fire monitoring schemes are required to ensure ecosystem function is maintained and ensure the persistence of forbs and their associated biodiversity; some of the least studied aspects of savannah ecology. Fire regimes are also being affected by programmes such as REDD+, which seek to reduce carbon emissions by modifying and/or preventing the occurrence of fire, often without a full understanding of the effect this will have on biodiversity and ecosystem function (Khatun et

al. 2016; Parr et al. 2014). It is therefore imperative that programmes such as REDD+ recognise the distinct nature of consumer-controlled biomes, the role that fire and herbivory play in maintaining them, and their intrinsic carbon storage capacity (Abreu et al. 2017; Bond and Parr, 2010; Ritchie, 2014).

CONCLUSIONS

Our results suggest that there is a clear distinction between brown worlds, where herbivores are the primary consumers of plant biomass, and black worlds, where fire is the primary consumer of plant biomass. The differences we found in the functional effects of these two consumers indicate that both are important for the maintenance of heterogeneity and diversity in savannah systems. However, we also found evidence that some of our response variables were primarily influenced by rainfall rather than fire or grazing, indicating that savannahs are driven by resources as well as consumers. The patterns we observed likely have cascading effects on other aspects of savannah ecology, most notably the distribution of wild herbivores, which may further emphasise the importance of maintaining both fire and herbivory in savannah systems.

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SUPPLEMENTARY MATERIAL

Table1: The effect of treatment and time on grass biomass, grass patchiness, grass quality, forb abundance and estimated forb species richness.

Response	Fixed effects	numDF	denDF	F-value	p-value	Significance
Biomass	Intercept	1	72	348.06	<0.0001	
	Treatment	2	12	29.07	<0.0001	***
	Time	6	72	17.03	<0.0001	***
	Treatment x Time	12	72	12.90	<0.0001	***
Strength of autocorrelation in average height	Intercept	1	58	17.96	0.0001	***
	Treatment	2	12	1.02	0.39	
	Time	6	58	1.30	0.27	
	Treatment x Time	12	58	1.68	0.09	
Scale of autocorrelation in average height	Intercept	1	58	53.54	<0.0001	***
	Treatment	2	12	2.16	0.15	
	Time	6	58	0.94	0.47	
	Treatment x Time	12	58	1.10	0.38	
Strength of autocorrelation in maximum height	Intercept	1	69	9.10	0.00	***
	Treatment	2	12	0.36	0.70	
	Time	6	69	0.64	0.69	
	Treatment x Time	12	69	2.52	0.01	*
Scale of autocorrelation in maximum height	Intercept	1	69	46.82	<0.0001	***
	Treatment	2	12	0.18	0.83	
	Time	6	69	1.19	0.32	
	Treatment x Time	12	69	0.93	0.51	
Strength of autocorrelation in biomass	Intercept	1	72	65.85	<0.0001	***
	Treatment	2	12	3.52	0.06	
	Time	6	72	1.34	0.25	
	Treatment x Time	12	72	1.06	0.41	
Scale of autocorrelation in biomass	Intercept	1	72	153.68	<0.0001	***
	Treatment	2	12	3.90	0.05	.
	Time	6	72	1.37	0.24	
	Treatment x Time	12	72	1.24	0.27	
C:N ratio	Intercept	1	22	0.03	0.85	
	Treatment	2	12	8.87	0.003	***
	Time	2	22	95.75	<0.0001	***
	Treatment x Time	4	22	7.48	0.00	***
Forb abundance	Intercept	1	72	173.43	<0.0001	***
	Treatment	2	12	0.58	0.58	
	Time	6	72	19.85	<0.0001	***
	Treatment x Time	12	72	3.74	0.0002	**
Estimated forb species richness	Intercept	1	72	60.71	<0.0001	***
	Treatment	2	12	2.38	0.13	
	Time	6	72	9.56	<0.0001	***
	Treatment x Time	12	72	0.88	0.57	
Percentage of forbs flowering	Intercept	1	72	20.21	<0.0001	***
	Treatment	2	12	3.42	0.067	
	Time	6	72	5.40	0.001	**
	Treatment x Time	12	72	0.70	0.75	

Table 2: The effect of treatment and time on forb community composition.

Predictor	Df	Sums of squares	Mean squares	F model	R ²	Pr(>F)	Significance
Treatment	2	5.67	2.84	12.76	0.16	0.00	***
Time	28	15.18	0.54	2.44	0.42	0.00	***
Treatment:Time	20	4.80	0.23	1.08	0.13	0.20	
Residuals	47	10.44	0.22	-	0.29	-	
Total	97	36.01	-	-	1.00	-	

Table 3: The percentage of the dissimilarity (up to 50%) between treatments explained by the abundance of each forb species.

Species	Control:wildebeest			Control:Burnt			Burnt:wildebeest				
	% variation explained	Mean abundance control	Mean abundance wildebeest	Species	% variation explained	Mean abundance control	Mean abundance burnt	Species	% variation explained	Mean abundance burnt	Mean abundance wildebeest
<i>Melhania</i> spp.	20.43	22.69	5.14	<i>Melhania</i> spp.	24.76	22.69	16.71	<i>Melhania</i> spp.	14.33	16.71	5.14
46	18.17	8.03	31.80	48	13.93	0.00	16.25	46	12.53	0.00	31.80
<i>Clerodendrum</i> spp.	6.19	6.97	0.17	<i>Clerodendrum</i> spp.	5.93	6.97	0.00	48	11.95	16.25	0.00
<i>Sida</i> spp.	4.87	2.66	0.83	46	5.58	8.03	0.00	<i>Commelina</i> spp.	3.99	3.21	1.80
<i>Rubiaceae</i> spp.	3.90	0.46	2.57	<i>Sida</i> spp.	4.59	2.66	0.14	<i>Gnaphalium</i> spp.	3.04	12.93	0.03
<i>Tephrosia</i> spp.	3.30	2.17	9.14	<i>Cucurbitaceae</i> spp.	4.51	0.00	3.21	<i>Rubiaceae</i> spp.	2.95	0.04	2.57
<i>Asparagus</i> spp.	2.72	0.00	1.37	<i>Gnaphalium</i> spp.	3.38	0.03	12.93	86	2.67	1.29	0.34

Table 4: The individual values for forb species which are characteristic of each treatment.

Species	Treatment			p
	Burnt	Control	Wildebeest	
<i>Asteraceae</i> spp.	0.01	0	0.39	0.001
48	0.46	0	0	0.001
<i>Sida</i> spp.	0	0.42	0.04	0.001
<i>Talinum</i> spp.	0.46	0	0.01	0.001
<i>Clerodendrum</i> spp.	0	0.53	0	0.001
<i>Dipcadi</i> spp.	0.21	0	0	0.001
<i>Pupalia</i> spp.	0.18	0	0	0.001
<i>Commelina</i> spp.	0	0.01	0.25	0.003
<i>Sterculiaceae</i> spp.	0.18	0	0	0.003
<i>Asparagus</i> spp.	0	0	0.19	0.004
<i>Triumfetta</i> spp.	0	0.01	0.2	0.006
<i>Combretum</i> spp.	0	0	0.14	0.006
46	0	0.09	0.34	0.007
72	0.2	0.01	0.01	0.007
<i>Ruellia</i> spp.	0	0	0.19	0.008
<i>Justicia</i> spp.	0	0	0.16	0.008
110	0.16	0	0	0.019
90	0.11	0	0	0.021
<i>Rubiaceae</i> spp.	0	0.02	0.22	0.022
<i>Solanum</i> spp.	0	0.16	0.01	0.024
37	0	0	0.14	0.024
<i>Melhania</i> spp.	0.21	0.38	0.07	0.027
100	0.11	0	0	0.029
<i>Commelina</i> spp.	0.14	0	0.01	0.036
<i>Hibiscus</i> spp.	0	0.01	0.15	0.038

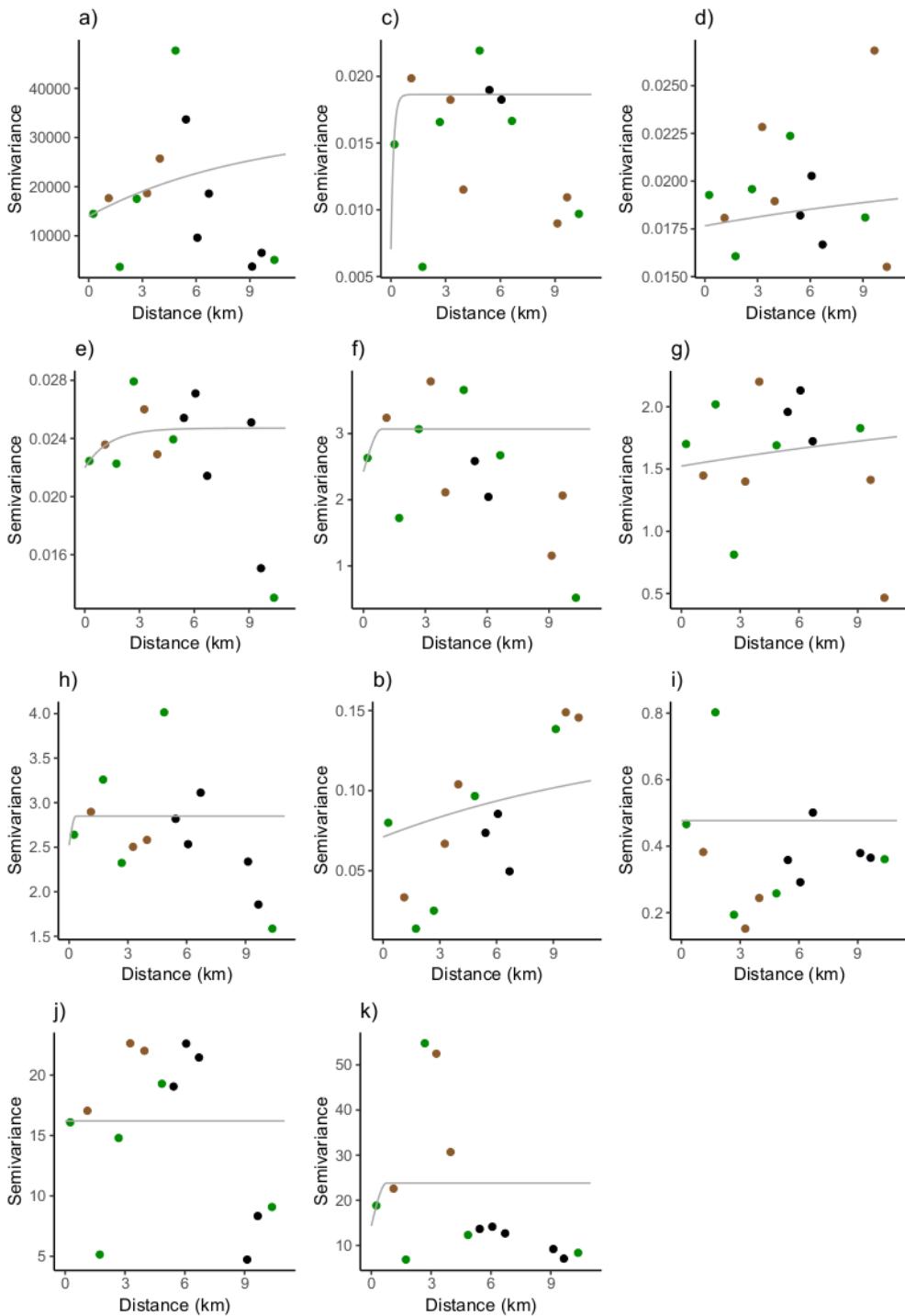


Figure 1: Semi-variograms for: a) grass biomass, b) strength of autocorrelation in vegetative height, c) scale of autocorrelation in vegetative height, d) strength of autocorrelation in inflorescence height, e) scale of autocorrelation in inflorescence height, f) strength of autocorrelation in biomass, g) scale of autocorrelation in biomass, h) grass quality, i) forb abundance, j) forb richness, and k) the percentage of forbs flowering. Burnt plots are in black, wildebeest plots in brown and control plots in green.

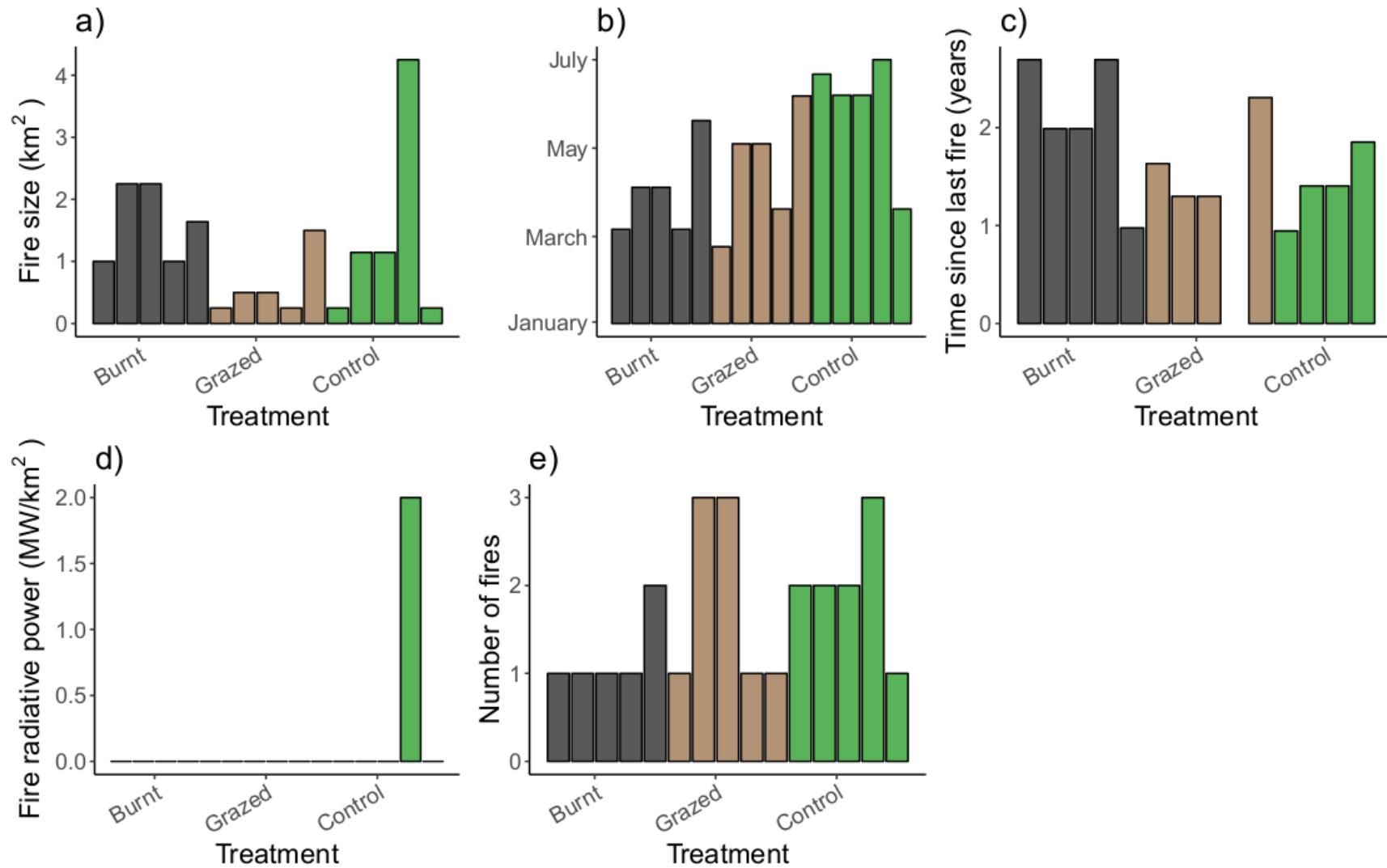


Figure 2: The fire histories of each plot: a) median fire size, b) median fire data, c) median time since last fire, d) median fire radiative power, e) total number of fires. Surveys of burnt plots are in black, wildebeest plots in brown and control plots in green.

Table 5: Differences in fire histories between treatments. There was insufficient data to test fire radiative power.

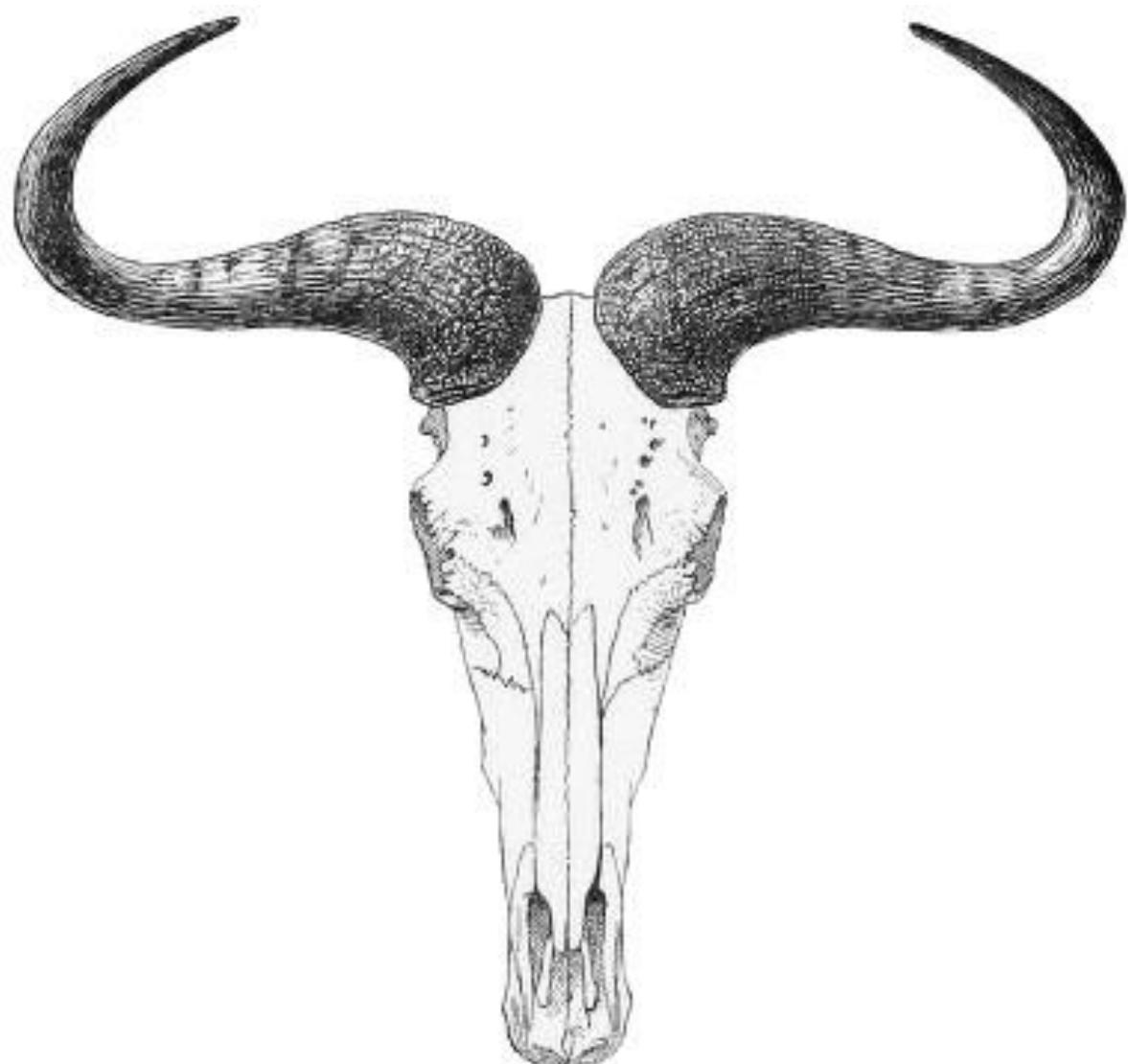
Fire characteristic	df	Deviance	p	Significance
Size	2	2.93	0.273	
Time since last fire	2	1.04	0.185	
Number of fires	2	1.733	0.255	

Table 6: Difference in the date of fires between each treatment.

Fire characteristic	df	F	p	Significance
Date	2	3.258	0.074	

Chapter 4

Direct and indirect effects of fire and grazing on mammalian herbivore communities



Cover illustration:

Skull of a blue wildebeest *Connochaetes taurinus* Burchell, the most abundant herbivore in the Serengeti-Mara. From *The Book of Antelopes* (Sclater & Oldfield, 1894).

ABSTRACT

1. Fire and herbivores are key consumers in savannah systems. Both consume large quantities of vegetative biomass but have contrasting effects on vegetation characteristics. It is important to understand how these contrasting vegetation characteristics cascade to effect other aspects of savannah systems, such as the distribution of mammalian herbivores.
2. Using a large scale experimental approach, we determined how mammalian herbivore distribution varied in response to fire and grazing by the wildebeest migration and examined the vegetation characteristics which might underly these patterns.
3. We found that burnt areas attracted Thompson's gazelles, but that a preference for short-grass areas, regardless of treatment, was more general. Grass quality was important in determining the distribution of wildebeest and topi, but Thompson's gazelle and warthog were attracted to short, but not high quality, grass.
4. Our results suggest that the vegetation resulting from both fire and grazing can have characteristics which are attractive to mammalian herbivores. They support the theories that both forage quality and a reduction in predation risk drives herbivore preference for areas of short-grass and show that the relative importance of these factors varies between species.

Keywords: Fire, grazing, herbivores, wildebeest, savannah, ecosystem interactions, habitat choice, consumers, Serengeti, forb

INTRODUCTION

African savannahs are dynamic systems featuring seasonal rainfall cycles, frequent disturbance by fire, and diverse assemblages of large mammalian herbivores (Scholes & Archer, 1997; Owen-Smith, 2013). These herbivores are similarly dynamic, moving constantly, often migratory, positioning themselves to maximise their fitness in a landscape of numerous, shifting biotic and abiotic factors operating at different spatial and temporal scales (McNaughton, 1985; Fryxel et al. 1988). Herbivores, in turn, have important impacts upon savannah systems, affecting ecosystem structure, composition, and function (Augustine and McNaughton, 1998; Sankaran et al. 2008). Therefore, in addition to being a fundamental goal of ecology, understanding how and why individuals distribute themselves through space and time is necessary for the successful management of both savannah systems and herbivore populations themselves. Furthermore, savannahs are under considerable pressure from climate change and increasing human populations, and compared with other taxa, large mammalian herbivores have been disproportionately affected by population decline and extinction (Dirzo et al. 2014; Andela et al. 2017; Chapter 2). It is important that we understand the habitats and conditions needed by our remaining mammalian herbivores to prevent cascading extinctions which may have significant adverse effects on ecosystem structure and function (Keesing & Young, 2014; Ripple et al. 2015).

Fire and herbivory are key ecological and evolutionary drivers in savannah systems (Bond & Keeley, 2005). Both consume significant quantities of vegetative biomass, but do so in contrasting ways, varying in their selectivity, effect on woody cover, frequency, and geographic extent (Anderson et al. 2007; Chapter 2). This contrast creates heterogeneity in vegetation characteristics which has cascading effects on other aspects of savannah ecosystems, such as how mammalian herbivores distribute themselves across the landscape (Fuhlendorf et al. 2009). Many studies have documented the utilization of burnt areas by mammalian herbivores (e.g. Vesey-Fitzgerald, 1971; Frost, 1984; Wilsey, 1996) and attributed this preference to increased grass quality (McNaughton, 1976; Archibald et al. 2005) and reduced predation risk (Eby et al. 2014; Hopcraft et al. 2014). Several studies have also focused on the creation of grazing lawns – highly productive areas of short grass which can form if grazing pressure is sufficiently heavy, which continue to attract grazers

and require grazing to be maintained (e.g. McNaughton, 1984; Archibald & Bond, 2004; Hempson et al. 2014). However, few studies have compared mammalian herbivore utilization of burnt, grazed and unburnt areas simultaneously, and also examined the vegetation characteristics which are driving these preferences. Eby et al. (2014) concluded that non-nitrogen nutrients drove the distribution of impala (*Aepyceros melampus* Lichtenstein) but were not able to determine which vegetation characteristics were driving the distribution of other herbivore species. In the Serengeti-Mara ecosystem of East Africa, fire and grazing by the annual migration of approximately 1.4 million wildebeest (*Connochaetes taurinus* Burchell) have similar effects on grass structure but contrasting effects on grass quality and forb communities (Chapter 2). Studying how mammalian herbivores distribute themselves across the heterogeneous landscape created by these contrasting consumers, and the vegetation characteristics underlying these patterns can help explain herbivore ecology and the role fire and grazing play in maintaining savannah heterogeneity.

The response of mammalian herbivores to vegetation characteristics varies depending on the morphology and physiology of the herbivore concerned (Hoffman, 1989). Of particular importance is the distinction between browsers, which feed primarily on the leaves of woody plants or forbs (dicots), and grazers, which feed primarily on grass (monocots). A continuum exists between these two categorisations, and many species can alter their diet if needed, for example during a drought (Shipley, 1999). Of equal importance is whether herbivores are foregut ruminants, which seek out high quality food, or hindgut ruminants, which consume large quantities of poor quality food, but will also take advantage of high quality areas (Hoffman, 1989). Both fire and wildebeest grazing remove large quantities of grass biomass, but only fire increased grass quality (Chapter 2). We might therefore expect foregut ruminants to be most abundant in burnt areas with low biomass and high quality and hindgut ruminants to be present in areas with high biomass but low quality. Herbivores are not only affected by the value of vegetation as a resource; the effect of vegetation on predation risk, or perceived predation risk, is also an important determinant of herbivore distribution (Frost, 1984; Hopcraft et al. 2014). Herbivores sacrifice resource intake to avoid predators (Mduma & Sinclair, 1994) but may be more responsive to environmental factors, such as vegetation structure, which increase the risk of predation than to direct predation

risk (Davies et al. 2016). Both fire and wildebeest grazing reduce grass height (Chapter 2), increasing line of sight and decreasing cover for predators (Hopcraft et al. 2005). This reduces predation and makes these areas attractive for certain herbivores (Anderson et al. 2016). Small body size is correlated with many of the attributes which make a species likely to prefer recently burnt areas, with different studies suggesting this may be due to both resource (Wilsey, 1996) and predation (Eby et al. 2014) effects.

Using a large-scale experiment, we examined the effect that fire and grazing by the wildebeest migration had on the distribution of resident mammalian herbivores and investigated the vegetation characteristics which may be driving the patterns we observed. We described mammalian herbivore distribution using: total abundance, total biomass, species richness, community composition, and investigated interspecies differences in responses to fire and grazing using the abundance of the eight most abundant species in our study. Finally, we used the vegetation characteristics we calculated in Chapter 2 to model how vegetation was driving herbivore distribution and investigate the relative importance of grass structure and quality. We anticipate a higher abundance of selective grazers and species vulnerable to predation (those with small body size) in burnt and grazed plots, and a higher abundance of bulk grazers in control plots. These patterns will be primarily driven by grass biomass, height and quality. Species such as wildebeest, topi (*Damaliscus lunatus jimela* Matschie), hartebeest (*Alcelaphus buselaphus cokii* Günther), Thompson's gazelles (*Eudorcas thomsonii* Günther) and Grant's gazelles (*Nanger granti* Brooke) will be associated with short grass areas of high quality, whilst buffalo (*Syncerus caffer* Sparrman) and zebra (*Equus quagga* Boddaert) will be more abundant in bunch grass areas with high biomass and low quality. Mixed feeders such as impala may be associated with areas of high forb abundance.

METHODS

Study area

Data collection was carried out in the Western Corridor region of northern Tanzania (2.0185°S, 34.2199°E). The Western Corridor is defined by the Grumeti and Mbalageti Rivers, which run parallel to each other towards Lake Victoria in the west. Lake Victoria heavily influences the rainfall and soil type in the Western Corridor. The mean annual rainfall is between 800 and 1400 mm per year and occurs in two distinct wet seasons, one from October to January and another from March to May (Norton-Griffiths et al. 1975). This high rainfall means that fires are frequent in the Western Corridor (Chapter 1). Alluvial deposits from old lake beds are the primary soil type, with the granite which underlies this more apparent and on hilltops and ridges (Jaeger, 1982). Broad-leaved *Terminalia* woodlands are the dominant vegetation on these hilltops and ridges whilst lower areas contain both woodlands and open plains dominated by *Themeda triandra* with occasional *Acacias* and *Balanytes*. Whilst the movement of the wildebeest migration is hard to predict, it will usually arrive in the Western Corridor around May, at the start of the long dry season, and move on by July (Hopcraft et al. 2015). The Western Corridor contains several protected areas: Serengeti National Park, Grumeti Game Reserve and Ikona Wildlife Management Area, and is surrounded by non-protected village lands to the north and west, and Ikorongo Game Reserve to the east (Fig. 1).

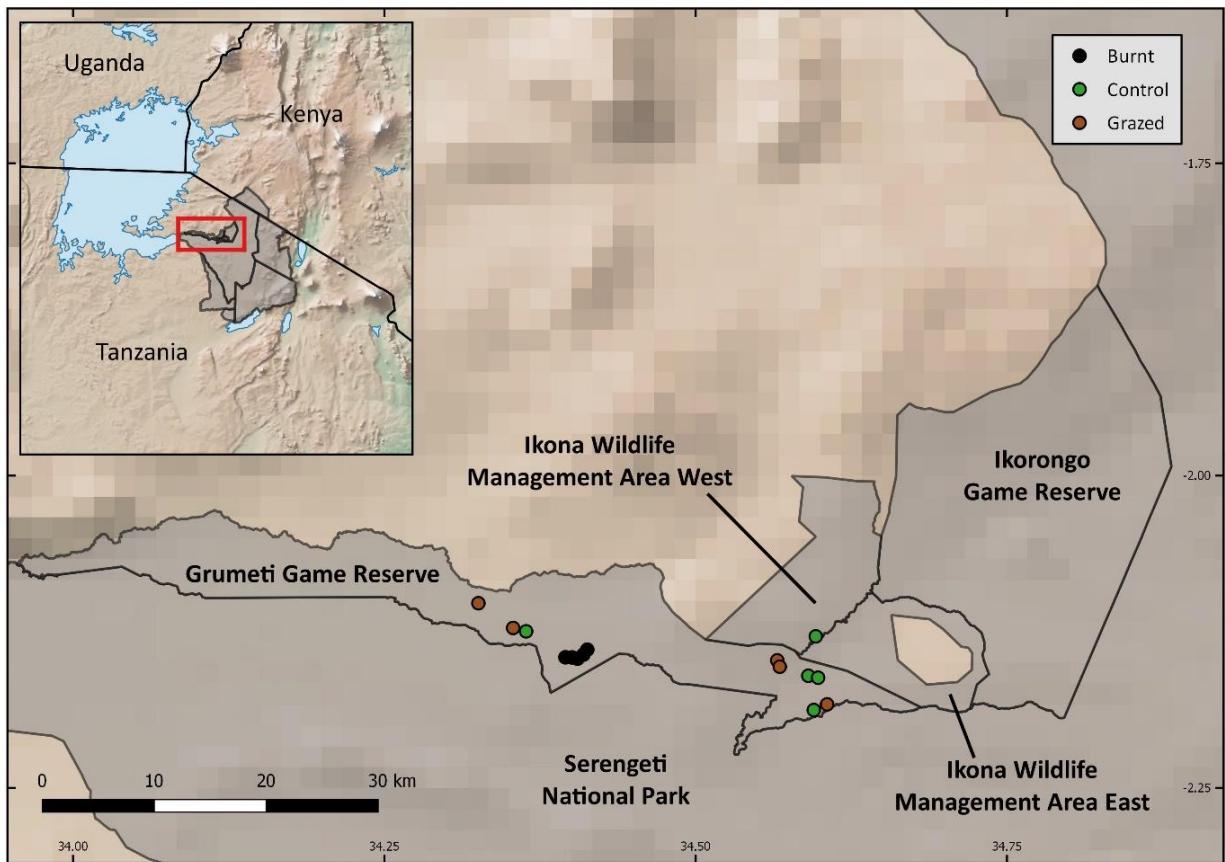


Figure 1: Map of study area with the location of survey plots. Burnt plots are black, wildebeest plots brown and control plots green. The base map is of elevation (made with Natural Earth) with protected areas shown in grey.

Data collection

Our data collection occurred within the same experimental design described in Chapter 3. We established 15 50 x 50 m (0.25 ha) plots, distributed evenly between three treatments: 1) burnt with resident herbivores, 2) unburnt but grazed by the wildebeest migration and resident herbivores or 3) unburnt and ungrazed by the wildebeest migration, but with resident herbivores (control). We surveyed these plots six times between mid-August and late September 2016 and once in mid-January 2017. Surveys were grouped into sets, a set being one survey of each plot, from one to seven. Plots in our burnt treatment burnt on 16th July 2016 and wildebeest arrived in Grumeti from the start of June 2016.

Data on vegetation were collected as described in Chapter 3 but in brief: We took measurements of the biomass, vegetative height, and inflorescence height of grass at 2 m intervals along two 50 m transects per plot. We collected data on the carbon to nitrogen ratio (as a proxy for grass quality) in each plot in August, September and January, we identified all forbs in 2 x 1 m belt transects per plot to species level and recorded whether each individual forb was flowering. In addition to the data described in Chapter 2 we scored the percentage of bare ground (0-25, 26-50, 51-75, 76-100) at 2m intervals along two 50 m transects per plot.

We placed a single ‘Bushnell Trophy Cam HD Aggressor No-Glow’ camera trap in each plot to record the presence, or absence, of mammalian herbivores. To standardise sampling effort, we placed camera traps so that the entirety of the plot was within the frame and set them to capture an image once every 15 minutes, independently of detecting movement. Camera traps were set up during the first survey of a plot, remained in the field for the entire duration of the study, and were removed at the end of the last survey of a plot.

Data processing

We sorted our camera trap images to remove images at night (when nothing was visible), images obstructed by e.g. rain, mist, glare or animals, disturbances such as tourist vehicles or surveys, and images which had been triggered by movement. We then recorded the number of individuals of each species present within the survey plot in each image. Wildebeest were included amongst the species as they can be both migratory and resident.

We aggregated the data from all the images from a plot within a five-day period (hereafter time-periods) to generate: the total abundance of all mammalian herbivores, the species richness, and the abundance of each species. Using Serengeti-specific values for individual biomass from Sachs (1967) where possible, or else values from Kingdom et al. (2013), we also calculated the total biomass of all mammalian herbivores and the biomass of each species for each period.

By selecting different time-periods we generated two datasets: firstly, a dataset which spanned the entire study period, allowing us to examine the trends in mammalian herbivore distribution through time. Time-periods for this dataset ran continuously from the start of August 2016 until the end of September 2016 (survey sets 1-6), for every other week between from the end of September 2016 until mid-January 2017 (to minimise the effort required to sort and process our camera trap images), and then for a single additional time period in mid-January 2017 (survey set 7). Secondly, we selected seven time-periods which matched the seven survey sets of the vegetation surveys detailed in Chapter 2, allowing us to model mammalian herbivore distribution against vegetation characteristics.

Despite our efforts to standardise sampling effort, the number of images between time-periods varied as a result of obstructions, disturbances and technical problems with our camera traps. We removed all time-periods from our datasets with less than 120 images (50% of the theoretical number of images in a time-period, based on four images for 12 hours for five days), as below this threshold we did not consider the data to be representative. For our remaining data we controlled for the number of images by dividing our mammalian herbivore variables (with the exception of species richness) by the number of images and multiplying by 4, thereby expressing our variables per hour rather than as totals for the time-period.

Data analysis

To examine how mammalian herbivore distribution varied with treatment and time, we used our first dataset to model each variable with treatment, time and an interaction between the two as fixed effects and plot as a random effect. Then, using our second dataset, we modelled our mammalian herbivore variables against the vegetation characteristics we calculated in Chapter 3: grass biomass, vegetative height, and inflorescence height, percentage of bare ground, C:N ratio (as a proxy for quality), forb abundance, forb species richness, and the percentage of individual forbs flowering. We also included plot and time as random effects. We only had data on C:N ratio for three of seven surveys therefore we performed models both with and without C:N ratio and reported both sets of results.

With the exception of species richness, to ensure our residuals met our model assumptions, we used binomial linear mixed-effects models to test the relationship between our mammalian herbivore response variables, treatment and time. For species richness we used a linear mixed effects model. Time was included in these models as a numeric variable with values from 1-32 representing the time-period of the data. To test the relationship between our mammalian response variables and vegetation we used linear mixed effects models. In our vegetation models time was included as a factor, with levels from 1-7, to represent the seven sets of surveys during our data collection. If included as a continuous variable the unequal distribution of surveys throughout our study period would mean the final set of surveys exerted a disproportionate influence on our results. For all models we centred and scaled our explanatory variables to minimise the effects of multicollinearity and assessed the distribution and homoscedasticity of our residuals using diagnostic plots.

We calculated the distance between our mammalian communities using Bray-Curtis dissimilarity indices and visualised the results using non-metric multidimensional scaling (NMDS). We used permutational multivariate analyses of variance (PERMANOVAs) (Oksanen et al. 2017) to analyse the effects treatment and time were having on the distances communities, and partitioned beta diversity into nestedness and turnover (Baselga et al. 2017). We identified which species of mammalian herbivore were contributing most to the dissimilarity of communities using similarity percentages (SIMPER) (Clarke, 1993) and used indicator values (IndVal) (Dufrene & Legendre, 1997) to calculate a quantitative index of the fidelity (the proportion of the individuals of a given species that are in a treatment) and specificity (the proportion of the plots in a given treatment that contain a given species) of a species to a treatment. We assessed the strength of the spatial autocorrelation in each response variable using empirical and fitted semi-variograms based on the residuals of each model. All analyses were carried out in R version 3.2.3 (R Core Team, 2015).

RESULTS

We recorded a total of 21,050 individuals from 15 species in 57,170 camera trap images throughout our study period. Wildebeest, zebra, Thompson's gazelle, topi, impala, buffalo, warthog (*Phacochoerus africanus* Gmelin) and baboons (*Papio Anubis* Lesson) were the most abundant species (Fig. 2a), whilst wildebeest, zebra, buffalo, elephant (*Loxodonta africana* Blumenbach), topi, eland (*Taurotragus oryx* Pallas), giraffe (*Giraffa camelopardalis tippelskirchii* Matschie), and impala made up the most biomass (Fig. 2b). The abundance (Fig. 3a), biomass (Fig. 3b) and richness (Fig. 3c) of mammalian herbivores remained relatively constant throughout our study period with no significant differences over time or between treatments (Supplementary Material Table 1).

