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**The influence of fire on savanna fauna: implications for
conservation management**

By Teegan Deborah Susan Docherty

Department of Biosciences

Durham University

March 2019

Submitted for the degree of Doctor of Philosophy

Declaration

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Teegan Docherty

March 2019

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Dedication

This thesis is dedicated to Dougal MacTavish who has been a constant source of inspiration throughout this work. Due to his vision, determination, resilience, and inestimable hard work, an incredible reserve and the wildlife it harbours are protected. Those who have had the opportunity to visit Mankwe Wildlife Reserve will—like me—be forever changed.

Abstract

Fire is an important natural disturbance that acts as a major driver of community dynamics and ecosystem function. While fire is increasingly used as a management tool to conserve and manage biodiversity in fire-prone systems, key gaps remain in our understanding of how biological communities respond to fire and the mechanisms driving community assembly. In this thesis, I evaluated the effects of long-term variation in fire regimes on large herbivorous mammals, birds and invertebrates in a South African savanna system. I tested the hypothesis that fire-mediated landscape heterogeneity (pyrodiversity) promotes biodiversity. First, I evaluated this hypothesis for large mammals by examining the relationship between their density and the diversity of fire age-classes on the landscape. Second, I tested this hypothesis for birds by assessing the effects of the diversity and configuration of fire age-classes on species richness and functional diversity at multiple spatial scales. Next, I evaluated how interactions between fire regimes and climate influenced invertebrate communities. Lastly, I assessed whether the indirect effects of fire on avian insectivores were mediated by vegetation structure or food availability. I surveyed for large mammals, birds and invertebrates across a landscape that represented approximately three decades of variation in fire age-classes and fire frequency. I did not find landscape-level pyrodiversity promoted the diversity or density of savanna fauna. Instead, I found that the extent of recently burned (<1-year post-fire) habitat and distance to water were the greatest predictors of large mammal density and that the extent of recently burned and unburned (≥ 10 -years post-fire) habitat were important predictors of avian species richness and functional diversity at two spatial scales (100 ha and 500 ha). I reveal that time-since-fire and fire frequency had opposing and interacting influences on grass-layer and ground-layer invertebrate communities, and these relationships were strongly mediated by seasonal rainfall. Lastly, relationships between fire and avian insectivores were mediated by vegetation structure and invertebrates, and these relationships were regulated by functional traits (i.e., niche breadth and body mass). In this thesis, I have demonstrated the long-term impact that fire regimes have on savanna communities. I suggest that fire management will be enhanced by a mechanistic understanding of fire-fauna relationships and consideration of trophic and climatic interactions. Current fire management practices have led to an insufficient extent of late-seral savanna and efforts should be taken to increase the amount of this habitat to increase faunal diversity, function and ecosystem resilience. Furthermore, management strategies to reduce burning during periods of low rainfall are likely to maximise the diversity and abundance of invertebrates and the species that rely on them.

List of Abbreviations

AIC	Akaike information criterion (pg. 29)
AICc	Akaike's information criterion corrected for small sample size (pg. 53)
CDS	Conventional distance sampling (pg. 28)
CWM	Community weighted mean (pg. 28)
DSM	Density surface modeling (pg. 26)
EDF	Estimated degrees of freedom (pg. 35)
FREQ	Fire frequency (pg. 31)
FRI	Fire return interval (pg. 69)
GAMM	Generalized additive mixed models (pg. 30)
GLMM	Generalised linear mixed model (pg. 69)
GrL	Grass length (pg. 68)
MWR	Mankwe Wildlife Reserve (pg. 27)
MCDS	Multiple covariate distance sampling (pg. 28)
PA	Protected area (pg. 4)
PQM	Point centred quarter method for measuring tree density (pg. 68)
PNP	Pilanesberg National Park (pg. 27)
REML	Restricted maximum likelihood (pg. 30)
SEM	Structural equation modeling (pg. 90)
SHAPE	Mean shape complexity of fire patches within a landscape (pg. 51)
ShD	Shrub density (pg. 68)
SHDI	Shannon habitat diversity index (pg. 31)
ShHt	Shrub height (pg. 87)
TrD	Tree density (pg. 68)
TSF	Time since fire (pg. 9)

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Chapter 1

General Introduction



1.1 BACKGROUND

Global climates, human and wildlife populations, habitats, and land-use are changing at unprecedented rates, presenting diverse challenges for conservation. With these changes come changes to disturbance regimes (Turner 2010). For example, climate change has significant effects on both abiotic (e.g., fire; Archibald et al. 2010; drought; Prugh et al. 2018) and biotic (e.g., insects, Kurz et al. 2008; herbivores, Perry et al. 2015) disturbance agents. Whether in the form of drought, tropical storms, wildfires, or disease outbreaks, evidence suggests that altered disturbance regimes have significant impacts on ecosystems (Wilson et al. 2006; Chergui et al. 2018) with mounting global evidence of species loss (Dirzo et al. 2014; Murphy & Romanuk 2014; Barlow et al. 2016).

Understanding the ecological effects of changes to disturbance regimes, such as changes in the frequency or intensity of disturbances, has been a long pursuit of ecological theory (Sousa 1979; White & Pickett 1985). Disturbance processes operate at a range of scales and are an important source of spatial and temporal heterogeneity (Sousa 1984). These dynamic processes affect ecosystems by disrupting the current state of habitat and altering community structure, resource availability and environment conditions (White & Pickett 1985). Many ecosystems have natural and anthropogenic disturbances acting simultaneously, which interact to produce enhanced ecological effects (Turner 2010). Wilson et al. (2006) documented significant declines in coral cover and fish diversity due to changes in concurrent natural and anthropogenic disturbance regimes such as terrestrial run-off, coral bleaching and disease outbreaks. Furthermore, rates of coral cover loss are faster at sites that have experienced a hurricane compared to sites that have not (Gardner et al. 2005). Evidence suggests that communities that are influenced by natural disturbances are more vulnerable to anthropogenic disturbances and environmental change (Short & Wyllie-Echeverria 1996; Wilson et al. 2006). Therefore, research that evaluates the sensitivity of species to disturbance and integrates the interactive effects of multiple disturbance processes is needed to better understand and predict the response of biological communities to changing disturbance regimes.

There is a critical need for effective conservation and management strategies in light of shifting disturbance regimes and predicted biodiversity loss. This requires improved understanding of how species and communities respond to changing disturbance regimes, particularly vulnerable species and communities. Research has shown that biological communities respond to the cumulative effects of repeated disturbances on habitat, revealing that long-term data on disturbance history is needed to

understand the current state of communities (Hobbs et al. 2007). Furthermore, studies must be conducted at a spatial scale that is commensurate with the scale of the disturbance in order to best inform management practices (Spasojevic et al. 2016a). While some species experience dramatic declines resulting from changes in disturbance regimes, others show little effect (Seiler et al. 2009). Many species, particularly plants, demonstrate remarkable coping mechanisms in disturbance-prone habitats (Spasojevic et al. 2016a). The ability to cope with disturbance has important implications for fire resistance and resilience and depends on both intrinsic (e.g., a species biology and genetics) and extrinsic (e.g., frequency or intensity of disturbance) factors (Dawson et al. 2011). Understanding determinants of ecological resistance and resilience to disturbance regimes can help inform conservation management (Nimmo et al. 2015).

Fire is an important disturbance process worldwide with major ecological and socio-economic consequences. Global estimates of burned area suggest that up to 380 Mha burn annually releasing approximately 2.1 Pg of carbon emissions (Chuvieco et al. 2016). Fire can have devastating impacts on human life, property and livelihoods, which increase as growing human populations encroach on wildlands (Attiwill & Adams 2013; San-Miguel-Ayanz et al. 2013). Projections suggest that the size and frequency of fires will continue to increase around the world with paralleled increases in the challenges and costs to managing fire (Westerling et al. 2006; Attiwill & Adams 2013; Barbero et al. 2015). The European Commission spends more than \$3 billion (USD) every year to suppress wildfires (Elia et al. 2016). Similarly, the costs of fire suppression for the United States government continue to rise with annual costs reaching \$2.9 billion in 2017 (NICF 2019). Yet, policies that promote the suppression of fire are often ineffective and unsustainable (North et al. 2015) and have led to the loss of natural fire regimes, native habitat and biodiversity (Bock & Bock 1992; Conway & Kirkpatrick 2007; Vogel et al. 2007; Corace et al. 2014). A comprehensive understanding of how ecosystems and biodiversity respond to fire is required for the development of ecologically sustainable fire management policies (Driscoll et al. 2010).

Changes in fire regimes resulting from changes in anthropogenic and climatic drivers are significant and have lasting effects on habitats and biological communities (Sankaran et al. 2005; Corace et al. 2014; Gosper et al. 2015). This project examines the response of wildlife to fire regimes in savanna ecosystems, which are the most fire-prone systems on earth (Chuvieco et al. 2016). Monitoring the effects of fire on biodiversity has been more comprehensive in some fire-prone

ecosystems and regions, particularly in Australia, than others. The research presented in this thesis takes place in southern Africa where prescribed fire is widely used as a management tool in savanna systems and is an important component of protected area (PA) management (Van Wilgen 2009). Yet, there has been very little ecological evaluation of fire management practices in this region. Empirical evidence is needed to inform and evaluate fire policies and to make predictions about how shifting fire regimes will affect future populations. In this thesis, I aim to garner a better understanding of the response of savanna fauna to fire regimes and to identify functional traits and ecological interactions that influence that response.

In this chapter, I review the impact fire has on wildlife, with a focus on savanna ecosystems. I provide a brief review of fire management, including the methods used in savanna systems and in South African PAs. The goal of this review is to examine and discuss the information available on the effects of fire on wildlife, with a focus on large herbivorous mammals, birds and invertebrates, and to identify important knowledge gaps. I discuss how an improved understanding of fauna-fire relationships and the mechanisms underlying them will improve fire management policy. Lastly, I summarise the principal conclusions of this review and their implications for conservation, and I outline the aims and objectives of this thesis.

1.2 FIRE

Fire has been a natural disturbance agent in ecosystems for hundreds of millions of years (Bond & Keeley 2005). While most terrestrial ecosystems can burn under suitable environmental conditions, some ecosystems are highly flammable (Pausas et al. 2017). The frequency and variability in the occurrence of fire depends on many environmental (Archibald et al. 2013; Lehmann et al. 2014) and anthropogenic (Chuvieco et al. 2008; Chergui et al. 2018) factors. Fires vary globally from slow-combusting, smoldering peatland fires, to fast-combusting grassland fires, to extreme, high-intensity eucalyptus forest fires (Ndalila et al. 2018; Huang & Rein 2019) and are an integral agent of change in fire-prone systems influencing ecosystem structure and function (Bond & Keeley 2005).

The ecological effects of fire on biota are diverse. Fire can greatly influence species diversity, density, and distribution worldwide (Sankaran 2005; Klop & van Goethem 2008). This includes a role in controlling pathogens, disease and insect outbreaks (Dickman & Cook 2007; Fyumagwa et al. 2007; Kurz et al. 2008). For example, in alpine forests, fire is known to control fungal pathogens (Dickman &

Cook 2007) and outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) (Kurz et al. 2008). Fire also plays a role in soil composition and nutrient budgets, with major impacts on the distribution and cycling of carbon and nitrogen (Bastias et al. 2006). During combustion, minerals from aboveground vegetation are transferred to the soil surface and ash-layer affecting decomposition processes, soil micro-organisms, plants, and invertebrates (MacLean et al. 1983; Broza & Izhaki 1997). While fire affects the current state of habitats and populations, it has also played a role throughout history as a driver of biological evolution, global biogeochemical cycles, and biome transformations (Bond et al. 2003; Pausas & Parr 2018). For example, fire contributed to the conditions in the late Tertiary era that favoured the expansion of fire-dependent C4 grasslands and savannas around the world (Bond et al. 2003; Keeley & Rundel 2005).

1.3 SAVANNAS

Savannas are the world's most flammable biome, comprising approximately 75% of the global annual burned area (Chuvieco et al. 2016). Globally, savannas make up approximately 20% of the land surface and contribute to an estimated 30% of terrestrial net primary production (Scholes & Archers 1997; Field et al. 1998). In Africa, approximately half of the land surface is savanna habitat, and much of this savanna has a high density and frequency of fires, coupled with a long annual burning season (Du Toit & Cumming 1999; Chuvieco et al. 2008). African savanna ecosystems are of high socio-economic value as they are the cradle sites of human history, the source of many important native crops (e.g., millet, sorghum and cotton), and the home to diverse cultures and large human populations (Olsson 2010; Olsson & Ouattara 2013; Parr et al. 2014). Moreover, savannas provide important productive land for agriculture and livestock (Parr et al. 2014). Along with the cultural and social importance of savannas, they are recognized for their high levels of biodiversity and ecosystem services (Bengtsson et al. 2019). For example, savannas sequester approximately 15% of the world's carbon and play an important role in water and nutrient cycling (Townsend & Douglas 2000; Grace et al. 2006; Parr et al. 2014). Yet, despite their extent and importance, these grassy ecosystems are poorly understood and poorly protected (Bond & Parr 2010).