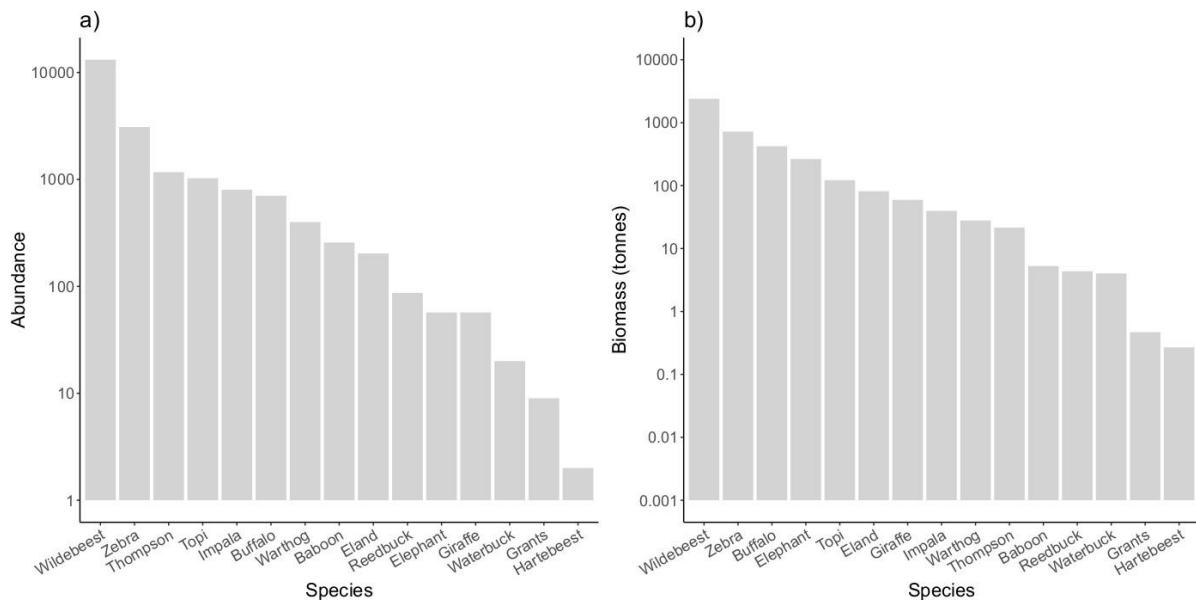


Figure 2: The a) abundance and b) biomass of the 15 species of mammalian herbivore we observed during our study.

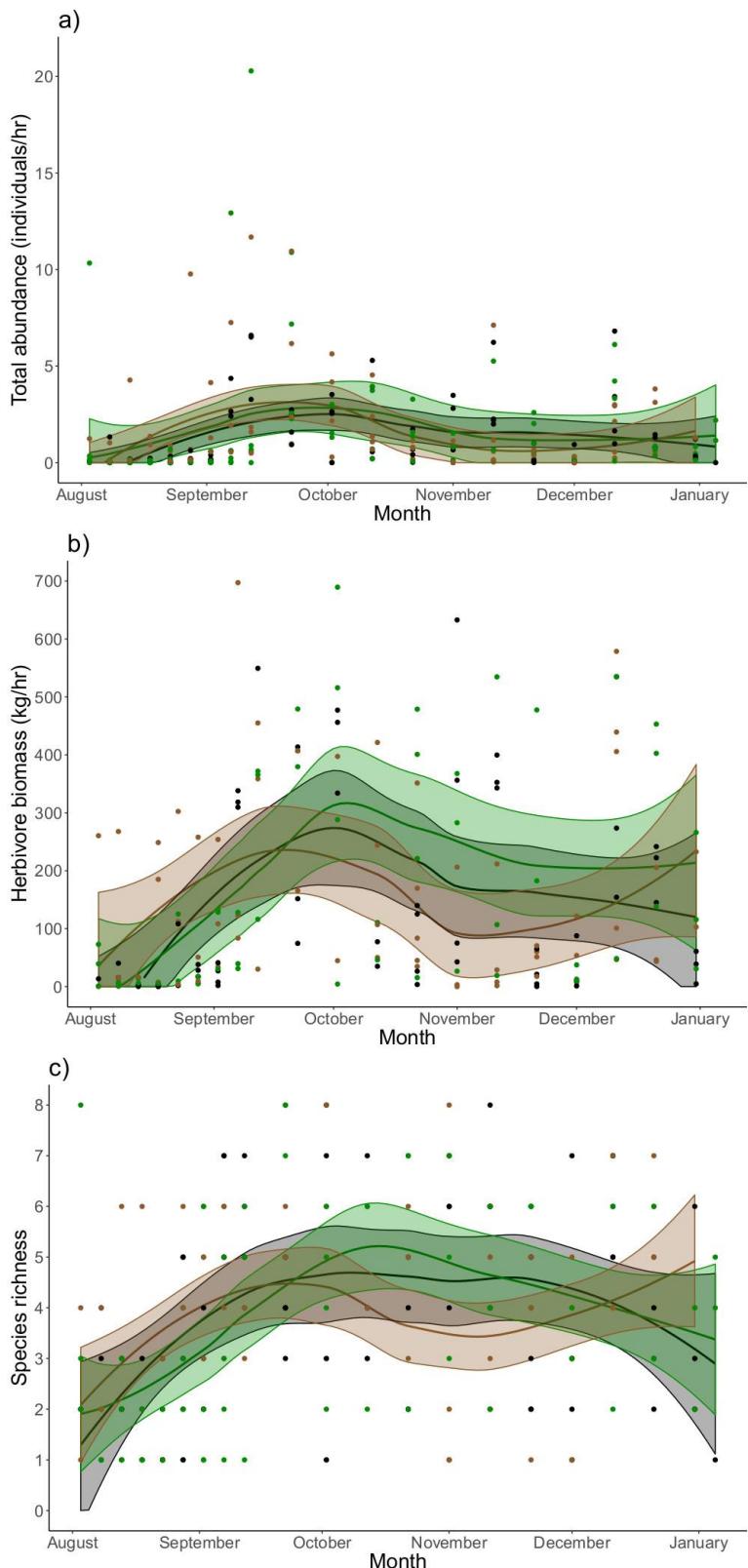


Figure 3: The temporal trends in a) the total abundance, b) the total biomass, and c) the species richness, of mammalian herbivores. Surveys of burnt plots are shown in black, wildebeest plots in brown and control plots in green.

The abundance of wildebeest (Fig. 4a), zebra (Fig. 4b), topi (Fig. 4c), and buffalo (Fig. 4f) did not differ significantly with treatment or time. Thompson's gazelles were significantly more abundant in burnt plots throughout the sampling period (Fig. 4d). Warthog abundance changed over time, increasing over the wet season in burnt plots but remaining constant in grazed and control plots and was equal among treatments (Fig. 4g). Baboon abundance was initially high in burnt plots but increased over time in control and wildebeest plots, whilst decreasing in burnt plots (Fig. 4h). Impala abundance differed significantly between treatments, and changed over time, with differing rates of change depending on treatment: impala were most abundant in wildebeest plots, where their abundance peaked at the start of the rainy season before declining (Fig. 4e; Supplementary Material Table 2). The relationship between the abundance of a species and the biomass of the same species are identical, therefore we did not model these data but graphs of species biomass through time are included in Supplementary Material Fig. 1.

The composition of mammalian herbivore communities was significantly different in our three treatments, with the composition of communities in each treatment also changing over time (Fig. 5; Supplementary Material Table 3). The majority of the Bray-Curtis dissimilarity (96%) between communities was explained by turnover, with wildebeest, zebra and Thompson's gazelle accounting for the majority of the dissimilarity between treatments (Supplementary Material Table 4). Our IndVal analysis strongly suggested that Thompson's gazelle and warthog were characteristic of burnt plots, baboon of wildebeest plots, and buffalo of control plots. Wildebeest characterised both burnt and wildebeest plots and zebra and impala characterised both wildebeest and control plots (Supplementary Material Table 5).

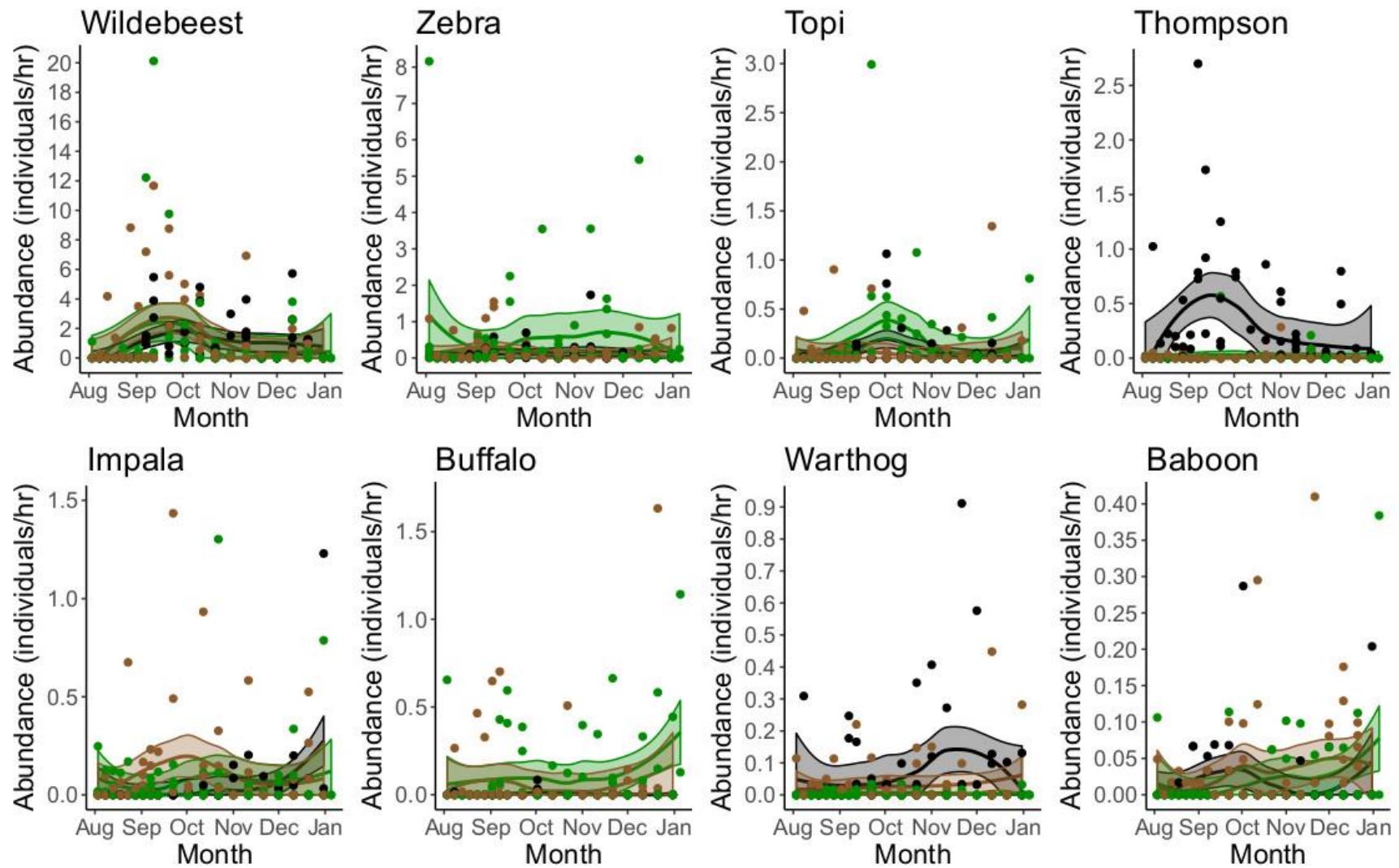


Figure 4: Temporal trends in the abundance of the eight species of mammalian herbivore which were most abundant during our study.

Surveys of burnt plots are shown in black, wildebeest plots in brown and control plots in green.

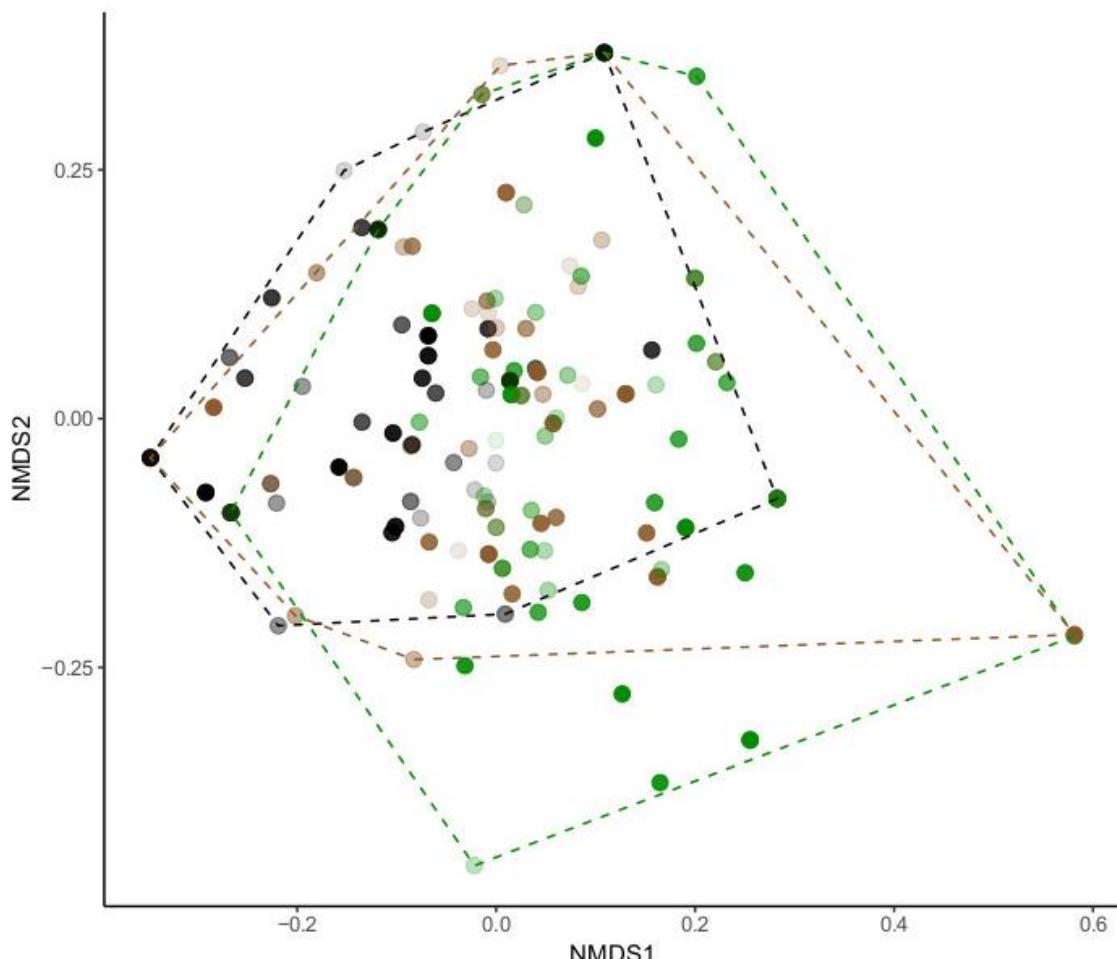


Figure 5: The similarity of mammalian herbivore communities in our study. Surveys of burnt plots are in black, wildebeest plots in brown and control plot in green. Shading represents time: darker points are more recent surveys.

The total abundance and total biomass of mammalian herbivores were predicted by grass biomass and vegetative height, with greater herbivore abundance and biomass in areas with low grass biomass and shorter grass (Fig. 6; Fig. 7). Mammalian herbivore species richness was predicted by both vegetative and inflorescence height, and by forb abundance, with the highest mammalian species richness in areas with a vegetative height of 5-10 cm, an inflorescence height of around 10 cm, and high forb abundance (Fig. 8; Supplementary Material Table 6).

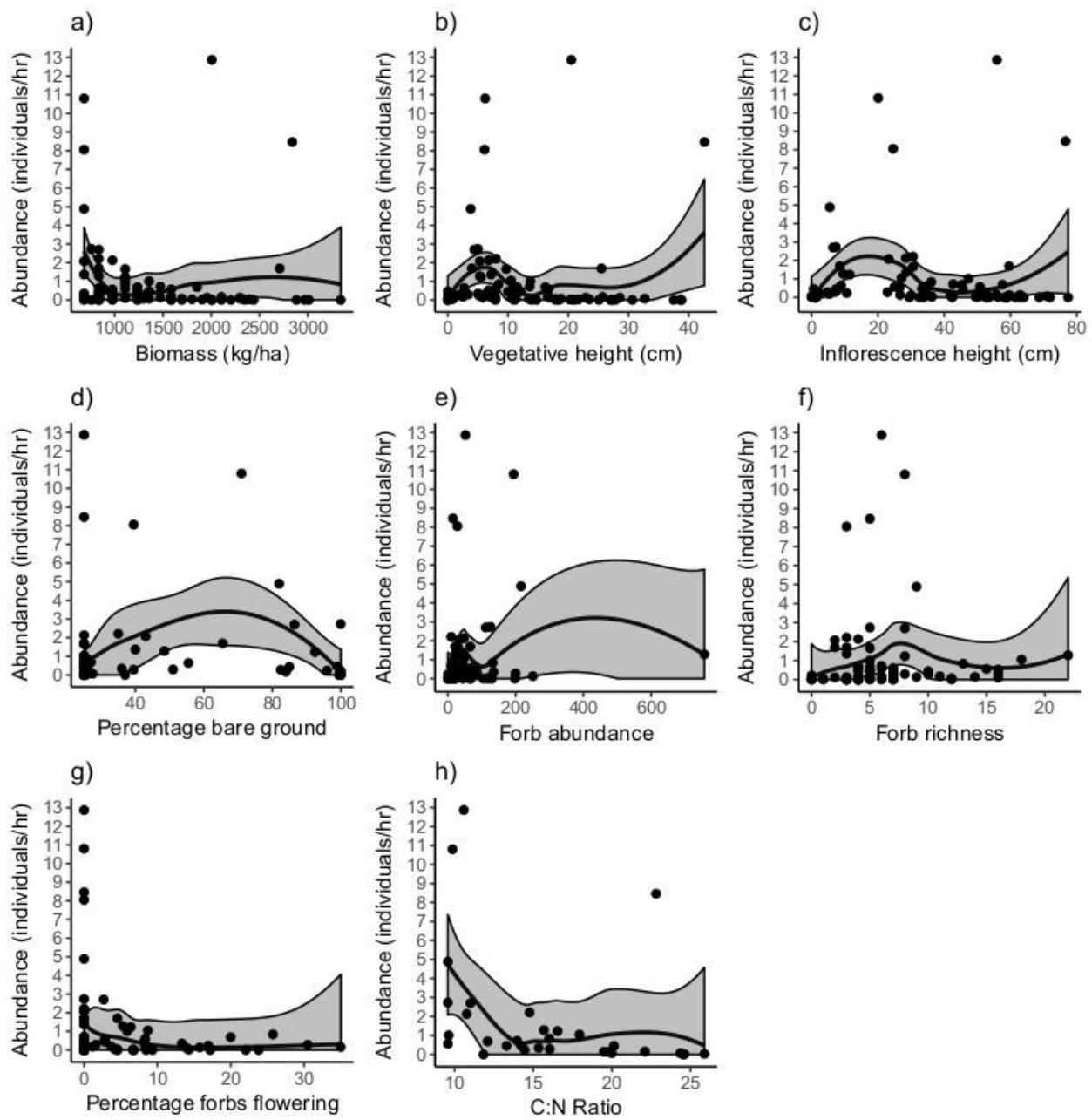


Figure 6: The relationship between the total abundance of mammalian herbivores and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

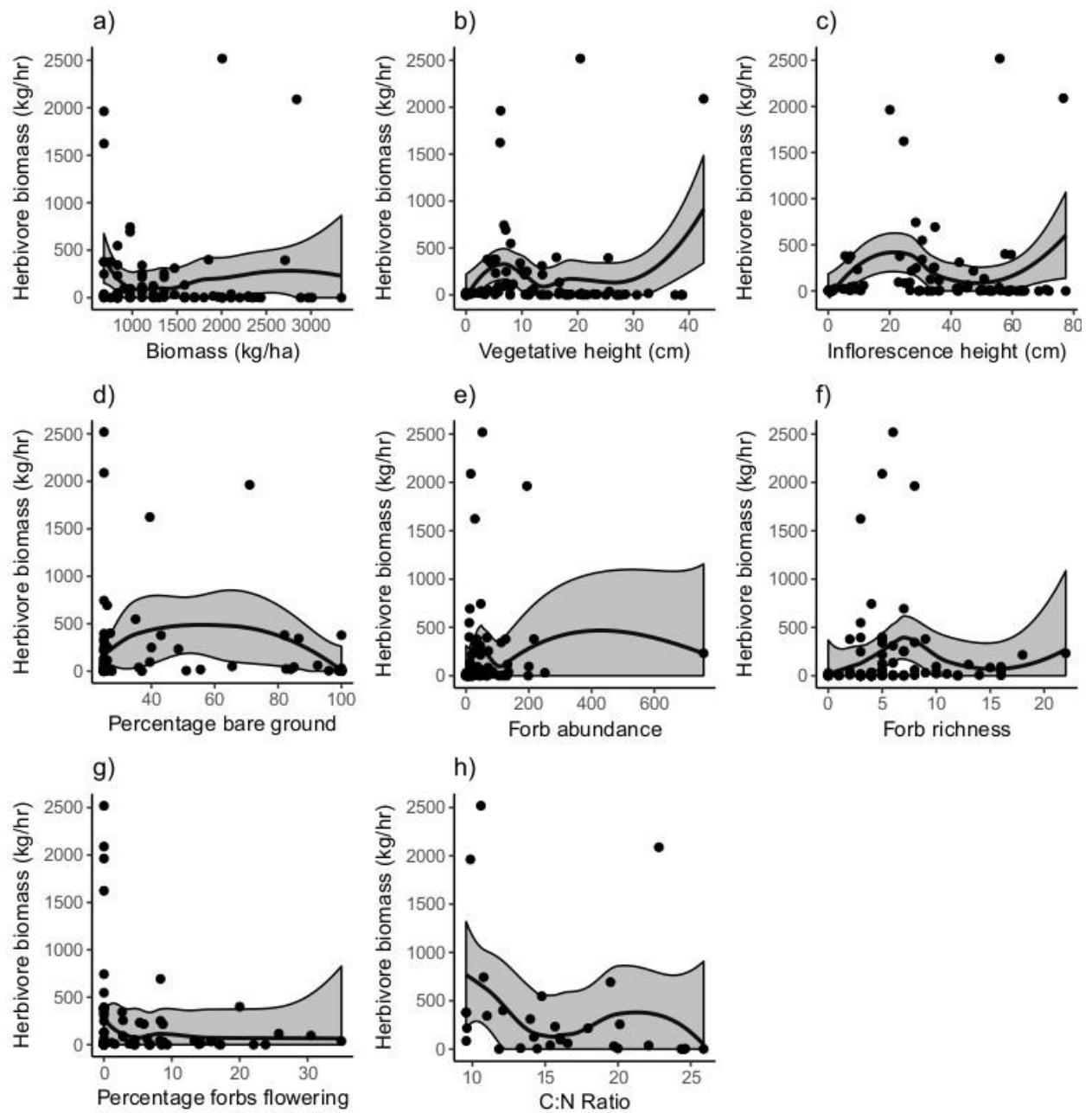


Figure 7: The relationship between the total biomass of mammalian herbivores and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

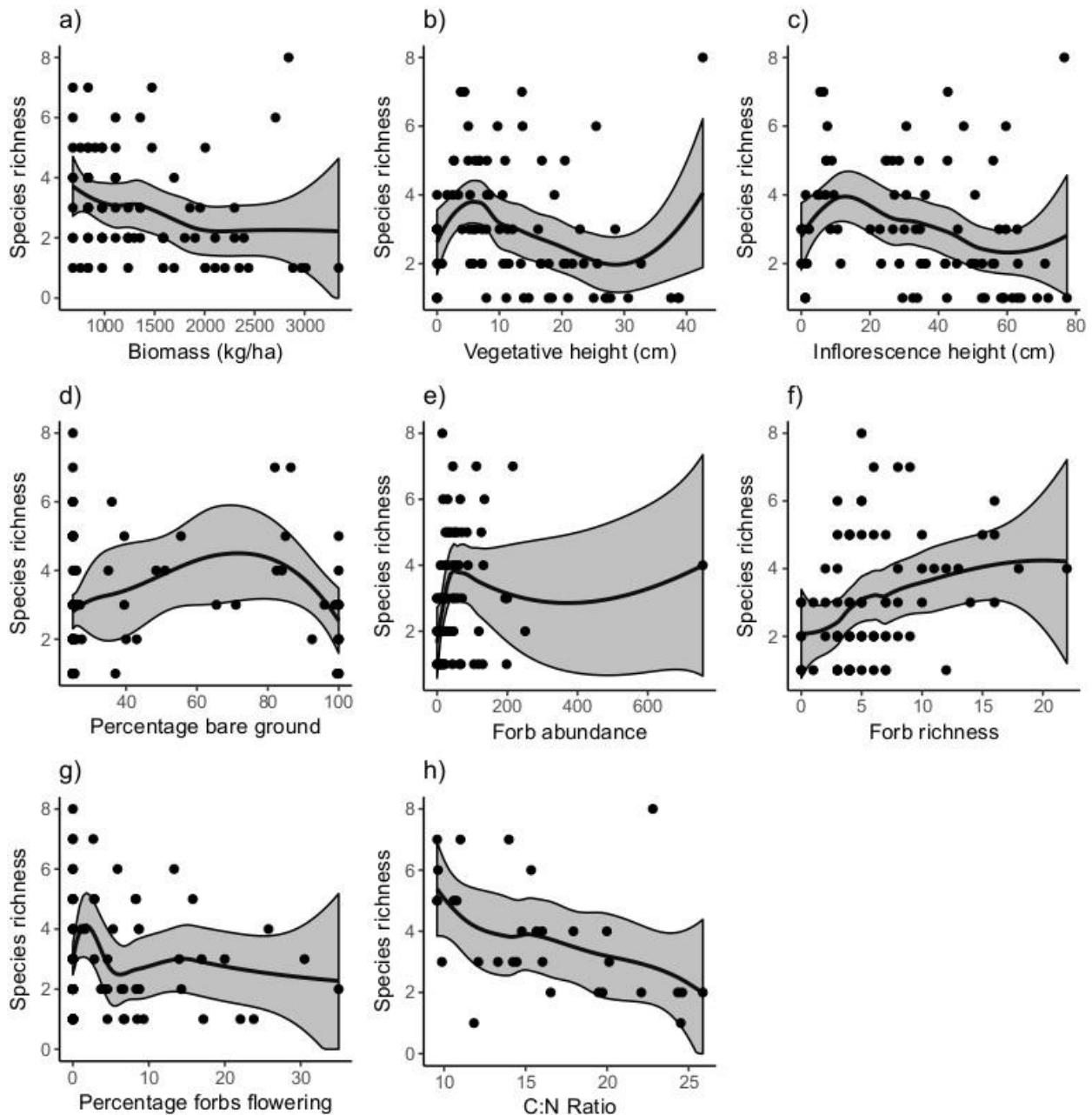


Figure 8: The relationship between the species richness of mammalian herbivores and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

The abundance of topi (Supplementary Material Fig. 4), impala (Supplementary Material Fig. 6) and buffalo (Supplementary Material Fig. 7) was not predicted by any vegetation characteristics. The abundance of wildebeest (Supplementary Material Fig. 2) was predicted by grass biomass with more wildebeest in area with low biomass, zebra by grass biomass

and vegetative height with greater abundance in areas with high biomass and vegetative height greater than 30cm (Supplementary Material Fig. 3), Thompsons's gazelle by grass biomass and vegetative height with greater abundance in areas with low biomass and vegetative height <10cm (Supplementary Material Fig. 5), warthog by inflorescence height with more warthog in short grass areas (Supplementary Material Fig. 8), and baboon by the percentage of bare ground and forb abundance with more baboons in areas with a higher percentage of bare ground and low forb abundance (Supplementary Material Fig. 9; Supplementary Material Table 7; Supplementary Material Table 8).

Including C:N ratio in our models changed the results. Although grass biomass and vegetative height remained significant predictors of total herbivore abundance (Fig. 6) and total herbivore biomass (Fig. 7), C:N ratio itself also became a significant predictor of total herbivore abundance. Mammalian herbivore species richness was no longer explained by inflorescence height and forb abundance, but grass biomass and C:N ratio became significant predictors (Supplementary Material Table 9). The direction of effects did not change, with higher total abundance, biomass and species richness in areas of short, low biomass grass. Total herbivore abundance and species richness were higher in plots with low C:N ratio (higher quality grass). For individual species, C:N ratio was a significant predictor of wildebeest and topi abundance (Supplementary Material Fig. 2; Supplementary Material Fig. 4). With C:N ratio included in our models none of our vegetation characteristics predicted the abundance of Thompson's gazelle (Supplementary Material Fig. 5), impala (Supplementary Material Fig. 6), buffalo (Supplementary Material Fig. 7), warthog (Supplementary Material Fig. 8) or baboons (Supplementary Material Fig. 9). Zebra abundance was still positively predicted by vegetative height (Supplementary Material Fig. 3; Supplementary Material Table 10; Supplementary Material Table 11). We found evidence of weak spatial structure in the relationships between our response variables, treatment and time (Supplementary Material Fig. 10).

DISCUSSION

Our results suggest that mammalian herbivore species respond differently to the vegetation characteristics created by fire and wildebeest grazing. Treatment did not affect the total abundance, biomass or species richness of mammalian herbivores but did affect community composition and the abundance of Thompson's gazelle, impala, and baboon. Both the quantity and quality of grass were important in explaining the patterns we observed. Total herbivore abundance, biomass, species richness, and the abundance of wildebeest, Thompson's gazelle, and warthog were highest in short-grass areas, suggesting that both fire and wildebeest grazing can create vegetation characteristics which are attractive to mammalian herbivores. Conversely, zebra were most abundant in areas of longer grass. Areas with high quality grass had higher total herbivore abundance and richness, and higher abundances of wildebeest and topi. Our results concur with established theories that mammalian herbivore distribution is driven by both food availability and predation risk, suggesting that some species are more responsive to food availability and others to predation risk (e.g. Wilsey, 1996, Eby et al. 2014). They suggest that fire may facilitate grazing and predator avoidance, whilst wildebeest grazing facilitates only predator avoidance.

There is a substantial body of literature establishing the preference of many mammalian herbivores for burnt areas (e.g. Vesey-Fitzgerald, 1971; Wilsey, 1996; Archibald & Bond, 2004; Eby et al. 2014; Donaldson et al. 2018). It may therefore be surprising that we detected no difference in total abundance, total biomass or species richness between our treatments. There are several possible explanations for this: 1) With the exception of zebra, wildebeest were more abundant than all other species by an order of magnitude and also constituted the most biomass. A peak in wildebeest abundance in September suggests that migratory herds returned to our study area during this period. The abundance and ubiquity of migrating wildebeest may have masked any preferences shown by resident herbivores. 2) Zebra were the second most abundant species in our study. Whilst wildebeest were most abundant in areas of short, highly nutritious grass, which are most likely to occur in burnt areas, zebra were most abundant in areas of longer grass, which are most likely to occur in control areas (Chapter 2). These contrasting patterns amongst the two most abundant

species in our study could confound an examination of the effect of treatment on total abundance and biomass). In Chapter 3 we established that fire and wildebeest grazing had similar effects on grass structure but only burning resulted in higher quality grass. Grass biomass and height were the dominant predictors of mammalian herbivore distribution, with the highest abundance in short-grass areas, regardless of treatment. Given the above, examining herbivore distribution through aggregate measures such as total abundance and total biomass does not appear to be particularly useful. Treatment did affect the composition of mammalian herbivore communities. That species richness does not change between treatments, but community composition does, and that the differences in community composition between treatments are driven by turnover, suggests that different species dominate different treatments, and this cancels out any differences in species richness.

We also detected significant effects of treatment on the abundance of Thompson's gazelles, impala, and baboon. Thompson's gazelles were characteristic of burnt areas, whilst impala and baboon abundance shifted between treatments throughout our study. Previous studies of mammalian responses to burnt areas in the Serengeti-Mara (Wilsey, 1996; Eby et al. 2014) have reported that wildebeest, zebra, topi, Thomson's gazelle, impala, warthog, and Grant's gazelle show a preference for burnt areas. They also note smaller species show a preference for burnt areas, attributing this to both resource and predation benefits (Green et al. 2015). Our results concur with these findings. Thompson's gazelles were the smallest species we observed, and they are likely to seek out short-grass area for both nutritional and predation benefits (Wilsey ,1996; Eby et al. 2014). However, they were most abundant in areas where grass was short, regardless of grass quality. This suggests that predation risk may play a greater role in determining their distribution than forage quality. Many predators will take Thompson's gazelle, but they have been shown to be more vulnerable to lion (*Panthera leo* Linnaeus 1758) and leopard (*Panthera pardus* Linnaeus 1758) in wooded areas. Cheetah (*Acinonyx jubatus* Schreber 1775) hunt primarily in the open areas and are Thompson's gazelle's main predator, however cheetahs need to get close so even in open areas less cover for cheetahs would give gazelles an advantage (Borner et al. 1987). Impala abundance was not predicted by any of our vegetation characteristics but Eby et al. (2014) found that impala distribution was determined by the concentrations of non-nitrogen

nutrients, such as copper, potassium and magnesium, which we did not measure. Impala are also mixed feeders, which make the vegetation characteristics they are responding to more difficult to predict than other species (Hempson et al. 2015). Baboon abundance was highest in areas with a high percentage of bare ground and low forb abundance. We observed baboons feeding on the bulbs of sedges, which were common across study plots but most abundant in sandy areas with little or no grass cover. Baboons may have selected these areas because of a greater abundance of sedges or because they were easier to locate and extract in areas with lots of bare ground (J. Probert, pers obs; Fig. 9).



Figure 9: Baboons were observed feeding on the fleshy roots of sedges growing in areas with little grass cover.

Both the quantity and quality of grass were important in predicting herbivore distribution. The total abundance, biomass and species richness were all higher in short-grass areas with low grass biomass. When included in our models, higher grass quality also predicted higher total abundance and species richness of mammalian herbivores. Given the correlation between smaller body size and preference for high quality food (Hoffman, 1989) it makes sense that grass quality would be associated with total abundance but not biomass (Eby et

al. 2014; Green et al. 2015). Grass biomass and height also drove the distribution of individual species, but the direction of response varied with species. Wildebeest, Thompson's gazelle, and warthog were most abundant in short-grass areas whilst zebra were most abundant in area with taller grass. Adding grass quality to our models made it the only significant predictor of wildebeest and topi abundance. These results match our knowledge of the biology of these species as wildebeest and topi are selective grazers which will preferentially feed on high quality grass (McNaughton, 1985; Murray & Brown, 1993).

There are some caveats which mean that our results should be interpreted with some caution: 1) It is impossible to tell whether changes in the significance of other covariates resulting from the inclusion of grass quality in our models is a result of grass quality predicting responses better or the removal of data necessary to include grass quality. 2) The clustered positioning of our burnt plots was necessitated by the occurrence of a single fire within the central portion of Grumeti Game Reserve at the start of our study period. There was evidence of weak spatial autocorrelation in some of our response variables which could not be accounted for in our models. Whilst these issues must be acknowledged, and almost certainly account for some of the variation in our models, our results make sense given our knowledge of mammalian herbivore biology and the findings of previous studies, so we feel they are unlikely to result in erroneous conclusions.

CONCLUSIONS

This was the first study to document both the direct and indirect effects of fire and wildebeest grazing on the distribution of sympatric mammalian herbivores in the Serengeti-Mara. We found that fire and grazing created areas that differed in attractiveness to different species, creating spatial heterogeneity in species assemblage composition across the landscape. Not all of the herbivore species which were more abundant in these short-grass areas were attracted to high-quality grass, perhaps reflecting the relative importance of predation for these species (Eby et al. 2014; Hopcraft et al. 2014). Our results suggest that both fire and wildebeest grazing can concentrate resident grazers by creating areas of short-grass which are attractive to many herbivores. Further testing is needed to determine if grazing by resident herbivores can create and maintain grazing lawns throughout the wet

season, which would in turn influence the movement of the migration the following year, providing high quality, but brief, foraging opportunities.

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SUPPLEMENTARY MATERIAL

Table 1: The effect of treatment and time (week) on the abundance (individuals/hr), biomass (kg/hr) and species richness of mammalian herbivores.

Response variable	Covariate	Df	Chisq	p	Significance
Abundance	Intercept	1	5.115	0.024	*
	Treatment	2	3.957	0.138	
	Time	1	0.416	0.519	
	Treatment: Time	2	5.656	0.059	
Biomass	Intercept	1	5.115	0.024	*
	Treatment	2	3.957	0.138	
	Time	1	0.416	0.519	
	Treatment: Time	2	5.656	0.059	
Richness	Intercept	1	36.667	0.000	***
	Treatment	2	0.955	0.620	
	Time	1	3.222	0.073	
	Treatment: Time	2	0.577	0.749	

Table 2: The effect of treatment and time (week) on the abundance(individuals/hr)/biomass (kg/hr) of the eight most abundant species of mammalian herbivore.

Species	Covariate	Df	Chisq	p	Significance
Wildebeest abundance	Intercept	1	0.669	0.413	
	Treatment	2	1.957	0.376	
	Time	1	3.237	0.072	
	Treatment:Time	2	0.962	0.618	
Zebra abundance	Intercept	1	1.918	0.166	
	Treatment	2	0.647	0.724	
	Time	1	0.978	0.323	
	Treatment:Time	2	0.255	0.880	
Topi abundance	Intercept	1	2.555	0.110	
	Treatment	2	0.519	0.771	
	Time	1	0.040	0.842	
	Treatment:Time	2	1.588	0.452	
Thompson's gazelle abundance	Intercept	1	0.438	0.508	
	Treatment	2	9.614	0.008	***
	Time	1	0.554	0.457	
	Treatment:Time	2	0.845	0.655	
Impala abundance	Intercept	1	15.400	0.000	***
	Treatment	2	11.550	0.003	**
	Time	1	10.955	0.001	***
	Treatment:Time	2	11.305	0.004	**
Buffalo abundance	Intercept	1	4.813	0.028	*
	Treatment	2	0.124	0.940	
	Time	1	0.995	0.318	
	Treatment:Time	2	4.455	0.108	
Warthog abundance	Intercept	1	4.282	0.039	*
	Treatment	2	1.617	0.446	
	Time	1	4.060	0.044	*
	Treatment:Time	2	2.653	0.265	
Baboon abundance	Intercept	1	0.024	0.877	
	Treatment	2	6.886	0.032	*
	Time	1	3.901	0.048	*
	Treatment:Time	2	11.790	0.003	**

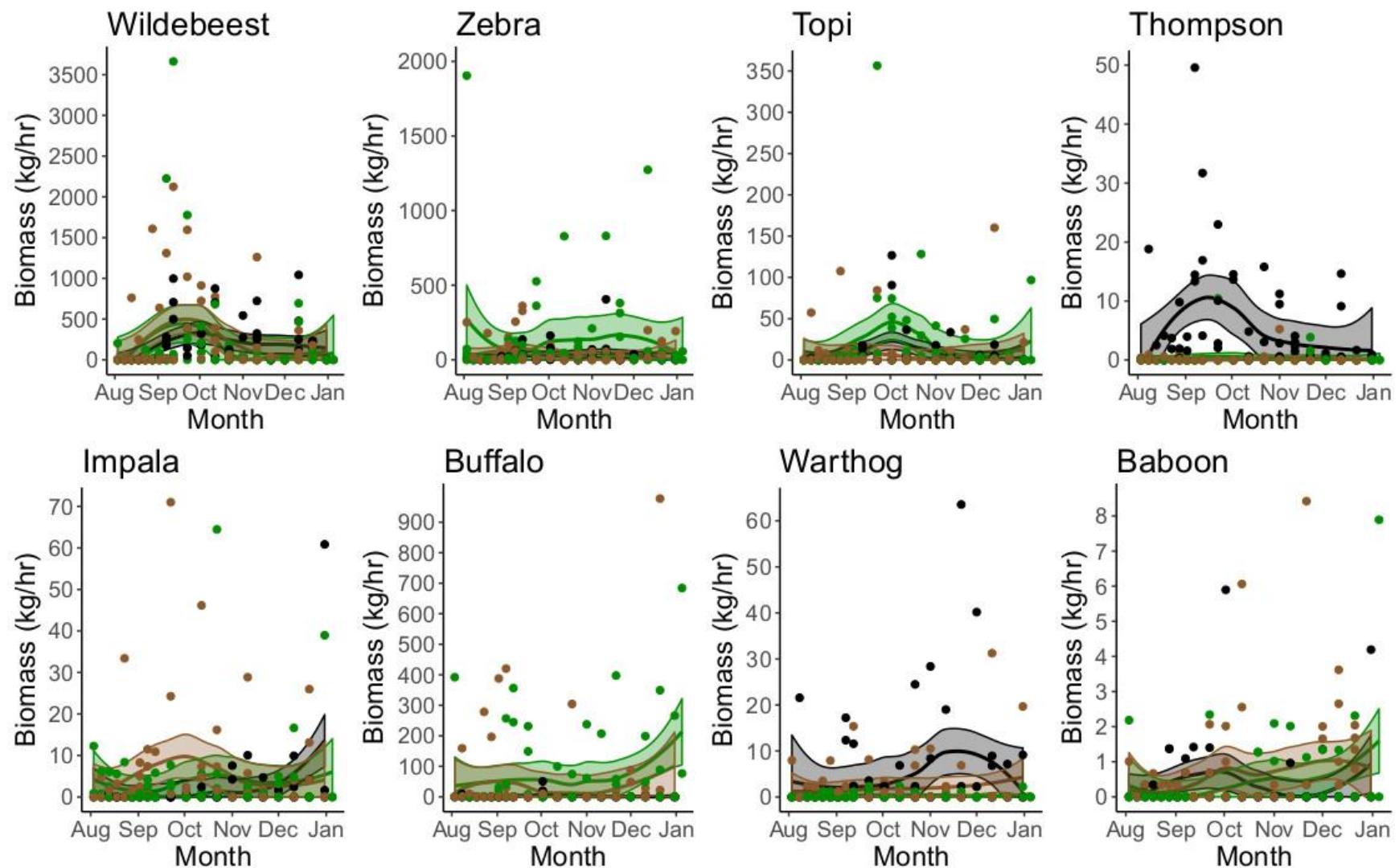


Figure 1: Temporal trends in the biomass of the eight species of mammalian herbivore which were most abundant during our study. Surveys of burnt plots are shown in black, wildebeest plots in brown and control plots in green.