Savannas are one of the most threatened biomes, having lost over 80% of their past global extent (Hoekstra et al. 2004; Ellis et al. 2010). Pervasive threats to savannas include habitat loss and degradation from human encroachment, unsustainable agricultural activities (e.g., overgrazing and

intensive cultivation), desertification, shrub encroachment and forest invasion, and inappropriate fire regimes (Maphisa et al. 2009; Bond & Parr 2010; Driver et al. 2012). The South African savanna, with its exceptional biodiversity, is recognized worldwide as an important priority for conservation (Reyers et al. 2001). South Africa is home to some very large, well-known PAs such as Kruger National Park. However, less than 7% of land in South Africa is formally protected (Driver et al. 2012). With no progress towards expanding the PA system, PAs in South Africa are characterised as having underfunded conservation policies and distressed management authorities (Secretariat of the Convention on Biological Diversity 2012). Nevertheless, an additional 30% of South Africa's land cover is classified as private PAs (Bingham et al. 2017). The recent boom in private PAs in South Africa has the potential to disproportionately contribute to the protection of biodiversity; however, very little is known about the conservation value of these land holdings (Cousins et al. 2008; Clements et al. 2019). Concerns about private PAs include insufficient conservation goals, mammal-centric management policies and harmful fire management practices (Cousins et al. 2008). Therefore, making sure that effective conservation strategies and management practices are developed is key to the conservation of savanna ecosystems.

1.4 FIRE REGIMES

The pattern and history of fire within an ecosystem is often described as a fire regime. As a multidimensional process, fire can be characterized by attributes such as frequency, intensity, size, season and age (Archibald et al. 2013). These attributes describe the spatial and temporal variation of repeated fires at a particular location (Archibald et al. 2013). Characterising fire regimes is important for 1) monitoring shifts in fire disturbance, 2) evaluating the response of biodiversity to fire regime changes, 3) estimating emissions (e.g., CO₂) from fire, 4) planning fire management, and 5) predicting the response of fire regimes to altered human and climatic drivers (Archibald et al. 2013; Moreno & Chuvieco 2013). However, how to best characterise a fire regime and at what temporal and spatial scale remains contentious, and can depend on the study at hand, the habitat, underlying geology and region (Smit et al. 2010; Hempson et al. 2017; Kelly & Brotons 2017). Fire regimes are constrained and influenced by environmental processes (e.g., climate and nutrient cycling), geology, habitat, and human activity (Archibald et al. 2013; Smit et al. 2013). For example, in Kruger National Park in South Africa, Smit et al. (2013) found that areas of the park with basaltic soils were more fire prone than areas with

granitic soils. Furthermore, in the Mediterranean, fire regimes are largely climate driven with an association between high temperatures, drought and fire (Pausas & Fernández-Muñoz 2012; Gouveia et al. 2016). In most regions of the world, natural fire regimes have been altered or lost due to anthropogenic factors such as fire suppression and management, land-use change, human encroachment, agricultural expansion and climate change (Van Wilgen 2009; Driscoll et al. 2010; Midgley & Bond 2015; Gouveia et al. 2016). In southern Africa, these factors have contributed to fire regimes characterised by larger, more frequent fires (Pricope & Binford 2012). Savanna systems are associated with multiple types of fire regimes, presumably depending on the climate and fuels present in a particular region (Archibald et al. 2013). In southern Africa, arid savannas comprise variable fire regimes that experience fire return intervals that range from approximately 2 to 5 years and fire seasons that range from 4 to 7 months (Archibald et al. 2013).

1.4.1 Managed fire regimes

Fire is a significant disturbance process because it is both naturally and human generated. In savannas, prior to human settlement, natural ignitions from lightning were the main cause of fires; however, now humans ignite most fires – either intentionally or unintentionally (Archibald 2016). Humans have an extensive history of intentionally burning the land (Bowman et al. 2011). In Australia for example, indigenous people have burned the land for thousands of years (Russell-Smith et al. 2003). While the objectives of indigenous fire practices are diverse and evolving, they include maintaining and restoring habitat conditions and have resulted in fire regimes characterised by highly-patchy fires (Russell-Smith et al. 2003).

In South African PAs, fire management has evolved from methods promoting a stable-state (i.e., fire suppression and containment) to methods promoting large-scale variability and flux (Van Wilgen 2009). Methods to suppress fire were widely used up until the 1970's and led to significant species loss and habitat transformation around the world (Carlson et al. 1993; Bagne & Purcell 2011; Smith et al. 2013). Yet, fire suppression is still practiced worldwide (Elia et al. 2016; NICF 2019), including in National Parks (Pricope & Binford 2012). In the 1970's in South Africa, there was a growing acceptance of the application of prescribed fire as a management tool (Van Wilgen 2009). In Kruger National Park and elsewhere a method called 'block burning' was practiced principally to intensively manage large mammal populations (Bond & Archibald 2003). Similar to methods of burning used for

livestock management, large blocks of land were burnt on a regular rotation to optimize the density of grass sward and woody vegetation for large grazers (Bond & Archibald 2003). These methods, which are still used on small game reserves and private land throughout Southern Africa, are considered to be 'homogeneous' fire management due to the rigid control placed on burn prescription such as season, weather conditions, size and frequency (Mulqueeny et al. 2010).

In the 1980's, 'heterogenous' fire management methods were developed in Kruger and Pilanesberg National Parks (Brockett et al. 2001; Van Wilgen 2009). These contemporary burning methods are called patch-mosaic burning and are rooted in the ecological theory that increased landscape heterogeneity will result in increased biodiversity (MacArthur & MacArthur 1961). By applying fires that vary in time and space for biodiversity conservation, these fire management practices are based on the assumption that 'pyrodiversity promotes biodiversity' (Martin & Sapsis 1991). Over time, a landscape mosaic emerges consisting of burned patches of varying spatiotemporal characteristics, such as post-fire age, shape, size and season of burn (Parr & Andersen 2006). Variations of these methods are now employed worldwide, including Australia (Andersen et al. 2005; Taylor et al. 2012; Sitters et al. 2014b), North America (Halofsky et al. 2011; Holcomb et al. 2014) and across southern Africa (Uys & Hamer 2007; Mulqueeny et al. 2010; Pricope & Binford 2012). However, the lack of sufficient data and research that supports the pyrodiversity promotes biodiversity relationship has been identified as a major shortcoming of these methods in South Africa and elsewhere (Parr & Brockett 1999; Van Wilgen et al. 2003, 2011; Parr & Andersen 2006; Driscoll et al. 2010; Kelly et al. 2017).

Fire management strategies in South Africa have evolved from a single taxon focus (i.e., large grazing mammals) to a holistic biodiversity focus. However, it appears that scientific evidence has had little effect on change in fire management policy in South Africa, other than providing theoretical ecological frameworks (e.g., heterogeneity promotes biodiversity) for evolving fire management (Bond & Archibald 2003). Furthermore, the ecological effects of these management shifts have not been documented. For example, there is no apparent ecological evidence to support the abandonment of block burning methods in Kruger National Park and other PAs in South Africa (Bond & Archibald 2003). And there is only one study (of three rare antelope species) evaluating the ecological effect of contemporary patch mosaic burning methods in South African PAs (Pacifi et al. 2015). Currently, patch mosaic burning in Kruger and Pilanesberg National Parks are guided by fire-related goals such as maximizing spatiotemporal variation, reducing fuel loads, limiting area burnt and mitigating

infrastructure damage (Brockett et al. 2001; Van Wilgen & Biggs 2011; Van Wilgen et al. 2014). Furthermore, the ecological outcomes of these fire management strategies are narrowly focused on maintaining an acceptable quality of grazing habitat and reducing woody vegetation cover (Van Wilgen et al. 2014), and do not include monitoring the effects of fire management on savanna biodiversity. Misapplication of prescribed fire and inappropriate fire regimes can result in species declines and significant risk of extinction (Vogel et al. 2007; Corace et al. 2014; Abreu et al. 2017). With increases in fire prescription globally, there is a great need for studies that evaluate the ecological effects of fire management, particularly in savanna systems (Mulqueeny et al. 2010; Pricope & Binford 2012; North et al. 2015; NICF 2019).

1.4.2 Spatiotemporal attributes of fire regimes

The individual spatial and temporal fire attributes (e.g. size, intensity, frequency, and seasonality) that comprise a fire regime may each have a significant independent or combined effect on biological communities (Archibald 2016). Time-since-fire (hereafter TSF) is a common temporal attribute investigated in fire-faunal studies, with some species exhibiting a specific successional response that may indicate resource requirements related to a unique seral stage (Fox 1982; Watson et al. 2012b; Sitters et al. 2014a; Eby et al. 2014). Whereas some species reveal short-term responses to fire, favouring recently burned, early-successional habitat (Krook et al. 2007; Hutto 2008; Eby et al. 2014), species in Australian shrubland small mammals (Kelly et al. 2011) and birds (Taylor et al. 2012) respond to very long post-fire chronosequences (105 and 35 years post-fire, respectively). Another important fire regime characteristic that features prominently in ecological theory is variation in disturbance frequency (Connell et al. 1978; Sousa 1979). Fire frequency, which is often measured by the fire return interval (time between fire events), has an enduring impact on savanna vegetation structure (Sankaran et al. 2008; Smit et al. 2010). Frequent burning reduces the nutrient content of soils with limiting effects on vegetation productivity and invertebrate communities (Bastias et al. 2006). Savanna sites that had repeated fires over 64 years had 36% and 38% less carbon and nitrogen respectively compared to unburnt sites (Pellegrini et al. 2018). While most savanna studies evaluate short-term faunal responses (e.g., 3 years post-fire; e.g., Dean 1987, O'Reilly et al. 2006, Eby et al. 2014) or short fire return intervals (e.g., biennial burns, e.g., Parr et al. 2004; Uys & Hamer 2007; Cianciaruso et al. 2010; Maravalhas &

Vasconcelos 2014), it is important that a full range of TSF or fire return intervals are integrated into studies to ensure the detection of long-term responses to fire regimes (Driscoll et al. 2010).

As discussed above, contemporary patch-mosaic burning methods attempt to maximize pyrodiversity on the landscape. Pyrodiversity is commonly characterised as variation in TSF or fire frequency (Parr et al. 2004; Davies et al. 2012) which capture the temporal heterogeneity of a fire regime. A major gap in our understanding of savanna fire regimes is how the spatial attributes of a fire regime influence savanna fauna. The effects of the spatial structure of a landscape on biodiversity are well studied in agricultural mosaic and fragmentation research with the shape, extent, size and configuration of habitat patches influencing biodiversity patterns (Debinski et al. 2001; Bennett et al. 2006; Haslem & Bennett 2008; Tscharntke et al. 2012; Fabian et al. 2013). However, despite the widespread use of prescribed fire regimes that maximize variability in spatial patterns (e.g., patch mosaics), very few studies have evaluated the influence of fire-mediated spatial variability on fauna (but see Sitters et al. 2014). Landscape structure can affect movement and dispersal which influence a species ability to persist on a burned landscape (Nimmo et al. 2018). For example, dispersal to and use of adjacent unburnt habitat patches has been documented as an important fire survival strategy (Gandar 1982; Yarnell et al. 2008; Murphy et al. 2010). Furthermore, species are influenced by the spatial distribution of resources, the structure of habitat and ecological processes at multiple spatial scales (Tscharntke et al. 2012). A recent study at the continent scale found that the richness of African mammals and birds was positively related to pyrodiversity. However, a continental scale study may overlook the value of small habitat patches which play a large role in the conservation of biodiversity, particularly of rare, specialist or range restricted species (Wintle et al. 2019). Furthermore, this broad scale cannot evaluate the effects of pyrodiversity at the scale of fire prescription. Methods evaluating spatial landscape structure and scale, if applied to a burn mosaic, may allow us to better identify patterns in the distribution of savanna fauna to guide the application of fire to accommodate the dispersal abilities and resource requirements of vulnerable savanna species.

Many environmental factors and processes can interact with fire regimes to create habitat heterogeneity at a variety of scales. These include abiotic factors, such as rainfall, topography, hydrology, and soils, and biotic processes, such as herbivores: e.g. elephants, termites, grazing ungulates, and invasive species (du Toit et al. 2003; Setterfield et al. 2010; Moranz et al. 2014; Pacifici et al. 2015). Fine-scale heterogeneity (<1 ha) resulting from interactions between prescribed fire,

vegetation structure, invasive species, and grazing is an important predictor of species distribution (Price et al. 2010; Sitters et al. 2015). In semiarid savanna, the relationship between fire and rainfall is very important. Vegetation structure responds to variability in fire frequency and rainfall in the short-term (grasses) and in the long-term (trees; Scanlon et al. 2005; Smit et al. 2010). Rainfall was found to be the main driver of pyrodiversity in African savannas, with the highest pyrodiversity in low rainfall regions ($< 650 \text{ mm yr}^{-1}$; Hempson et al. 2017). Global fire data show that the variation in fire frequency in savannas is related to interannual variation in rainfall (Chuvieco et al. 2008). Some savanna species' response to fire is mediated by rainfall (Blanche et al. 2001; Vasconcelos et al. 2009; Beale et al. 2018) and may be related to the interactive effects of fire and rainfall on grass and woody vegetation structure in savannas (Sankaran et al. 2005; D'Onofrio et al. 2018). An understanding of interactions of fire regimes with other environmental processes represents a major gap in fire-fauna research (Driscoll et al. 2010). Quantifying the cumulative and interactive effects of multiple environmental drivers is critical for developing robust and adaptive conservation strategies that can manage all potential interaction outcomes (Côté et al. 2016).

1.4.3 Impacts of fire regimes on large herbivorous mammals

South African PAs are home to much of the world's extant megafauna making them important areas for conservation. While fire management is an important component of PA conservation plans, so too is tourism, which generates important revenue for PA management and conservation (Pacifci et al. 2015). Tourists are most interested in seeing large mammals (Lindsey et al. 2007) and the density and diversity of large mammals are directly related to tourist revenue in Southern Africa (Arbieu et al. 2018). Therefore, understanding how fire policy affects the diversity, density and distribution of large mammals is a key component of savanna conservation and PA management. Despite a relatively large body of literature on the response of large herbivorous mammals (*hereafter* large mammals) to fire, our understanding of this response is hindered by short-term studies, small spatial scales and lack of replication. (see systematic review of the literature in Table A1.1). For example, over 80% of studies conducted in savanna habitat have investigated the effects of fire within 2 years of burning (see Table A1.1), limiting our understanding the long-term effects of fire regimes on large mammals. Furthermore, most of these studies have compared large mammal communities between one or more burned areas

to unburned areas in a control-impact design, demonstrating our limited understanding of how large mammals respond to variation in fire regimes at larger-landscape scales.

Coined the “magnet effect” by Archibald et al. (2005), many studies around the world have demonstrated mammalian herbivore attraction to recently burned grassland habitats (Oliver et al. 1978; Vinton et al. 1993; Sankaran 2005; Klop et al. 2007; Eby et al. 2014) due to the high nutrition content of post-fire grass regrowth (Hobbs et al. 1991; Allred et al. 2011; Eby et al. 2014). In addition to common grazers like zebra and wildebeest, studies have demonstrated that rare antelope including oribi (Rowe-Rowe 1982; Everett et al. 1991), sable (Parrini & Owen-Smith 2009), bontebok (Beukes 1987), and mountain reedbuck (Rowe-Rowe 1982), preferentially select recently burned savanna. Many mammals have specific habitat requirements, such as oribi that prefer a biennial spring burn (Everett et al. 1991) and common eland who only forage on burnt habitats in the wet season (Rowe-Rowe 1982). Evidence suggests that selection of post-fire habitat occurs on short temporal scales, with densities of mammals on burn patches often declining within one year post-fire (Rowe-Rowe 1982; Gureja & Owen-Smith 2002; Tomor & Owen-Smith 2002; Eby et al. 2014; Cherry et al. 2018); however, this finding is confounded by the lack of studies evaluating habitat selection in relation to long-term fire regimes.

African savannas are naturally heterogeneous environments, with variation in rainfall (Hempson et al. 2015b), water bodies (Owen-Smith 2004), tree cover (Klop et al. 2007), and soils (Pacifci et al. 2015) influencing the distribution of large mammals. Understanding the landscape characteristics most relevant for habitat selection can help resolve the relative influence fire has on the density and distribution of wildlife using a savanna mosaic. Studies of the response of mammals to fire-mediated heterogeneity (pyrodiversity) are limited mainly to small and medium sized mammals in Australia (Griffiths et al. 2015; Radford et al. 2015; Davies et al. 2018). Little support was garnered for pyrodiversity-biodiversity hypothesis in medium sized mammals in Australian savanna (Radford et al. 2015; Davies et al. 2018). Only one study has evaluated the pyrodiversity biodiversity assumption with large mammals in African savanna (Beale et al. 2018). At a broad, continental scale Beale et al. (2018) demonstrated that large mammal richness increased with pyrodiversity and that this relationship was enhanced in wet savannas (>650 mm rainfall yr⁻¹). At a smaller landscape scale, Pacifci et al. (2015) evaluated the effect of fire management in a region of Kruger National Park on the density and distribution of three rare antelopes. They determined that large mammal response to variation in fire regime attributes (e.g., frequency and intensity) was species-specific (Pacifci et al. 2015). Landscape-

scale studies (e.g., reserve or region) can provide an enhanced understanding of the distribution of animal patterns in relation to landscape-level spatiotemporal patterns and ecosystem functions (Parr & Chown 2003). Furthermore, such studies provide ecological evidence at spatial scales that correspond to the scale of fire prescription, making them highly useful for land managers.

Spatial scale is important to consider among large herbivores because differences in body size and vagility may cause species to respond differently to the heterogeneity of resources on the landscape (Cromsigt et al. 2009). Species-specific characteristics (e.g., body size, foraging strategy, metabolic needs) underlie patterns of resource selection on a burned mosaic (Sensenig et al. 2010) that vary with forage quality (Lemon 1968), competition (Rowe-Rowe 1982; Pacifici et al. 2015), and predation risk (Eby & Ritchie 2012). For example, large-bodied mammals may be more evenly distributed across a heterogeneous savanna landscape due to a wider dietary tolerance and lower predation risk (Cromsigt & Olff 2006). Whereas, small herbivores select the high quality forage in open burned areas with heightened visibility (Sensenig et al. 2010).

When studying the response of wildlife to fire it is important to consider how variation in detection probability may affect data quality (Pastro et al. 2014). Fire simplifies habitat, removing the grass-layer and vegetation cover, potentially increasing the probability of detecting individuals in burned habitat. The probability of detecting an animal can vary with species, age, sex and habitat (Buckland et al. 2009). This is particularly relevant for large mammals due to key characteristics that can affect detection such as crypsis, habitat preference (e.g., open grassland vs woodland), herd size and body size. While fire has been shown to affect the detection of forest birds (Buckland et al. 2009), it has not been evaluated in mammals. However, studies have shown that detection varies with habitat structure for large mammals, supporting the hypothesis that fire affects detection probability (Bukombe et al. 2015). Thus, studies that evaluate the effects of fire management on abundance need to incorporate detection probabilities to obtain robust data that is comparable across variable fire regimes.

1.4.4 Impacts of fire regimes on birds

Disturbance processes, including fire, influence avian communities via changes in habitat structure and vegetation resources, altering food and foraging substrates, nest sites, predation, shelter and competition (Brawn et al. 2001). Studies show that bird communities and species respond to the size (Lindenmayer et al. 2014), age (Watson et al. 2012b), frequency (Lindenmayer et al. 2008; Reside et

al. 2012) and severity (Tingley et al. 2016) of fires. Post-fire succession in forests affects species occupancy rates suggesting that birds associate with vegetation resources of a particular seral state (Watson et al. 2012b; Tingley et al. 2016). The majority of studies investigating the effects of fire regimes on birds have been conducted in shrublands and forests (Smucker et al. 2005; Taylor et al. 2012; Sitters et al. 2014b; Hutto & Patterson 2016; Tingley et al. 2016; Prowse et al. 2017). Comparatively, very few studies have been conducted in savanna systems, even though the effects of fire on birds are thought to be greatest in habitats with simple physiognomies, such as vegetation characterised by a single low stratum (e.g., grasslands), due to the moderating effects of habitat structure (Barton et al. 2014). Post-fire recovery of avian diversity and community composition is slowest in habitats with the simplest habitat structure (Lindenmayer et al. 2008), emphasizing the need for studies that evaluate the response of birds to fire in savanna.

The pyrodiversity-biodiversity relationship has received some support from research on avian communities in forest habitats, where variation in fire age (Sitters et al. 2014b) and severity (Tingley et al. 2016) have a positive effect on species richness. However, in contrast, little to no support for the relationship has been found in Australian shrubland (Taylor et al. 2012, 2013a; Kelly et al. 2014) and woodland (Burgess & Maron 2016; Prowse et al. 2017). Instead, these studies found that the extent of long unburnt habitat (e.g. >10 years since fire) had the greatest effect on avian diversity, supporting the idea that birds associate with a particular seral state on the landscape. Furthermore, avian studies of the pyrodiversity-biodiversity relationship reveal that this relationship varies with habitat type (Sitters et al. 2014b), climate (Sitters et al. 2014b; Beale et al. 2018), and topography (Lindenmayer et al. 2014), as well as interactions with biotic processes like herbivory (Fuhlendorf & Harrell 2006), limiting the applicability of generalizations from these studies to other systems. It is also important to note that the pyrodiversity-biodiversity relationship varies with spatial scale (Burgess & Maron 2016). As highly mobile organisms, birds respond to spatial variation in resources at multiple spatial scales (Kremen et al. 2007). In Australian woodland, small scale (<1ha) fire-mediated heterogeneity was a significant predictor of avian richness (Sitters et al. 2015; Burgess & Maron 2016). However, in Australian shrubland and woodland, landscape-scale pyrodiversity had little effect on avian richness (Taylor et al. 2012, 2013a; Kelly et al. 2014; Burgess & Maron 2016; Prowse et al. 2017).

Species-specific responses may also have contributed to the inconsistencies in results among pyrodiversity studies. Functional traits such as dispersal ability (Watson et al. 2012a), body size (Prowse

et al. 2017), and feeding guild (Burgess & Maron 2016) may underpin a species response to pyrodiversity. In addition, a pyrodiversity response can vary with age (Stillman et al. 2019), site fidelity (Lindenmayer et al. 2014), trophic interactions (Ponisio et al. 2016), and range size (Beale et al. 2018). For example, young forest birds are negatively associated with pyrodiversity because they are more likely to select habitat with increased cover and lower predation risk (Stillman et al. 2019). Range-restricted species are thought to increase with pyrodiversity due to the increase in rare niches (Beale et al. 2018). Understanding the mechanisms that govern a species fire response (e.g., functional traits or trophic interactions) are vital to understanding the dynamics of community assembly, species loss and ecosystem functioning in fire-prone systems (Hooper et al. 2005). Functional traits and functional diversity have yet to be considered for evaluating the effects of fire management on savanna fauna in southern Africa. However, a functional understanding of fire response is critical to understanding fire resilience (Spasojevic et al. 2016a). Studies in plants have shown that particular functional traits (e.g., regeneration traits; Lucrecia Lipoma et al. 2016) or high levels of functional diversity (Spasojevic et al. 2016a) result in fire resilience and distinct fire-tolerant communities.

With the exception of a few studies, most research investigating the effects of fire on savanna birds has been conducted in tropical savannas in Northern Australia (Valentine et al. 2007, 2012; Legge et al. 2008; Reside et al. 2012) and Brazil (Cavalcanti & Alves 1997; Cintra & Sanaiotti 2005) and oak-savanna in the United States (Davis & Peterson 2000; Grundel & Pavlovic 2007). However, variation in site characteristics, habitat relationships and disturbance response often limit the application of ecological evidence among regions (Pastro et al. 2014; Kelly & Brotons 2017). Research on the effects of fire on birds in African savanna consist of observations at a single fire (Dean 1987; Mills 2004) and studies conducted at very small spatial scales (O'Reilly et al. 2006; Krook et al. 2007; Gregory et al. 2010). Consistent with studies from Mediterranean shrubland and coniferous forests (Hutto 1995a; Herrando et al. 2002), studies in savanna identify changes in avian community composition post-fire (O'Reilly et al. 2006; Krook et al. 2007; Bouwman & Hoffman 2007). African savanna studies reported increases in avian diversity (O'Reilly et al. 2006; Bouwman & Hoffman 2007) and abundance post-fire (Gregory et al. 2010), which may result from temporary influx of short-grass specialist species (Krook et al. 2007), large-bodied ground foragers (Manry 1982) and generalist species (Prowse et al. 2017). While the short time scales evaluated in savanna bird studies (<4 years since fire; O'Reilly et al. 2006; Krook et al. 2007; Valentine et al. 2007, 2012) may be adequate for assessing some components of

fire-fauna dynamics, these time frames limit our ability to understand the effects of fire regimes on habitat succession and community assembly processes and prevent the meaningful evaluation of fire management policies which are applied at longer temporal scales.