Table 3: The effect of treatment and time on the community composition of mammalian herbivores.

Predictor	Df	Sum of squares	Mean squares	F model	R2	Pr(>F)	Significance
Treatment	2	5.819	2.909	12.966	0.110	0.001	***
Set	1	0.248	0.248	1.103	0.005	0.364	
Treatment:Set	2	1.457	0.729	3.247	0.028	0.001	***
Residuals	202	45.328	0.224	-	0.858	-	
Total	207	52.852	-	-	1.000	-	

Table 4: The percentage of the dissimilarity between treatments explained by the abundance of each mammalian herbivore species.

Control:wildebeest				Control:Burnt				Burnt:wildebeest			
Species	% variation	Mean abundance	Mean abundance	Species	% variation	Mean abundance	Mean abundance	Species	% variation	Mean abundance	Mean abundance
	explained	control	wildebeest		explained	control	burnt		explained	burnt	wildebeest
Wildebeest	30.66	0.18	0.11	Wildebeest	31.40	0.11	0.24	Wildebeest	37.40	0.24	0.18
Zebra	24.21	0.06	0.13	Thompson	18.21	0.00	0.13	Thompson	18.37	0.13	0
Impala	10.01	0.03	0.02	Zebra	17.24	0.13	0.05	Zebra	14.98	0.05	0.06
Topi	8.88	0.02	0.05	Topi	8.01	0.05	0.02	Impala	7.33	0.01	0.03
Buffalo	7.40	0.01	0.03	Impala	6.50	0.02	0.01	Warthog	6.55	0.03	0.01
Baboon	4.87	0.01	0.01	Buffalo	4.80	0.03	0.00	Topi	5.14	0.02	0.02
Warthog	4.26	0.01	0.00	Warthog	4.65	0.00	0.03	Baboon	4.08	0.01	0.01
Eland	2.16	0.00	0.01	Baboon	2.52	0.01	0.01	Buffalo	3.09	0.00	0.01
Thompson	1.87	0.00	0.00	Giraffe	2.00	0.01	0.00	Giraffe	1.03	0.00	0
Elephant	1.80	0.00	0.00	Reedbuck	1.45	0.03	0.00	Eland	0.95	0.00	0
Giraffe	1.66	0.00	0.01	Elephant	1.24	0.00	0.00	Grants	0.47	0.00	0
Reedbuck	1.63	0.00	0.03	Eland	1.20	0.01	0.00	Elephant	0.42	0.00	0
Waterbuck	0.50	0.00	0.00	Grants	0.43	0.00	0.00	Waterbuck	0.15	0.00	0
Grants	0.09	0.00	0.00	Waterbuck	0.31	0.00	0.00	Hartebeest	0.04	0.00	0
Hartebeest	0.00	0.00	0.00	Hartebeest	0.04	0.00	0.00	Reedbuck	0.00	0.00	0

Table 5: Indicator Values (IndVal) for the mammalian herbivore species which are characteristic of each treatment.

Species	Treatment			p
	Burnt	Control	Wildebeest	
Baboon	0.039	0.042	0.152	0.030
Buffalo	0.002	0.190	0.057	0.001
Eland	0.006	0.043	0.019	0.490
Elephant	0.000	0.069	0.004	0.020
Giraffe	0.014	0.079	0.010	0.073
Grants	0.035	0.000	0.002	0.072
Hartebeest	0.014	0.000	0.000	0.283
Impala	0.034	0.138	0.211	0.030
Reedbuck	0.000	0.024	0.000	0.195
Thompson	0.604	0.001	0.004	0.001
Topi	0.088	0.162	0.059	0.174
Warthog	0.221	0.006	0.078	0.002
Waterbuck	0.000	0.027	0.003	0.200
Wildebeest	0.259	0.065	0.185	0.028
Zebra	0.093	0.292	0.134	0.045

Table 6: The effect of vegetation on the abundance (individuals/hr), biomass (kg/hr) and species richness of mammalian herbivores.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Abundance	Biomass	1	32.953	32.953	10.673	0.002	**
	Vegetative height	1	30.506	30.506	9.880	0.002	**
	Inflorescence height	1	0.131	0.131	0.042	0.837	
	Percentage bare ground	1	3.619	3.619	1.172	0.283	
	Forb Abundance	1	0.433	0.433	0.140	0.709	
	Forb Richness	1	0.023	0.023	0.008	0.931	
	Percentage forbs flowering	1	2.365	2.365	0.766	0.384	
Biomass	Biomass	1	1040617.729	1040617.729	7.388	0.009	*
	Vegetative height	1	994980.838	994980.838	7.064	0.010	*
	Inflorescence height	1	6141.561	6141.561	0.044	0.835	
	Percentage bare ground	1	27338.730	27338.730	0.194	0.661	
	Forb Abundance	1	37224.404	37224.404	0.264	0.609	
	Forb Richness	1	28897.205	28897.205	0.205	0.653	
	Percentage forbs flowering	1	166936.285	166936.285	1.185	0.280	
Richness	Biomass	1	4.100	4.100	2.282	0.137	
	Vegetative height	1	18.157	18.157	10.106	0.002	**
	Inflorescence height	1	15.895	15.895	8.847	0.004	**
	Percentage bare ground	1	3.492	3.492	1.944	0.168	
	Forb Abundance	1	9.100	9.100	5.065	0.028	*
	Forb Richness	1	4.260	4.260	2.371	0.132	
	Percentage forbs flowering	1	1.386	1.386	0.771	0.383	

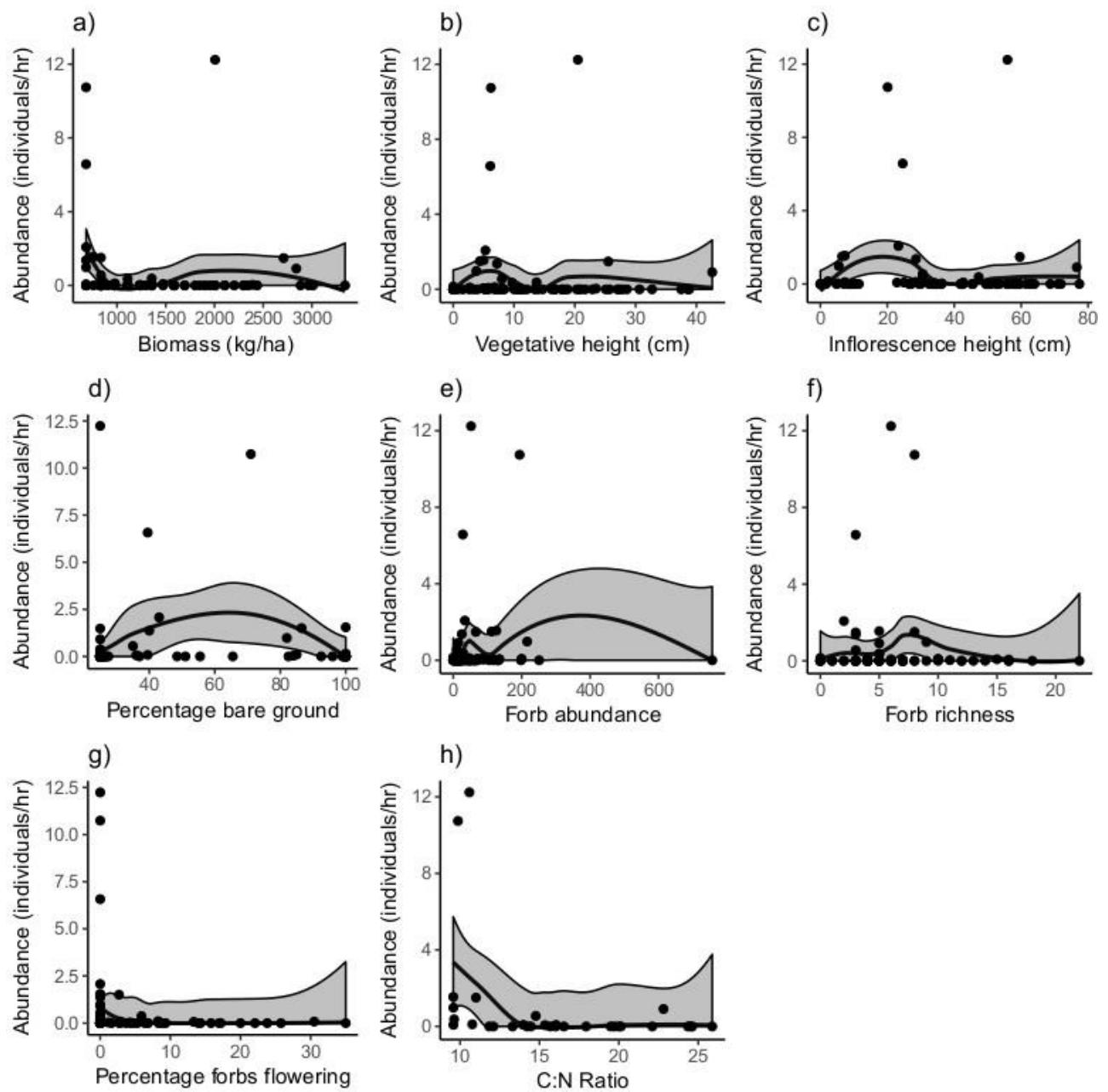


Figure 2: The relationship between wildebeest abundance and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

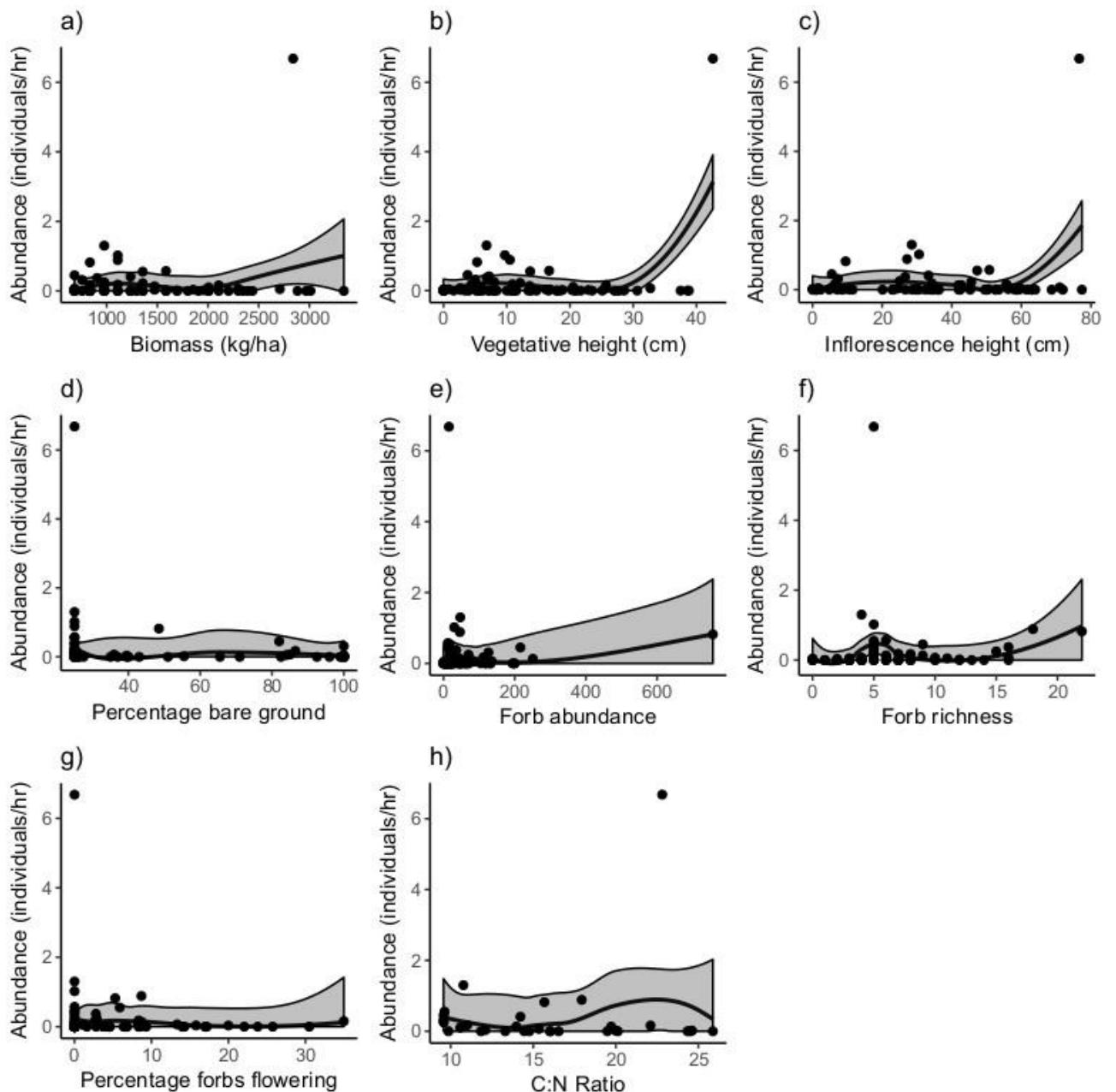


Figure 3: The relationship between zebra abundance and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

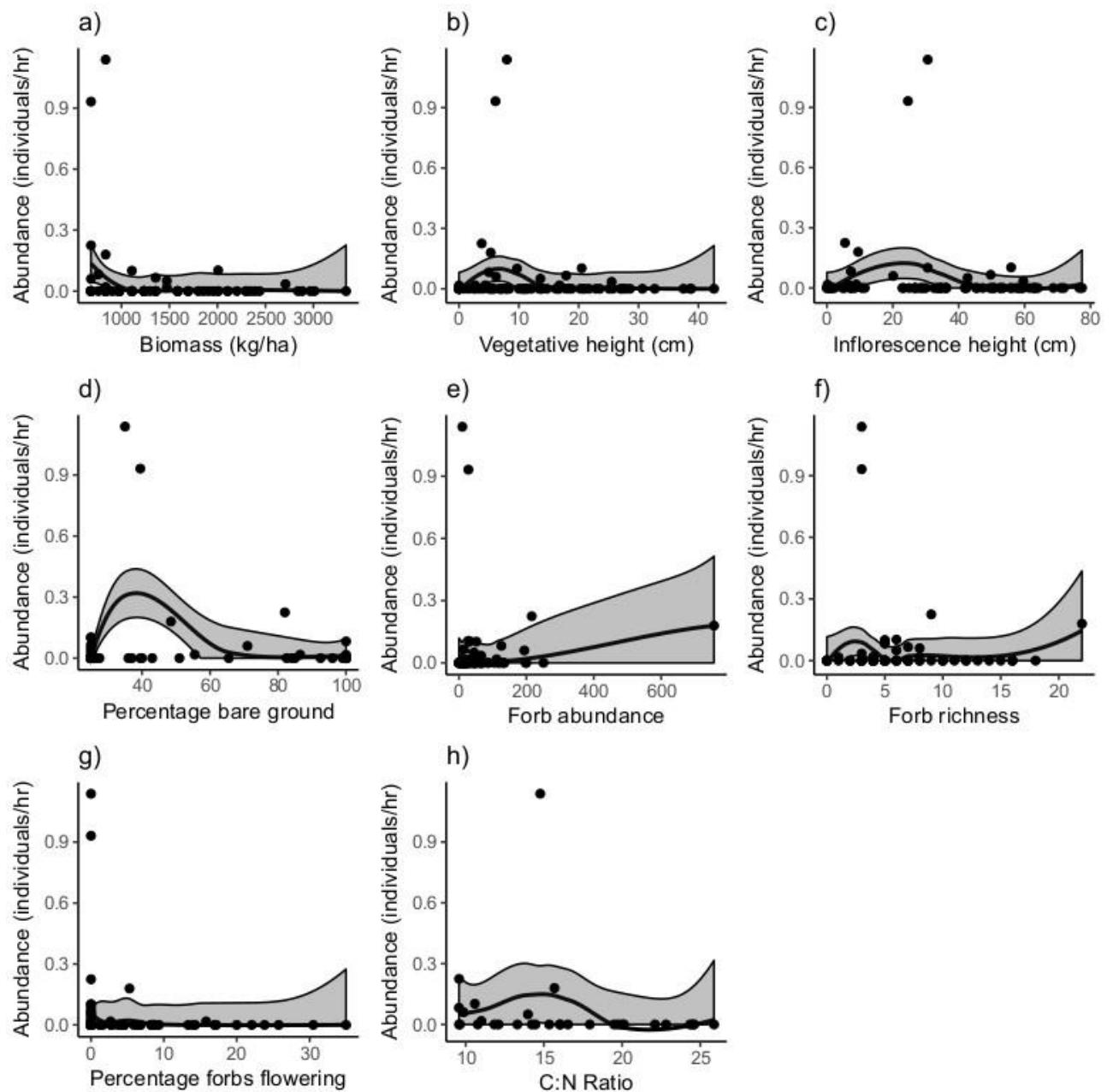


Figure 4: The relationship between topi abundance and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

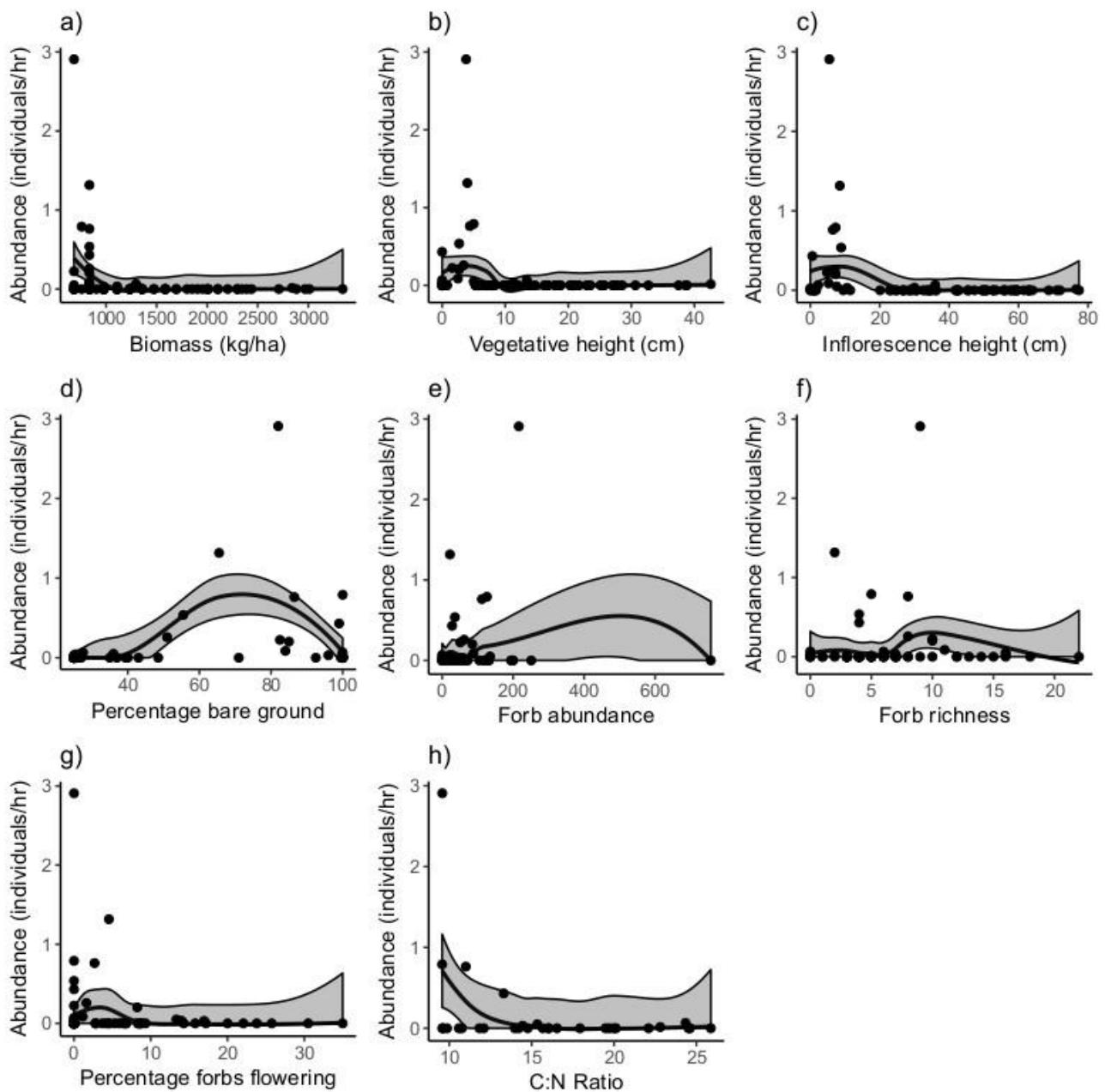


Figure 5: The relationship between Thompson's gazelle abundance and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

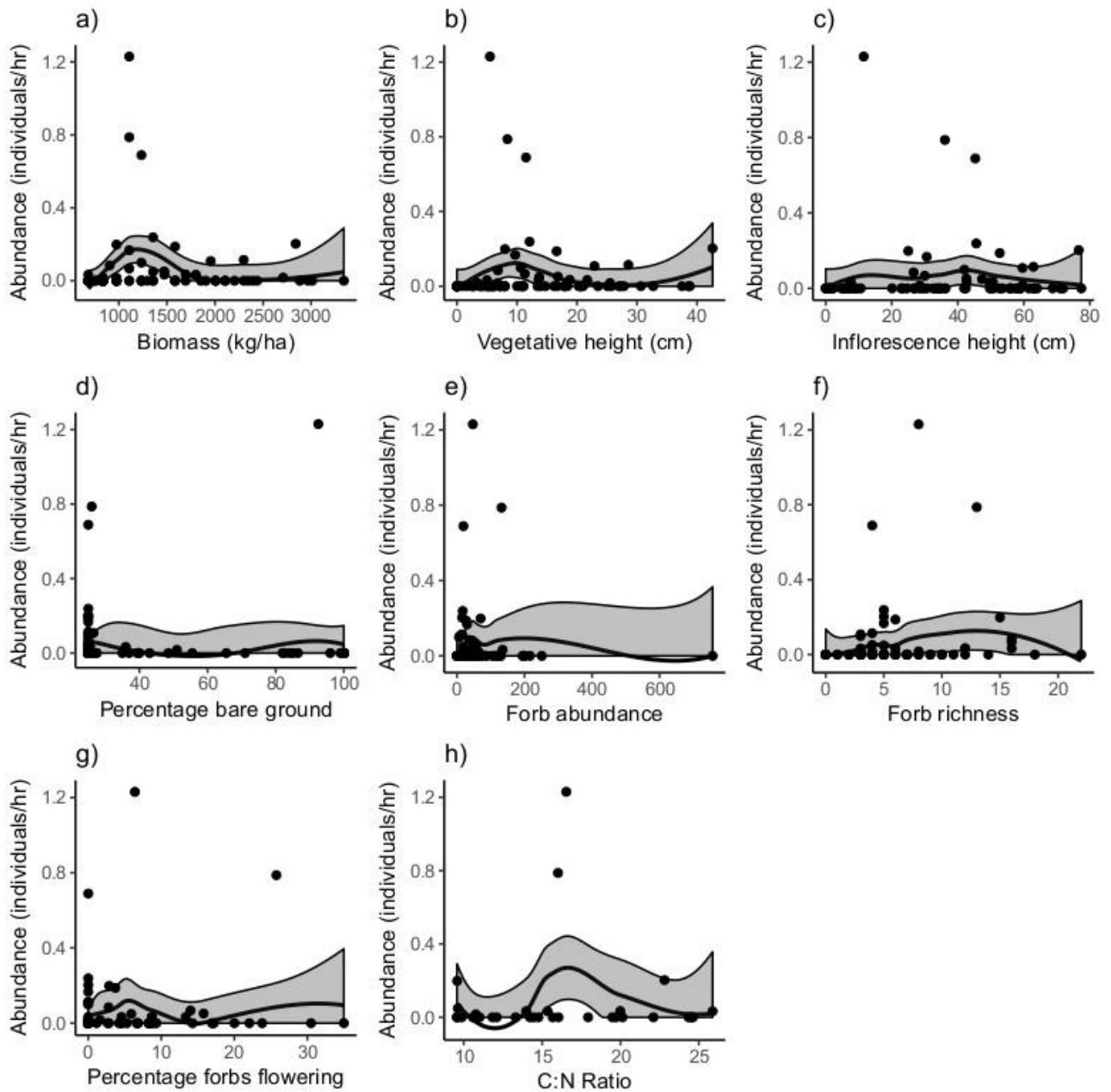


Figure 6: The relationship between impala abundance and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

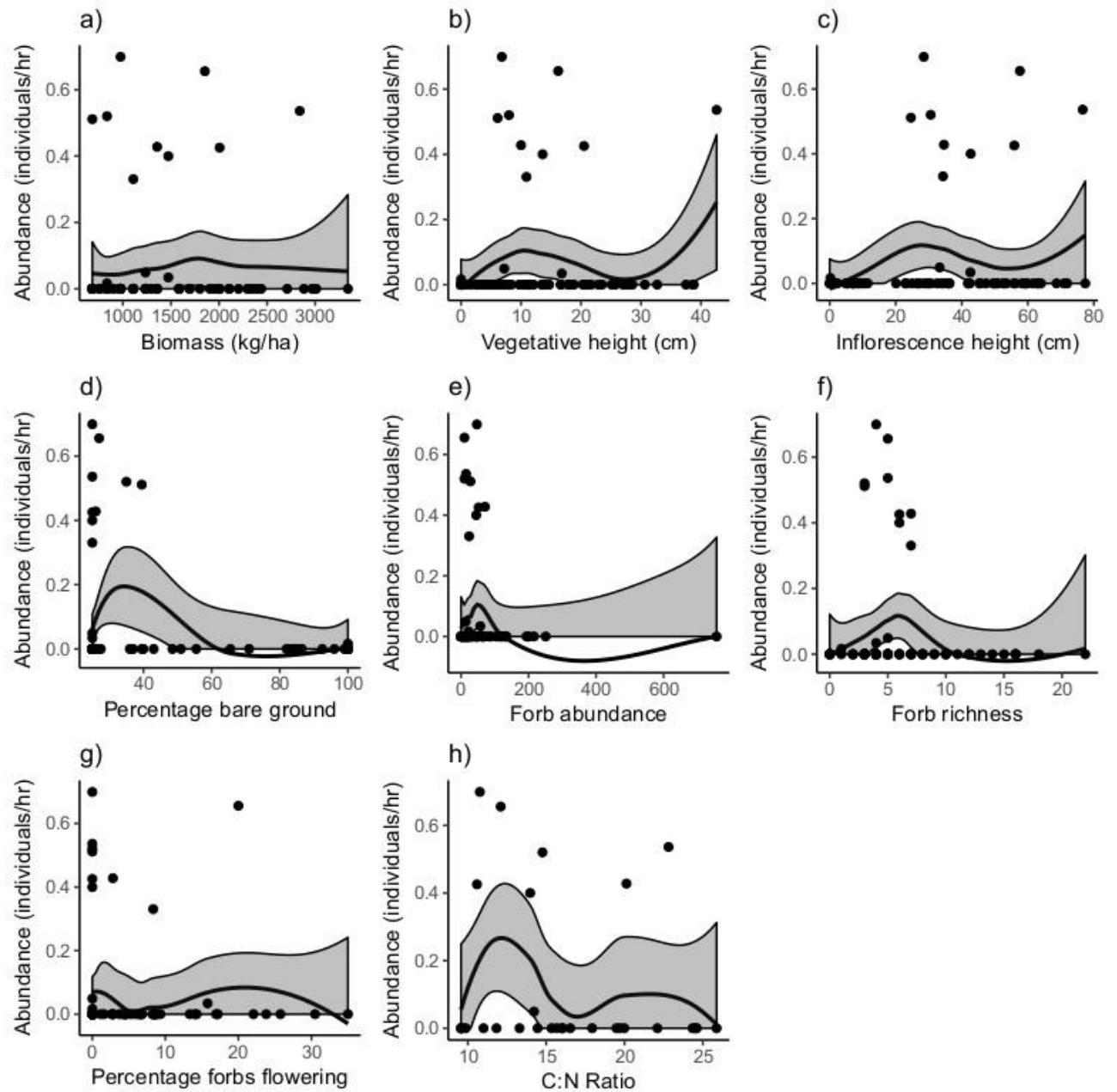


Figure 7: The relationship between buffalo abundance and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

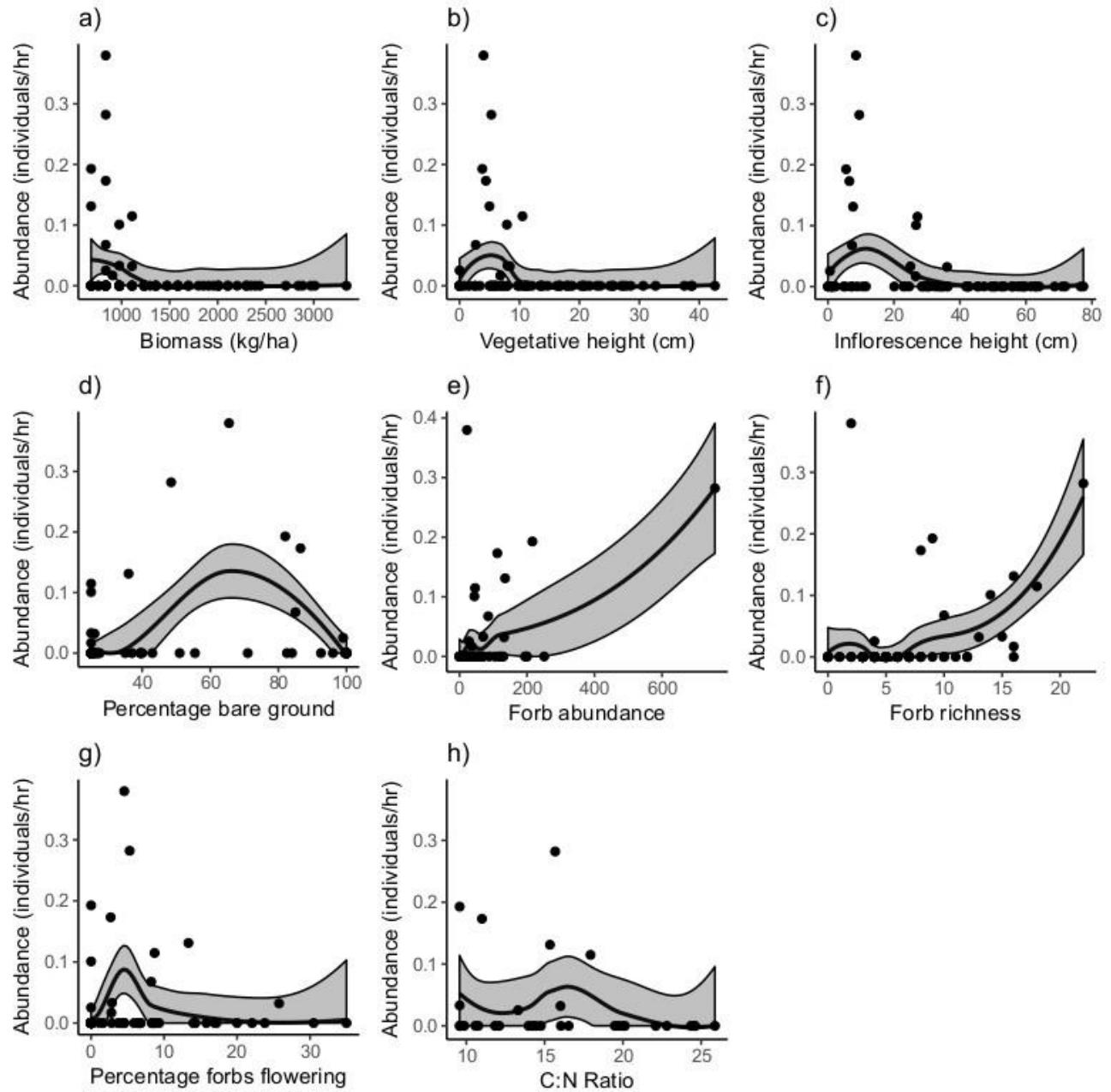


Figure 8: The relationship between warthog abundance and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

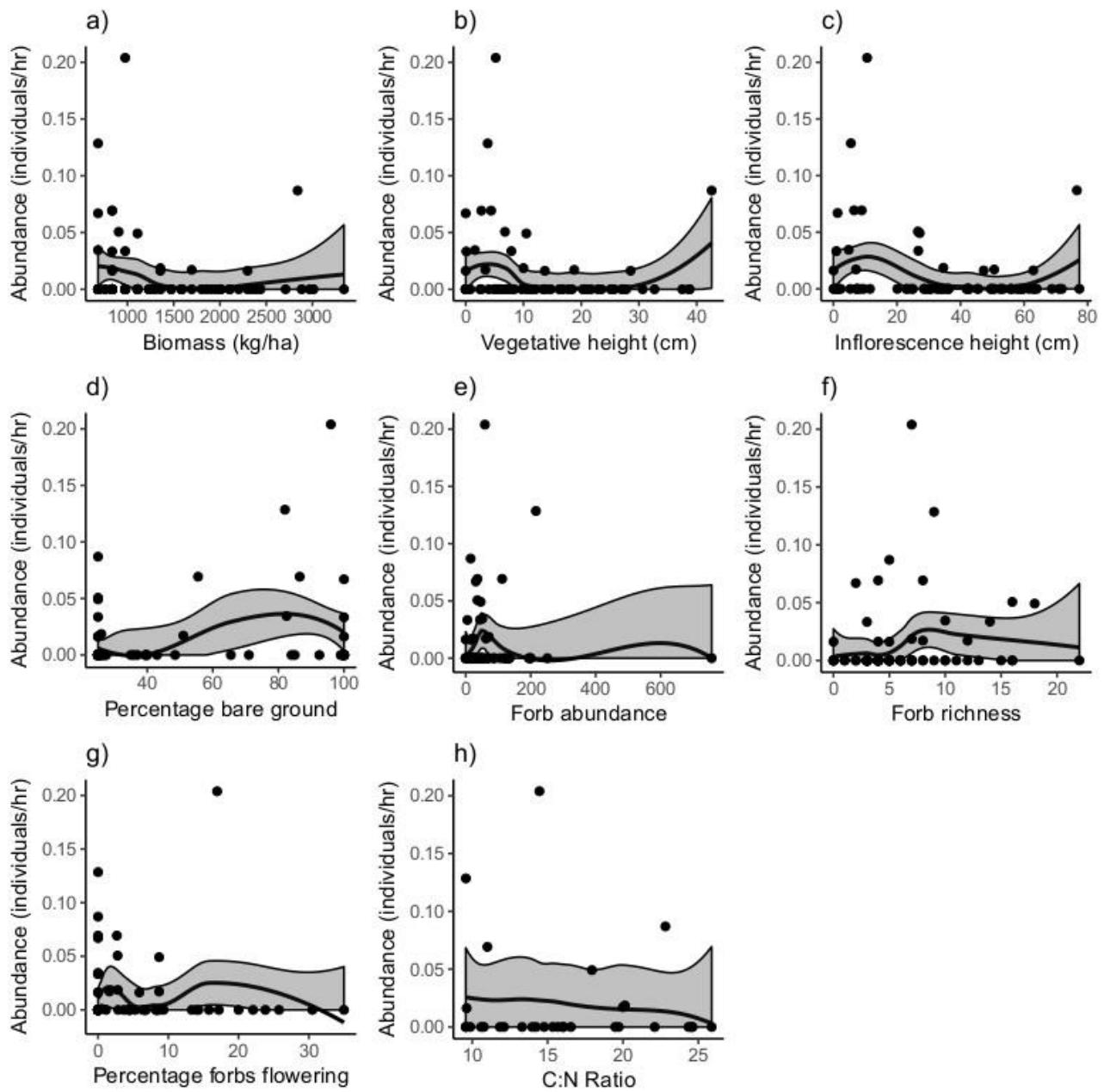


Figure 9: The relationship between baboon abundance and: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) forb abundance, f) forb species richness, g) the percentage of forbs flowering, and h) the carbon:nitrogen ratio.