Globally, avian feeding guilds respond to shifts in disturbance regimes due to altered trophic interactions with prey and vegetation resources (Edwards et al. 2013a; Hamer et al. 2014; Vollstädt et al. 2017). However, there is a limited body of research that evaluates functional group response to fire in savanna birds, with the majority of studies based on observations of birds using an area before and after a single fire event (Dean 1987; Mills 2004; Bouwman & Hoffman 2007). Preference for early-successional post fire habitats by insectivores in savannas (Dean 1987), grasslands (Bouwman & Hoffman 2007) and forests (Hutto 1995; Smucker et al. 2005) is likely the result of short-term opportunists using ephemeral resources. For example, woodpecker species are known to increase in abundance following fire due to increases in nesting (i.e., cavities) and foraging resources resulting from standing dead wood (Koivula & Schmiegelow 2007; Hutto 2008). Birds, such as the fork-tailed drongo (*Dicrurus adsimilis*) in South Africa, may be nomadic during the fire season, tracking foraging opportunities on recently burned habitats across a large region (Dean 1987; Bouwman & Hoffman 2007). Large-bodied terrestrial insectivores such as lapwings, coursers, and thick-knees are another group that favour burned grassland in South Africa (Engelbrecht 2001; Little et al. 2013), supporting the idea that open habitat with short grass is preferred by birds that are visual predators due to increased prey detectability and foraging efficiency (Devereux et al. 2006; Chouteau 2007). Many post-fire insectivores are short-grass specialists that will remain on a burnt patch until substantial grass re-growth occurs (Krook et al. 2007). Correlative evidence has suggested that invertebrate food availability could be a key factor determining avian habitat selection on a burned landscape (Haugaasen et al. 2003; Herrando et al. 2005). However, further research is needed to assess the impact of fire on food resources and trophic interactions as a possible mechanism underlying avian response to fire.

1.4.5 Impacts of fire regimes on invertebrates

Understanding how invertebrates respond to variation in fire regimes is important because they comprise the bulk of global biodiversity (approximately 70% in biomass and species), they are essential food resources for insectivorous and carnivorous vertebrates and they provide valuable ecosystem services, such as pollination, seed dispersal, decomposition and nutrient cycling (Losey & Vaughn

2006; Hamer 2010). Nonetheless, in Africa, ecological studies of invertebrates are scarce (Hamer 2010) as is their inclusion in protected area biodiversity monitoring and conservation plans (McGeoch et al. 2011).

Invertebrates are sensitive to environmental disturbance owing to their small size, limited dispersal abilities, specialized microhabitat requirements, host-interactions, and vulnerable life history stages (Evans 1984; Vasconcelos et al. 2009; Podgaiski et al. 2013). However, varied and often conflicting effects of fire on community structure have been reported for invertebrates. For example, fire has led to increases in the abundance of ants (Andersen 1991; York 1999; Sackmann & Farji Brener 2006) and beetles (Muona & Rutanen 1994) and the diversity of spiders (Moretti et al. 2004). Elsewhere fire has led to decreases in the abundance of grasshoppers (Bock & Bock 1991) and caterpillars (Little et al. 2013) and the diversity of butterflies (Akite 2008). Direct effects of fire on invertebrates include mortality and forced emigration (Andersen & Müller 2000), while indirect effects of fire are mainly attributed to responses to altered habitat structure such as leaf litter depth (Vasconcelos et al. 2009), grass height (Radford & Andersen 2012); and floral composition (Ponisio et al. 2016). Nevertheless, the mechanisms driving these indirect responses are poorly understood and may include altered predation rates (Belovsky et al. 1990), microclimate (e.g., temperature or humidity; Niwa and Peck 2009), shelter (Brennan et al. 2011; Podgaiski et al. 2013), and foraging resources and substrates (Ponisio et al. 2016). Only two invertebrate studies have investigated the pyrodiversity-biodiversity relationship in savanna, revealing that variability in fire season and frequency had a positive effect on ants in Neotropical savanna (Maravalhas & Vasconcelos 2014) and little to no effect on termites in South African savanna (Davies et al. 2012).

Rapid recovery of invertebrate communities post fire (e.g., 6 months) has been documented in ecosystems worldwide (Izhaki et al. 2003; Parr et al. 2004; Radford & Andersen 2012; Calcaterra et al. 2014). In addition, some invertebrates have revealed little or no response to fire (Davies et al. 2012; Andersen et al. 2014). Such resilience is characteristic of ants in a range of fire-prone habitats (Izhaki et al. 2003; Barrow et al. 2007; Parr & Andersen 2008; Pryke & Samways 2012a; Andersen et al. 2014). In African savannas, resilience has been reported for both ants and termites (Parr et al. 2004; Barrow et al. 2007; Parr & Andersen 2008; Davies et al. 2012). Resilience in wingless, ground-active invertebrates likely results from the ability to survive fire events by taking refuge below ground (Davies et al. 2012; Pryke & Samways 2012b). Furthermore, resilience may stem from the persistence of

resources needed by ground-active invertebrates across post-fire successional stages despite changes in above-ground vegetation (Teasdale et al. 2013). Ant response to fire may not be generally representative of invertebrate taxa, particularly of more fire-sensitive invertebrate groups. Thus, the dominant focus on ants in fire research may have led to the overestimation of invertebrate fire resilience (Andersen 1991; Parr et al. 2004; Barrow et al. 2007; Parr & Andersen 2008; Calcaterra et al. 2014) and data for a wider range of invertebrate taxa are needed.

In the longer-term, fire may influence invertebrate resources through successional processes, nutrient cycling and trophic interactions (Bastias et al. 2006; Ponisio et al. 2016). Nevertheless, research on the response of invertebrates to long-term fire regimes is limited. However, studies of the response of communities to time-since-fire in Australian shrubland revealed that Coleoptera (beetles), Diptera (flies) and Lepidoptera (butterflies and moths) were most abundant >40 years post-fire (Friend & Williams 1996; Teasdale et al. 2013). Here, the abundance of some invertebrate taxa (e.g., spiders) were found to track post-fire succession, while the peak abundance of others (e.g., grasshoppers and butterflies) coincided with a particular seral state (Teasdale et al. 2013). These taxa may be at risk of local extinction if local fire management is not applied at appropriate temporal scales and does not maintain long unburned areas (Driscoll et al. 2012; Teasdale et al. 2013). While shrublands demonstrate congruence between invertebrate populations and post-fire succession, studies in savanna have revealed that this response is contingent on rainfall, with a post-fire response only detectable with increasing rainfall (Blanche et al. 2001; Davies et al. 2012). Rainfall and fire have interactive effects on vegetation productivity, structure and phenology; however, rainfall also affects invertebrate survival, host-interactions, reproduction, and life-history stages (Butterfield & Coulson 1997). For example, increases in humidity that mark the beginning of the rainy season cue the termination of diapause in some beetle species (Tanaka et al. 1987). Therefore, savanna invertebrate research should investigate the interactive effects of fire and rainfall.

1.5 IMPLICATIONS FOR FIRE MANAGEMENT AND CONSERVATION

Disturbance regimes are vital processes in most ecosystems. In savannas, understanding the effect fire regimes have on wildlife is important for conservation. There is a need for conservation plans and fire management strategies that are supported by ecological evidence and tailored for local systems (Kelly & Brotons 2017). Nonetheless, currently, evidence of faunal relationships with fire comes

primarily from Australian ecosystems. To develop effective PAs, practitioners require ecological evidence on the response of biodiversity to key environmental stressors, such as fire regimes, climate and land-use change, and how these responses vary under shifting conditions (Ferraro & Pressey 2015). Such evidence will help practitioners develop holistic fire management strategies that integrate information regarding biodiversity (e.g., species, traits, and functions), habitat, ecosystem services and trophic interactions rather than just a narrow focus on reducing fuel loads, area burnt, and fire hazards (Bowman & Legge 2016). In addition, evaluating the ecological outcomes and causal effects of management decisions and interventions over the long-term is an important component of any conservation plan (Baylis et al. 2016). For South African PAs, an important first step for fire management evaluation will include evaluating the assumption that pyrodiversity promotes biodiversity.

This review reveals many shortcomings and gaps in our understanding of the response of savanna fauna to fire regimes and contemporary fire management practices. I summarise these shortcomings into four key knowledge gap areas: 1) evidence that pyrodiversity promotes biodiversity in savanna systems, 2) the relationships between savanna fauna and long-term fire regimes, 3) how other environmental processes (e.g., rainfall) alter these relationships, and 4) a mechanistic understanding of these relationships. Generalizations about the effects of fire on fauna are difficult to make because fire response is determined by many factors such as study species or group, spatial scale, geographic region, habitat type, and climate (Blanche et al. 2001; Moretti et al. 2004; Vasconcelos et al. 2009; Nimmo et al. 2014; Pastro et al. 2014). While many large African mammals select recently burned habitat in the short-term (up to 1 year post-fire; e.g., Eby et al. 2014), an understanding of how they respond to landscape-scale variation resulting from a long-term fire regime is lacking. Birds demonstrate varied responses to pyrodiversity in Australia; however, apart from on a continental scale (i.e., Beale et al. 2018), this response has yet to be studied in savanna systems. Landscape-scale studies are important for capturing the full range of variation in fire regimes, environmental stressors, habitat structure and species distributions. Furthermore, studies conducted at the same scale as fire prescription (e.g., landscape-scale) allow for meaningful evaluation of fire management policy (Pacifi et al. 2015). Evidence suggests that bird functional groups, particularly avian insectivores in savanna habitat, respond to temporal variation in fire regimes (Valentine et al. 2012). Investigating functional traits can lead to the identification of species that demonstrate resilience or sensitivity to fire, as well as the mechanisms underlying these fire responses (Spasojevic et al. 2014).

However, as outlined above our knowledge of faunal resilience to fire in savannas is constrained by a narrow focus on ants. Exploring fire resilience, and the mechanisms governing it (e.g., functional diversity), in other taxa in response to long-term fire regimes will be important for the conservation of savanna biodiversity (Nimmo et al. 2015). Such an understanding can identify management actions to promote the persistence of species and functions in the face of changing disturbance regimes (Nimmo et al. 2015).

Carefully designed studies are needed to address these key knowledge gaps and inform fire management. For this project, I am addressing this need by developing ecological evidence to support fire management in southern African savanna systems and PAs. I use this thesis to address the knowledge gaps outlined above, evaluate current fire management, and provide recommendations to support future decision-making. Below I outline the aims and objectives of this thesis.

1.6 AIMS AND OBJECTIVES

1. To test the pyrodiversity promotes biodiversity (PPB) hypothesis

Here, I assess the response of large mammals (Chapter 2) and birds (Chapter 3) to pyrodiversity at Mankwe Wildlife Reserve and Pilanesberg National Park, the latter being the site where patch-mosaic burning was first developed and has yet to be evaluated (Brockett et al. 2001). As discussed in section 1.4.3, density is important for the management of large mammals for conservation and tourism, thus this thesis represents one of the first attempts to evaluate the relationship between pyrodiversity and large mammal density (Chapter 2). I then expand on this relationship and evaluate how pyrodiversity affects functional diversity using birds at multiple spatial scales (Chapter 3).

2. To assess how community structure responds to interactions between fire and climate

I aim to develop a better understanding of the effects of interactions between fire and other environmental processes on fauna. As discussed in section 1.4.2 and 1.4.5, fire regimes and climate can interact to influence savanna vegetation and faunal community structure. Firstly, I evaluate the interactive effects of fire and rainfall on two communities of invertebrates (Chapter 4). Secondly, I evaluate the relative and interactive effects that fire, rainfall, and season have on trophic interactions among vegetation structure, invertebrates and avian insectivores

(Chapter 5). Such an understanding is important for making predictions about the effects of changing disturbance regimes and for informing conservation policy.

3. To understand the mechanisms underlying community response to variation in fire regimes

Knowledge of the mechanisms underlying how animals respond to fire is important for making predictions of responses to shifts in fire regimes and for developing sustainable conservation plans. A functional trait approach can reveal important mechanisms underlying shifts in community structure in response to changing fire regimes. First, I evaluate the effects of pyrodiversity on trait-based indices of functional diversity in birds (Chapter 3). Next, I evaluate how functional traits (i.e., niche width and body mass) influence the response of avian insectivores to fire and climate. Lastly, communities can respond indirectly to fire regimes via changes in habitat structure or food resources, I evaluate support for these causal mechanisms by examine trophic relationships between vegetation structure, invertebrates and avian insectivores (Chapter 5).

Chapter 2

The impact of fire regimes on the spatial distribution and densities of large herbivores



White rhinoceros (*Ceratotherium simum*)

2.1 ABSTRACT

Fire is an important agent of disturbance in savanna systems, influencing habitat structure and species distribution. Prescribed burning is an important conservation tool in fire prone habitats and is widely used to manage populations of large herbivorous mammals. However, the effects of long-term fire histories and their component fire characteristics (i.e., time-since-fire, frequency and heterogeneity) on large herbivore densities are poorly understood. Here, I used a three-step approach to estimating densities of large mammalian herbivores in two protected areas in South Africa. First, variability in large mammal detection was modeled in relation to the fire regime and ecological variables. Second, large mammal densities were modeled across a gradient of post-fire ages. Third, density surface models were used to investigate the effects of fire attributes and ecological variables on the density and distribution of large herbivores at the landscape-scale. The results of this study demonstrate that detection of large mammals is affected by prescribed burning. In general, the density of large grazers decreased as time-since-fire increased, whereas browser species were unaffected. Furthermore, individual species and the large mammal community respond to different fire and landscape variables; however, the proportion of recently burned habitat (<1-year-old) and distance to water were stronger predictors of animal densities than diversity of fire-age classes and fire frequency. These findings demonstrate that there is a lasting effect of burning on resource selection by large mammals and reveals that resource selection is influenced by multiple landscape features such as burn extent, proximity to water, and habitat type. This study describes an approach that supports the development of fire management strategies to conserve large mammal species and communities in savannas and other fire-prone landscapes.

2.2 INTRODUCTION

Fire is an important agent of disturbance in ecosystems worldwide including coniferous forests (Tingley et al. 2016), chaparral and coastal shrubland (Malanson & Westman 1985; Herrando et al. 2002), grasslands (Allred et al. 2011), and savannas (Higgins et al. 2007). Fire alters vegetation structure at multiple spatial and temporal scales, acting as a major source of habitat heterogeneity (Levick et al. 2012). In savanna systems, fire can reduce the herbaceous layer in the short-term, while over the long-term repeated fires can reduce shrub encroachment and tree cover (Higgins et al. 2007). Post-fire changes in vegetation and resource availability can influence the densities and distribution of biota (Archibald & Bond 2004). Many studies have demonstrated the attraction of herbivorous mammals to recently burned grassland (Oliver et al. 1978; Vinton et al. 1993; Sensenig et al. 2010), due to post-fire grass regrowth that is high in protein (Lemon 1968; Parrini & Owen-Smith 2009), nitrogen (Knapp 1985; Eby *et al.* 2014), and other nutrients (Eby *et al.* 2014). The spatial distribution of herbivores based on the distribution of forage resources can vary with differences in body mass and diet (Wilsey 1996; Hempson et al. 2015a). Due to the role fire plays in wildlife distribution and habitat use, prescribed burning is an important conservation tool in fire prone habitats (Andersen et al. 2012; Kelly et al. 2017) and is widely used to manage populations of large herbivorous mammals (Pacifci et al. 2015; Bielski et al. 2018).

In savanna systems, land managers have used prescribed burning to meet multiple objectives including reducing shrub encroachment, preventing large wildfires (Van Wilgen 2009), conserving large mammals by improving the nutritive quality of forage (Parrini & Owen-Smith 2009), and facilitating animal visibility to enhance the experience of visiting tourists (Klop & van Goethem 2008). More recently, to promote and conserve biodiversity, managers of National Parks (Brockett et al. 2001; Pacifci et al. 2015) and game reserves (Mulqueeny, Goodman, & O'Connor, 2010) across South Africa have begun to prescribe fires that are varied spatially and temporally across the landscape (Brockett et al. 2001; Parr & Andersen 2006). This fire-mediated heterogeneity has been termed *pyrodiversity* (Martin & Sapsis, 1991) and results in a landscape mosaic of burn patches. Nevertheless, while these burning methods are based on the established ecological relationship that habitat heterogeneity promotes niche and species diversity (MacArthur & MacArthur 1961; Tilman 1982), the generality of this relationship has been questioned (Parr & Andersen 2006). In particular, the response to pyrodiversity may be species-specific (Taylor et al. 2013a), or contingent on either habitat type (e.g.

coniferous forests; Ponisio et al., 2016; Tingley et al., 2016) or climate (e.g. rainfall; Beale et al., 2018). Furthermore, work in highly fire-prone savannas has demonstrated faunal resilience to changes in pyrodiversity (Davies et al. 2012; Andersen et al. 2014). Given that the density and diversity of large herbivores in African savanna has been attributed to the inherent heterogeneity of the savanna landscape (Vrba 1992; Du Toit & Cumming 1999), investigating the effects of fire-driven heterogeneity on large herbivorous mammals is fundamentally important. Moreover, while previous studies have investigated the effects of landscape-scale heterogeneity in vegetation (Cromsigt et al. 2009), rainfall (Fryxell et al. 2005), and soils (Grant & Scholes 2006) on large herbivore density and distribution, the effects of fire-mediated heterogeneity is still poorly understood.

Most research documenting how herbivorous mammals respond to fire has followed the control-impact approach comparing recently burned habitat to unburned habitat, with the majority of studies comparing sites that are less than 1-year post-fire to control sites (described only as unburned or greater than 1-year post fire; see Table A1.1). While some post-fire changes in resource availability are short-lived (Eby et al. 2014), changes to habitat structure (Higgins et al. 2007), floral composition (Bond et al. 2008), and landscape heterogeneity (Kelly et al. 2011) can be long lasting. Some species respond to long post fire successional gradients (e.g. >40 years; Kelly et al., 2011) and rely on late seral state habitat (Taylor et al. 2012). Furthermore, individual fire variables such as fire frequency (Archibald et al. 2005) and size (Kimuyu et al. 2017) can influence the distribution of large herbivores at variable spatial and temporal scales.

African savannas are complex, heterogeneous environments with substantial variation in water availability (Owen-Smith 2004), tree cover (Klop et al. 2007), and soils (Pacifci et al. 2015), each of which impact upon large herbivore distributions. Understanding the landscape characteristics most relevant for habitat selection can help resolve the relative role that fire plays in determining the density and distribution of large herbivores on a savanna mosaic. Habitat selection on a burned landscape has been related to the nutritive quality of foraging resources (Lemon 1968), competition among herbivores (Rowe-Rowe 1982), and changes in predation risk due to changes in vegetation structure (Eby & Ritchie 2012). Species-specific characteristics (e.g., body size, foraging strategy, metabolic needs) underlie hypotheses of resource selection on a patch mosaic, driven by allometric relationships with forage quality (Sensenig et al. 2010). It has been hypothesized that whilst small herbivores mainly select the

low quantity, high quality forage in burned areas, large bodied herbivores forage more often on high quantity vegetation, often in unburned areas, to maximize their energetic and nutritional intake (Sensenig et al. 2010). Large bodied species may also be more evenly distributed across a landscape due to a wider dietary tolerance (Cromsigt & Olff 2006).

Reliable estimation of animal abundance and density is an important baseline for effective management and conservation planning (Buckland et al., 2001). Counts of animals that are not adjusted to account for variation in detection can introduce considerable error into estimates of abundance or density (Dénes et al. 2015). This can also obscure community patterns across environmental gradients (Tingley & Beissinger 2013) and bias inference made from relationships with ecological covariates (Gu & Swihart 2004). Distance sampling methods allow for robust estimation of abundance and can account for factors contributing to imperfect detection (e.g., ranging patterns, crypsis, variation in body size and group size, and variable vegetation structure; Buckland, Rexstad, Marques, & Oedekoven, 2015). Despite savanna conditions being appropriate for these methods (Bukombe et al. 2015), they have rarely been used to quantify large ungulates in savanna systems (but see M'soka et al., 2017). Density surface models (DSM) are an additional tool that allows ecologists to build spatial models of the relationships between population abundance and environmental covariates, whilst also incorporating detection probabilities from distance sampling (Miller et al. 2013). DSMs have been used to investigate the densities of marine mammals (Katsanevakis 2007), large carnivores (Durant et al. 2011), and more recently ungulates (Schroeder et al. 2014; Valente et al. 2016). For example, they have been used to estimate the densities of large mammals over long-time frames (Durant et al. 2011), to tease apart patterns of niche segregation among ungulate species (Schroeder et al. 2014) and to examine the spatially explicit role of environmental variables on ungulate distribution (Valente et al. 2016), which are important steps in understanding how large herbivore distributions relates to a fire regime.

In this study I use landscape-scale fire data from almost three decades of fires in two protected savanna systems in South Africa to examine the relationship between large herbivore distribution and burning. I use distance sampling techniques to relate the abundance of large herbivorous mammals (hereafter large herbivores) to temporal and spatial characteristics of heterogeneous fire regimes. The present study has three aims. First, to model detection probabilities for large herbivores using distance sampling techniques. Second, to estimate large herbivore densities and biomass across a post-fire

chronosequence that serves as a framework for understanding resource selection within a savanna burn mosaic. Third, to evaluate the relative influence of multiple fire and ecological variables on mammal density and distribution. Specifically, I examine the importance of three characteristics of the fire regime, namely the extent of new burn, fire frequency and pyrodiversity on ungulate densities using DSM. The results of this chapter support recommendations for fire management regarding the application of prescriptive fire regimes for large herbivores.

2.3 METHODS

2.3.1 *Study Area*

The study was carried out at Pilanesberg National Park (PNP; 49,500 ha) and Mankwe Wildlife Reserve (MWR; 4,680 ha) in North West Province, South Africa. These two sites are approximately 5 km apart and have fenced perimeters. In these areas, the wet season extends from October to March and mean annual rainfall is approximately 630 mm (Brockett et al. 2001). The habitat is a sourish-mixed bushveld and contains open grasslands interspersed with discontinuous woodland (Acocks 1988). MWR employs a modified rotational fire regime where established blocks of habitat are burnt every four to five years whilst preserving some unmanaged blocks that have not been burnt in ten years or more. At PNP, the fire regime is based on the 'patch mosaic burning' method and is one of the locations where these methods were first formalized (Brockett et al. 2001). Here, savanna burning attempts to mimic natural fire regimes and fire is varied in space and time to create a heterogeneous mosaic of fire patches. Most fires (>80%) in these study areas occur between May and August.

2.3.2 *Line transect surveys*

Driven surveys for large herbivores were conducted twice over two sampling years once at the beginning of the wet season (September to November 2014 and 2015) and once at the end of the wet season (January to March 2015 and 2016). Twelve line transects (7 at PNP and 5 at MWR; see Figure A2.1) were undertaken. Surveys were conducted two or three times per season for a total of 9 surveys per transect line. These were placed along existing roads and ranged from 2.9 km to 11.0 km in length, with herbivores surveyed from within a vehicle. Driven surveys were conducted by two observers, one driver spotting on one side of the road and the other observer spotting on the other side of the road. Surveys were conducted within four hours of sunrise and three hours of sunset to survey during peak

activity and avoid the hottest time of the day. The direction, time of day, and vehicle-side of the observers were rotated during repeat surveys of each transect to reduce sampling bias. Between observations, the vehicle was driven at 10-15 km/hr. Due to the proximity of a reserve boundary, one transect was surveyed as a one-sided transect. Observations of animals were recorded as single-species groups. Each time a group of animals was encountered the location of the vehicle, time, group size, and distance and angle to the centre of the group were recorded. The distance was recorded using a laser rangefinder (Leica Rangemaster CRF 1600) and the location of the vehicle was recorded using a handheld Global Positioning System (GPS) unit. The GPS unit had a horizontal accuracy of approximately 4-5 meters. The location of the group was later mapped using the location coordinates, distance and angle. The function 'NEAR' in ArcGIS 10.1 (ESRI 2010) was used to estimate the perpendicular distance of the group from the transect line.

2.3.3 Vegetation and fire mapping

The vegetation and fire history within the study area was mapped separately using Landsat 5 and 8 surface reflectance imagery (30 m resolution) in Quantum GIS (QGIS 2016). To locate individual fire patches, Landsat data was displayed on a computer screen using the bands red, middle infrared, and near-infrared in blue, green, and red colours (Bowman et al. 2003; Jones et al. 2013). The boundary of every fire (including unburned interior areas) occurring between January 1989 and March 2016 was hand digitized at a constant scale (1:25,000). Each fire patch was assigned an age-class based on the calendar year in which it burned. To verify the dates of ignition derived from Landsat data, I used fire maps provided by the land managers for each study area. In a few cases where no ignition date data was available for old fires, I acquired the apparent month of ignition from Landsat imagery and set the ignition date as the 15th of that month. In addition, the vegetation at the study sites was mapped using Landsat 8 images. Vegetation was mapped as either tree covered (hereafter woodland) or open grassland with an object-based, segmentation resulting in discrete patches of woodland amongst open savanna grassland.

2.3.4 Statistical analyses

Detection probabilities and density estimates

A two-step approach was used for density estimation. In the first step I estimated detection functions and conducted conventional distance sampling (CDS) and multiple covariate distance sampling (MCDS) using Distance 7.0 (Thomas et al. 2010). I estimated densities for all species combined and for individual species with at least 60 observations. Following recommended good practice (Buckland et al. 2015), I conducted exploratory analyses of the data including: plotting histograms of sightings using different distance grouping bins, evaluating the effects of covariates on the distances at which animals were detected during surveys, evaluating the use of different truncation distances with data, and investigating data for cluster-size bias. Density estimates, \hat{D} , of mammals were estimated using the equation:

$$\hat{D} = \frac{n\hat{E}(s)}{2wL\hat{P}_a}$$

Where n is the number of observed groups (clusters) of animals, $\hat{E}(s)$ is the estimate of the mean cluster size in the population, \hat{P}_a is the probability of detecting a cluster within the truncation distance w , and L is the total length of the transect. The average size of observed groups can often increase with increasing distance from the line (cluster size-bias). Consequently, I used a size-bias regression between the detection probability and observed cluster size (Buckland et al., 2001). In all analyses the slope was not significantly different from zero ($p > 0.15$) demonstrating a lack of size bias and, as a result, I used $\hat{E}(s) = \bar{s}$ as the mean observed cluster size. A 500-m truncation distance (w) was found to be appropriate for most species and I maintained this truncation distance across all species for simplified comparisons. Three standard distance-based detection functions (uniform, half-normal and hazard-rate) that are commonly used with line transects were fit to the data with cosine or polynomial series adjustments (Buckland et al. 2001).