Table 7: The effect of vegetation on the abundance of wildebeest, zebra, topi and Thompson's gazelles.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Wildebeest abundance	Biomass	1	11.213	11.213	4.362	0.041	*
	Vegetative height	1	3.730	3.730	1.451	0.232	
	Inflorescence height	1	1.814	1.814	0.706	0.404	
	Percentage bare ground	1	4.752	4.752	1.849	0.178	
	Forb Abundance	1	0.047	0.047	0.018	0.893	
	Forb Richness	1	0.355	0.355	0.138	0.712	
Zebra abundance	Percentage forbs flowering	1	0.728	0.728	0.283	0.596	
	Biomass	1	2.220	2.220	4.869	0.030	*
	Vegetative height	1	5.911	5.911	12.966	0.001	**
	Inflorescence height	1	0.952	0.952	2.089	0.152	
	Percentage bare ground	1	0.001	0.001	0.002	0.966	
	Forb Abundance	1	0.037	0.037	0.080	0.778	
Topi abundance	Forb Richness	1	0.036	0.036	0.080	0.778	
	Percentage forbs flowering	1	1.054	1.054	2.312	0.132	
	Biomass	1	0.044	0.044	2.063	0.156	
	Vegetative height	1	0.019	0.019	0.902	0.346	
	Inflorescence height	1	0.000	0.000	0.022	0.883	
	Percentage bare ground	1	0.008	0.008	0.351	0.555	
Thompson's gazelle abundance	Forb Abundance	1	0.016	0.016	0.759	0.388	
	Forb Richness	1	0.000	0.000	0.022	0.882	
	Percentage forbs flowering	1	0.004	0.004	0.177	0.675	
	Biomass	1	0.358	0.358	4.782	0.032	*
	Vegetative height	1	0.348	0.348	4.636	0.034	*
	Inflorescence height	1	0.014	0.014	0.192	0.663	
	Percentage bare ground	1	0.139	0.139	1.855	0.177	
	Forb Abundance	1	0.010	0.010	0.128	0.722	
	Forb Richness	1	0.080	0.080	1.069	0.305	
	Percentage forbs flowering	1	0.000	0.000	0.001	0.973	

Table 8: The effect of vegetation on the abundance of impala, buffalo, warthog and baboon.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Impala abundance	Biomass	1	0.000	0.000	0.004	0.951	
	Vegetative height	1	0.029	0.029	0.995	0.322	
	Inflorescence height	1	0.079	0.079	2.675	0.108	
	Percentage bare ground	1	0.075	0.075	2.534	0.117	
	Forb Abundance	1	0.121	0.121	4.102	0.051	
	Forb Richness	1	0.032	0.032	1.101	0.300	
Buffalo abundance	Percentage forbs flowering	1	0.013	0.013	0.426	0.516	
	Biomass	1	0.006	0.006	0.279	0.600	
	Vegetative height	1	0.004	0.004	0.203	0.654	
	Inflorescence height	1	0.003	0.003	0.126	0.724	
	Percentage bare ground	1	0.045	0.045	2.105	0.153	
	Forb Abundance	1	0.056	0.056	2.608	0.116	
Warthog abundance	Forb Richness	1	0.003	0.003	0.119	0.732	
	Percentage forbs flowering	1	0.008	0.008	0.353	0.555	
	Biomass	1	0.000	0.000	0.025	0.874	
	Vegetative height	1	0.006	0.006	2.295	0.134	
	Inflorescence height	1	0.011	0.011	4.348	0.041	*
	Percentage bare ground	1	0.002	0.002	0.758	0.387	
Baboon abundance	Forb Abundance	1	0.002	0.002	0.843	0.363	
	Forb Richness	1	0.007	0.007	2.973	0.091	
	Percentage forbs flowering	1	0.000	0.000	0.007	0.933	
	Biomass	1	0.001	0.001	1.629	0.206	
	Vegetative height	1	0.002	0.002	2.492	0.118	
	Inflorescence height	1	0.000	0.000	0.000	0.993	

Table 9: The effect of vegetation, including C:N ratio, on the abundance (individuals/hr), biomass (kg/hr) and species richness of mammalian herbivores.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Abundance	Biomass	1	30.329	30.329	4.903	0.037	*
	Vegetative height	1	33.683	33.683	5.445	0.028	*
	Inflorescence height	1	8.671	8.671	1.402	0.248	
	Percentage bare ground	1	13.814	13.814	2.233	0.148	
	C:N ratio	1	65.094	65.094	10.522	0.003	**
	Forb Abundance	1	2.079	2.079	0.336	0.568	
	Forb Richness	1	0.944	0.944	0.153	0.700	
	Percentage forbs flowering	1	13.212	13.212	2.136	0.157	
Biomass	Biomass	1	1338952.735	1338952.735	5.247	0.031	*
	Vegetative height	1	1609622.887	1609622.887	6.307	0.019	*
	Inflorescence height	1	260888.689	260888.689	1.022	0.323	
	Percentage bare ground	1	144272.645	144272.645	0.565	0.460	
	C:N ratio	1	1665303.644	1665303.644	6.525	0.060	
	Forb Abundance	1	9597.918	9597.918	0.038	0.848	
	Forb Richness	1	3828.925	3828.925	0.015	0.904	
	Percentage forbs flowering	1	767135.725	767135.725	3.006	0.096	
Richness	Biomass	1	12.459	12.459	6.289	0.019	*
	Vegetative height	1	30.193	30.193	15.241	0.001	**
	Inflorescence height	1	2.600	2.600	1.313	0.263	
	Percentage bare ground	1	0.791	0.791	0.399	0.534	
	C:N ratio	1	38.907	38.907	19.639	0.000	***
	Forb Abundance	1	5.251	5.251	2.650	0.117	
	Forb Richness	1	1.183	1.183	0.597	0.447	
	Percentage forbs flowering	1	1.097	1.097	0.554	0.464	

Table 10: The effect of vegetation, including C:N ratio, on the abundance of wildebeest, zebra, topi and Thompson's gazelles.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Wildebeest abundance	Biomass	1	10.452	10.452	1.493	0.234	
	Vegetative height	1	3.728	3.728	0.532	0.473	
	Inflorescence height	1	13.384	13.384	1.912	0.180	
	Percentage bare ground	1	11.255	11.255	1.607	0.217	
	C:N ratio	1	35.692	35.692	5.097	0.033	*
	Forb Abundance	1	0.910	0.910	0.130	0.722	
	Forb Richness	1	2.254	2.254	0.322	0.576	
Zebra abundance	Percentage forbs flowering	1	6.225	6.225	0.889	0.355	
	Biomass	1	3.231	3.231	3.672	0.068	
	Vegetative height	1	10.596	10.596	12.042	0.002	**
	Inflorescence height	1	0.298	0.298	0.339	0.566	
	Percentage bare ground	1	0.013	0.013	0.015	0.905	
	C:N ratio	1	1.699	1.699	1.930	0.223	
	Forb Abundance	1	0.007	0.007	0.008	0.929	
Topi abundance	Forb Richness	1	0.114	0.114	0.129	0.722	
	Percentage forbs flowering	1	1.768	1.768	2.010	0.169	
	Biomass	1	0.077	0.077	2.737	0.112	
	Vegetative height	1	0.037	0.037	1.318	0.263	
	Inflorescence height	1	0.000	0.000	0.015	0.903	
	Percentage bare ground	1	0.036	0.036	1.287	0.269	
	C:N ratio	1	0.298	0.298	10.577	0.003	**
Thompson's gazelle abundance	Forb Abundance	1	0.140	0.140	4.965	0.036	
	Forb Richness	1	0.073	0.073	2.589	0.122	
	Percentage forbs flowering	1	0.024	0.024	0.842	0.368	
	Biomass	1	0.256	0.256	1.227	0.285	
	Vegetative height	1	0.386	0.386	1.844	0.192	
	Inflorescence height	1	0.033	0.033	0.159	0.694	
	Percentage bare ground	1	0.106	0.106	0.509	0.484	

Table 11: The effect of vegetation, including C:N ratio, on the abundance of impala, buffalo, warthog and baboon.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Impala abundance	Biomass	1	0.002	0.002	0.053	0.821	
	Vegetative height	1	0.000	0.000	0.006	0.940	
	Inflorescence height	1	0.000	0.000	0.006	0.940	
	Percentage bare ground	1	0.044	0.044	1.166	0.295	
	C:N ratio	1	0.001	0.001	0.020	0.895	
	Forb Abundance	1	0.020	0.020	0.532	0.473	
	Forb Richness	1	0.054	0.054	1.429	0.245	
Buffalo abundance	Percentage forbs flowering	1	0.001	0.001	0.014	0.906	
	Biomass	1	0.000	0.000	0.011	0.918	
	Vegetative height	1	0.020	0.020	0.490	0.492	
	Inflorescence height	1	0.008	0.008	0.199	0.660	
	Percentage bare ground	1	0.098	0.098	2.386	0.136	
	C:N ratio	1	0.171	0.171	4.160	0.287	
	Forb Abundance	1	0.118	0.118	2.882	0.103	
Warthog abundance	Forb Richness	1	0.005	0.005	0.122	0.730	
	Percentage forbs flowering	1	0.021	0.021	0.524	0.476	
	Biomass	1	0.000	0.000	0.006	0.940	
	Vegetative height	1	0.003	0.003	1.170	0.296	
	Inflorescence height	1	0.004	0.004	1.701	0.206	
	Percentage bare ground	1	0.000	0.000	0.052	0.821	
	C:N ratio	1	0.003	0.003	1.166	0.525	
Baboon abundance	Forb Abundance	1	0.010	0.010	3.779	0.068	
	Forb Richness	1	0.001	0.001	0.317	0.582	
	Percentage forbs flowering	1	0.000	0.000	0.161	0.692	
	Biomass	1	0.001	0.001	0.444	0.511	
	Vegetative height	1	0.002	0.002	1.092	0.306	
	Inflorescence height	1	0.000	0.000	0.002	0.962	
	Percentage bare ground	1	0.005	0.005	2.618	0.119	

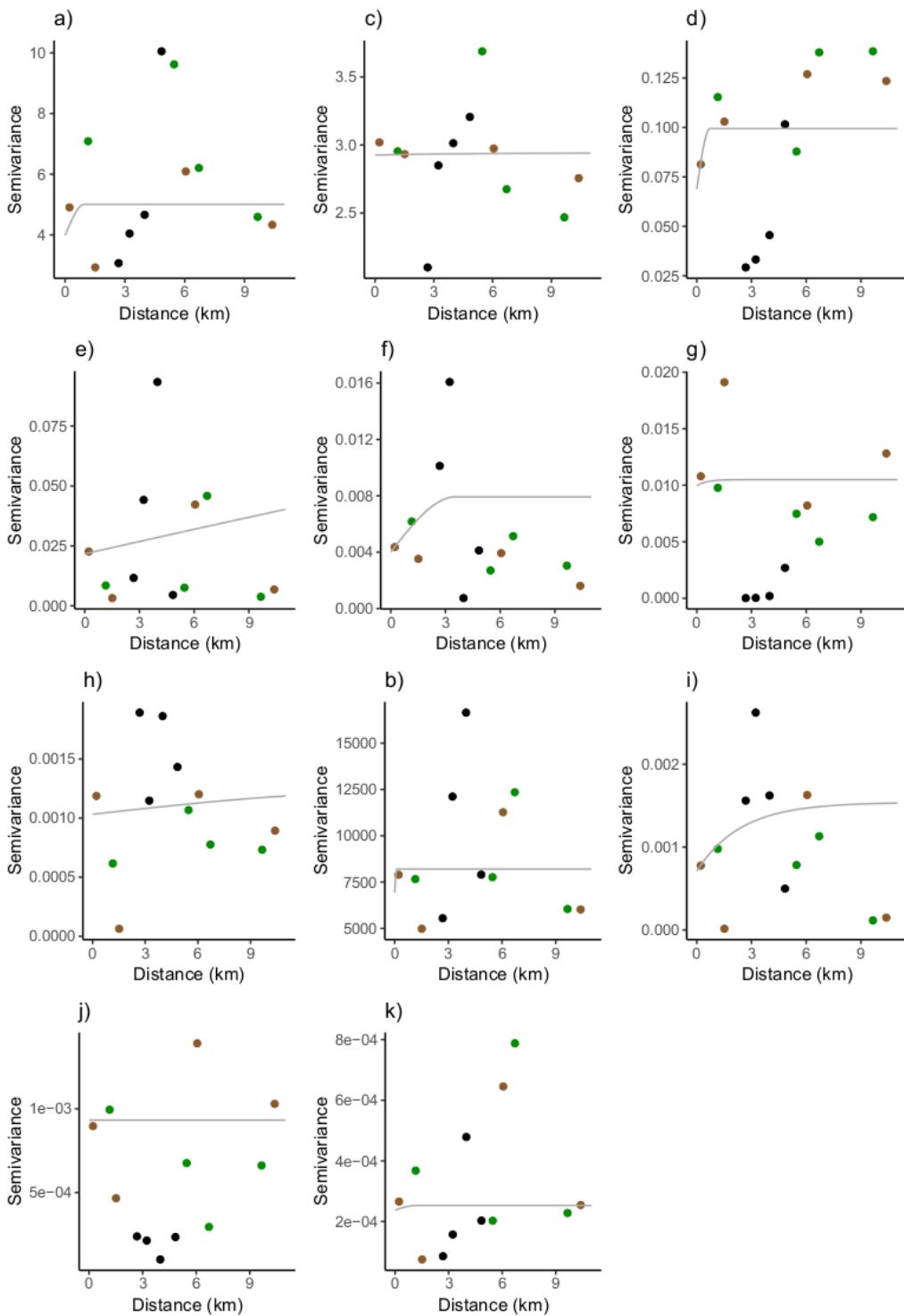
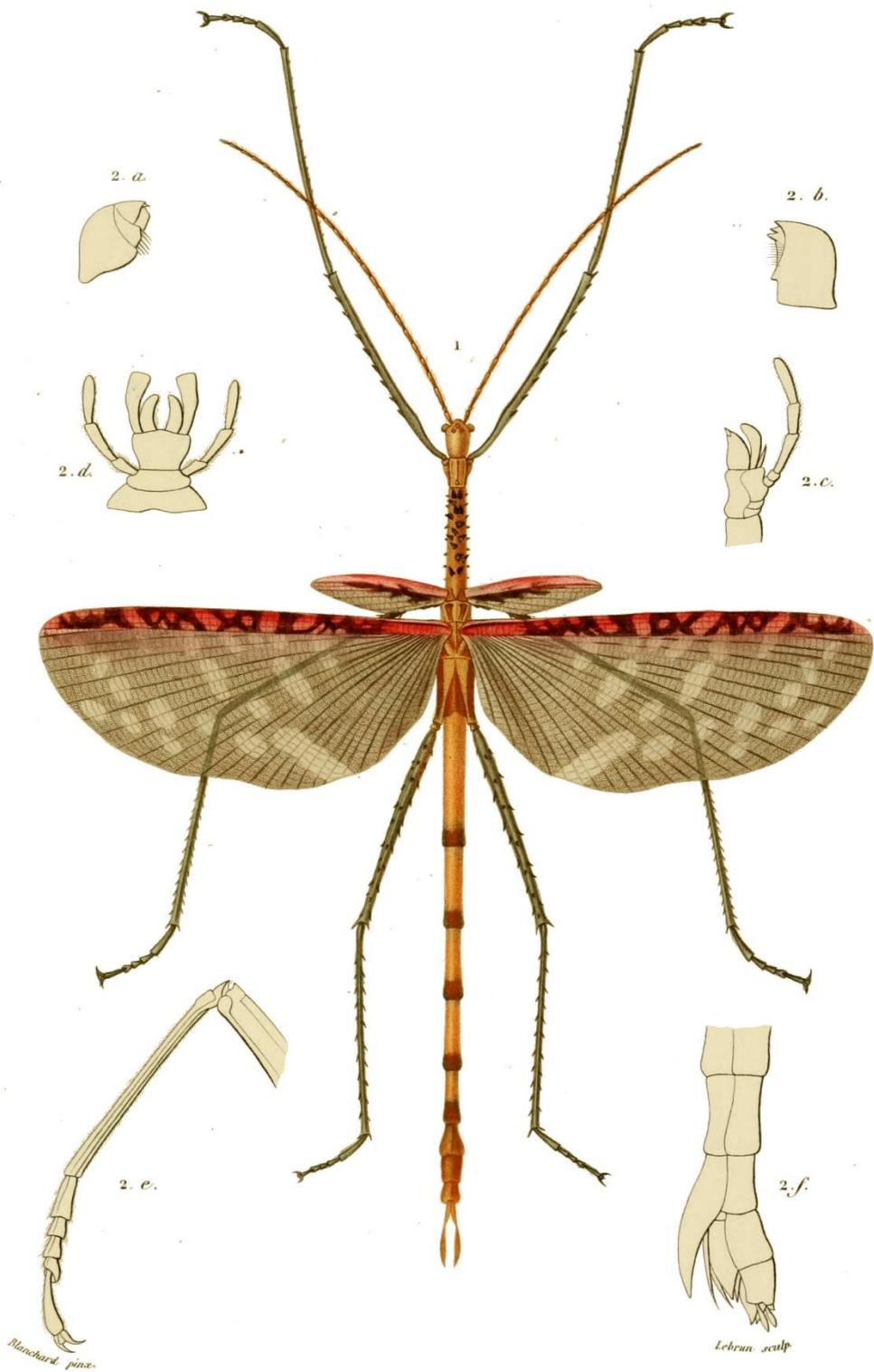


Figure 10: Semi-variograms for: a) total abundance, b) total biomass, c) species richness, d) wildebeest abundance, e) zebra abundance, f) topi abundance, g) Thompson's gazelle abundance, h) impala abundance, i) buffalo abundance, j) warthog abundance, and k) baboon abundance. Burnt plots are shown in black, wildebeest plots in brown and control plots in green.

Chapter 5

Fire and grazing have strong contrasting effects on invertebrate communities



Cover illustration: *Cyphocrana titan*, modified from *Dictionnaire universel d'histoire naturelle* (D' Orbigny, 1849).

ABSTRACT

1. Despite constituting the majority of faunal diversity in savannahs, and carrying out many important functions, invertebrates have received relatively little research attention. We have a poor understanding of how they are directly affected by fire and grazing, and how indirect effects on vegetation cascade to affect invertebrates, making it hard to predict how management actions, and changing savannah dynamics will affect invertebrate communities.
2. Using a large scale natural experimental approach, we investigated the response of invertebrates to fire and grazing by the wildebeest migration in the Serengeti-Mara ecosystem of East Africa. We linked the variation we observed in invertebrate responses to differences in vegetation characteristics created fire and grazing.
3. Fire and grazing had significantly different effects on invertebrates. Both reduced the abundance, biomass and richness of invertebrates but fire caused greater reductions than grazing. Wildebeest grazing affected foliage-dwelling invertebrates but had no effect on most ground-dwelling invertebrates, and a positive effect on ant abundance.
4. Foliage-dwelling invertebrates were affected by grass biomass and height, but invertebrates also responded to rainfall, increasing in abundance during the wet season. Ants recovered rapidly from the effects of fire and grazing but spiders declined throughout our study period.
5. Our results show that diversity exists in invertebrate responses to fire and grazing depending on the ecological niche of the taxa being examined. Maintaining habitat heterogeneity is therefore key to maintaining invertebrate abundance and diversity. Consumers affect invertebrates directly through mortality and indirectly through their effects on vegetation, but invertebrates are also affected by bottom-up processes such as rainfall. Global changes in fire, grazing and rainfall may have important consequences for invertebrate communities.

Keywords: Fire, grazing, herbivores, wildebeest, savannah, consumers, Serengeti, forb

INTRODUCTION

Despite constituting the majority of savannah faunal diversity (Ulys & Hamer, 2006) invertebrates remain an understudied component of savannah ecology (Andersen & Lonsdale, 1990; Davies et al. 2016). Studies have indicated that invertebrates play an important role in pollination, decomposition, nutrient cycling, pest control, seed dispersal and herbivory (Davies et al. 2016; Greenslade & Smith, 2010; Risch et al. 2015; Uys & Hamer, 2007) but our understanding of how they are affected by, and interact with, processes shaping savannah systems is poor (e.g. Parr & Chown, 2004). Given the frequency of fires and the abundance of mammalian herbivores in many African savannahs, there is a key knowledge gap that needs addressing in order to facilitate the management of savannahs for biodiversity. Greater understanding of invertebrate responses to fire and grazing would allow informed decisions concerning the effects of management actions on savannah biodiversity, and potentially provide a useful tool in successfully implementing management objectives (Parr et al. 2004; Ulys & Hamer, 2006).

Most studies of faunal responses to fire and grazing in savannahs have focused on mammals (Andersen & Lonsdale, 1990; Davies et al. 2016), despite the significant role invertebrates play as consumers in savannah systems (La Pierre et al. 2015). Those studies that have focused on invertebrates have produced conflicting results, with both positive and negative effects reported on various taxa, in different locations, over a range of temporal scales (Doamba et al. 2014; Greenslade & Smith, 2010; Parr, Bond & Robertson 2002; Ulys & Hamer, 2006). For example, Branson (2005) found that burning negatively affected Orthoptera abundance but not species richness one-year post-fire, whilst Greenslade & Smith (2010) found the abundance and richness of Orthoptera and Hymenoptera was higher on burnt plots, and the abundance and richness of Araneae was lower 18 months post-fire. In relation to grazing, Gibson et al. (1992) found the abundance and species richness of spiders increased as grazing intensity decreased, with the highest abundance and richness in ungrazed plots. Welch & Kondratieff (1991) found that light and heavy grazing had no effect on grasshopper density or species composition in the short-term, but that grasshopper density was higher in lightly grazed areas following decades of grazing, and Hutchinson and King (1980) found that ants were most abundant when grazing was most intense. In

addition to the lack of a clear consensus, most studies focus on either fire or grazing rather than contrasting the effects of both in a single ecosystem (Swengel, 2001) or focus on a single taxonomic group (Yekwayo et al. 2018). There is also a lack of research in Africa in particular and, given the context dependent nature of faunal responses to fire (Barrow et al. 2006), it is unclear to what extent findings from research in North America (e.g. Branson, 2005; Jackson et al. 2012), Australia (e.g. Andersen et al. 2014; Greenslade & Smith, 2010), or even other regions in Africa (e.g. Parr et al. 2004; Doamba et al. 2014), can be extrapolated elsewhere.

The short-term effects of an individual fire or grazing event may be substantially different to the long-term effects of fire and grazing regimes and it is important to distinguish between them (Parr et al. 2004). Short-term effects are usually direct, resulting from mortality and displacement, but also altered microclimate and resource availability, whilst long-term effects are the result of changes in vegetation structure and therefore habitat suitability. In her review of invertebrate responses to a variety of management strategies Swengel (2001) concluded that both fire and grazing were likely to cause direct invertebrate mortality, resulting in sharp declines immediately post-disturbance. Fire generally causes greater mortality than grazing (Bulan & Barrett, 1971), but in both cases, levels of mortality are highly dependent on invertebrate life history stage, mobility, ecological niche, and the timing, intensity and patchiness of the fire or grazing (Uys & Hamer, 2006). The lowest mortality occurs in groups that are either highly mobile (e.g. grasshoppers) or able to seek refuge underground (e.g. ants and termites) or in fallen wood (e.g. some beetles) (Dana 1991; Deyrup 1996; Van Wieren, 1998). It should also be noted that mortality may continue for several weeks post-disturbance as a result of starvation and exposure (Warren et al. 1987; Bale et al. 2002). The recovery of invertebrate populations in burnt and grazed areas is dependent on the distance to a source population, invertebrate mobility, and food and habitat preference (Swengel, 2001). Post-burn vegetation may be attractive to herbivorous invertebrates, both because of the lush, high quality regrowth, and because of reduced plant defences resulting from the temporary release from invertebrate herbivory (Henderson, 1981; Awmack & Leather, 2002).

As with the effects of individual fire and grazing events, the impact of fire and grazing regimes are context dependent, varying with habitat, rainfall, taxa and invertebrate functional type. For example, responses can vary depending on taxon type, Uys & Hamer (2006) found that the richness of epigaeic, winged and wingless invertebrates was highest in plots burnt once every two years, compared with plots which burnt annually, once every 18 months, and unburnt plots. However, fire frequency in the same experiment had little impact on soil invertebrates. The long-term impacts of fire frequency are likely an indirect result of the effects of fire and grazing regimes on vegetation structure and composition, microclimate and refuge availability. Evans (1984, 1988) found that frequent fire decreased forb cover and that forb-feeding species of grasshopper were therefore less common in frequently burnt plots. York (1999) found reduced arthropod richness and abundance in frequently burnt plots (approximately every three years) compared with unburnt plots and concluded that this was a result of a reduced volume of litter, reduced moisture, and simplified habitat structure. Some groups, particularly ants, have been shown to be highly resilient to both long-term fire regimes and long-term grazing regimes (Whitford et al. 1990; Parr et al. 2004).

In Chapter 3 we demonstrated that the similarity in the effects of fire and grazing on vegetation was superficial: whilst both disturbances remove grass biomass, patchiness in the distribution of this biomass, grass quality and the effect on forb communities were significantly different. Building on this work, here we quantified how invertebrate distribution varied over time in response to fire and grazing, and explicitly linked this variation to vegetation characteristics. We used sweep netting and pitfall traps to sample two microhabitats and describe invertebrate distribution using 13 measures collected over a six-month period in the Western Corridor region of the Serengeti-Mara ecosystem: the total abundance of all invertebrates (number of individuals), the richness (number of orders), the total biomass (combined weight of all orders, for sweep nets only), the community composition, and the abundance (number of individuals) of the three most abundant orders. By doing so we aimed to understand how the different vegetation characteristics which arise from disturbance by fire or grazing by the wildebeest migration cascade to affect invertebrate communities. We anticipated that burning would initially result in a larger decrease in invertebrate abundance and richness than grazing, due to higher direct

mortality and more complete removal of habitat. However, given the long association with fire and grazing, invertebrate communities were likely to be resilient to these disturbances and so variation in invertebrate distribution would rapidly become a function of vegetation structure, complexity, and quality. We expected diversity on burnt and wildebeest plots to increase with time and for invertebrate community composition to become more homogenous with time as a result of increased structural complexity in recovering vegetation. Finally, we predicted the relative importance of vegetation characteristics to differ based on the microhabitat they were sampled from, with grass quantity (height and biomass) more important for invertebrates sampled using sweep nets.

METHODS

Study area

Our data collection took place in the Western Corridor region of the Serengeti-Mara ecosystem (2.0185° S, 34.2199° E). Located in Tanzania, the Western Corridor contains several protected areas: Serengeti National Park, Grumeti Game Reserve and Ikona Wildlife Management Area, and is surrounded by non-protected village lands to the north and west, and Ikorongo Game Reserve to the east (Fig. 1). Lake Victoria lies just to the west and heavily influences both rainfall and soil type in the Western Corridor. At between 800 and 1400 mm per year the mean annual rainfall is amongst the highest in the ecosystem. It occurs in two distinct wet seasons, one from October to January and another from March to May (Norton-Griffiths et al. 1975). The soil is dominated by alluvial deposits from old lake beds, underlain by granite which becomes more apparent on hilltops and ridges (Jaeger, 1982). These hilltops are covered largely with broad-leaved *Terminalia* woodlands whilst lower areas contain a matrix of woodlands and open *Themeda triandra* plains with occasional *Acacias* and *Balanytes*. The Grumeti River is also surrounded by broad-leaved riverine forest (Sinclair, 1979). Fires are frequent in the Western Corridor due to the high rainfall (Chapter 2). The wildebeest migration will usually arrive around May, at the start of the long dry season, and move on by July but its movement is highly variable (Hopcraft et al. 2015).

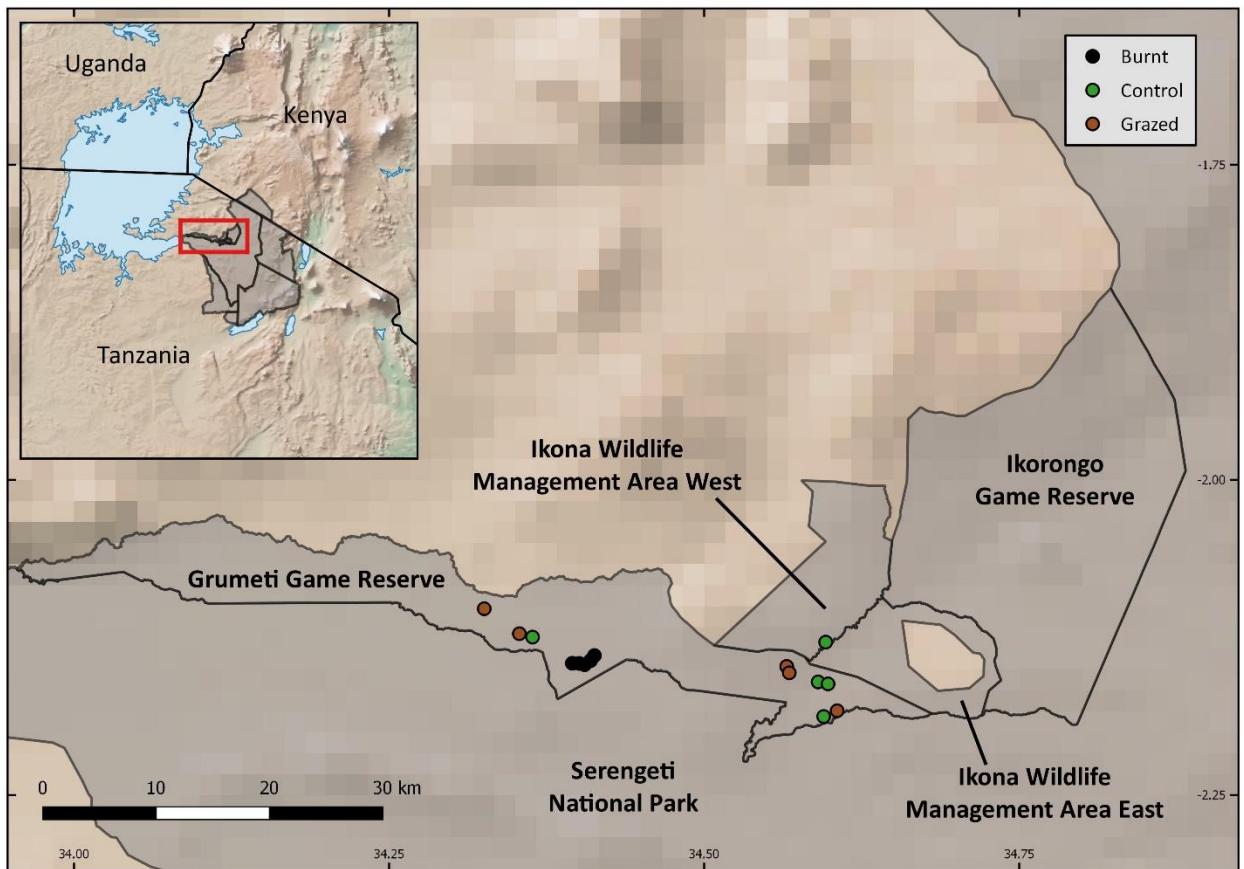


Figure 1: Map of study area with the location of survey plots. Burnt plots are black, wildebeest plots brown and control plots green. The base map is of elevation (made with Natural Earth) with protected areas shown in grey.

Data collection

Our data collection was carried out within the same experimental set-up described in Chapters 3 and 4. We sampled 15 50 x 50 m (0.25 ha) plots, split equally between three treatments: 1) burnt with resident herbivores, 2) unburnt but grazed by the wildebeest migration and resident herbivores or 3) unburnt and ungrazed by the wildebeest migration, but with resident herbivores (control). We surveyed all plots six times between mid-August and late-September and a seventh time in mid-January 2017. Plots in our burnt treatment burnt in mid-July and wildebeest arrived in Grumeti from the start of June.

Data on vegetation were collected as described in Chapter 2 but in brief: measurements of the biomass, vegetative height, and inflorescence height of grass were collected at 2 m

intervals along two 50 m transects per plot. Data on grass quality (carbon to nitrogen ratio) were collected in each plot in August, September and January, and all forbs in 2 x 1 m belt transects per plot were identified to species level. In addition to the data described in Chapter 3 we scored the percentage of bare ground (0-25, 26-50, 51-75, 76-100) at 2 m intervals along two 50 m transects per plot.

Invertebrates were collected using two techniques: sweep netting and pitfall trapping, to capture communities in different microhabitats. Sweep netting was carried out along 2 x 50 m line transects per plot with one figure-eight sweep per 1 m travelled. This was done in advance of collecting data on vegetation to minimise the disturbance of invertebrates prior to sweep netting. Pitfall traps were set up during the first set of surveys and collected for survey sets two to six. There was insufficient time to carry out pitfall trapping for the seventh set of surveys in January. Fifteen pitfalls were placed in each plot, arranged in a 5 x 3 grid. Each trap was partially filled with a solution of propylene glycol and water to aid in the capture and preservation of invertebrates. Contents of all pitfall traps for a single survey were amalgamated into a single container in the field. Captured invertebrates from sweep nets and pitfall traps were counted and each individual was identified to order level. Ants (Formicidae) were abundant in pitfall traps and therefore were identified to Family level. Sweep net samples were also dried in an electric oven at 60 ° for 4 hours and the combined dry weight of each order was recorded.

Data processing

Data from sweep nets and pitfall traps were treated separately throughout data processing and analysis. For sweep nets, in each survey we calculated: the total abundance of all invertebrates (number of individuals), the richness (number of orders), the total biomass (combined weight of all orders), the community composition, and the abundance (number of individuals) of each order. In 57 of 75 surveys (76%) we found at least one pitfall trap had been destroyed (Supplementary Materials Fig. 1). In order to partially control for this variability in survey effort we excluded surveys where more than 50% of the pitfall traps had been destroyed (4 surveys, 5%). For pitfall traps, in each survey we calculated: the

abundance of all invertebrates (number of individuals), the richness (number of orders), the community composition, and the abundance (number of individuals) of each order.

Data analysis

To investigate the patterns in our invertebrate response variables we modelled them against treatment and time. Then, hypothesising that the patterns we observed in each treatment over time were partly the indirect effects of vegetation characteristics, we modelled our invertebrate response variables against the vegetation characteristics we calculated in Chapter 3: grass biomass, vegetative height, inflorescence height, percentage of bare ground, carbon to nitrogen ratio (as a proxy for quality), forb abundance, forb species richness, and the percentage of individual forbs flowering. We included time and an interaction between time and each covariate in our vegetation models and plot as a random effect in all models.

We used linear mixed effects models (LMMs), centred and scaled numerical explanatory variables to minimise the effects of multicollinearity and assessed the distribution and homoscedasticity of our residuals using diagnostic plots. We included time as a factor, with levels from 1-7, to represent the seven sets of surveys during our data collection. If included as a continuous variable, the unequal distribution of surveys throughout our study period would mean the final set of surveys exerted a disproportionate influence on our results (see Chapter 3 for more detailed discussion). We assessed the strength of the spatial autocorrelation in each response variable using empirical and fitted semi-variograms based on the residuals of each model.

We used Bray-Curtis dissimilarity indices to calculate the distance between our invertebrate communities and visualised the results using non-metric multidimensional scaling (NMDS). We analysed these differences using permutational multivariate analyses of variance (PERMANOVAs) (Oksanen et al. 2017), partitioned beta diversity into nestedness and turnover (Baselga et al. 2017) and identified which invertebrate orders were contributing most to the dissimilarity using similarity percentages (SIMPER) (Clarke, 1993). We also used indicator values (IndVal) (Dufrene & Legendre, 1997) to identify which species were

characteristic of a treatment using quantitative index which calculates the fidelity (the proportion of the individuals of a given species that are in a treatment) and specificity (the proportion of the plots in a given treatment that contain a given species) of a species to a treatment. All analyses were carried out in R version 3.2.3 (R Core Team, 2015).

RESULTS

We captured a total of 27,870 individual invertebrates, 1774 (6%) from sweep netting and 26,096 (94%) from pitfall traps. There were differences between the samples in our sweep nets and our pitfall traps, with sweep netting capturing fewer individuals per survey (mean of 17) than pitfall traps (mean of 368) and differences in the orders best represented in the samples from each method. In sweep nets Orthoptera, Araneae, Hemiptera, Coleoptera and Acari were the five most abundant orders, making up 28%, 25%, 17%, 8% and 4% of the total number of individuals respectively (Fig. 2a). The composition of pitfall traps was dominated by the Formicidae, making up 71% of individuals, followed by Araneae (10%), Coleoptera (6%), Blattodea (4%) and other Hymenoptera (3%) (Fig. 2b).

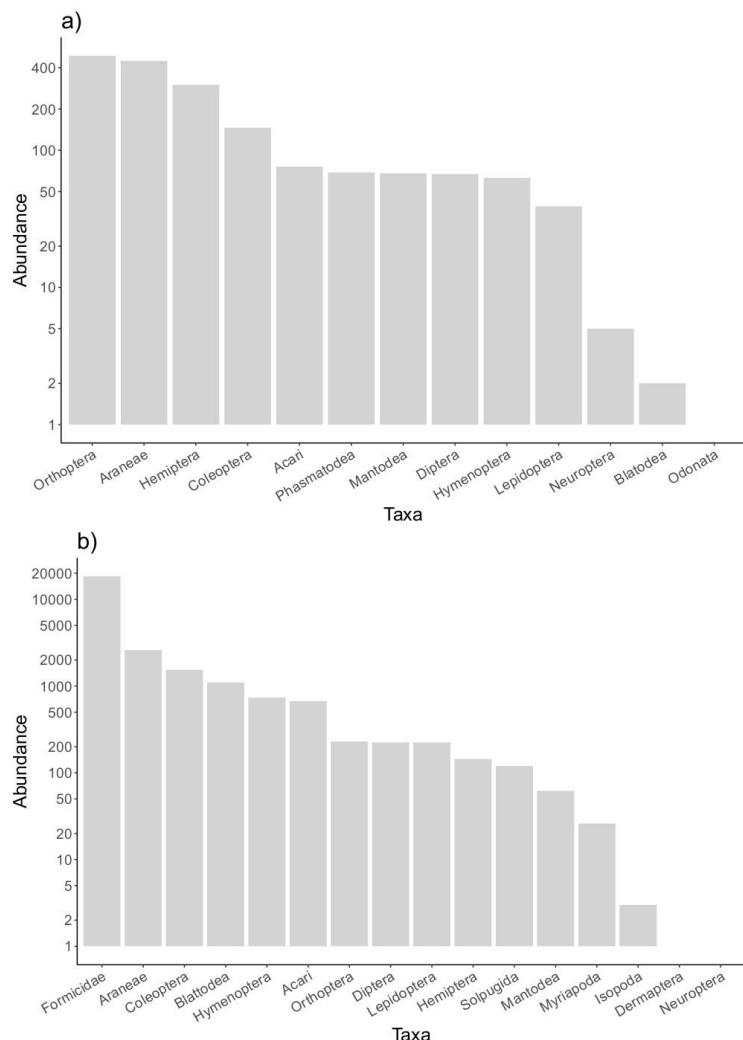


Figure 2: The total number of individuals captured by order for a) sweep nets, and b) pitfall traps. Note that scales are logged.

Abundance and richness

Treatment and time significantly affected the total abundance of invertebrates found in both sweep nets (Fig. 3a) and pitfall traps (Fig. 3b), with the effects of time varying between treatments (Supplementary Material Table 1). In both methods there was a decrease in abundance over the course of the dry season, with abundance in sweep nets increasing again by January. In burnt areas, no individuals were caught with sweep netting until the final set of surveys in January, i.e. after rains in the wet season.

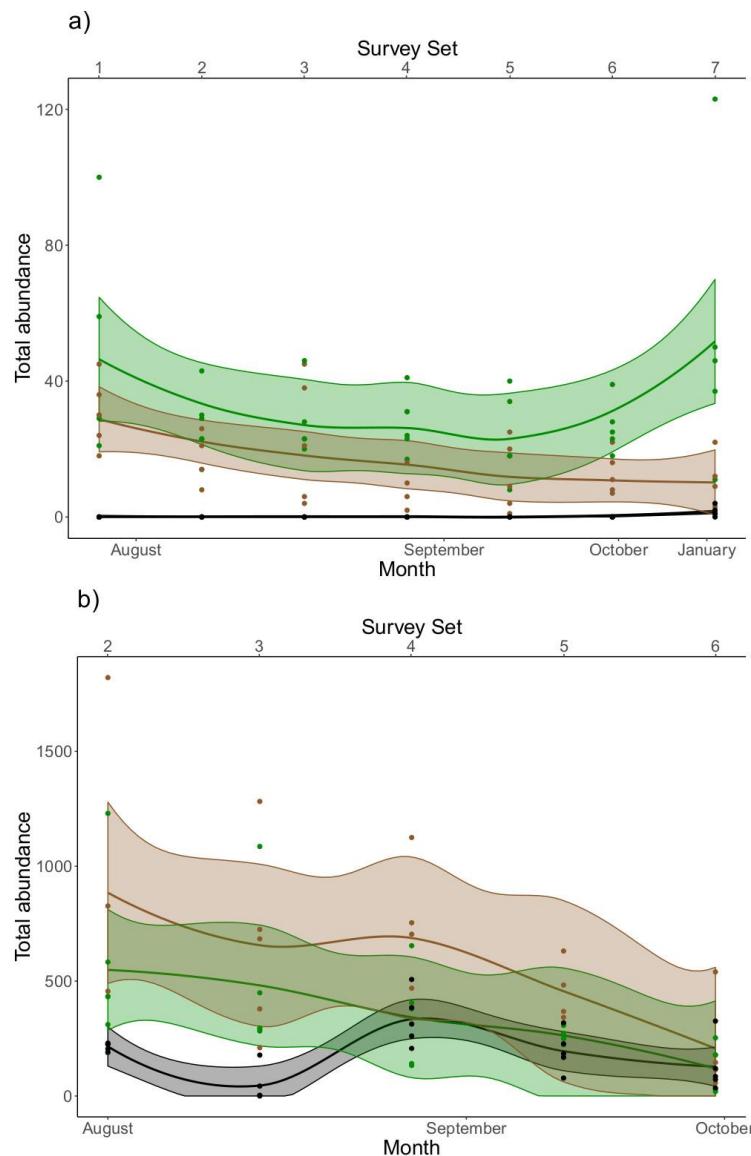


Figure 3: The temporal trends in a) the total invertebrate abundance of sweep nets, and b) the total abundance of pitfall traps. Surveys of burnt plots are shown in black, wildebeest plots in brown and control plots in green.

Treatment also significantly affected the richness of sweep nets (Fig. 4a). As sweep netting captured no individuals in burnt plots for all but the final set of surveys, this also meant richness was zero for survey sets one to six. Richness in pitfall traps differed among treatments, varied over time, and varied at different rates depending on treatment (Supplementary Material Table 1). On burnt plots, richness in pitfalls declined sharply during the dry season, recovering with the onset of the rains (Fig. 4b).

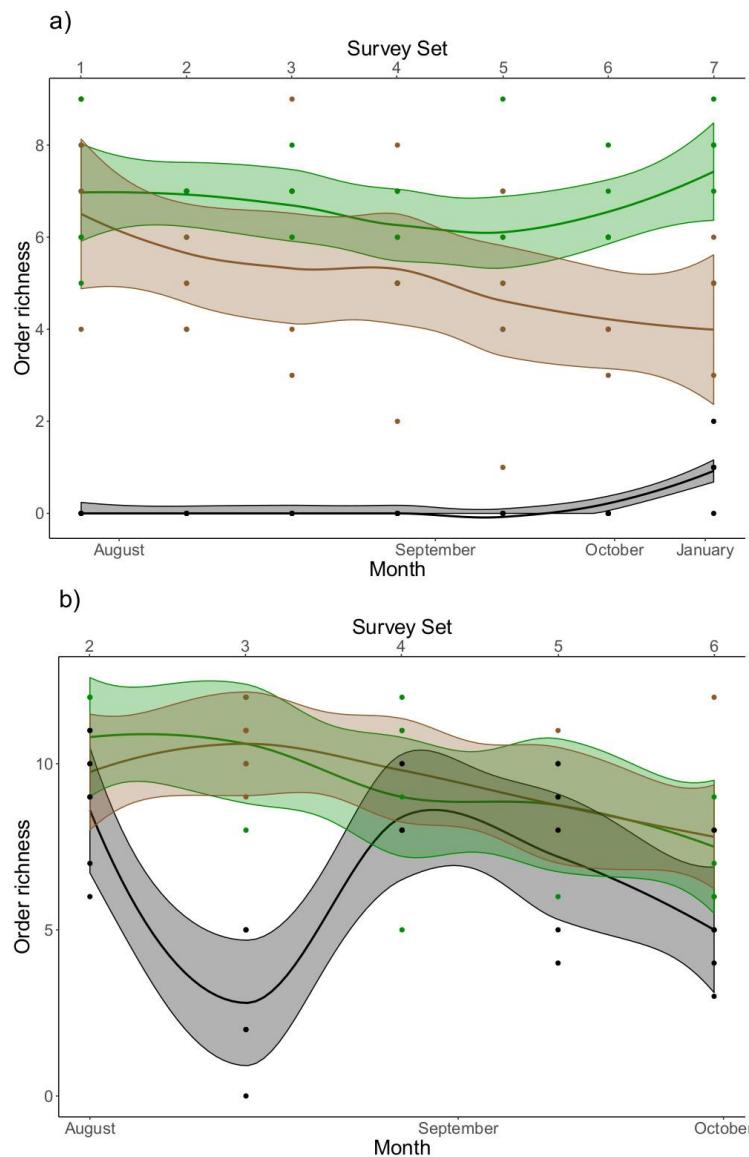


Figure 4: The temporal trends in a) the total richness of sweep nets, and b) the total richness of pitfall traps. Surveys of burnt plots are shown in black, wildebeest plots in brown and control plots in green.

Biomass

The dry weight of the invertebrates in our sweep nets was dominated by Orthoptera (81%), followed by Phasmatodea (9%), Hemiptera (4%), Araneae (3%) and Mantodea (2%).

Treatment and time both had a significant effect on invertebrate biomass in sweep nets, with virtually no biomass in burnt areas throughout our study. We also found a significant interaction between treatment and time with the invertebrate biomass in control plots increasing rapidly with the arrival of the rains whilst invertebrate biomass in grazed and burnt plots stayed constant, showing remarkably little recovery even in January when there had been several months of rainfall (Fig. 5; Supplementary Material Table 1).

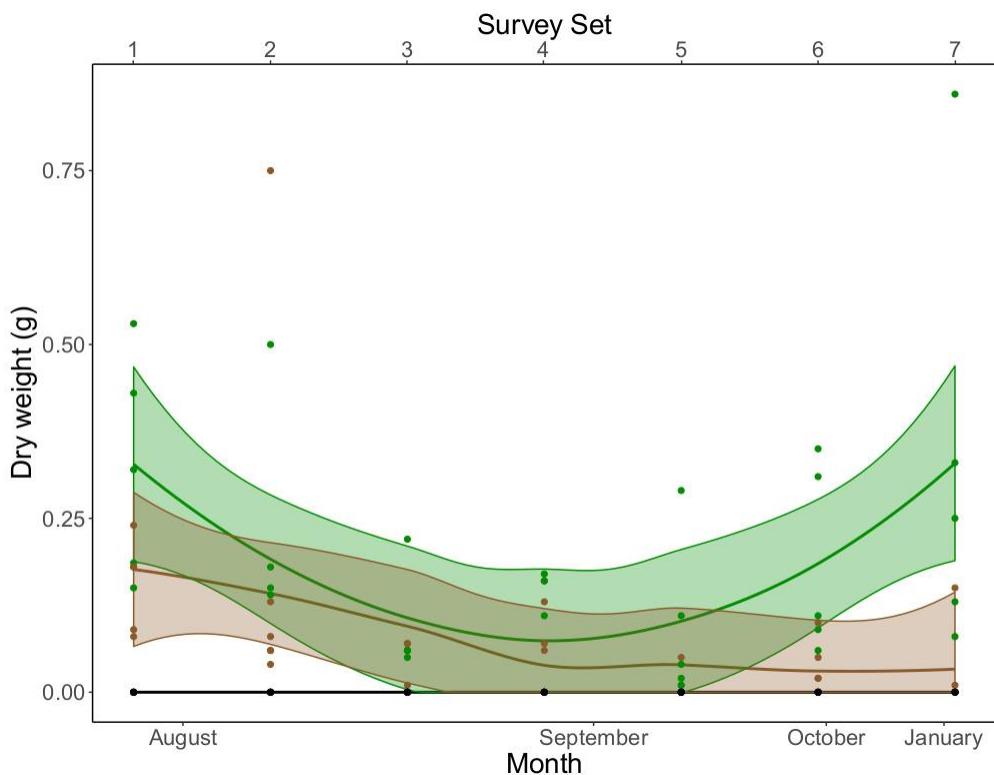


Figure 5: The temporal trends in total invertebrate biomass in sweep nets. Surveys of burnt plots are shown in black, wildebeest plots in brown and control plots in green.

Order abundance

The abundance of Orthoptera (Fig. 6a) varied significantly with treatment and time, and at different rates depending on treatment. Orthopteran abundance in wildebeest plots

declined consistently over time and, whilst abundance in control plots declined over the dry season, it increased sharply at the start of the rainy season. Araneae abundance (Fig. 6b) differed significantly between treatments, with greater abundance in control and wildebeest plots than burnt plots but did not vary over time. The abundance of Hemiptera (Fig. 6c) differed significantly between treatments and changed over time, decreasing over the dry season and increasing over the wet season.

In pitfall traps, the abundance of Formicidae (Fig. 6d) was affected by treatment and time, declining steadily over the course of our study, with the lowest abundance in burnt plots and the highest in grazed plots. Araneae abundance (Fig. 6e) differed significantly between treatments, over time, and changed at different rates depending on treatment: increasing over the dry season in control and wildebeest plots before declining sharply at the start of the rainy season, initially declining in burnt plots before peaking in late August and then declining. Coleopteran abundance was not predicted by either treatment or time (Fig. 6f; Supplementary Material Table 1) but appeared lowest in control plots and highly variable in burnt and wildebeest plots.

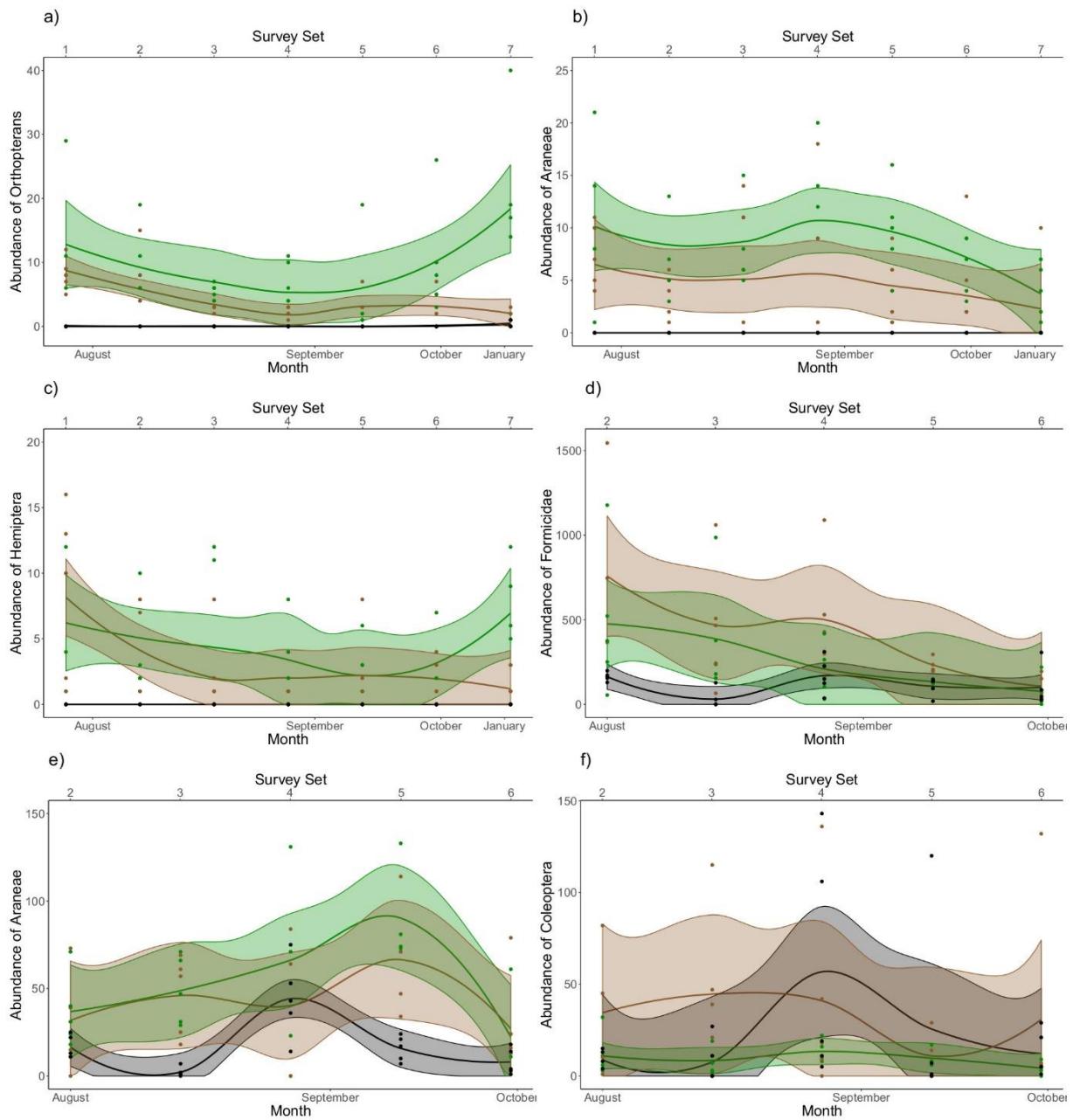


Figure 6: The temporal trends in the abundance of: a) Orthoptera, b) Araneae, and c) Hemiptera, in sweep nets, and d) Formicidae, e) Araneae, and f) Coleoptera, in pitfall traps. Surveys of burnt plots are shown in black, wildebeest plots in brown and control plots in green.

Community composition

Treatment significantly affected invertebrate community composition in both sweep nets (Fig. 7a) and pitfall traps (Fig. 7b). Community composition in pitfall traps also became more

homogenous over time (Supplementary Material Table 2). In sweep nets there was no overlap between invertebrate communities in burnt plots and those in control and wildebeest plots, presumably driven by the extremely low abundances collected on burnt plots. Invertebrate communities in control plots were largely positioned within those in wildebeest plots, with greater variation in the communities found in wildebeest plots. In pitfall traps communities in burnt plots occupied the greatest space, with communities in control and wildebeest plots positioned within this space and showing a high degree of overlap.

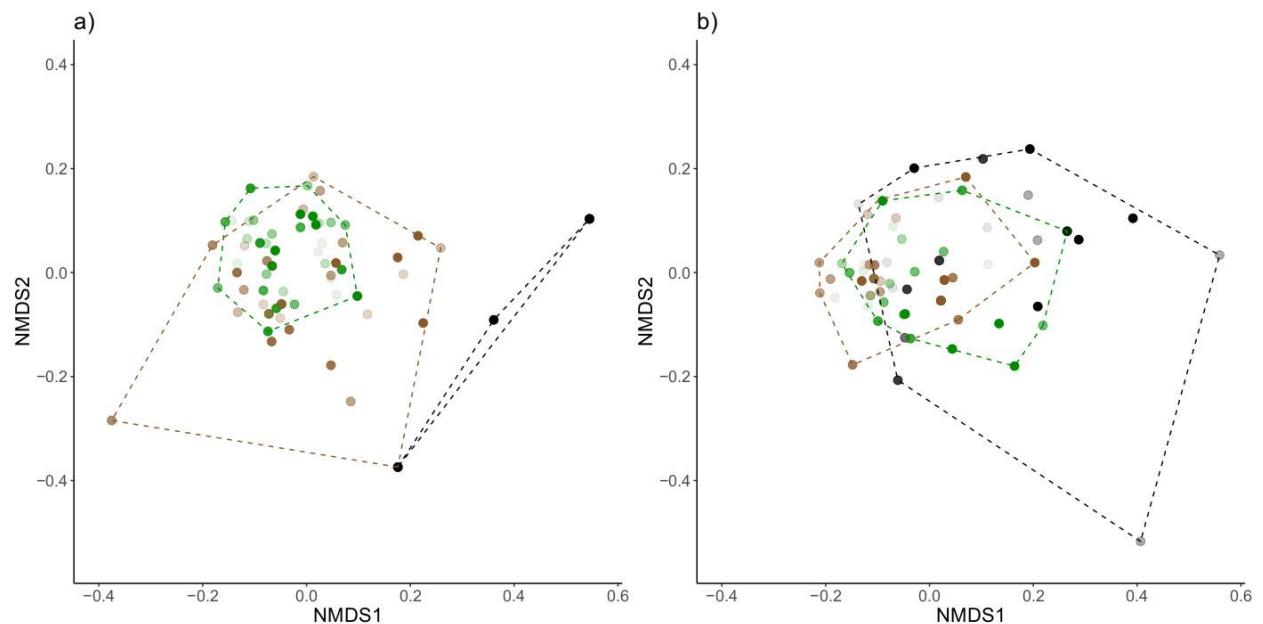


Figure 7: The similarity of the invertebrate communities in a) sweep nets, and b) pitfall traps. Surveys of burnt plots are in black, wildebeest plots in brown and control plot in green. Shading represents time: darker points are more recent surveys.

Turnover explained 88.6% of the dissimilarity between invertebrate communities in sweep nets and 80.9% of the dissimilarity in invertebrate communities in pitfall traps. For both survey methods, the most abundant species drove the dissimilarity between treatments (Supplementary Material Tables 3 & 4). Acari, Araneae, Coleoptera, Hemiptera, Lepidoptera, Mantodea, Orthoptera and Phasmatodea were all characteristic of control plots in sweep nets, whilst in pitfall traps Acari (specifically ticks) were characteristic of control plots, and to a lesser extent wildebeest plots, and Hemiptera were characteristic of wildebeest plots (Supplementary Material Tables 5 & 6).

Vegetation effects

Inflorescence height predicted the total abundance and order richness in sweep nets with both abundance and richness increasing with height (Fig. 8; Fig. 10). Biomass predicted total abundance in pitfall traps, with higher abundance in plots with low biomass (Fig. 9; Supplementary Material Table 7). Order richness in pitfall traps and invertebrate biomass in sweep nets were not predicted by any of our vegetation characteristics (Fig 10; 11; Fig. 12; Supplementary Material Table 7).

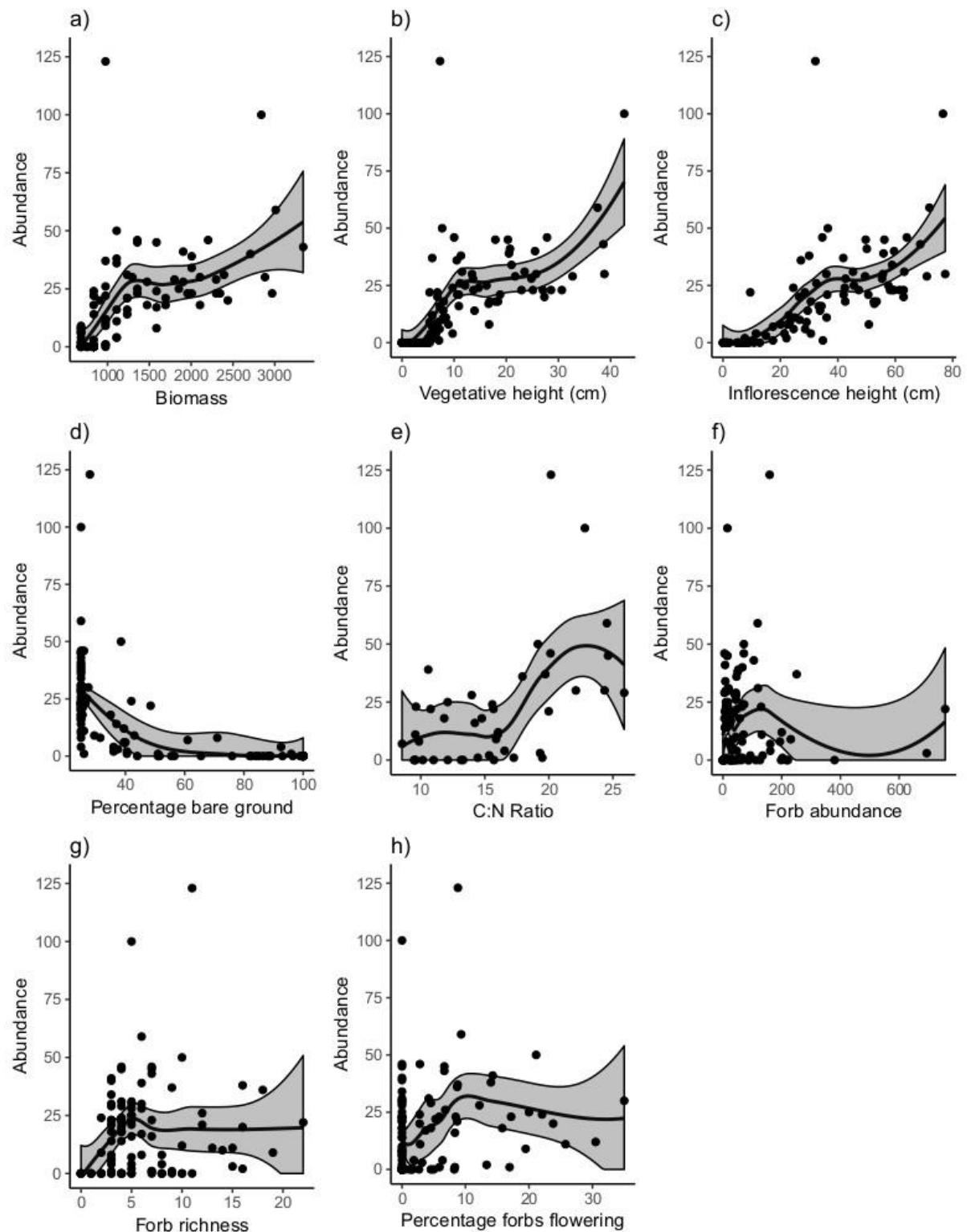


Figure 8: Variation in total invertebrate abundance in sweep nets against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

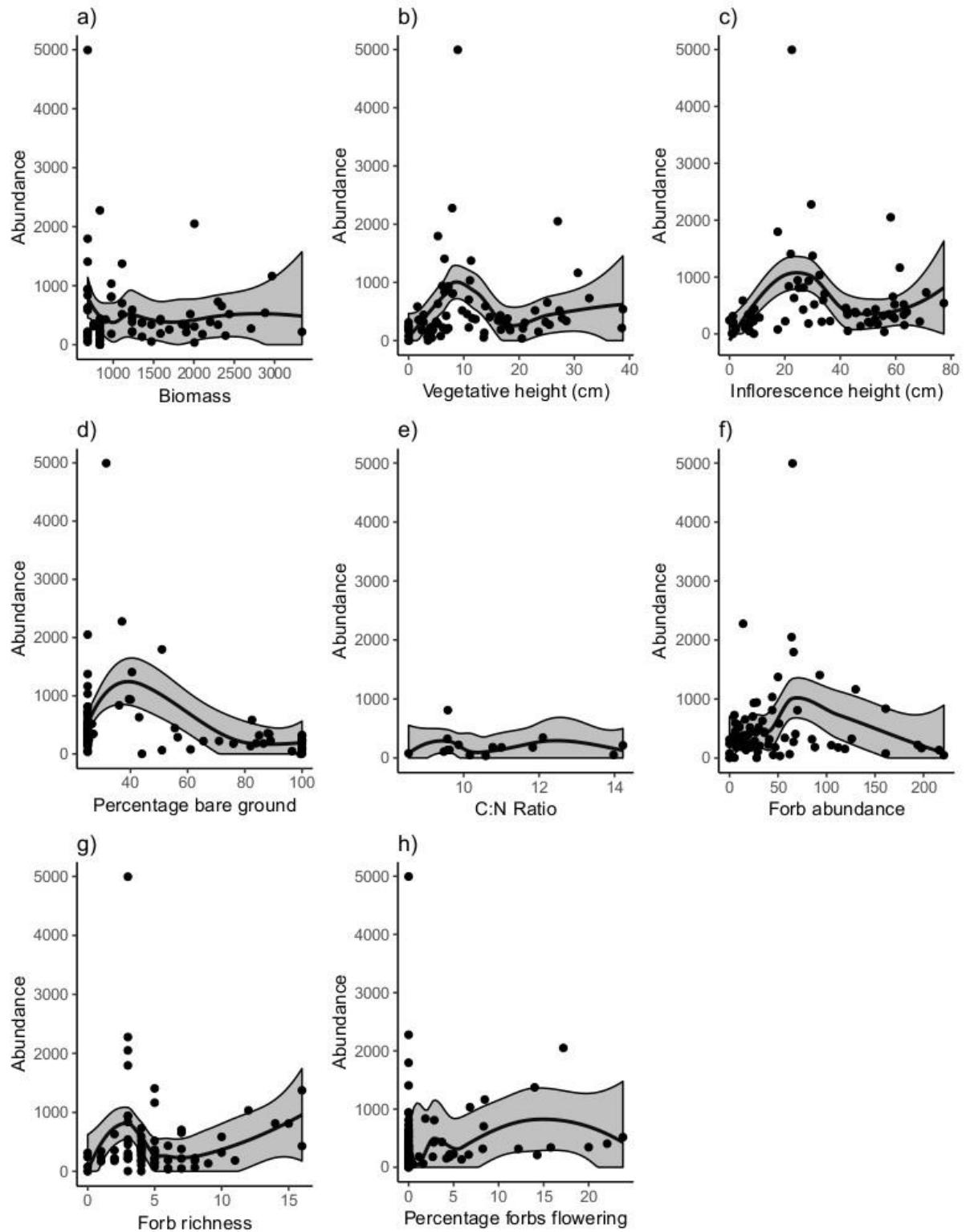


Figure 9: Variation in total invertebrate abundance in pitfall traps against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

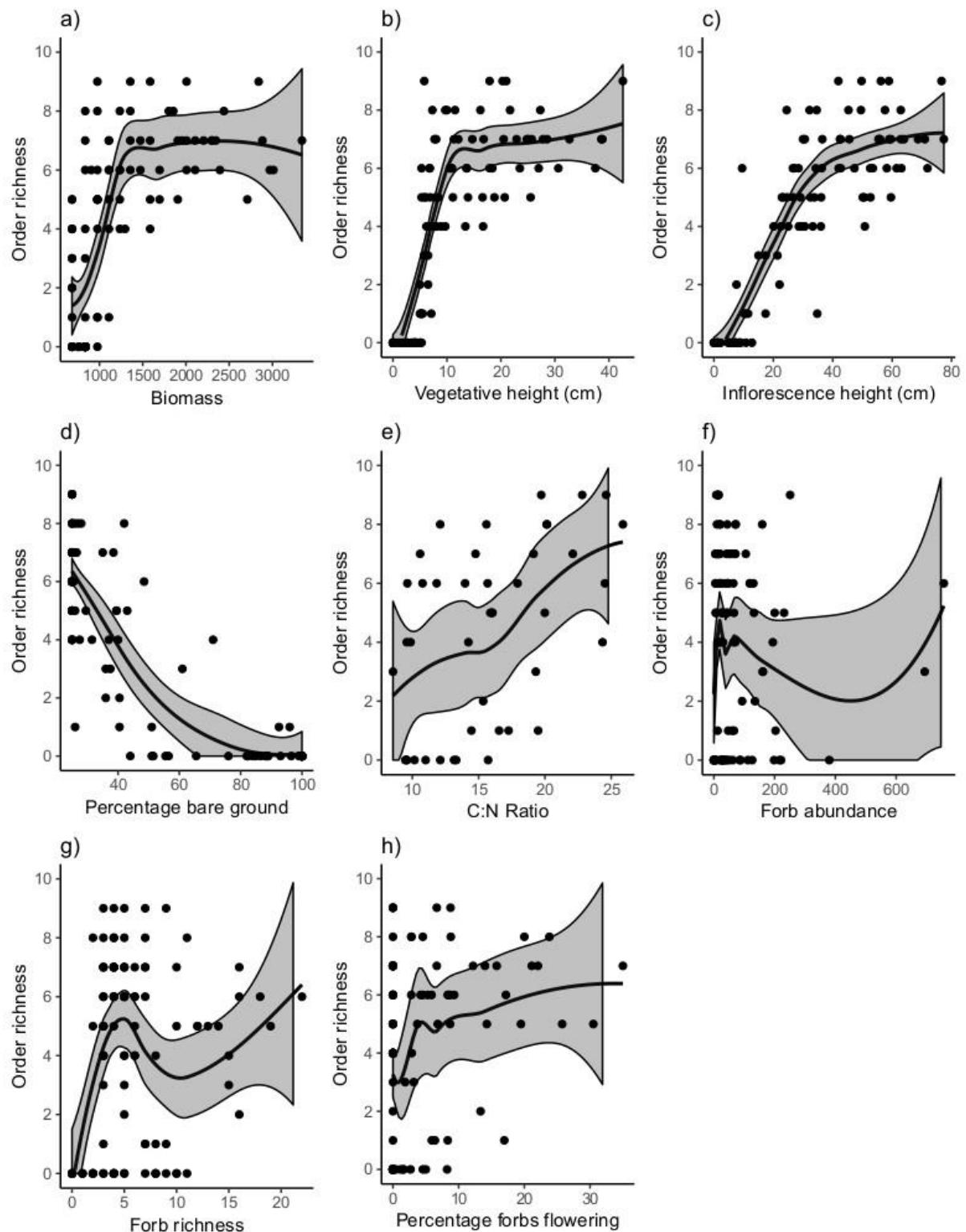


Figure 10: Variation in order richness in sweep nets against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

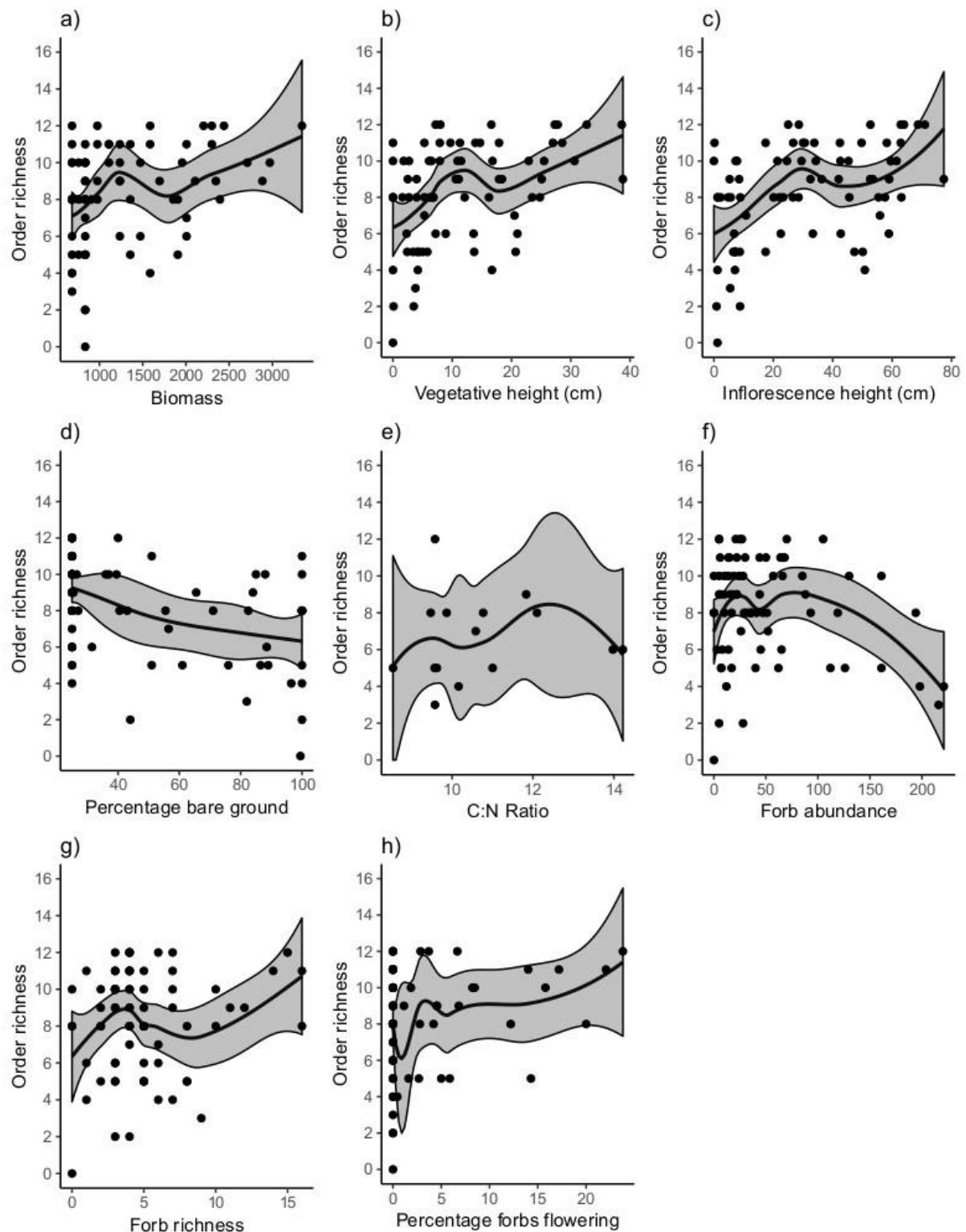


Figure 11: Variation in order richness in pitfall traps against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

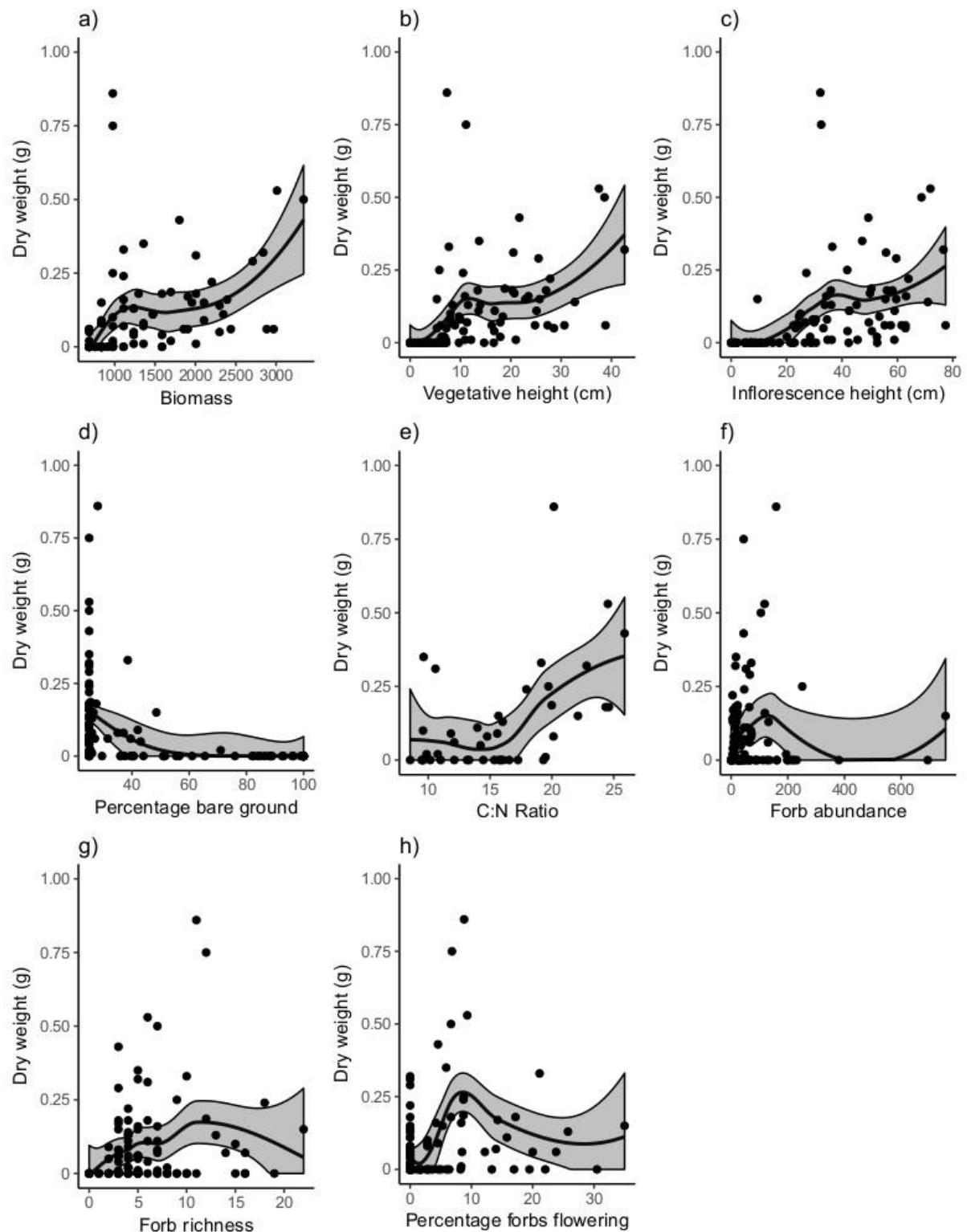


Figure 12: Variation in invertebrate biomass in sweep nets against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

In sweep nets the abundance of Orthoptera (Supplementary Material Fig. 2) and Araneae (Supplementary Material Fig. 3) were not predicted by any vegetation characteristics but Hemiptera were significantly more abundant in plots with high biomass and vegetative height (Supplementary Material Fig. 4; Supplementary Material Table 8). In pitfall traps Formicidae were more abundant in plots with low biomass and higher vegetative height (Supplementary Material Fig. 5), Araneae abundance (Supplementary Material Fig. 5) was not predicted by any vegetation characteristics and Coleoptera were more abundant in plots with low forb abundance (Supplementary Material Fig. 5; Supplementary Material Table 9). Including grass quality in our models did not change the results for the total abundance, order richness or invertebrate biomass in sweep nets (Supplementary Material Table 10). The abundance of Orthoptera and Araneae were still not predicted by any vegetation characteristics, but Hemipteran abundance was significantly higher in plots with high biomass and vegetative height, and in plots where a lower percentage of forbs were flowering (Supplementary Material Table 11). We found evidence of weak spatial structure in some of our response variables (Supplementary Material Fig. 9).

DISCUSSION

Our study is one of the first to compare the short-term effects of concurrent fire and grazing on savannah invertebrates and to explicitly link these effects to vegetation characteristics.

We found significant differences in the effects of fire and grazing on total invertebrate abundance, biomass, richness, community composition, and in the abundance of individual orders. Fire reduced invertebrate abundance, biomass and richness more than grazing but the effects of wildebeest grazing were mixed and dependent on habitat requirements.

Grazing caused decreases in foliage-dwelling taxa but had no effect on most ground-dwelling taxa, and a positive effect on ant abundance. In some instances, these differences were driven by vegetation characteristics, particularly differences in grass biomass and height, but changes over time show that invertebrates are also clearly responding to factors such as rainfall and predation which we did not quantify in our study. Ground-dwelling invertebrate abundance and taxon richness recovered rapidly in burnt plots. Our results suggest that fire and grazing by the wildebeest migration have substantially different effects on invertebrate communities, although for some taxa these effects are short-lived.