Initially, CDS models with no covariates were fitted as the null model and then MCDS models used stepwise addition of covariates to assess the effects of different covariates on detection functions. The best detection function model was selected based on the Akaike's information criterion (AIC), while taking into account distance data histograms and goodness-of-fit tests (Buckland et al., 2015; Burnham & Anderson, 2002). For density analyses of all species combined, the covariate *species* was included in models to account for differences in detectability among species. An additional seven covariates that

were anticipated to influence detectability were selected *a priori*. Side of vehicle was included as a covariate (a factor with two levels) to account for potential differences in detection probabilities between the driver and the passenger. A daylight covariate was included as the minimum of the number of minutes after sunrise or until sunset to indicate the proximity to peak activity (which occurs around sunrise and sunset for most large herbivores in this system). Year (a factor with two levels) and season (a factor with two levels; early or late in rainy season) were also included as covariates, to account for potential differences in detection among years and among seasons. A vegetation covariate (a factor with two levels; grassland or woodland) was included to indicate habitat type. Time-since-fire (hereafter TSF) was included as a covariate to account for potential differences in the detection of animals arising from differences in the vegetation structure (e.g., grass height) among habitats. TSF describes the fire age-class of the area in which the observed group was detected (or in which most of the group was detected, if the group spanned fire age-classes) and ranges from 1 to 11 years old. Fire ages from 8 to 11 years were pooled to achieve an area comparable to other age-classes. Exploratory analysis showed that including TSF as a categorical variable had a better fit to the data than as a continuous variable, consequently this variable was included in the analysis as a factor with eight levels.

Densities and the detection function of mammal species were estimated at the global and stratum (i.e. TSF) level. Initially, I estimated the densities of animals separately for each site (i.e., PNP and MWR) but, as this changed neither the detection function nor the density results, I combined sites in all analyses. Density of the commonest species were used to compute biomass estimates (kg/km²) for each burn treatment using mean adult body mass values from Hempson et al. (2015). Common species were those that had sufficient observations (>60 clusters) to perform individual species density analyses.

Landscape-level density surface modeling

The second stage of analyses involved using the detection functions calculated in stage one to build density surface models to examine the relationships between large herbivore densities and multiple landscape variables. Analyses were conducted using the 'dsm' package (Miller et al. 2013) within program R (R Development Core Team 2016). Transect lines were divided into 500m segments and density was modeled within the resulting 162 segments across the study area for each sampling season. Segments were 500m long and 1,000m wide (2 x the truncation distance). Five landscape

covariates were derived for each segment (see Landscape Variables below). The top MCDS model for all species was used to estimate the detection function for the density surface models.

Generalized additive mixed models (GAMMs) were used to examine the relationship between the density of animals in each segment and the landscape variable. A quasi-poisson error structure and a logarithmic link function were used (Buckland et al., 2015). In addition, the models contained the variable site (i.e., MWR or PNP), to account for site specific spatial variation, and the random effect transect-ID, to account for the repeated surveys over time. I used restricted maximum likelihood (REML) estimation of the smoothness parameters (Wood 2011). Model fit was evaluated using the percentage deviance explained and the adjusted R^2 value for each model (Wood et al. 2016). The top density surface model was selected among the set of candidate models using the percentage deviance explained. I examined the distributions of model residuals to confirm that normality assumptions were not violated. In addition, I examined the residuals for spatial autocorrelation among segments using visual inspection of a correlogram; no evidence of spatial dependence was found.

The fire and vegetation raster layers were used to produce landscape-level spatial covariates for the study site using Fragstats 4.0 (Mcgarigal et al. 2012). The amount of recently burnt habitat in the landscape mosaic was described by the proportion of a transect segment that is newly burned (NEW), which includes all burns that have occurred within 1 year of the survey. To characterize the landscape burn-age heterogeneity (i.e., pyrodiversity) I calculated the Shannon habitat diversity index (SHDI), which summarised the diversity of fire age classes in a transect segment using the number of age-classes and their proportional area (Mcgarigal et al. 2012). To assess the effects of fire frequency (FREQ) I calculated how many times a transect segment had burned in the known fire history (i.e., between 1989 and the time of the survey). To examine the influence of tree cover on mammal density I included the proportion of the transect segment that was woodland (WOOD). Finally, I used ArcGIS 10.1 (ESRI 2010) to measure the distance from the centre of a transect segment to the nearest permanent waterbody (e.g., dams and watering pans) within the study sites (WATER). None of these landscape variables were strongly correlated (Pearson correlation coefficient: $r < 0.5$ in all cases).

2.4 RESULTS

Over the two years, 693 km of surveys (PNP = 482.5 km, MWR = 210.5 km) were conducted, resulting in 1176 observations of groups of large mammal species (8874 individuals). Sightings of 21 mammal species were recorded; however, I removed waterbuck (*Kobus ellipsiprymnus*) and hippopotamus (*Hippopotamus amphibius*) from the dataset as these species were almost exclusively associated with waterbodies in the study region. In addition, I removed 4 species that were observed less than 4 times during surveys over the two years (see Table A2.2). Of the remaining 15 species, I estimated individual species density for six common species (with >60 clusters): impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga burchellii*), giraffe (*Giraffa giraffa*), greater kudu (*Tragelaphus strepsiceros*), and warthog (*Phacochoerus africanus*). For both combined species and individual species, observations declined with distance from the transect line (Figure 2.1). Hazard-rate models with a polynomial series adjustment offered the best model fits for detection function. MCDS analyses evaluated the influence of covariates on the probability of detecting a cluster of animals. No covariate consistently influenced the detection function across species (Table 2.1).

The model of best fit for combined species included the covariates *species* and *TSF* (Table 2.1). The model of best fit for the detection of impala included the covariate *daylight*. The Cramer-von Mises goodness-of-fit test (C-vM) for impala detection was not significant ($p = 0.995$), indicating a good fit of the model to the data. The model of best fit for the detection of warthogs was influenced by *TSF* and *season* and was a good fit to the data (C-vM: $p = 0.980$; Table 2.1). The top detection model for plain's zebra included the *side* of the vehicle and was a good fit to the data (C-vM: $p = 0.998$; Table 2.1); however, this model had similar support to the null model ($\Delta AIC < 0.5$; Table 2.1). The models for the detection of blue wildebeest (C-vM: $p = 0.997$), greater kudu (C-vM: $p = 0.820$), and giraffe (C-vM: $p = 0.961$) were a good fit to the data; however, adding covariates did not improve on the null models for these species (CDS; Table 2.1). Detectability broadly declined more rapidly for smaller species; the only exception being kudu, whose detectability declined more rapidly than might be expected for such a large species (Figure 2.1).

Table 2.1: Summary of detection function models with covariates, including AICc model fit scores, for combined species and individual species. Covariates included season, year, daylight: minutes from sunrise or sunset, side: vehicle side of observation; veg: vegetation type; TSF: time-since-fire (in years); species. CDS (conventional distance sampling) includes no covariates. K is the number of parameters in each model, P_a is the estimated proportion of animal clusters observed along the transect.

Species	Covariates	K	AIC _c	Delta AIC _c	P_a
All species	species + TSF	23	15026.55	0.00	0.331
	species	16	15046.23	19.68	0.343
	TSF	9	15086.18	59.63	0.330
	none (CDS)	2	15110.81	64.58	0.350
	season	3	15116.58	90.03	0.340
	daylight	3	15117.21	90.66	0.319
	veg	3	15117.44	90.89	0.334
	side	3	15119.23	92.68	0.320
	year	3	15119.90	93.35	0.301
Impala	daylight	3	2960.30	0.00	0.293
	none (CDS)	2	2961.28	0.98	0.289
	TSF	10	2967.50	7.21	0.273
	year	3	2983.47	23.17	0.419
	veg	3	2983.50	23.20	0.419
	side	3	2983.59	23.30	0.418
	season	3	2983.61	23.32	0.416
Wildebeest	none (CDS)	2	3807.34	0.00	0.439
	TSF	9	3807.55	0.22	0.443
	year	3	3808.88	1.54	0.449
	daylight	3	3808.97	1.64	0.424
	season	3	3809.37	2.04	0.439
	side	3	3809.40	2.07	0.447
	veg	3	3809.48	2.14	0.430
Zebra	side	3	2869.32	0.00	0.435
	none (CDS)	2	2869.76	0.43	0.460
	year	3	2871.21	1.89	0.481
	season	4	2871.29	1.97	0.473
	veg	3	2871.49	2.17	0.444
	daylight	3	2871.09	2.77	0.440
	TSF	9	2872.72	3.40	0.470
Kudu	none (CDS)	2	735.38	0.00	0.185
	side	3	746.96	11.58	0.339
	season	3	746.96	11.59	0.339
	daylight	3	746.97	11.59	0.339

Species	Covariates	K	AIC _c	Delta AIC _c	P _a
Giraffe	year	3	746.97	11.59	0.339
	veg	3	746.98	11.60	0.339
	TSF	7	755.25	19.88	0.354
	none (CDS)	2	628.38	0.00	0.472
	season	3	630.75	2.37	0.495
	year	3	630.75	2.37	0.495
	daylight	3	630.75	2.38	0.495
	side	3	630.78	2.40	0.495
	veg	3	630.79	2.41	0.496
Warthog	TSF	8	638.90	10.52	0.447
	TSF + season	9	1003.97	0.00	0.198
	TSF	8	1008.79	4.82	0.172
	season	3	1009.91	5.95	0.198
	none (CDS)	2	1010.43	6.46	0.200
	side	3	1012.41	8.45	0.203
	year	3	1012.43	8.46	0.202
	veg	3	1012.43	8.46	0.200
	daylight	3	1012.43	8.46	0.200

Densities and biomass for *total species combined* were highest in habitat burnt within the last year and decreased with increasing burn age (Figure 2.2). Similar declining densities were found for the grazers (i.e. blue wildebeest, plains zebra, and warthog) and the intermediate browser-grazer impala. This pattern of declining densities with increasing burn age was not observed in the two browser species: giraffe and greater kudu. The densities of the greater kudu were variable across the post-fire chronosequence, while the densities of giraffe peaked in habitats that had burned four years previously (Figure 2.3).

The deviation explained by the DSMs of best fit varied from 0.052 for greater kudu to 0.40 for blue wildebeest (Table 2.2). The DSM of best fit for *all species* contained all five of the landscape spatial covariates (NEW, SHDI, WOOD, WATER, FREQ). The proportion of new burn and distance to water were highly significant covariates in this model, while the proportion of woodland was weakly significant (Table 2.2). Pyrodiversity and fire frequency were not significant predictor variables of total species density. Total species density was positively related to the proportion of new burn, while density