As predicted, fire had a greater effect on invertebrates than grazing by the wildebeest migration (Swengel, 2001). However, the different sampling techniques we used produced different patterns (Teasdale et al. 2013). Sweep nets were devoid of invertebrates on burnt plots throughout most of our study. This suggests that, for those invertebrates captured by sweep netting, fire caused high initial mortality and that burnt areas remained either inaccessible or inhospitable throughout our study (Bulan & Barrett, 1971). Sweep netting samples foliage-dwelling invertebrates, and fire removed almost all foliage, effectively leaving no habitat for these groups. Wildebeest grazing also caused a reduction in invertebrate abundance, biomass and richness in sweep nets, but to a lesser degree than fire. It should also be noted that only control plots saw sharp increases in invertebrate abundance during the early wet season. This pattern confirms that impacts on invertebrates extend beyond directly mortality, and it is likely that reduced habitat complexity in burnt and grazed plots makes them suboptimal habitat (Langellotto & Denno, 2004).

In contrast with samples from sweep nets, invertebrate abundance and richness in pitfall traps dropped sharply between the first and second sampling periods before rising again for the remainder of our study. This suggests that ground-dwelling invertebrates are better able to survive fire than those that live in the vegetation, likely due to the ability to take refuge below ground (Dana 1991; Deyrup 1996; Van Wieren, 1998). However, whilst they may survive the initial disturbance, ground-dwelling invertebrates can subsequently succumb to exposure, predation, or lack of food (Warren et al. 1987; Bale et al. 2002). The decline during the dry season and recovery during the wet season suggests that desiccation may be the key cause of mortality in the weeks immediately post-fire as a result of the removal of cover and modification of the microclimate in burnt plots (York, 1999).

Invertebrate abundance was higher in wildebeest plots than control plots, a pattern which appeared to be driven by ant abundance since they dominate the ground fauna, and there was no difference in taxon richness. This suggests that wildebeest grazing has little effect on ground-dwelling invertebrates generally and has a positive effect on ant abundance. Hutchinson and King (1980) also observed ants to be most abundant in areas where grazing was most intense and attributed this to a preference of some species for establishing colonies in areas with a high percentage of bare ground. It is also possible that ants are responding to shifts in food resources or that areas with shorter grass are hotter and therefore attractive to thermophilic ants.

All taxa in sweep net samples were more abundant in control plots, which is expected given the niches sampled by sweep netting (Teasdale et al. 2013). The abundance, and particularly biomass, of sweep net samples were dominated by herbivorous taxa, especially Orthopterans and Hemipterans. These taxa increased during the wet season, possibly in response to increased vegetation quality or reduced mortality from desiccation (as a result of higher humidity) (York, 1999). Spiders declined throughout our study in all treatments. Invertebrate abundance and richness, particularly of spiders, has been linked to habitat complexity, as more complex habitats provide niches for a greater number of species, cover for invertebrate predators, and protection from vertebrate predators (Langellotto & Denno, 2004; Malumbres-Olarte et al. 2013). This might explain the decline in burnt and grazed plots (Greenslade & Smith, 2010), but does not explain the decline in control areas. Acari, Araneae, Coleoptera, Hemiptera, Lepidoptera, Mantodea, Orthoptera and Phasmatodea

were all characteristic of control plots demonstrating that treatment had strong effects on the abundance of foliage-dwelling invertebrates, even at a crude taxonomic level.

Pitfall traps were dominated by predatory invertebrates, and overwhelmingly by ants. Ants have been shown to be highly resilient to fire, likely in part due to their subterranean nesting habits (e.g. Parr et al. 2004; Andersen et al. 2014), so it is not surprising they were largely unaffected by the disturbances. Taxa in pitfalls showed contrasting relationships with treatment. Ants and spiders were least abundant in burnt plots, partly due to direct mortality, but other studies suggest it may also be due to limited prey, unfavourable microclimates, and the reduction in habitat complexity (Langelotto & Denno, 2004; Parr et al. 2004; Malumbres-Olarte et al. 2013). Beetle abundance was lowest in control plots and highly variable in burnt and wildebeest plots, but universally high in grazed plots. This may indicate dung beetles are attracted to wildebeest dung in grazed plots. Acari were characteristic of control plots, and to a lesser extent wildebeest plots, which suggests that burning was achieving one of its most commonly stated objectives in controlling tick populations.

Grass biomass and height were the most important vegetation characteristics in determining invertebrate distribution. In sweep nets both the total abundance and order richness were higher in plots with higher inflorescence height, whilst Hemipterans were more abundant in plots with high biomass and vegetative height. Multiple mechanisms may explain these patterns. For foliage-dwelling invertebrates (those most likely to be captured in sweep nets), a lack of grass means a lack of habitat and may also result in higher risk of predation by vertebrates (Gunnarsson, 1990) and exposure to more extreme temperature (York, 1999). In pitfall traps, total abundance was higher in areas of low biomass and ant abundance was higher in areas of low biomass but higher vegetative height. Habitat structure is known to cause bias in pitfall traps, with larger catches in areas of lower biomass, so it is likely that this bias is influencing these results (Melbourne, 1999). However, vegetation characteristics explained less of the patterns we observed than expected. The total abundance, biomass, richness and the abundance of Orthoptera and Hemiptera in sweep net samples appeared to increase during the rainy season. These increases may be due to more favourable microclimate conditions or they may have

lifecycles with dormancy during the dry season and emergence during the wet season (Uys & Hamer, 2006). For some taxa it is likely that a finer taxonomic resolution is needed to test the effects of vegetation (Teasdale et al. 2013). Different species within the same order may occupy contrasting niches, for example forb or grass feeding grasshoppers (Evans, 1984; 1988), or have contrasting life history strategies, for example predatory ground beetles and dung beetles. These contrasting ecological requirements within orders may respond differently to the same vegetation characteristics, obscuring any signal for the order as a whole.

There are several considerations which would improve our understanding of invertebrate responses to fire and grazing. As has already been mentioned, increasing taxonomic resolution would allow us to examine effects on functionally similar groups, reducing the noise in our models and giving more informative results. Identification of all the taxa to species, or even family, level is a significant challenge given the time and expertise required to identify such a large number of invertebrates morphologically. Molecular techniques such as meta-barcoding, meta-genomics, and next generation sequencing (Crampton-Platt et al. 2016; Hebert et al. 2016) may however make this process quicker in future. Secondly, variation in the timing and intensity of fire and grazing can have significant effects on invertebrates (Uys & Hamer, 2006). In the Serengeti-Mara the timing and spatial distribution of the migration is variable and fire can occur throughout the year across much of the system (Chapter 2). It is necessary to examine how variability in the timing and intensity of fire and grazing, and how this coincides with rainfall, affects invertebrate communities (Parr et al. 2004). Thirdly, our study examines only the short-term effects of individual fire and grazing events. The longer-term effects of fire and grazing regimes on vegetation structure and composition can have corresponding effects on invertebrate communities which have not been examined in our study (Evans, 1984; 1988; York, 1999; Parr et al. 2004; Uys & Hamer, 2006). Finally, there was evidence of weak spatial structure in our data, which is unsurprising given the clustering of our burnt plots. This was necessary given the logistical constraints of our study, and is an issue suffered by many studies on single fire events (see Parr & Chown, 2003), but a wider scale experiment with a more equal distribution of plots which encompassed multiple burnt areas would help to address this issue.

CONCLUSIONS

Our results demonstrate expected relationships between fire, grazing, vegetation and invertebrates. Fire almost universally reduced the abundance, biomass and species richness of invertebrates, whilst wildebeest grazing reduced the abundance, biomass and richness of foliage-dwelling invertebrates, but not of ground-dwelling invertebrates. Some taxa recovered rapidly, suggesting fire and grazing may have minimal long-term effects on them, whilst others were affected for the duration of our study. Our results suggest that homogenisation of either fire or grazing would have negative impacts on invertebrate communities in the Serengeti-Mara. Increases in livestock grazing have suppressed fire in some areas of the system (Chapter 2) and it is likely that this has severely reduced invertebrate abundance and species richness. Maintaining the heterogeneity of savannah is crucial to the persistence of invertebrate diversity within these systems.

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SUPPLEMENTARY MATERIAL

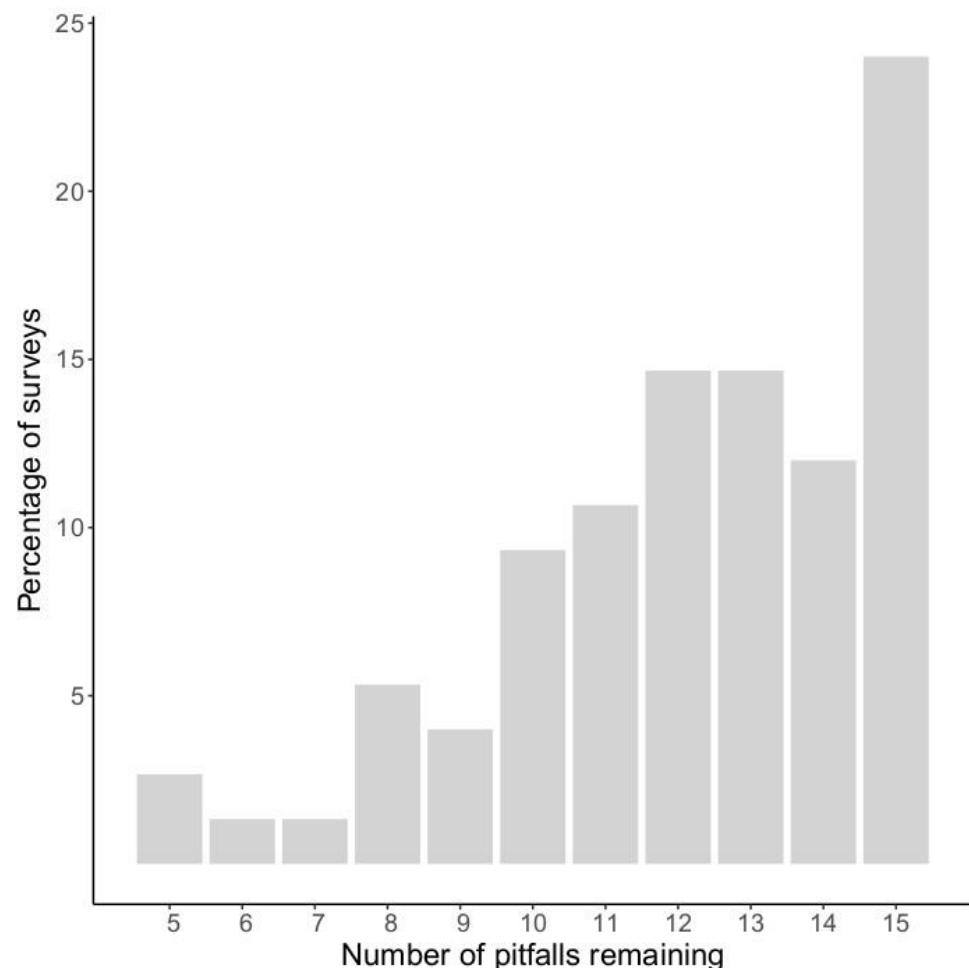


Figure 1: The number of pitfall traps remaining as a percentage of the total number of surveys (75).

Table 1: The effect of treatment and time on our invertebrate response variables.

Response variable	Sampling technique	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Total abundance	Sweep nets	Treatment	2	9225	4612.6	27.2	< 0.001	***
		Set	6	2412	402.0	2.4	0.038	*
		Treatment:Set	12	3436	286.4	1.7	0.088	
Total abundance	Pitfall traps	Treatment	2	1317423	658711.0	10.0	0.003	**
		Set	4	1294352	323588.0	4.9	0.002	**
		Treatment:Set	8	744216	93027.0	1.4	0.216	
Order richness	Sweep nets	Treatment	2	304	151.8	107.6	< 0.001	***
		Set	6	13	2.1	1.5	0.187	
		Treatment:Set	12	27	2.3	1.6	0.107	
Order richness	Pitfall traps	Treatment	2	139	69.5	20.3	< 0.001	***
		Set	4	70	17.6	5.1	0.001	**
		Treatment:Set	8	106	13.3	3.9	0.001	**
Invertebrate biomass	Sweep nets	Treatment	2	0	0.2	13.5	0.001	***
		Set	6	0	0.0	2.9	0.015	*
		Treatment:Set	12	0	0.0	1.8	0.063	
Orthoptera abundance	Sweep nets	Treatment	2	507	253.6	13.9	0.001	***
		Set	6	341	56.9	3.1	0.009	**
		Treatment:Set	12	547	45.6	2.5	0.009	**
Araneae abundance	Sweep nets	Treatment	2	693	346.5	23.1	< 0.001	***
		Set	6	190	31.7	2.1	0.062	
		Treatment:Set	12	133	11.1	0.7	0.706	
Hemiptera abundance	Sweep nets	Treatment	2	98	49.1	3.9	0.050	*
		Set	6	383	63.8	5.1	0.000	***
		Treatment:Set	12	279	23.3	1.8	0.057	
Formicidae abundance	Pitfall traps	Treatment	2	824885	412443.0	7.1	0.010	*
		Set	4	1147428	286857.0	4.9	0.002	**
		Treatment:Set	8	654119	81765.0	1.4	0.221	
Araneae abundance	Pitfall traps	Treatment	2	4628	2314.0	5.4	0.022	*
		Set	4	13448	3361.9	7.9	< 0.001	***
		Treatment:Set	8	8102	1012.8	2.4	0.031	*
Coleoptera abundance	Pitfall traps	Treatment	2	1755	877.6	1.1	0.361	
		Set	4	4977	1244.2	1.6	0.198	
		Treatment:Set	8	7144	892.9	1.1	0.363	

Table 2: The effect of treatment and time on community composition in sweep nets and pitfall traps.

Sampling technique	Covariate	Df	Sum of squares	Mean squares	F model	R ²	Pr(>F)	Significance
Sweep nets	Treatment	2	1.932	0.966	10.826	0.244	0.001	***
	Set	22	2.425	0.110	1.235	0.306	0.198	
	Treatment:Set	20	0.979	0.049	0.549	0.124	0.981	
	Residuals	29	2.587	0.089	-	0.327	-	
	Total	73	7.922	-	-	1.000	-	
Pitfall traps	Treatment	2	0.642	0.321	7.599	0.162	0.001	***
	Set	18	1.081	0.060	1.423	0.274	0.064	.
	Treatment:Set	13	0.581	0.041	0.983	0.147	0.471	
	Residuals	39	1.646	0.042	-	0.417	-	
	Total	73	3.950	-	-	1.000	-	

Table 3: The percentage of the dissimilarity between treatments explained by the abundance of each invertebrate order in sweep nets.

Control:wildebeest				Control:Burnt				Burnt:wildebeest			
Order	% variation explained	Mean abundance control	Mean abundance wildebeest	Order	% variation explained	Mean abundance control	Mean abundance burnt	Order	% variation explained	Mean abundance burnt	Mean abundance wildebeest
Araneae	24.19	8.23	4.6	Araneae	27.5	8.23	0	Orthoptera	23.53	4.114	0.5
Orthoptera	23.65	9.8	4.11	Orthoptera	25.72	9.8	0.5	Araneae	23.38	4.6	0
Hemiptera	15.66	5.49	3.09	Hemiptera	14.81	5.49	0	Hemiptera	17.01	3.086	0
Coleoptera	8.18	3.11	1.06	Coleoptera	6.48	3.11	0	Diptera	14.65	0.971	1.5
Mantodea	5.62	1.57	0.37	Diptera	5.76	0.77	1.5	Coleoptera	5.77	1.057	0
Acari	5.19	1.37	0.8	Phasmatodea	5.16	1.37	0	Acari	5.35	0.8	0
Phasmatodea	5.09	1.37	0.6	Mantodea	4.99	1.57	0	Phasmatodea	3.4	0.6	0
Diptera	4.99	0.77	0.97	Acari	4.74	1.37	0	Hymenoptera	2.7	0.714	0
Hymenoptera	3.91	1.09	0.71	Lepidoptera	2.41	0.8	0	Mantodea	2.21	0.371	0
Lepidoptera	2.88	0.8	0.31	Hymenoptera	2.1	1.09	0	Lepidoptera	1.56	0.314	0
Neuroptera	0.31	0.09	0.06	Blatodea	0.17	0.06	0	Odonata	0.3	0.029	0
Blatodea	0.2	0.06	0	Neuroptera	0.16	0.09	0	Blatodea	0.14	0	0
Odonata	0.13	0	0.03	Odonata	0	0	0	Neuroptera	0	0.057	0

Table 4: The percentage of the dissimilarity between treatments explained by the abundance of each invertebrate order in pitfall traps.

Order	Control:wildebeest			Control:Burnt			Burnt:wildebeest				
	% variation explained	Mean abundance control	Mean abundance wildebeest	Order	% variation explained	Mean abundance control	Mean abundance burnt	Order	% variation explained	Mean abundance burnt	Mean abundance wildebeest
Formicidae	65.14	251.24	465.52	Formicidae	58.91	251.24	119.17	Formicidae	62.61	465.52	119.17
Araneae	9.19	49.56	41.32	Araneae	16.25	49.56	18.04	Araneae	8.19	41.32	18.04
Coleoptera	5.45	9.20	31.56	Coleoptera	7.72	9.20	23.13	Coleoptera	7.48	31.56	23.13
Hymenoptera	3.19	7.76	13.44	Blattodea	4.89	3.40	12.42	Blattodea	7.28	31.40	12.42
Acari	6.33	3.88	22.88	Hymenoptera	3.77	7.76	9.08	Acari	6.10	22.88	0.08
Orthoptera	1.07	3.68	4.32	Orthoptera	1.62	3.68	1.58	Hymenoptera	3.55	13.44	9.08
Blattodea	5.87	3.40	31.40	Diptera	1.37	2.76	3.04	Orthoptera	1.25	4.32	1.58
Lepidoptera	0.99	3.28	4.28	Lepidoptera	1.33	3.28	1.58	Diptera	1.03	3.92	3.04
Diptera	0.89	2.76	3.92	Acari	1.24	3.88	0.08	Lepidoptera	0.90	4.28	1.58
Solpugida	0.81	2.52	2.44	Hemiptera	1.19	1.48	2.42	Hemiptera	0.75	2.00	2.42
Hemiptera	0.57	1.48	2.00	Solpugida	0.91	2.52	0.08	Solpugida	0.44	2.44	0.08
Mantodea	0.34	1.24	1.28	Mantodea	0.50	1.24	0.04	Mantodea	0.24	1.28	0.04
Myriapoda	0.14	0.40	0.32	Myriapoda	0.23	0.40	0.33	Myriapoda	0.14	0.32	0.33
Dermoptera	0.01	0.04	0.00	Isopoda	0.05	0.00	0.13	Isopoda	0.03	0.00	0.13
Neuroptera	0.01	0.00	0.04	Dermoptera	0.02	0.04	0.00	Neuroptera	0.01	0.04	0.00
Isopoda	0.00	0.00	0.00	Neuroptera	0.00	0.00	0.00	Dermoptera	0.00	0.00	0.00

Table 5: The individual values for invertebrate orders which are characteristic of each treatment for sweep nets.

Taxa	Treatment			p
	Burnt	Control	Wildebeest	
Acari	0.000	0.379	0.189	0.001
Araneae	0.000	0.623	0.266	0.001
Blatodea	0.000	0.057	0.000	0.311
Coleoptera	0.000	0.491	0.123	0.001
Diptera	0.008	0.150	0.188	0.195
Hemiptera	0.000	0.585	0.298	0.001
Hymenoptera	0.000	0.190	0.091	0.084
Lepidoptera	0.000	0.390	0.064	0.001
Mantodea	0.000	0.416	0.060	0.001
Neuroptera	0.000	0.034	0.011	0.775
Odonata	0.000	0.000	0.029	1.000
Orthoptera	0.000	0.681	0.269	0.001
Phasmatodea	0.000	0.517	0.113	0.001

Table 6: The individual values for invertebrate orders which are characteristic of each treatment for pitfall traps.

Taxa	Treatment			p
	Burnt	Control	Wildebeest	
Acari	0.000	0.020	0.219	0.010
Araneae	0.143	0.277	0.254	0.216
Blattodea	0.139	0.068	0.310	0.126
Coleoptera	0.232	0.104	0.278	0.422
Dermoptera	0.000	0.029	0.000	1.000
Diptera	0.101	0.240	0.148	0.166
Formicidae	0.177	0.234	0.287	0.369
Hemiptera	0.056	0.066	0.359	0.001
Hymenoptera	0.153	0.197	0.288	0.099
Isopoda	0.086	0.000	0.000	0.113
Lepidoptera	0.079	0.170	0.249	0.097
Mantodea	0.009	0.167	0.200	0.086
Myriapoda	0.033	0.123	0.033	0.223
Neuroptera	0.000	0.000	0.029	1.000
Orthoptera	0.063	0.230	0.214	0.246
Solpugida	0.022	0.103	0.131	0.460

Table 7: The effect of vegetation characteristics on total invertebrate abundance, order richness and biomass.

Response variable	Sampling technique	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Total abundance	Sweep nets	Biomass	1	114.492	114.492	0.606	0.440	
		Vegetative height	1	16.363	16.363	0.087	0.769	
		Inflorescence height	1	1053.260	1053.260	5.575	0.021	*
		Percentage bare ground	1	61.570	61.570	0.326	0.570	
		Forb Abundance	1	33.117	33.117	0.175	0.677	
		Forb Richness	1	633.175	633.175	3.352	0.077	
Total abundance	Pitfall traps	Percentage forbs flowering	1	195.992	195.992	1.037	0.311	
		Biomass	1	340844.739	340844.739	5.332	0.024	*
		Vegetative height	1	213892.537	213892.537	3.346	0.071	
		Inflorescence height	1	8666.803	8666.803	0.136	0.714	
		Percentage bare ground	1	67904.467	67904.467	1.062	0.306	
		Forb Abundance	1	38878.302	38878.302	0.608	0.438	
Order richness	Sweep nets	Forb Richness	1	606.984	606.984	0.009	0.923	
		Percentage forbs flowering	1	60294.150	60294.150	0.943	0.334	
		Biomass	1	5.555	5.555	3.907	0.052	
		Vegetative height	1	3.142	3.142	2.210	0.141	
		Inflorescence height	1	53.662	53.662	37.737	0.000	***
		Percentage bare ground	1	0.945	0.945	0.665	0.417	
Order richness	Pitfall traps	Forb Abundance	1	2.435	2.435	1.712	0.195	
		Forb Richness	1	1.166	1.166	0.820	0.369	
		Percentage forbs flowering	1	1.417	1.417	0.997	0.321	
		Biomass	1	0.601	0.601	0.137	0.712	
		Vegetative height	1	0.176	0.176	0.040	0.842	
		Inflorescence height	1	2.020	2.020	0.460	0.499	
Invertebrate biomass	Pitfall traps	Percentage bare ground	1	0.277	0.277	0.063	0.802	
		Forb Abundance	1	1.304	1.304	0.297	0.587	
		Forb Richness	1	6.359	6.359	1.448	0.232	
		Percentage forbs flowering	1	0.117	0.117	0.027	0.871	
		Biomass	1	0.001	0.001	0.048	0.828	
		Vegetative height	1	0.002	0.002	0.104	0.748	
Invertebrate biomass	Pitfall traps	Inflorescence height	1	0.011	0.011	0.747	0.390	
		Percentage bare ground	1	0.000	0.000	0.004	0.950	
		Forb Abundance	1	0.003	0.003	0.183	0.671	
		Forb Richness	1	0.040	0.040	2.601	0.117	
		Percentage forbs flowering	1	0.004	0.004	0.260	0.611	

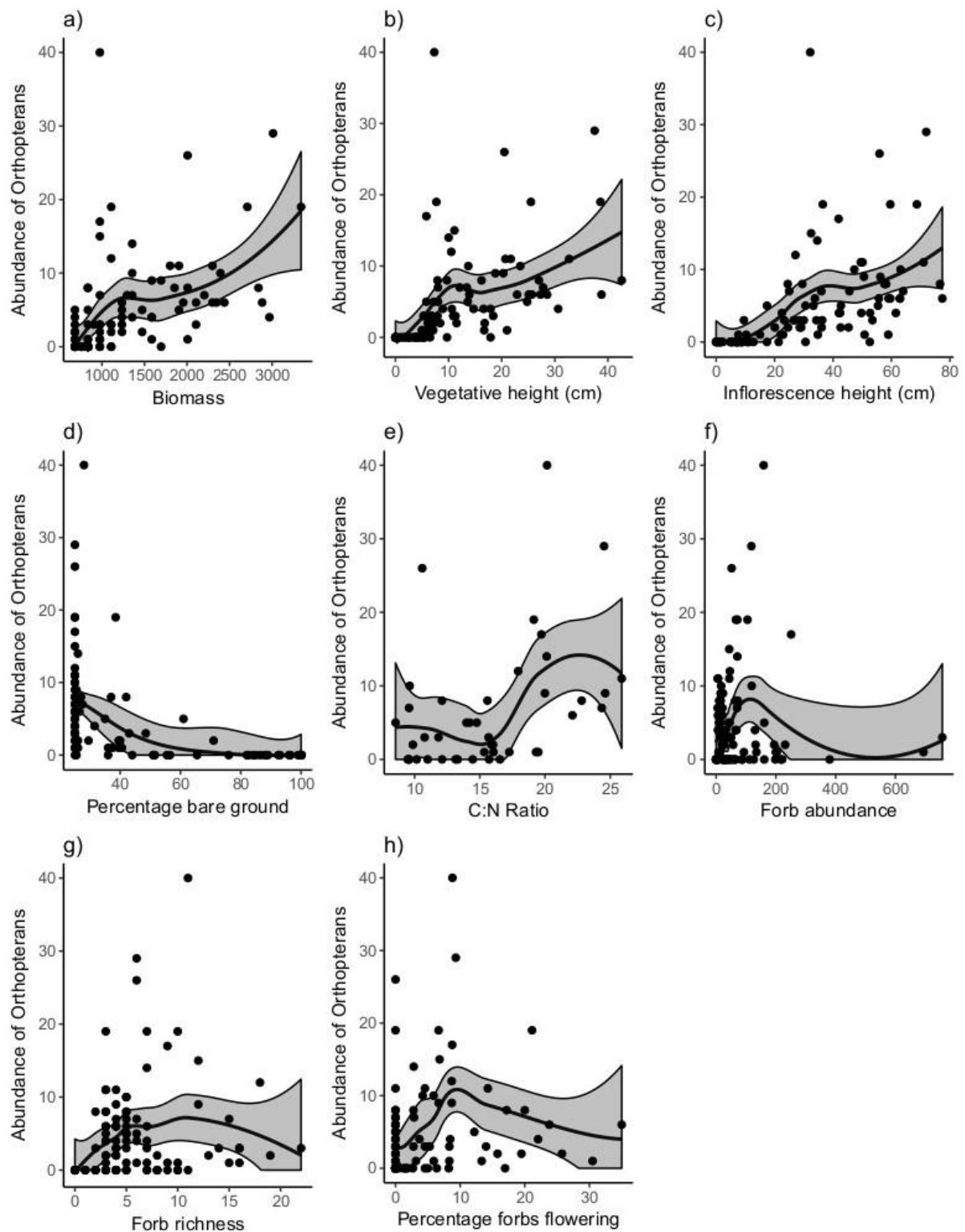


Figure 2: Variation in *Orthopteran* abundance in sweep nets against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

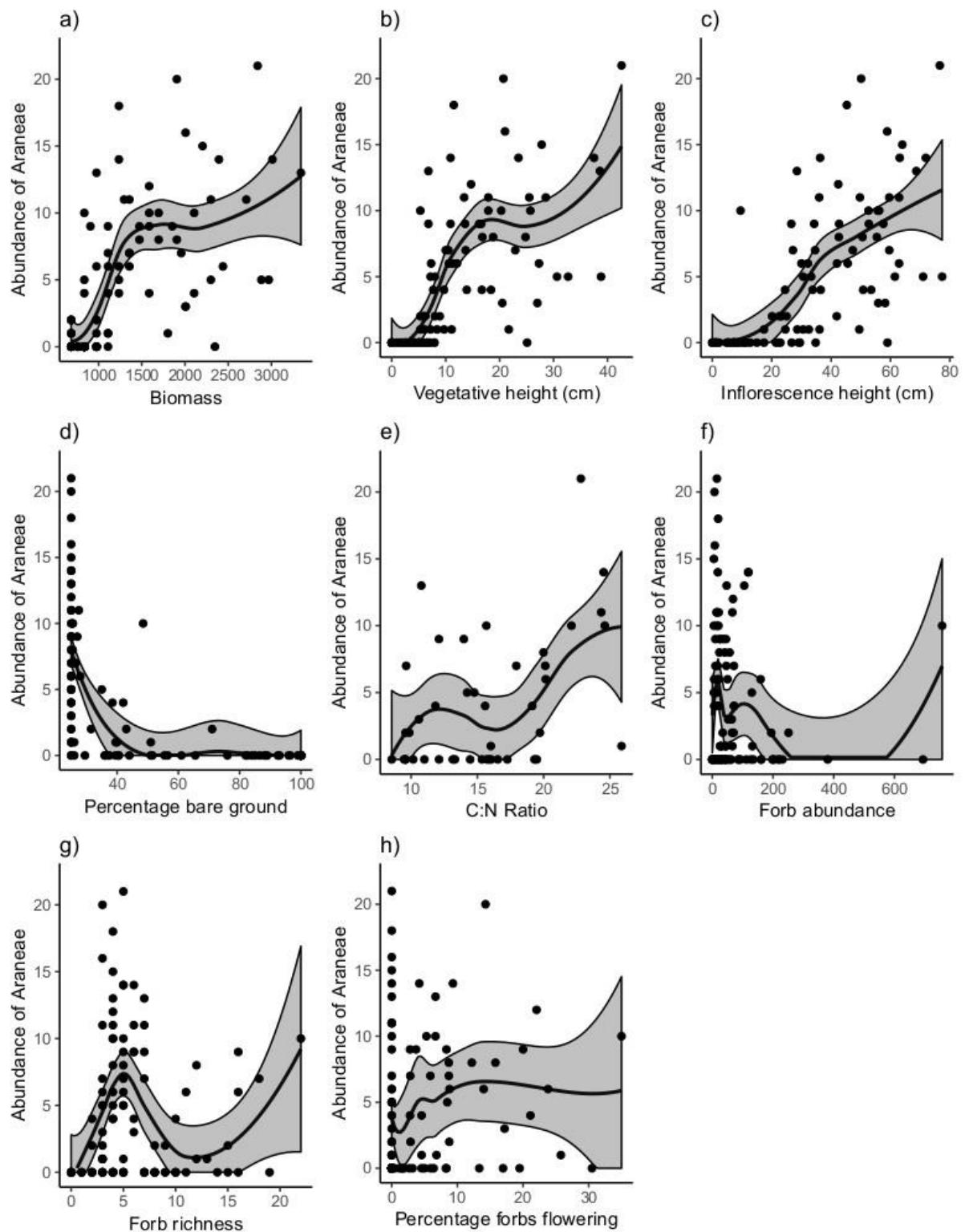


Figure 3: Variation in Araneae abundance in sweep nets against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

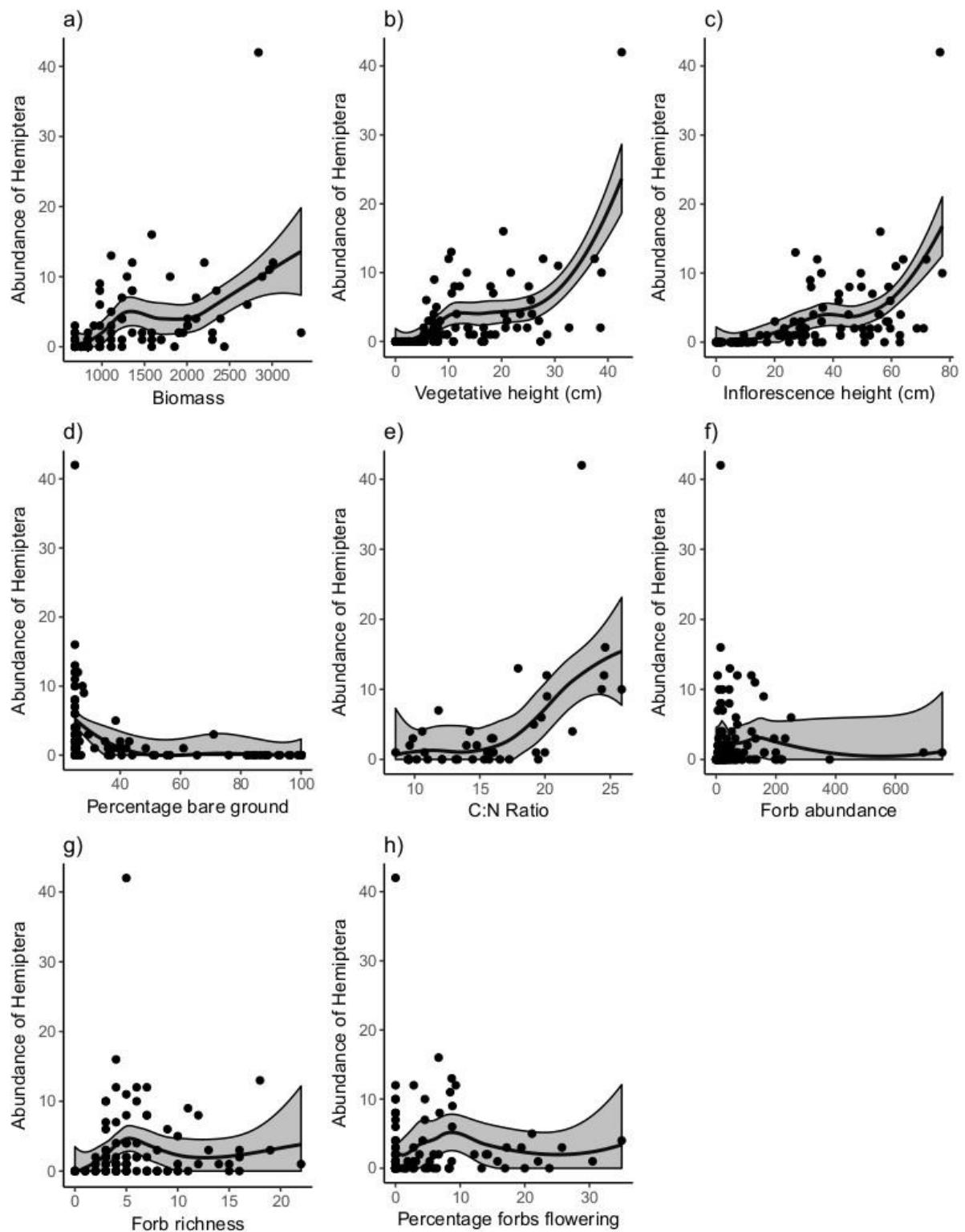


Figure 4: Variation in *Hemipteran* abundance in sweep nets against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

Table 8: The effect of vegetation characteristics on the abundance of the three most abundant orders in sweep nets.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Orthoptera abundance	Biomass	1	0.079	0.079	0.004	0.952	
	Vegetative height	1	15.194	15.194	0.692	0.408	
	Inflorescence height	1	65.806	65.806	2.998	0.087	
	Percentage bare ground	1	0.057	0.057	0.003	0.959	
	Forb Abundance	1	77.063	77.063	3.511	0.066	
	Forb Richness	1	36.071	36.071	1.644	0.203	
Araneae abundance	Percentage forbs flowering	1	52.532	52.532	2.394	0.125	
	Biomass	1	7.585	7.585	0.551	0.460	
	Vegetative height	1	0.704	0.704	0.051	0.822	
	Inflorescence height	1	36.010	36.010	2.616	0.109	
	Percentage bare ground	1	6.473	6.473	0.470	0.495	
	Forb Abundance	1	0.026	0.026	0.002	0.965	
Hemiptera abundance	Forb Richness	1	2.682	2.682	0.195	0.660	
	Percentage forbs flowering	1	6.072	6.072	0.441	0.508	
	Biomass	1	60.500	60.500	4.901	0.030	*
	Vegetative height	1	101.571	101.571	8.229	0.005	**
	Inflorescence height	1	2.952	2.952	0.239	0.626	
	Percentage bare ground	1	4.631	4.631	0.375	0.542	
	Forb Abundance	1	7.469	7.469	0.605	0.440	
	Forb Richness	1	1.690	1.690	0.137	0.712	
	Percentage forbs flowering	1	19.880	19.880	1.611	0.207	

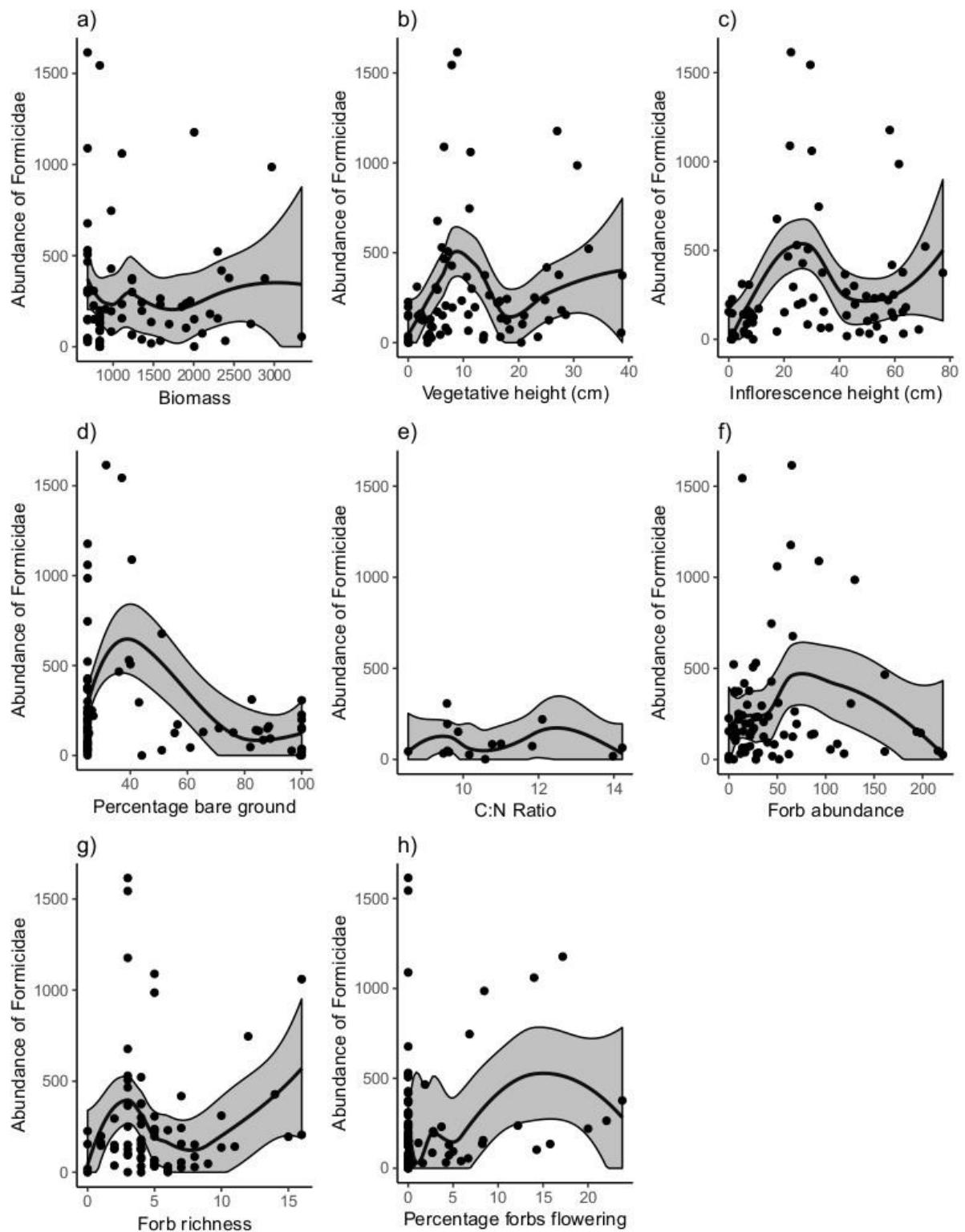


Figure 6: Variation in *Formicidae* abundance in pitfall traps against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

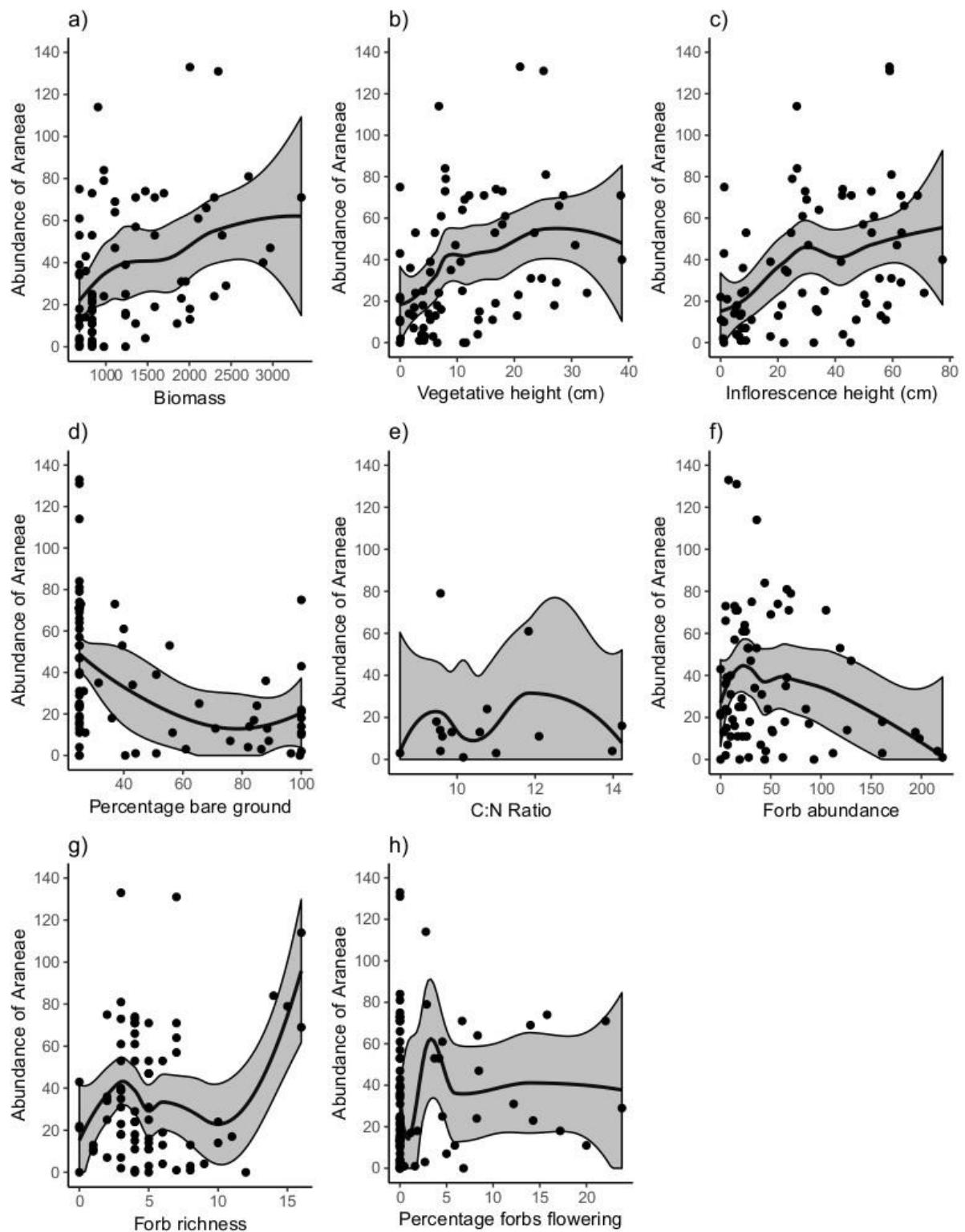


Figure 7: Variation in *Araneae* abundance in pitfall traps against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

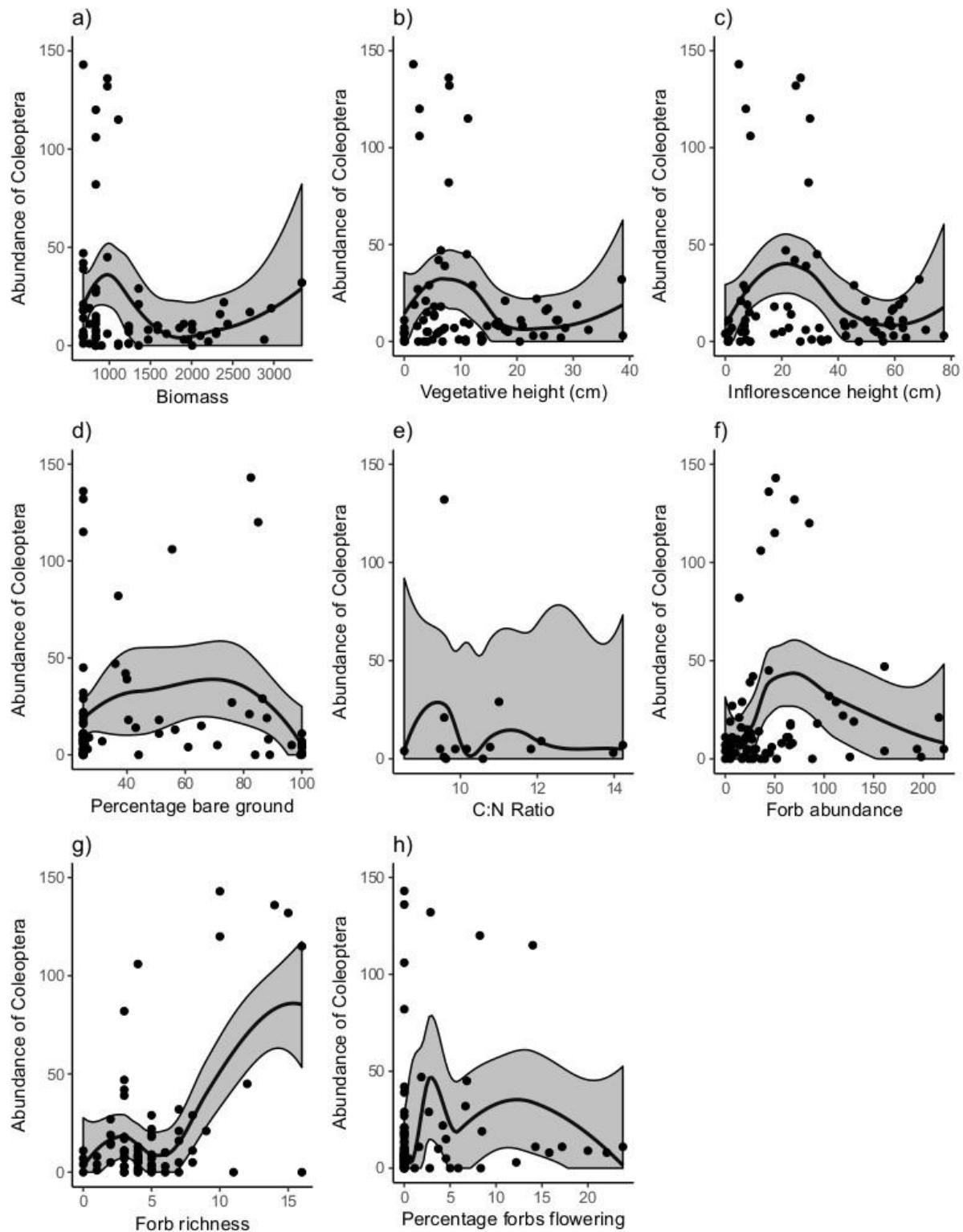


Figure 8: Variation in Coleopteran abundance in pitfall traps against the vegetation characteristics from Chapter 2: a) grass biomass, b) grass vegetative height, c) grass inflorescence height, d) the percentage of bare ground, e) C:N ratio, f) forb abundance, g) forb richness, h) the percentage of forbs flowering.

Table 9: The effect of vegetation characteristics on the abundance of the three most abundant orders in pitfall traps.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Formicidae abundance	Biomass	1	455320.735	455320.735	6.839	0.013	*
	Vegetative height	1	277159.211	277159.211	4.163	0.046	*
	Inflorescence height	1	26004.797	26004.797	0.391	0.535	
	Percentage bare ground	1	104591.838	104591.838	1.571	0.217	
	Forb Abundance	1	2000.272	2000.272	0.030	0.864	
	Forb Richness	1	14348.140	14348.140	0.216	0.644	
Araneae abundance	Percentage forbs flowering	1	195736.209	195736.209	2.940	0.092	
	Biomass	1	832.530	832.530	1.578	0.216	
	Vegetative height	1	5.392	5.392	0.010	0.920	
	Inflorescence height	1	91.237	91.237	0.173	0.679	
	Percentage bare ground	1	730.809	730.809	1.385	0.245	
	Forb Abundance	1	1491.915	1491.915	2.828	0.102	
Coleoptera abundance	Forb Richness	1	694.470	694.470	1.317	0.256	
	Percentage forbs flowering	1	382.008	382.008	0.724	0.398	
	Biomass	1	77.375	77.375	0.098	0.757	
	Vegetative height	1	16.477	16.477	0.021	0.886	
	Inflorescence height	1	852.791	852.791	1.077	0.306	
	Percentage bare ground	1	481.277	481.277	0.608	0.440	***
	Forb Abundance	1	16936.715	16936.715	21.384	0.000	
	Forb Richness	1	458.375	458.375	0.579	0.451	
	Percentage forbs flowering	1	30.220	30.220	0.038	0.846	

Table 10: The effect of vegetation characteristics, including C:N ratio, on the total invertebrate abundance, order richness and invertebrate biomass in sweep nets.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Total abundance	Biomass	1	226.533	226.533	0.575	0.454	
	Vegetative height	1	41.915	41.915	0.106	0.746	
	Inflorescence height	1	1297.459	1297.459	3.293	0.078	
	Percentage bare ground	1	227.909	227.909	0.578	0.452	
	C:N ratio	1	1572.612	1572.612	3.991	0.054	
	Forb Abundance	1	503.307	503.307	1.277	0.266	
	Forb Richness	1	39.972	39.972	0.101	0.752	
	Percentage forbs flowering	1	750.892	750.892	1.906	0.176	
Order richness	Biomass	1	8.000	8.000	3.663	0.065	
	Vegetative height	1	0.323	0.323	0.148	0.703	
	Inflorescence height	1	29.351	29.351	13.438	0.001	**
	Percentage bare ground	1	1.205	1.205	0.552	0.463	
	C:N ratio	1	0.013	0.013	0.006	0.942	
	Forb Abundance	1	0.038	0.038	0.017	0.897	
	Forb Richness	1	2.730	2.730	1.250	0.273	
	Percentage forbs flowering	1	0.247	0.247	0.113	0.739	
Invertebrate biomass	Biomass	1	0.002	0.002	0.131	0.720	
	Vegetative height	1	0.001	0.001	0.043	0.837	
	Inflorescence height	1	0.053	0.053	2.850	0.101	
	Percentage bare ground	1	0.013	0.013	0.668	0.419	
	C:N ratio	1	0.067	0.067	3.574	0.068	
	Forb Abundance	1	0.027	0.027	1.452	0.239	
	Forb Richness	1	0.002	0.002	0.099	0.755	
	Percentage forbs flowering	1	0.027	0.027	1.432	0.240	

Table 11: The effect of vegetation characteristics, including C:N ratio, on the abundance of the three most abundant orders in sweep nets.

Response variable	Covariate	Df	Sum of squares	Mean squares	F value	p	Significance
Orthoptera abundance	Biomass	1	1.617	1.617	0.034	0.855	
	Vegetative height	1	63.279	63.279	1.332	0.257	
	Inflorescence height	1	163.553	163.553	3.443	0.072	
	Percentage bare ground	1	11.714	11.714	0.247	0.623	
	C:N ratio	1	89.745	89.745	1.889	0.180	
	Forb Abundance	1	69.584	69.584	1.465	0.238	
	Forb Richness	1	12.194	12.194	0.257	0.616	
	Percentage forbs flowering	1	88.624	88.624	1.865	0.181	
Araneae abundance	Biomass	1	0.187	0.187	0.018	0.894	
	Vegetative height	1	27.907	27.907	2.686	0.111	
	Inflorescence height	1	1.043	1.043	0.100	0.753	
	Percentage bare ground	1	2.928	2.928	0.282	0.599	
	C:N ratio	1	1.148	1.148	0.111	0.742	
	Forb Abundance	1	3.278	3.278	0.315	0.580	
	Forb Richness	1	0.178	0.178	0.017	0.897	
	Percentage forbs flowering	1	31.667	31.667	3.048	0.090	
Hemiptera abundance	Biomass	1	73.840	73.840	4.834	0.036	*
	Vegetative height	1	121.747	121.747	7.970	0.009	**
	Inflorescence height	1	34.533	34.533	2.261	0.142	
	Percentage bare ground	1	50.582	50.582	3.311	0.079	
	C:N ratio	1	127.235	127.235	8.329	0.498	
	Forb Abundance	1	37.335	37.335	2.444	0.130	
	Forb Richness	1	11.611	11.611	0.760	0.393	
	Percentage forbs flowering	1	68.917	68.917	4.511	0.050	*

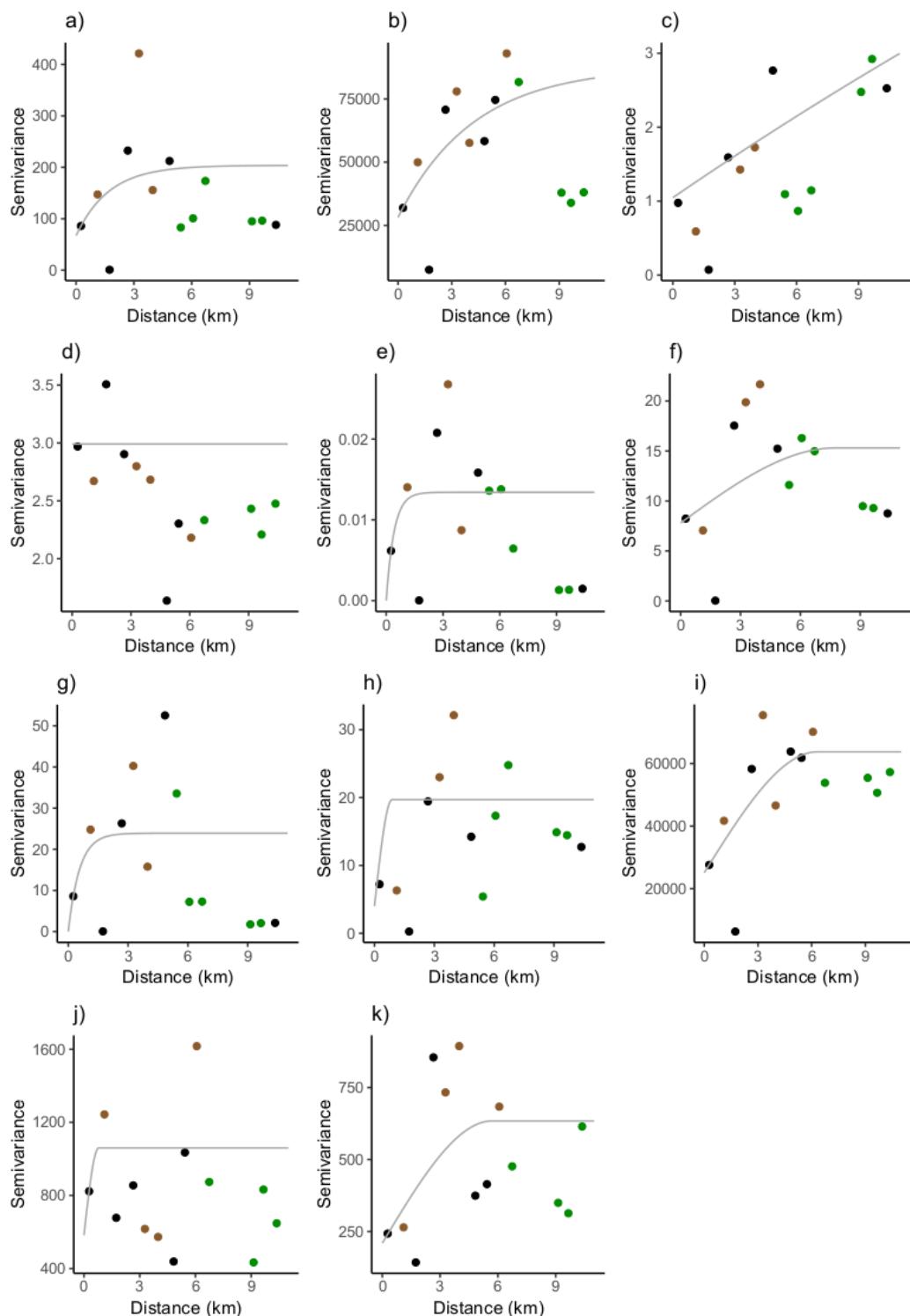
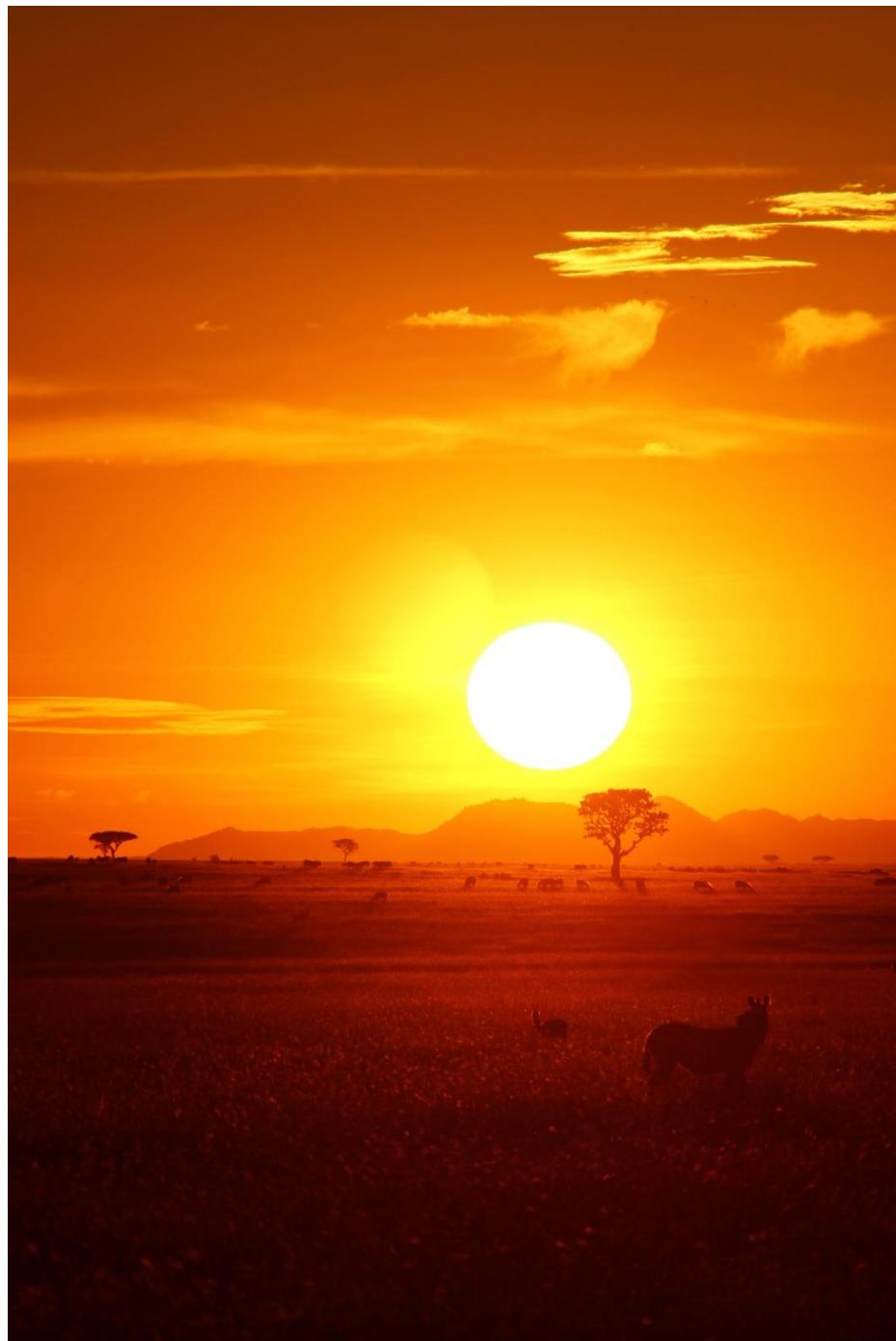


Figure 9: Semi-variograms for: total invertebrate abundance in a) sweep nets, and b) pitfall traps; order richness in c) sweep nets, and d) pitfall traps; e) invertebrate biomass in sweep nets; abundance in sweep nets of: f) Araneae, g) Orthopterans, and h) Hemiptera; abundance in pitfall traps of: i) Formicidae, j) Coleoptera, and k) Araneae. Burnt plots are shown in black, wildebeest plots in brown and control plots in green.

Chapter 6

Synthesis



Cover illustration:

Sunset over Nyati Plains, Grumeti Game Reserve, Tanzania. ©James Probert

Key findings

The main aim of this thesis was to better understand the roles of fire and herbivory in the ecology of the Serengeti-Mara and other consumer controlled systems. Using a combination of satellite and field data we described the fire regime of the Serengeti-Mara and examined the factors driving it, investigated how fire and grazing impact vegetation and how these effects cascade to affect mammalian and invertebrate communities. First, we described the spatial and temporal patterns of the Serengeti-Mara's fire regime and examined the biotic and abiotic factors which were driving those patterns. We showed that spatial patterns were driven by both the short and long term effects of rainfall, whilst declines in the number of fires and the area burnt were the result of increasing livestock populations. Second, we demonstrated that fire is fundamentally different from herbivory by quantifying the functional differences between fire and grazing by the wildebeest migration on vegetation. We showed that the two consumers had similar effects on vegetation structure but contrasting effects on grass quality and on forb communities. Third, we found that the contrasting vegetation characteristics created by fire and grazing caused differences in the local abundance of resident mammalian herbivores. Grass structure, grass quality and forb abundance were all significant in determining resident herbivore distribution, indicating that some species were driven more by nutrition and others by fear of predation. Finally, we observed variation in invertebrate responses to, and recovery from, fire and grazing dependent upon ecological niche.

Novelty and impact

There are many studies on fire in the Serengeti-Mara, and some have even described aspects of the fire regime using satellite data (e.g. Wilsey, 1996; Dempewolf et al. 2007), but none have done so as comprehensively as our study. It is necessary to accurately describe a process before it can be studied further or effectively manipulated. Our findings provide greater understanding of the main drivers of fire in the Serengeti-Mara and the surfaces we have generated will provide useful tools for future researchers. We also identify striking declines in the area burnt in some areas of the system, driven by increasing livestock density, which require urgent management attention.

As the two key consumers in savannah systems (Bond, 2005) it is important to understand the contrasting effects that fire and grazing have on savannah ecology. The wildebeest migration is similar to fire in its intensity and brevity but had very different effects on vegetation, resident mammalian herbivores, and invertebrates. Our findings underline the differences between areas where fire is the dominant consumer and where grazing is the dominant consumer. They highlight that the two consumers are not interchangeable, that the extinction of migrations of large mammalian herbivores from many systems will have fundamentally altered their ecology and that it is essential that we preserve those species which remain.

Changes in fire and herbivory

Throughout our planet's history there have been fluctuations in the form and intensity of fire and herbivory (Scott & Glasspool, 2006). However, as with many other aspects of our planet's ecology, human activities are causing changes beyond the range of natural variation which may have serious consequences for our natural world and ourselves. Andela et al. (2017) reported a global decline in the area burnt of nearly 25% between 1998 and 2015 and observed that the largest decreases were in savannah ecosystems. Our results provide a site-specific confirmation of these findings and provide a mechanism for why these declines are taking place. We identified a 40% decline in the number of fires between 2001 and 2014, and a 39% decline in the area burnt over the same period, driven by increasing livestock density. Our results are significant for two key reasons. First, where previously, protected areas in Africa experienced the most extensive fires (Archibald, 2016), the declines we observed took place within the protected areas of the Serengeti-Mara, and second, climate has typically been thought of as the primary determinant of the area burnt, whilst humans modify other aspects of fire regimes such as the season, location and intensity (van Wilgen et al. 2004; Smit *et al.* 2013; Archibald, 2016). However, we observed substantial modification of the area burnt as a result of human activities.

The IUCN defines a protected area as:

“A protected area is a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values.” (Dudley, 2008)

Large areas of the Serengeti-Mara’s network of protected area are not achieving the objectives stated in this definition. Human activities, specifically livestock grazing, are not sustainable, suppressing fire and likely resulting in changes in ecosystem state and the loss of biodiversity and ecosystem services. The displacement of wild herbivores by livestock is in itself an important change in the ecology of the system. Livestock have a very different set of functional traits to wild herbivores and consequently have different effects on vegetation (Hempson et al. 2015; 2017). Therefore, whilst we observed that the substitution of wild herbivores by livestock switched off fire, it is also possible there will be an increase in woody cover, increased methane emissions, and decreased lateral nutrient transfer (Hempson et al. 2017).

There is no simple solution to reducing livestock density and restoring fire. Kideghesho and Mtoni (2010) found deep negative attitudes towards protected areas amongst the human populations of the Serengeti-Mara. These stem from people feeling that land has been stolen from them to create protected areas, that they are being denied their right to hunt, graze and access water, from intense competition for land and resources and from receiving insufficient benefits from protected areas to offset these costs. Conversely, the resources of the Serengeti-Mara are not infinite and the persistence of the system in its current state (Fig. 1) requires the limitation of their exploitation by ever expanding human populations. Livestock have displaced wild herbivores across much of Africa (Archibald, 2016; Ogutu et al, 2016) so the changes we observed are likely to be much more widespread than the Serengeti-Mara. Establishing the extent and severity of the changes we observed, and acting to address them, should be an urgent focus of research and management attention.



Figure 1: The boundary between Grumeti Game Reserve and the bordering village lands. Foreground is the game reserve; the boundary (marked by a small stream) is clearly visible by the sharp transition to a thicket of *Acacia*. ©James Probert

Comparing the impacts of fire and herbivory

Fire and herbivores are the two major consumers of vegetative biomass globally (Bond, 2005). They shape consumer-controlled systems and the differences in their effects can have substantial impacts on ecosystem structure, composition and function. Despite this, our understanding of the contrasts between fire and herbivory is largely theoretical (e.g. Archibald & Hempson, 2016). Comparisons of the effects of fire and herbivory are hindered by a poor ability to quantify the multidimensional nature of herbivory, for example in terms of its intensity, timing and selectivity. We used the high intensity and short duration of grazing by the wildebeest migration as an analogue to fire to compare the effects of the two consumers on vegetation. This approach attempts to control for some of the variability encompassed within herbivory by examining the effects of short-duration, heavy grazing specifically.

Whilst this produced interesting results, there is a need for further research to more accurately describe herbivory and elucidate how it differs from fire. A key question is whether the wildebeest migration alone can facilitate the creation of grazing lawns in our study area. In our study, wildebeest grazing reduced grass biomass but did not increase grass quality. This may have several explanations: 1) the removal of biomass alone may not be enough to stimulate highly nutritious regrowth, 2) nutrient inputs from wildebeest dung and urine may not be significant, 3) the effects of wildebeest dung and urine may be temporally delayed beyond the duration of our study, or 4) the effect of the input of wildebeest dung and urine may be spatially larger than our study area. If wildebeest grazing does not generate grass which is higher quality than the surrounding landscape, it is less likely to facilitate the grazing of other herbivores. It has also been shown that small fires are needed to concentrate resident grazers (e.g. Donaldson et al. 2018) and it is possible that the scale of the wildebeest migration is too large to do this. Grazing lawns can be triggered by grazing alone (Hempson et al. 2015) but it is probable that the grazing of the wildebeest migration is too brief to trigger the creation of a grazing lawn. A final key factor is rainfall. The Western Corridor receives high rainfall, approximately 1400 mm, which means grass growth rates are high (Norton-Griffiths, 1975). In such a productive area a brief period of migratory grazing is unlikely to result in the creation of a lawn, suggesting fire may be more important in shaping vegetation structure in our study area.

Limitations of our study

The primary shortcomings in our study were the placement of plots for Chapters 3-5, and the fact that we were unable to sample our plots pre-treatment. There was a single fire within our study area at the correct time for our study, necessitating that our burnt plots would be clustered in this burnt area. Whilst there is evidence of weak spatial autocorrelation in some of our variables, it is not strong enough to invalidate our findings. A before-after-control-impact study was originally planned but the start of fieldwork was delayed due to permitting issues. This undoubtedly makes it difficult to determine whether our results were correlation or causation e.g. were forbs more abundant in our burnt plots because they had burnt or were they more likely to burn because there was a high abundance of forbs in them? However, there is a substantial body of literature on savannahs and

therefore we interpret our results with reference to this evidence. Given that many of our conclusions are supported by the results of other studies we feel confident of their robustness.

Future directions in savannah ecology

There are several areas which pose challenges to the progression of savannah ecology but also provide opportunities that could help drive the field forward: 1) The scale of savannahs versus the scale of research on savannah ecology, 2) describing the complexity and variability of herbivory, and 3) increasing integration between researchers and managers.

1) Savannahs cover a fifth of the planet's terrestrial surface and can be found in regions with different environmental conditions. They are complex systems with multiple drivers, responses and feedbacks operating at different spatial and temporal scales. Current funding mechanisms promote the replication of studies that are short-term, have limited sample sizes, and are relatively small-scale considering the extent of the ecosystems concerned. Given these constraints it can be difficult to extrapolate findings to other systems, or even beyond the peculiarities of individual studies. Several steps could help alleviate these problems:

a) The value of long-term experiments in aiding our understanding of complex biological systems is well established but few of these exist within savannah ecosystems. Increasing the number of such experiments and coordinating their design and data collection would help us to understand the causes, mechanics and tipping points of long term change in savannahs.

b) Despite the scarcity of long-term experiments, several savannah systems (e.g. Kruger National Park, the Serengeti-Mara, Mpala Community Conservancy, and Hluhluwe-iMfolozi) have been the subjects of long-term study and therefore numerous datasets exist for them. These datasets are typically managed ad-hoc and other researchers may not be aware of their existence or be able to access them. Central repositories of such datasets would improve our understanding of long term patterns within ecosystems and reduce barriers to

cross-system collaborations. Both of these endeavours would also increase the impact of individual datasets, provide greater value for money for funders, and promote open access to data.

c) New metrics need to be created to allow greater comparability between studies and study sites, and facilitate cross-system analyses. For example, describing the timing of fires as spring burns, autumn burns, early dry season burns and similar can be confusing for those not familiar with a particular system, obscure hypotheses and assumptions relating to the timing of factors such as rainfall, and hinder comparisons with other systems. Explicit measurements, such as the number of dry months before a fire takes place, where a dry month is defined as receiving less than a certain proportion of the annual rainfall, explicitly quantify how factors such as fuel moisture affect variability in fire characteristics and responses to fire and make studies more accessible and comparable.

2) It is critical that we develop the methods to describe herbivory in greater detail and with greater accuracy. Fire is multidimensional, it can be described by its size, season, frequency and intensity (Gill, 1975), and the availability of satellite data has made it possible to study the effects of variation in these characteristics at 250m resolution at a global scale (e.g. Bond & Keeley, 2005). Herbivory is also multidimensional, we recognise that grazers and browsers, foregut and hindgut ruminants, resident and migratory herbivores, invertebrate and mammalian herbivores, respond differently to changes in vegetation and effect vegetation differently, but at present we lack the tools to quantify and generate surfaces of variation in the intensity and timing of these axes at suitable spatial and temporal resolutions (Hempson et al. 2015; Archibald & Hempson, 2016).

3) The defining goal of Applied Ecology is to use ecological science to help answer management questions. However, examining the effects of management can be hindered by an unclear understanding of what management aims to do and what management actually achieves. This makes forming hypotheses and interpreting results challenging. For example, not all the protected areas in the Serengeti-Mara have fire management plans but all manage fire in some way. Speaking to managers may not produce accurate information because perceptions of why and how fire is managed, and what is achieved, varies between

decision makers (e.g. park wardens) and implementers (e.g. park rangers). For those areas which do have fire management plans, objectives may be arbitrary (e.g. burn every three years), objectives may lack underlying justification for the desired effects on savannah ecology, may not be specific to particular ecosystems or habitats (particularly in large protected areas with strong environmental gradients), and fire itself may not be monitored to ensure objectives are being met. Therefore, greater clarity is needed on what objectives management are pursuing, how they are pursuing them, and what is actually being achieved.

Concluding remarks

Over forty years after Whitaker coined the phrase, savannahs remain very much ecosystems uncertain. We now understand that consumers are vital in creating and maintaining these ecosystems, but our understanding of the effects of fire and herbivory and how they interact remains limited. Savannahs also face an uncertain future, with significant threats from increasing human populations, wild herbivore extinctions, and climate change. This thesis presents novel work which examines these two areas of uncertainty in the context of the Serengeti-Mara ecosystem of East Africa. Using satellite data, we described the ecosystem's fire regime, showed that rainfall had both short and long-term effects on fire characteristics, and demonstrated that large declines in the area burnt and number of fires were caused by increasing livestock density. With a large scale natural experiment, we showed that fire and grazing have different effects on vegetation, different direct effects on mammalian herbivores and invertebrates, and that vegetation characteristics create contrasting responses in mammalian herbivores and invertebrates. Further work is needed to continue to investigate how fire and herbivory shape savannah ecology. Particular emphasis should be placed on developing tools which improve our ability to describe herbivory, on understanding how changes in fire and herbivory will affect savannahs, and on how to mitigate these changes.

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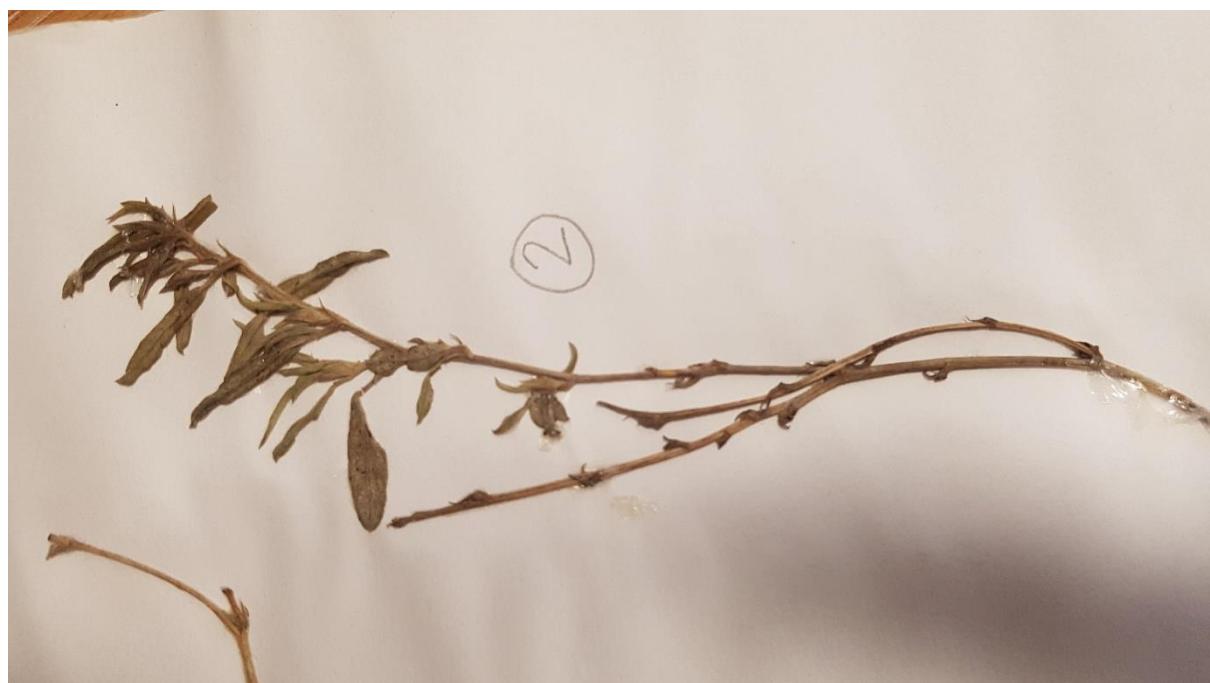
APPENDIX I

Forb herbarium

1 - *Tephrosia pumila*



2



3 – *Solanum incanum*



4 – Rubiaceae spp.



5 – *Sida* spp.



6 – *Clerodendrum* spp.



13



14



15 – *Triumfetta* spp.



16



17



18 – *Ruellia* spp.



19 – *Commelina* spp.



20 – *Justicia* spp.