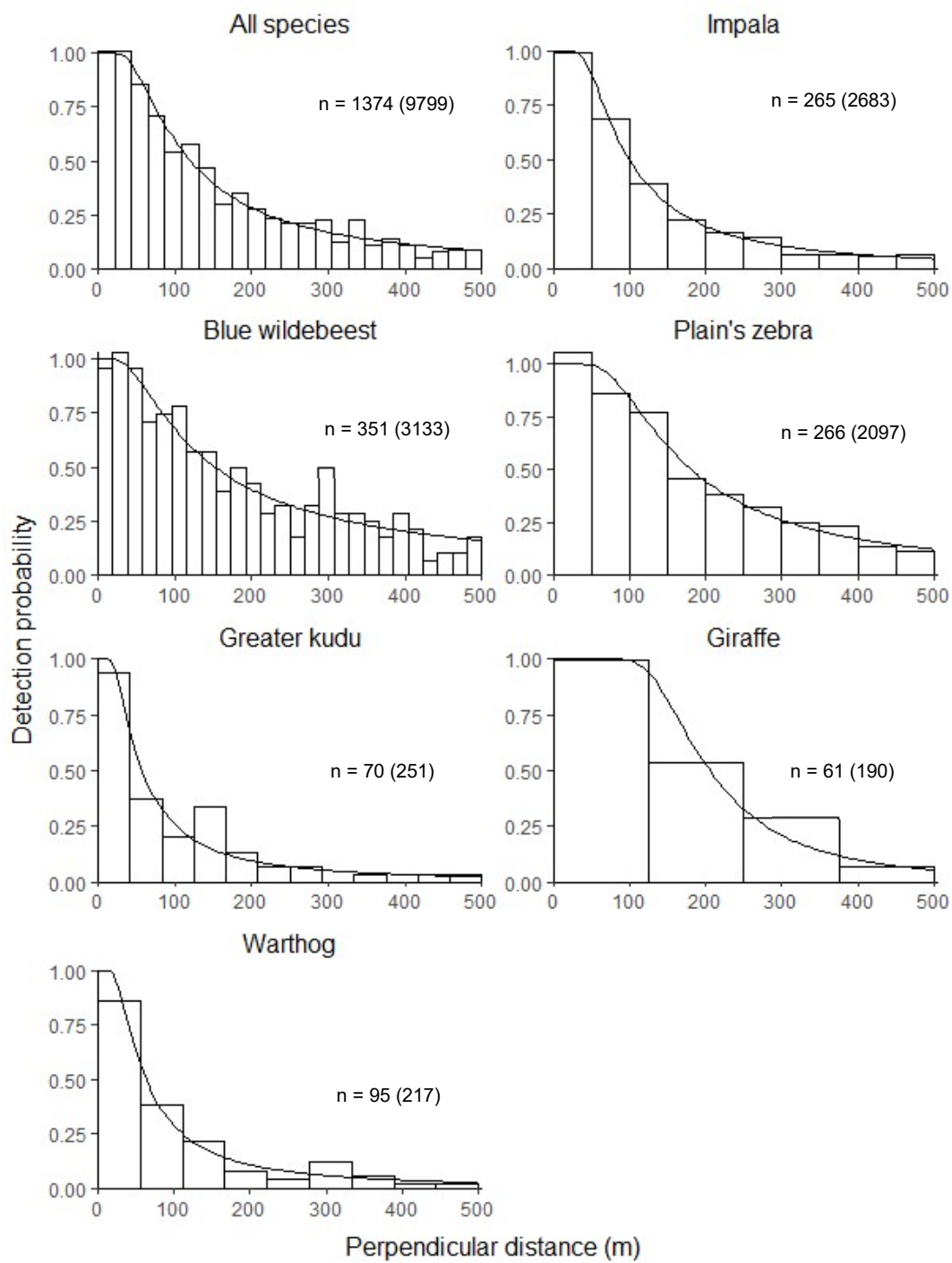


Figure 2.1 Histogram of detection distances for groups of animals with the fitted detection functions shown. Displayed are the number of groups and the number of individuals in parentheses observed during surveys.

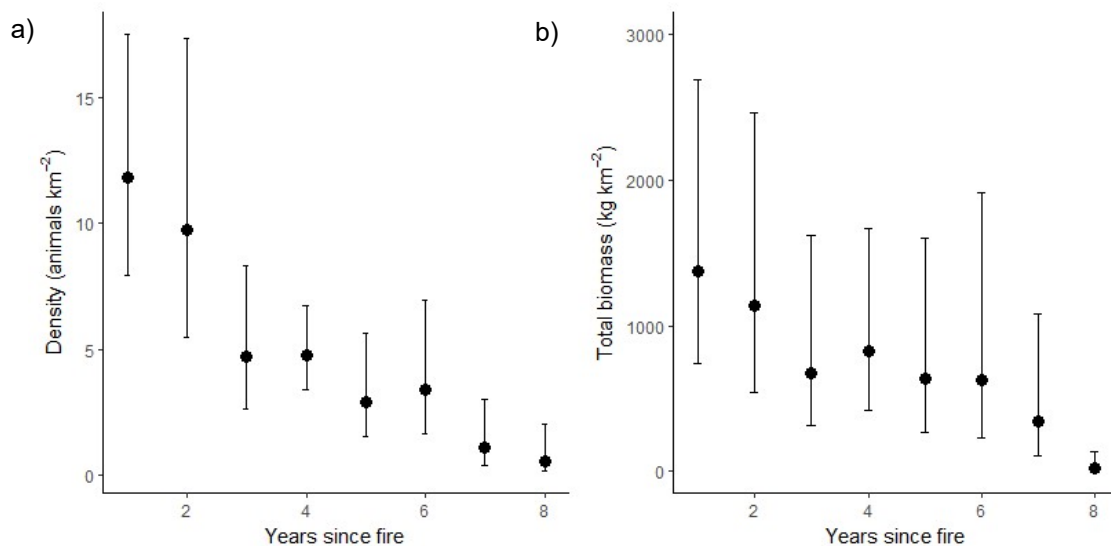


Figure 2.2 Mammalian response (per km²) to years since fire in relation to: a) the density of all species combined and b) total animal biomass (kg). Error bars are 95% confidence intervals.

decreased as distance to water and proportion of woodland increased (Figure 2.4). The DSM of best fit for impala and blue wildebeest demonstrated positive associations with the proportion of recently burned habitat on the landscape (Figure 2.4). The positive relationship observed between large mammal species and the proportion of new burn should be interpreted with caution. Inspection of these relationships (Figure 2.4) demonstrates wide confidence intervals that suggest the effect could be interpreted differently. Wide confidence intervals for this covariate are likely due to small sample sizes when the proportion of new burn is high. A negative association was found between the density of impala, blue wildebeest and plain's zebra and distance to water (Figure 2.4). The DSM of best fit for warthog density contained the significant predictor variables WOOD and WATER (Figure 2.4). The best fitting models for the greater kudu and giraffe did not contain any significant predictor variables.

2.5 DISCUSSION

This three-stage study of large herbivore 1) detection probabilities, 2) densities across a post-fire chronosequence, and 3) density surface models lends support to the proposed generality that large herbivores select recently burned savanna (<1-year post-fire). However, the data for grazers demonstrates that there is a lasting effect of burned habitat on resource selection across the gradient of fire age-classes. Density surface models demonstrated that large herbivores respond to a range of

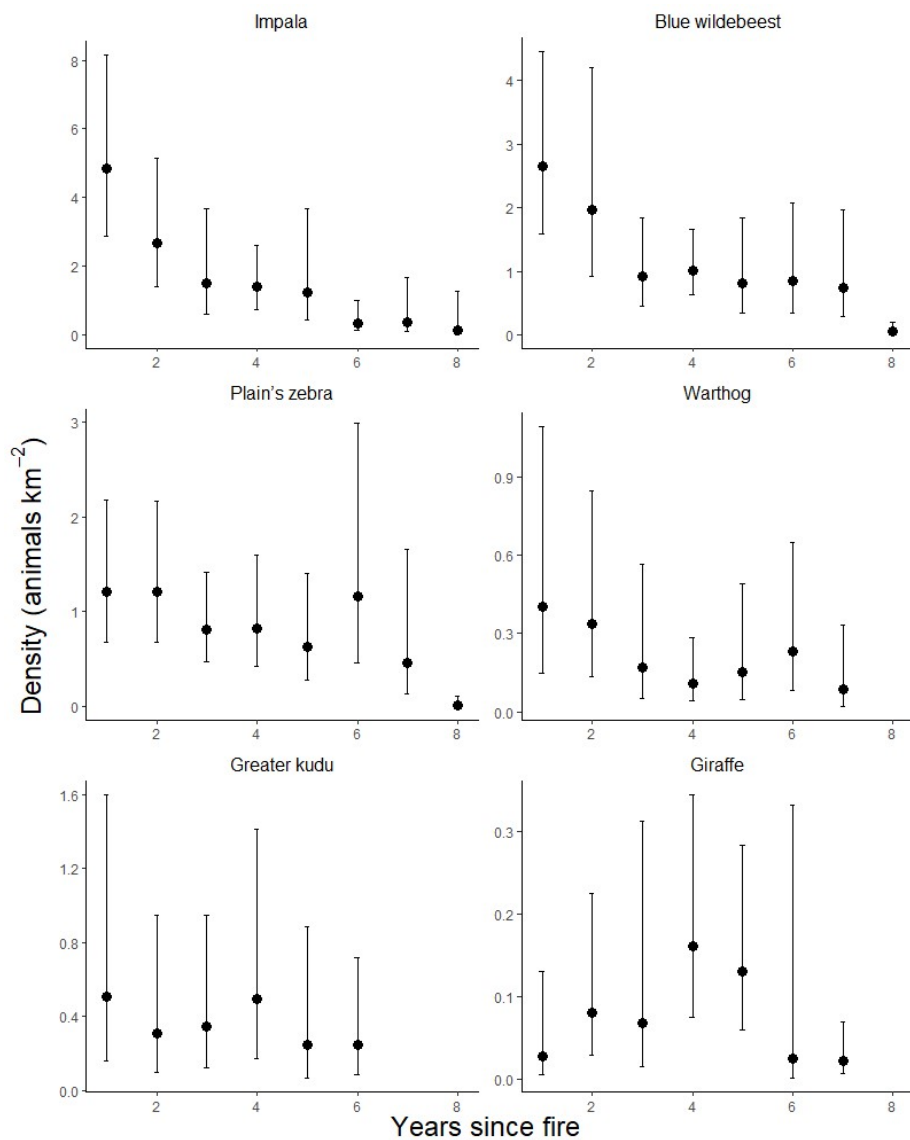


Figure 2.3 Densities of large herbivore species in habitat that varies in years since fire with 95% confidence intervals.

fire attributes and ecological variables on the landscape with burned habitat and areas close to water supporting the highest densities of large herbivores. Understanding the relative importance and effects of different fire and landscape variables is a critical step in the development of management strategies for the conservation of savanna species.

Table 2.2 Parameters for density surface models of the relationship between mammal densities (animals per km²) and landscape variables. Includes restricted maximum likelihood (REML) score, R² (adjusted), deviance explained, with the approximate *P* values and estimated degrees of freedom (edf) for each explanatory variable. Landscape variables include proportion of newly burned habitat (NEW), burn-age diversity (SHDI), proportion of woodland habitat (WOOD), distance to the nearest permanent waterbody (WATER), and fire frequency (FREQ). Only the top models are presented, however, see Table A2.4 for additional information on model selection.

Model	edf	<i>P</i>	REML	R ²	Deviance explained (%)
All Species					
NEW + SHDI + WOOD + WATER + FREQ			870.186	0.310	34.18
NEW	1.000	<0.001			
SHDI	1.000	0.089			
WOOD	1.799	0.045			
WATER	2.696	<0.001			
FREQ	1.000	0.335			
Impala					
NEW + SHDI + WOOD + WATER + FREQ			639.058	0.18	25.17
NEW	1.000	0.002			
SHDI	1.149	0.633			
WOOD	2.384	0.237			
WATER	1.000	<0.001			
FREQ	1.000	0.200			
Blue wildebeest					
NEW + SHDI + WOOD + WATER + FREQ			743.570	0.40	39.18
NEW	1.367	0.021			
SHDI	1.001	0.071			
WOOD	2.081	0.198			
WATER	2.739	<0.001			
FREQ	1.487	0.751			
Plain's zebra					
WOOD + SHDI + WATER			697.392	0.18	25.06
WOOD	1.284	0.354			
SHDI	1.000	0.236			
WATER	5.370	0.004			
Greater kudu					
NEW + SHDI + WATER + FREQ + WOOD			608.67	0.052	18.28
NEW	4.833	0.470			
SHDI	1.669	0.076			
WATER	2.680	0.314			
FREQ	2.443	0.300			
WOOD	1.037	0.566			
Giraffe					
SHDI + WATER + FREQ + WOOD			405.51	0.092	21.70
SHDI	1.003	0.939			
WATER	2.281	0.565			
FREQ	1.183	0.869			
WOOD	2.865	0.604			
Warthog					
SHDI + WATER + FREQ + WOOD			438.32	0.306	36.86
SHDI	2.264	0.596			
WATER	2.023	0.012			
FREQ	3.607	0.595			
WOOD	7.220	0.001			