21



(2)

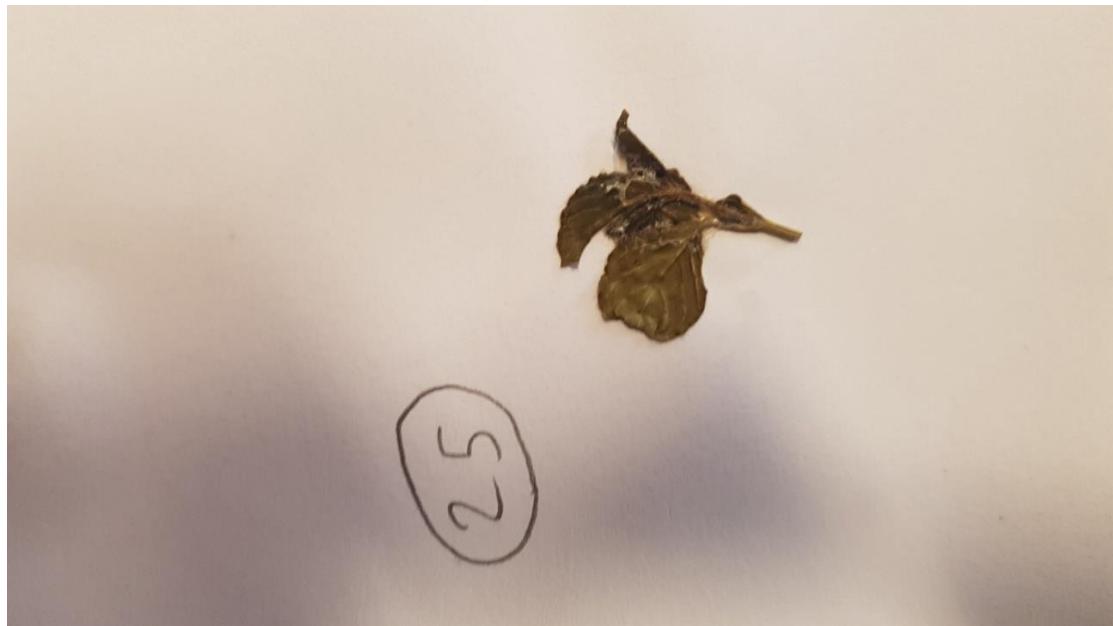
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243

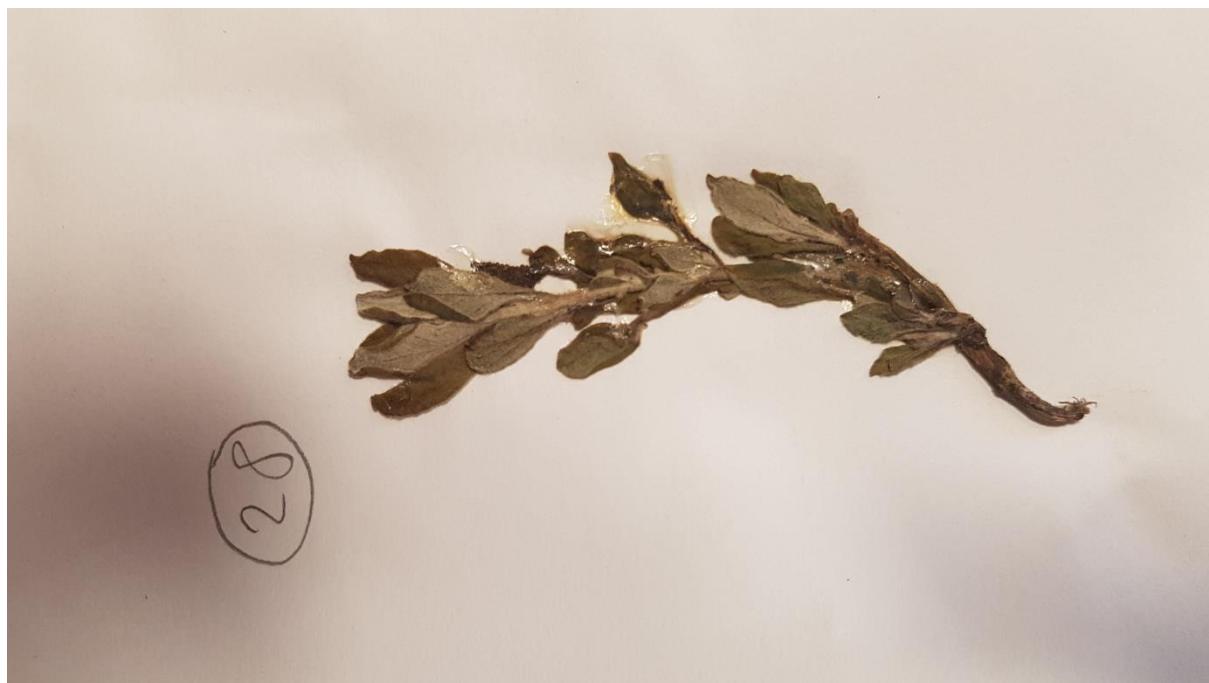
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27



28 – *Asteraceae* spp.



32



33



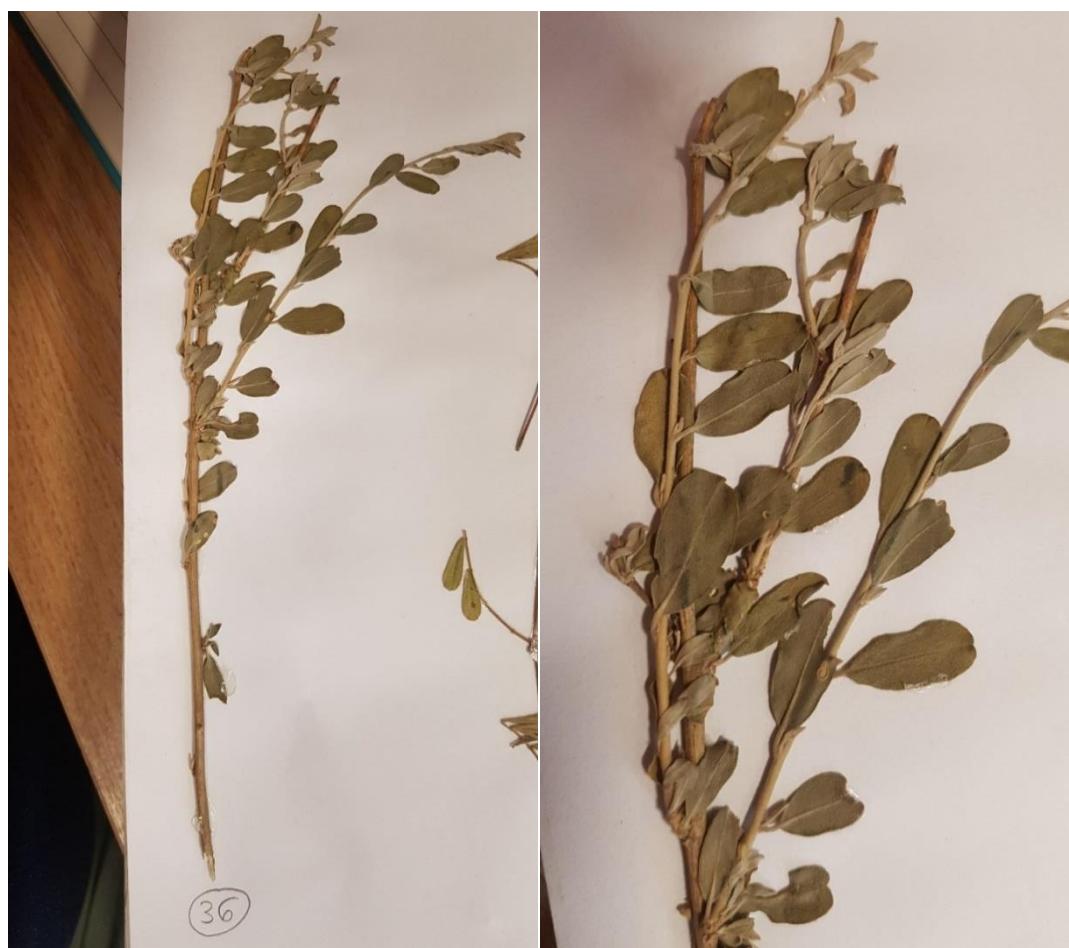
34



35 – *Justicia metamensis*



36 – *Fabaceae spp.*



37



39 – *Tephrosia* spp.



44



46



47



49 – *Asparagus* spp.



53



54 – *Combretum* spp.



55



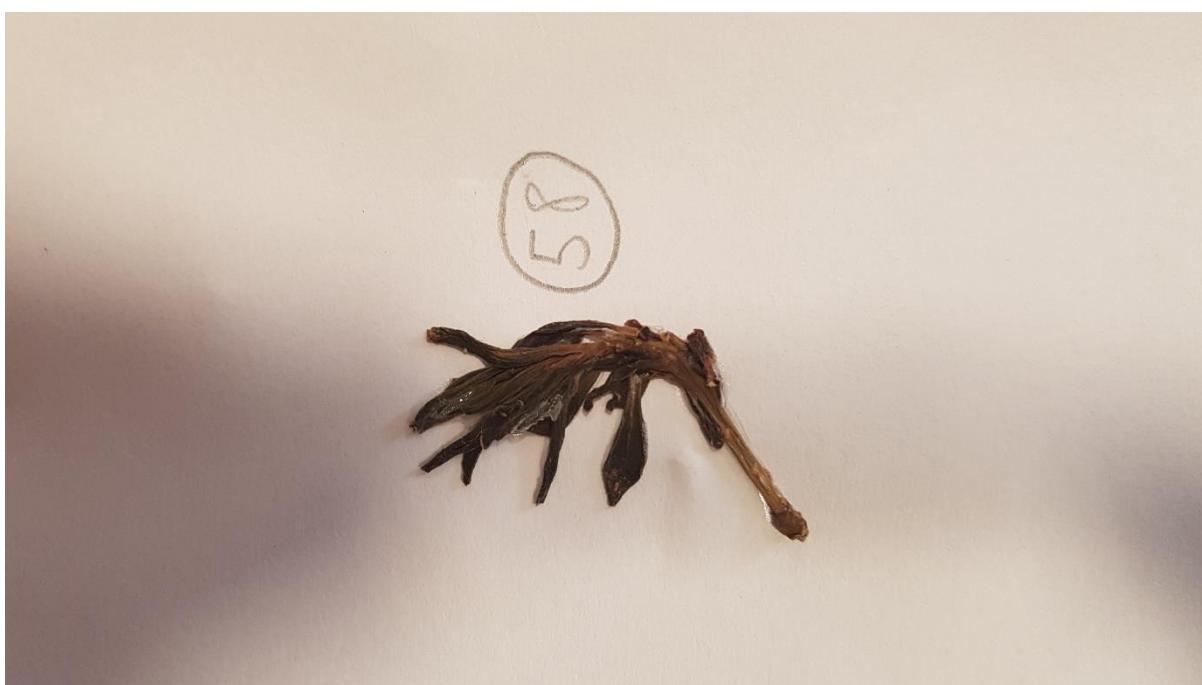
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57



58 – *Talinum* spp.



60



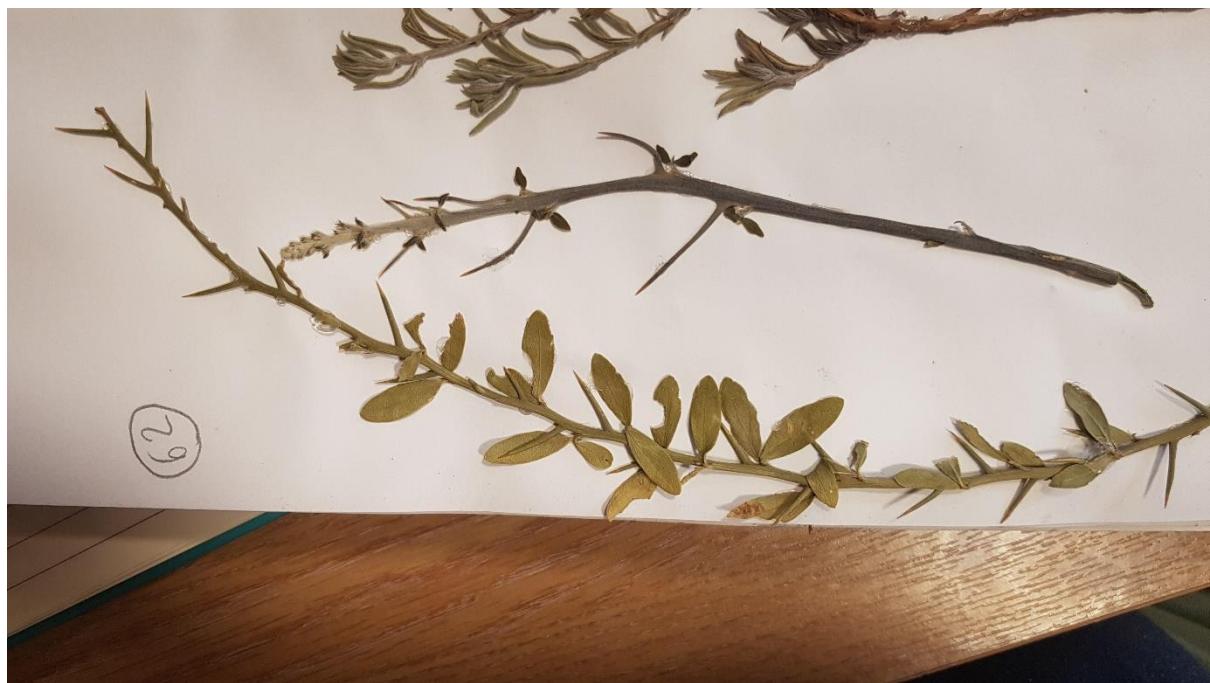
61



63 – *Hibiscus* spp.



62



64



65



66



68



69



72



73 – *Dipcadi* spp.



74 – *Sterculiaceae* spp.



75 – *Pupalia* spp.



76



77



78



79



80



82



83

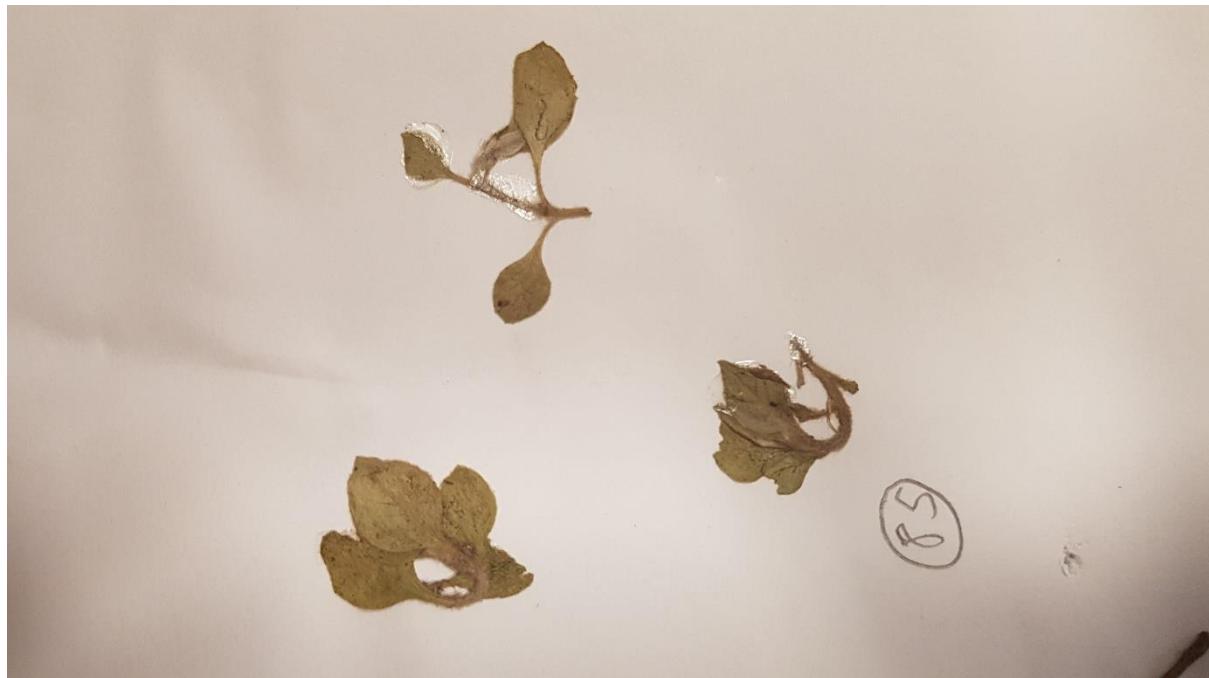


84



264

85



86 – *Commelina* spp.



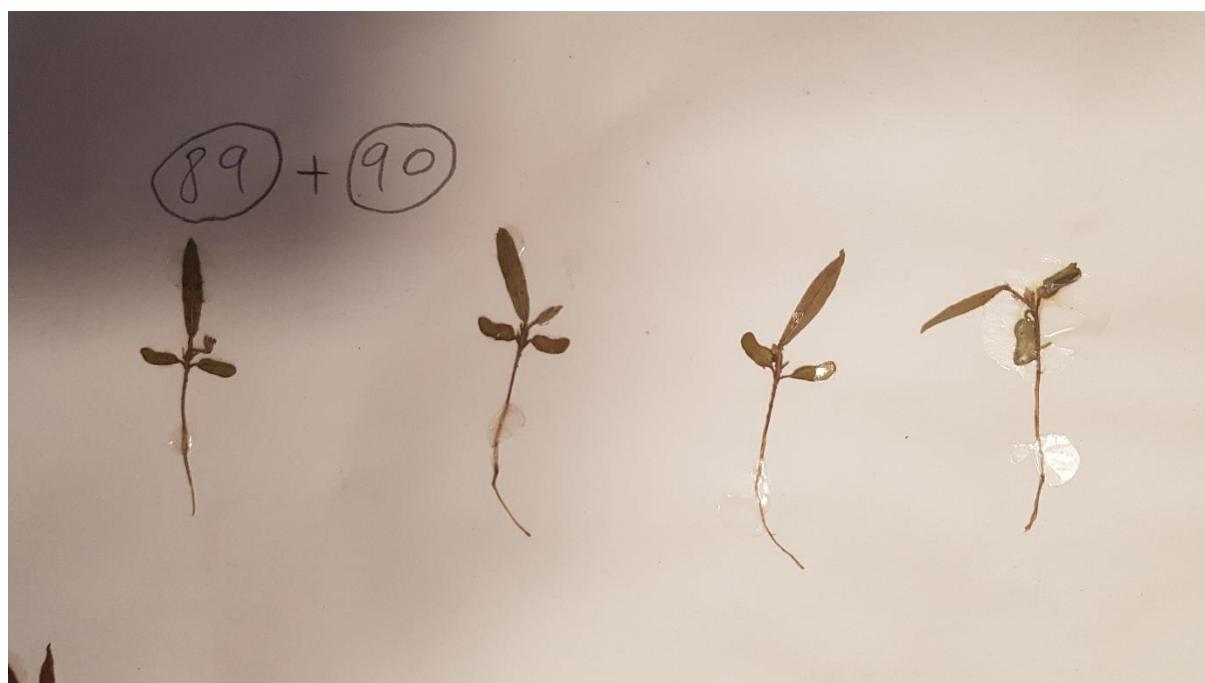
87 – *Cucurbitaceae* spp.



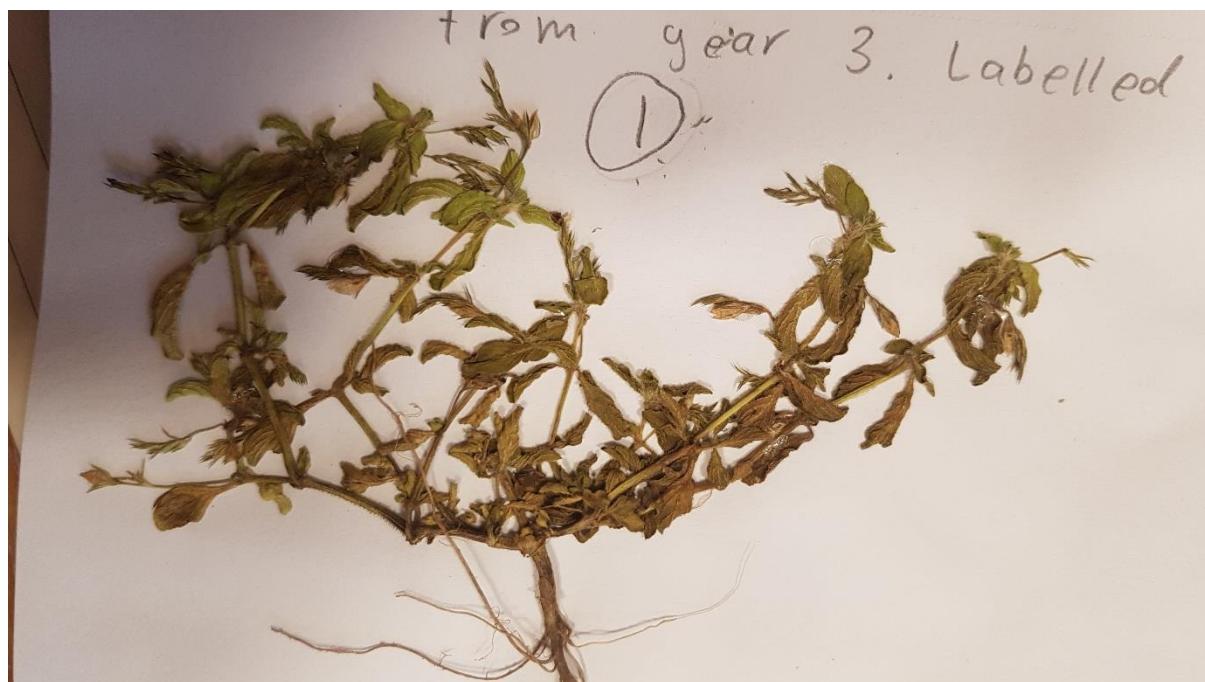
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89 – *Argyrolobium* spp.



92



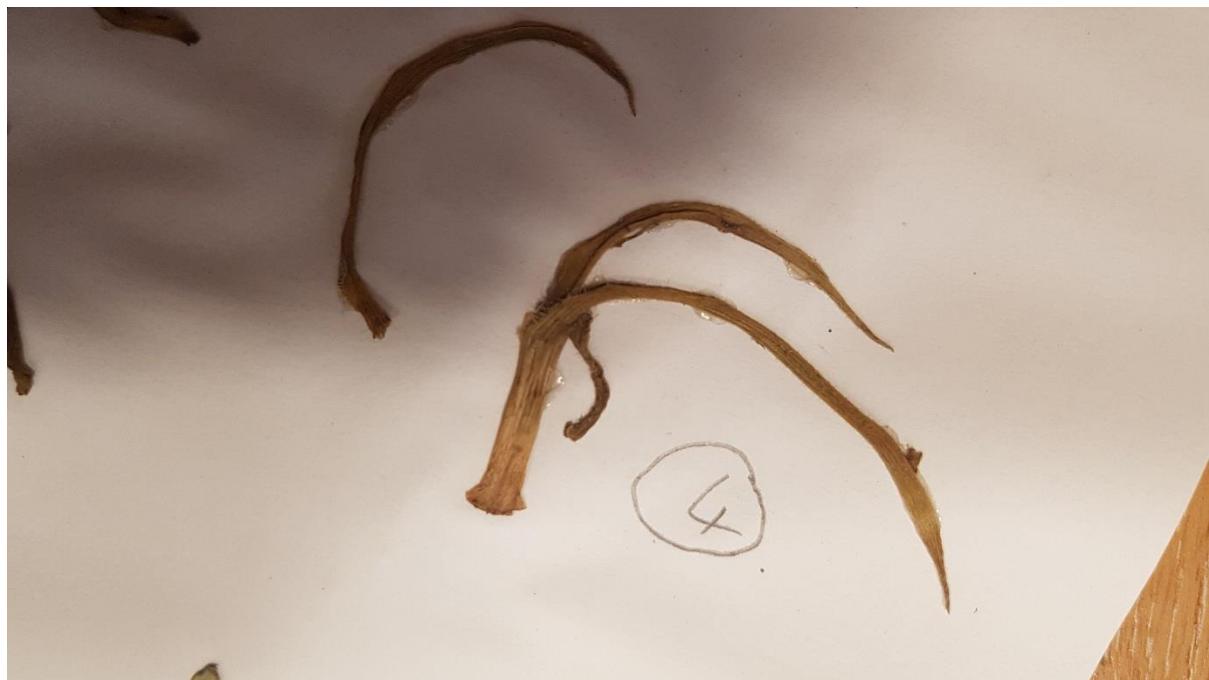
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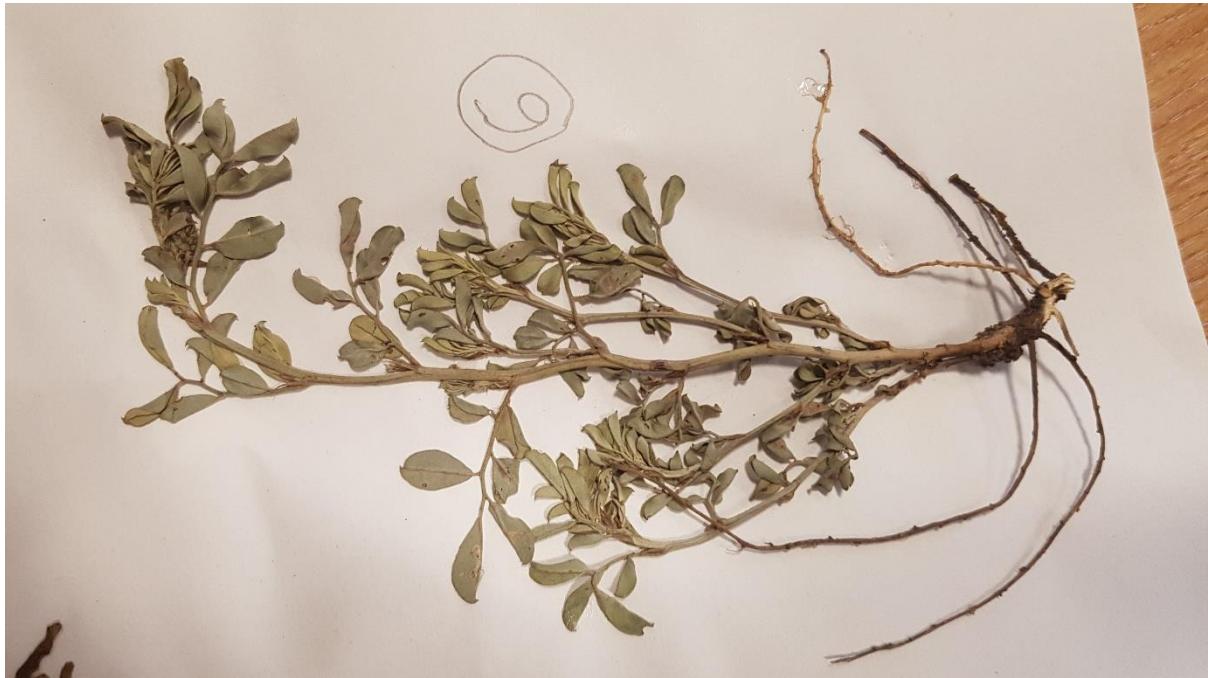
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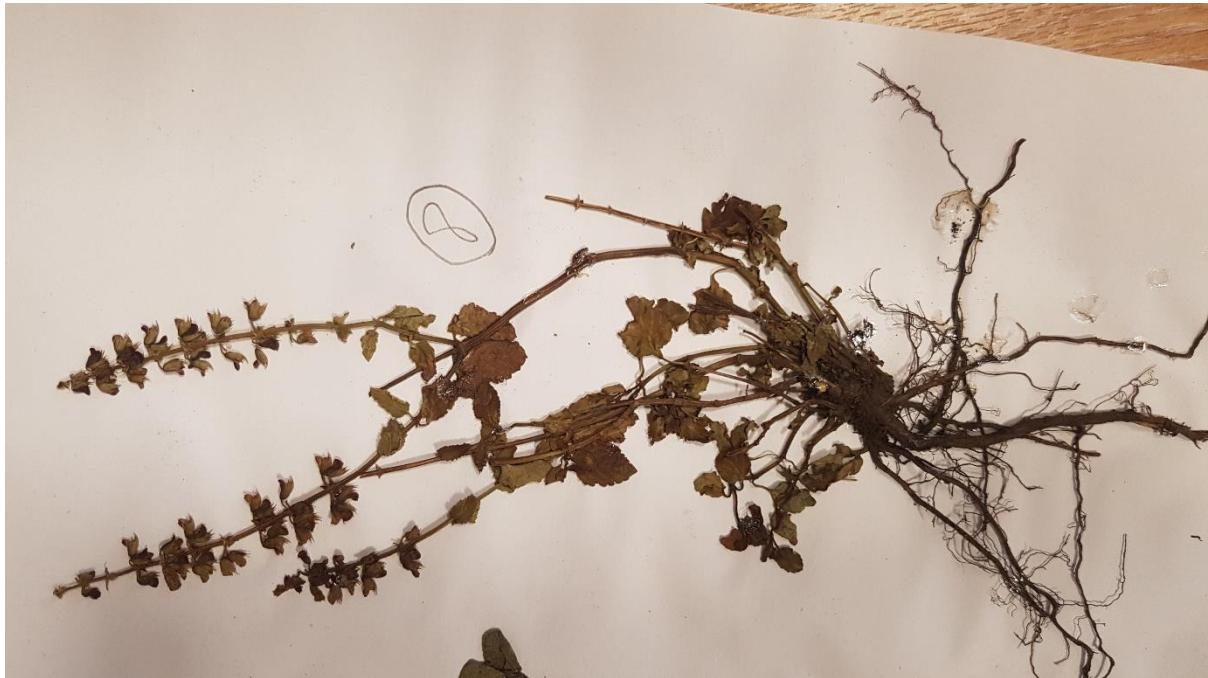
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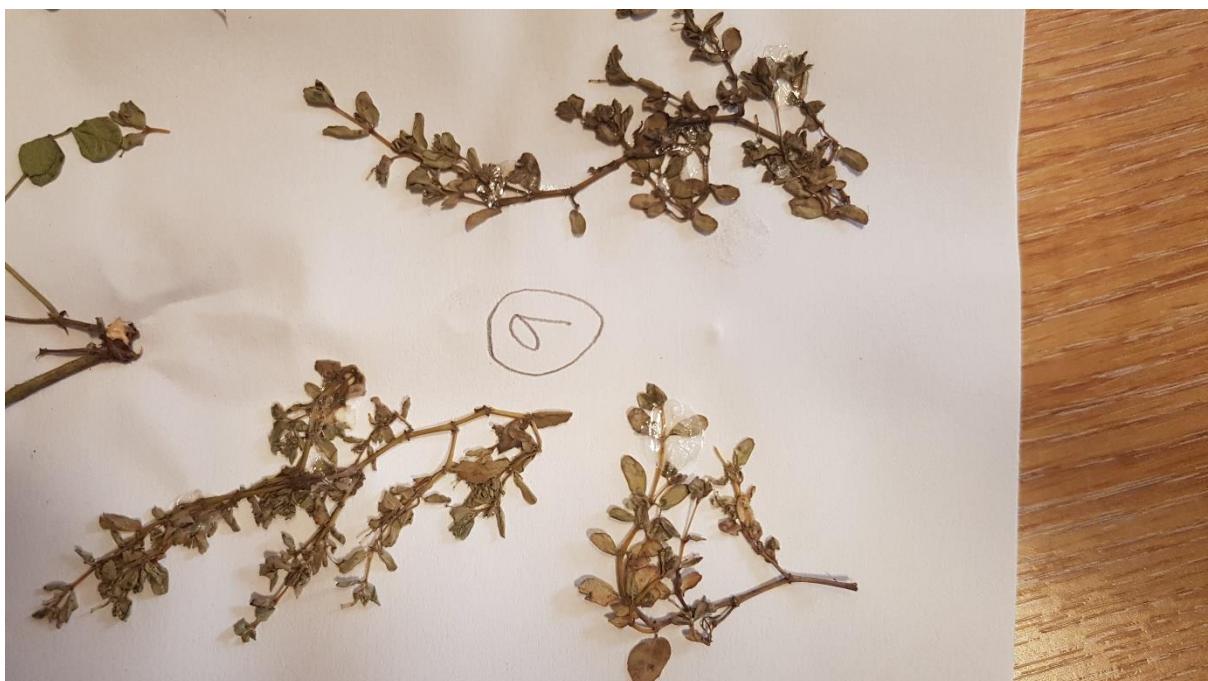
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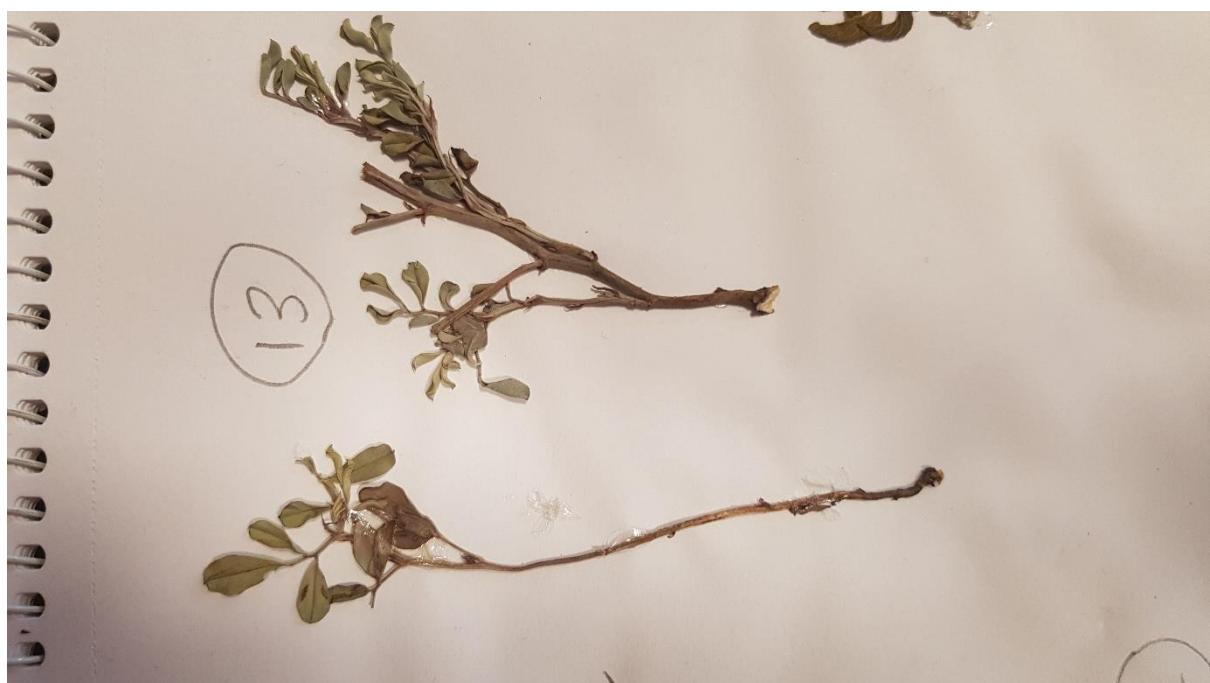
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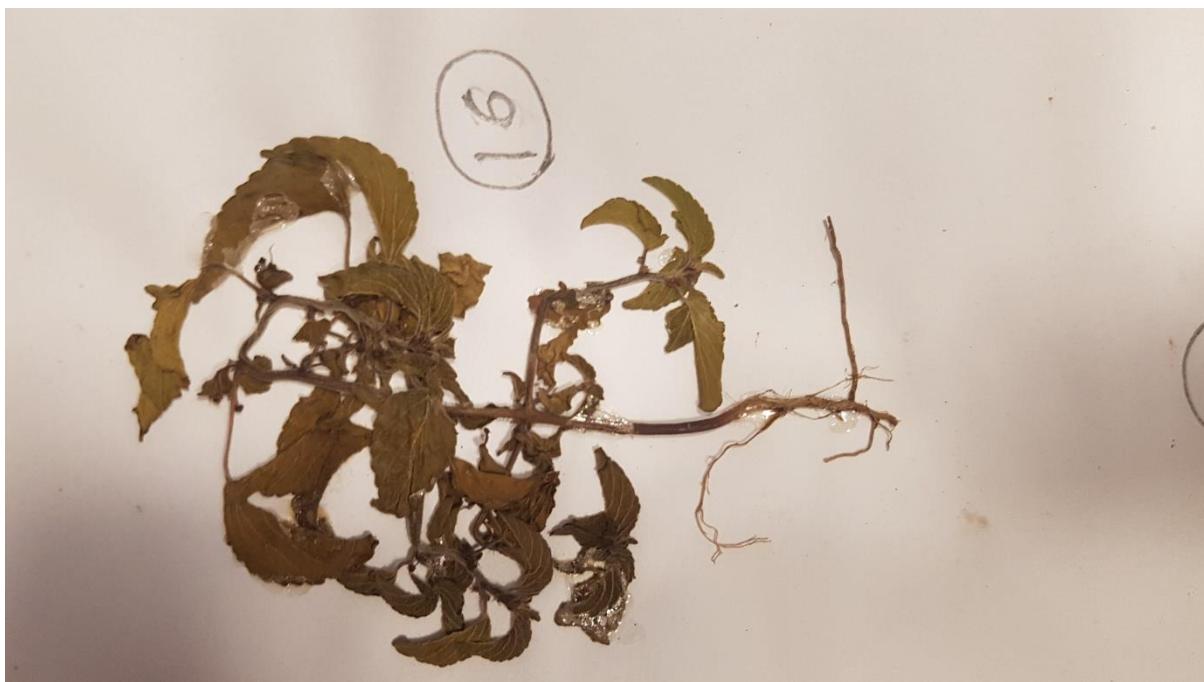
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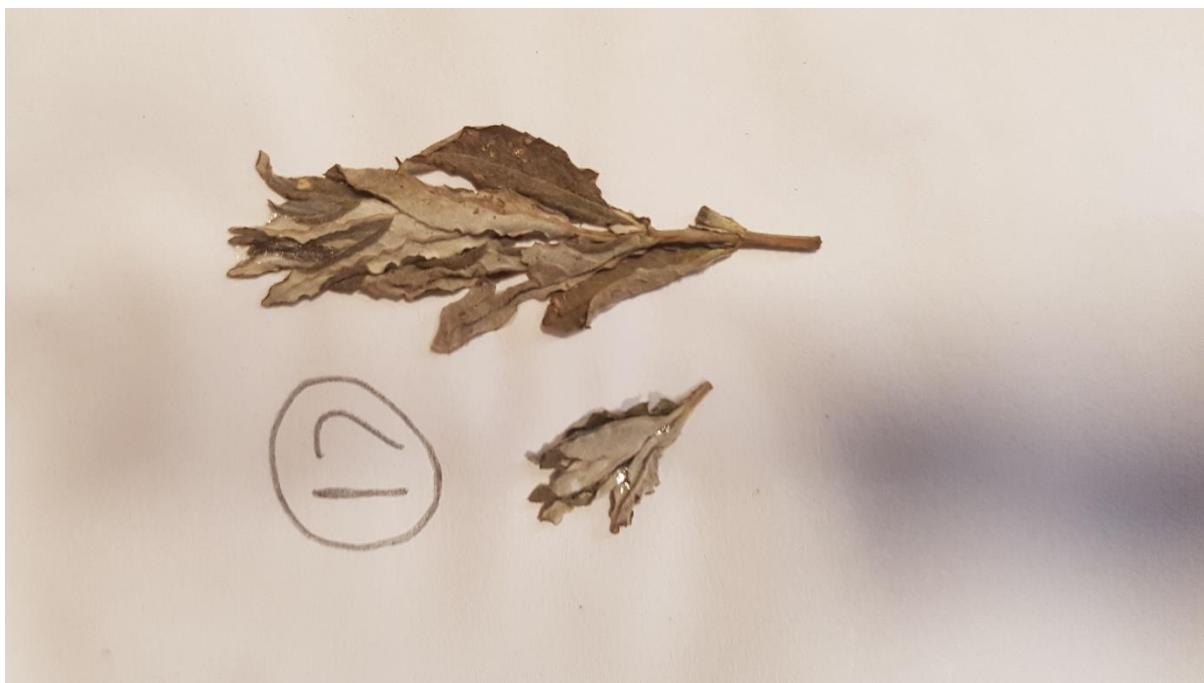
106



107 – *Lamiaceae* spp.



108



110 – *Ocimum* spp.



111 – *Gnaphalium* spp.



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