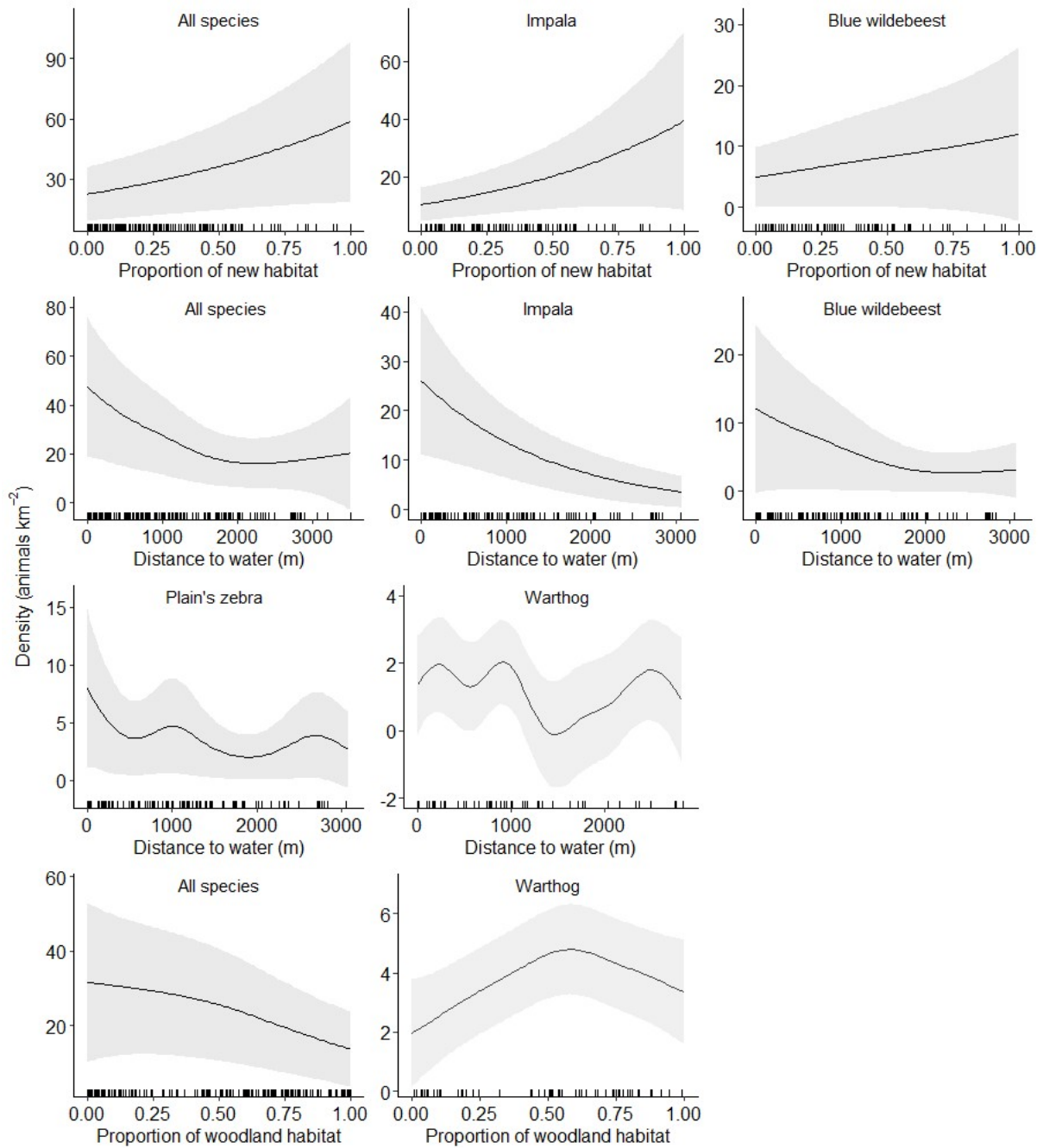


Figure 2.4 Responses of total mammal and individual species density to the proportion of new burn (<1-year), distance to water, and the proportion of woodland habitat on the landscape. Predictions and 95% confidence intervals from the top-ranked generalized additive mixed model are shown. The observed data are not displayed here in order to improve the visibility of the predicted relationships (lines). Rug plots of observed data values are shown on the x-axis.

Detection Probabilities

Imperfect detection of animals during surveys can introduce estimate error, underestimate population size, and obscure ecological patterns, hindering the reliability of count-based studies of large herbivore in savanna systems (Dénes et al. 2015). In this system, detection probability varied by species and was affected by fire age-class, season, and time of day (see Table 2.1). Notably fire age-class affected the detection of *all species*, highlighting the importance of accounting for this potentially confounding factor in fire studies (Pastro et al. 2014). The results also demonstrate that detection probability can drop significantly within short distances (<100 m) for species such as impala, warthog and kudu (Figure 2.1). This suggests that sampling designs that restrict mammal observation distance during sampling are unlikely to remove detection error (Moe et al., 1990; Tomor & Owen-Smith, 2002; Wallgren et al., 2009; Eby et al., 2014).

Densities across a fire gradient

While Australian mammals have been shown to respond to very long post-fire chronosequences (Kelly et al. 2011), the long-term effects of fire on large herbivore densities have rarely been studied in Africa. In this study, large herbivore densities indicated a lasting effect of burning across a post-fire chronosequence as demonstrated by a general decline in density with increasing fire age for all species combined and for grazers (i.e., wildebeest, zebra, and warthog) and the browser-grazer intermediate, impala. Research in African savanna has long suggested that large herbivores select new growth in burned areas due to higher nutritional content (Lemon et al. 1968; Sensenig et al. 2010); however, studies have demonstrated that elevated nutritional levels are temporary, resulting in habitat selection of new burn areas that lasts from a few months (Eby et al. 2014) up to 1 year (Parrini & Owen-Smith 2009). Unlike previous studies, the results of the present study did not find a temporary increase in large herbivore densities within the first-year post-fire. Instead these findings generally demonstrated a consistent decline in density over the 1 to 11 years post-fire. While evidence has shown that large mammals are selecting recently burned habitats due to the high nutritional quality of the available forage (Eby et al. 2014), the selection of older burn areas is less well understood. However, large mammals may select older burn areas because of the high quantity of forage (Belovsky 1997) or increase in vegetation cover for predator avoidance (Mduma & Sinclair 1994). In recently burned habitats, nutritional quality of grass is high but is limited in quantity, but as time-since-fire increases, grass density

increases and nutritional quality decreases (Allred et al. 2011). Therefore, this gradual decline in large mammal densities as time-since-fire increases may reflect a trade-off between forage quantity and forage quality (Belovsky 1997).

The lasting effects of fire on large herbivores may be the residual effects of fire on vegetation or a positive feedback loop where increased grazing (McNaughton 1984) and browsing (Bergstrom et al. 2000) on previously burned sites promotes regrowth of higher quality forage (Verweij et al. 2006). The distribution of grazing lawns—short-grass areas of high-quality forage promoted by grazing—is related to fire history (Archibald et al. 2005). Frequent fires have been shown to prevent overgrazing, allowing sites to recover lost grass biomass and reduce the spread of grazing-adapted grasses (Archibald et al. 2005). Therefore, fire return intervals at the study sites may be contributing to a balance between over-grazing and burning, improving the quality and quantity of grasses across the fire disturbance gradient.

In addition to changes in the grass layer, fire can also increase the quality and quantity of forage for browsers (Rutherford 1981; Carlson et al. 1993), leading to increased browsing on newly sprouted vegetation in post-fire areas (Klop et al. 2007; Bond et al. 2008). However, similar to previous studies (Klop et al. 2007; Isaacs et al. 2013), this study did not find a consistent relationship between time-since-fire and the densities of browser species (i.e., greater kudu and giraffe). Prior research has demonstrated that shifts in the structure and composition of woody species along a post-fire successional gradient can result in variable responses of browser species (Bond et al. 2008; Isaacs et al. 2013). Both browser species in the present study demonstrated high densities at intermediate post-fire ages, which may be the result of delayed post-fire benefits in browse quality or quantity (Carlson et al. 1993). Similarly, a previous study in South African savanna, found that giraffe and kudu were selecting 3 year old burns over 1-year old burns (Burkepille et al. 2016). Selection of mid-age burn areas (i.e., 4-5 years) by giraffe in this study may reflect post-fire availability or regeneration of preferred tree species (e.g., *Acacia karroo*; Bond et al. 2008) or tree size (e.g., 2-3 metres; Pellew 1983). Ultimately, these results show that browsers and grazers are distributed differently on the landscape, resulting in differential foraging pressure based on fire age.

Allometric scaling hypotheses predict that body mass will govern herbivore resource selection (Belovsky 1997). On a burned landscape it has been predicted that small herbivores rely on the high

quality forage of new burns, while larger herbivores are constrained by forage quantity of the older burns (Sensenig et al. 2010). Some previous studies have shown a positive relationship between burn age and body mass (Wilsey 1996; Sensenig et al. 2010). In contrast, this study found no relationship between body mass and time-since-fire, suggesting that body mass alone is inadequate to describe resource selection on a burn mosaic. Instead, other factors such as distance to water (Pacifci et al. 2015), habitat type (Watson et al. 2011), or predation risk (Eby & Ritchie 2012) are likely to have an important role in species-specific habitat selection. In addition, preference seen for new burns by both small and large bodied herbivores may be due to variability in factors such as the number of months since burning, rainfall, or grass composition creating spatial heterogeneity in the quality and quantity of forage available on recently burned areas (Sensenig et al. 2010).

Density surface models

Spatially-explicit DSMs are a valuable tool for ecologists because they represent an important advancement in methods for modelling the spatially-explicit relationships between animal abundance and multiple environmental covariates when detection is heterogeneous (Miller et al. 2013). Unlike conventional distance sampling, DSMs are less dependent on a random survey design (Valente et al. 2016), making them particularly appropriate for this study, since surveys were limited to existing road networks. While placing transects along roads may lead to biased densities due to large mammals avoiding roads (Ward et al. 2004), the estimated detection probabilities did not demonstrate avoidance behaviour, and decreased with distance (Figure 2.1).

Results from density surface modelling for total species, plain's zebra, blue wildebeest, and impala upheld the widely supported conclusion that grazers are positively related to recently burned areas. However, unlike the majority of studies that have investigated this relationship, the present study found that savanna mammals are responding to a complex and multivariate environment (*but see* Ritchie et al. 2008; Pacifci et al. 2015). Density of all species combined increased with the proportion of new burn and proximity to water and decreased with increasing woody cover. Moreover, density was not related to fire frequency or pyrodiversity (Table 2.2). Density surface models for individual species demonstrated species-specific responses to the suite of environmental covariates; however, I did not observe allometric patterns of resource use observed elsewhere (Sensenig et al. 2010), as both small (e.g., impala) and large (e.g., zebra and wildebeest) herbivores responded positively to the extent of

new burn and did not respond to pyrodiversity. Warthogs, the smallest herbivore in this study, did not respond to the extent of new burn despite being short-grass specialists (Kleynhans et al. 2011) and demonstrating the highest densities in the most recent burns (<1 year post-fire) when densities were compared across the fire disturbance gradient. Sensenig et al., (2010) found that gut-type affected resource selection on a burned landscape because hindgut fermenters (e.g., warthog and zebra) are limited by total forage quantity rather than quality. However, warthogs may also be supplementing their diet with other food sources (e.g., roots and rhizomes; Treydte et al. 2006) or selecting habitat at a smaller spatial scale than the scale of this study by selecting small habitat patches such as grazing lawns (Kleynhans et al. 2011).

The positive association between large herbivore distribution and water sources at the landscape scale is consistent with results from previous studies in African savanna (Traill 2004; Kimanzi et al. 2014), including rare antelope in South Africa (Pacifci et al. 2015), and has significant implications for management. The addition of artificial water sources in relation to the distribution and seasonality of natural sources in African savanna is a key management tool used by managers of protected areas (Owen-Smith 1996). Significant associations with water sources were found on the landscape for species with high water dependence (i.e., zebra, wildebeest, impala and warthog; see Table A2.2) and no association with water for species with low water dependence (i.e., giraffe, kudu). Water-dependent species tend to increase grazing around permanent water sources during the dry season and expand grazing into areas farther away from water sources that are less heavily grazed during the wet season (Owen-Smith 1996). Both years of surveys had lower than average rainfall (449 mm and 418 mm, respectively) and this may have increased large herbivore use of areas near water sources.

The pyrodiversity promotes biodiversity hypothesis has received support in forested habitats (Sitters et al. 2014b; Tingley et al. 2016); however, it has received little support in shrubland (Kelly et al. 2012; Taylor et al. 2012) or savanna habitats (Davies et al. 2012; Andersen et al. 2012). While the effects of pyrodiversity on diversity (Taylor et al. 2012; Sitters et al. 2014b) and occupancy (Tingley et al. 2018) have been investigated, this study is one of the first to investigate the relationship between a spatio-temporal measure of pyrodiversity and abundance (*but see* Davies et al., 2018). Pyrodiversity had a weak negative effect on total species density, and on the densities of blue wildebeest and greater kudu (Figure A2.2). Research by Beale et al., (2018) found a positive relationship between mammal

richness and pyrodiversity in Africa; however, they found that mammal richness in dry savanna (<650 mm annual rainfall) was not as responsive to pyrodiversity compared to mammal richness in wet savanna, supporting the idea that dry savanna taxa may be more resilient to fire disturbance in Africa (Parr et al. 2004) and Australia (Andersen et al. 2012). The present study did not find an effect of fire frequency on large herbivore density. Studies of the distribution of large herbivores have found variable responses to fire frequency relative to other environmental covariates; with no response reported in the Himalayas (Ahrestani et al. 2011) and responses in savanna habitat in South Africa (Pacifci et al. 2015) and Australia (Ritchie et al. 2008) that vary by species and season. Compared to pyrodiversity and fire frequency, other environmental variables such as proximity to water may be more important drivers of mammal density and distribution in dry savanna.

Pyrodiversity was measured at a scale (spatial and temporal) commensurate with the scale and application of prescribed fires making it a meaningful measure of management in this study area. However, it is possible that mammal species are responding to a different scale or measure of pyrodiversity (Beale et al. 2018). Spatial scale is important to consider among large herbivores because differences in body size and vagility may cause species to respond differently to the heterogeneity of resources (Cromsigt et al. 2009). Fine-scale heterogeneity is known to cause resource partitioning within a burn patch (Cromsigt & Olff 2006; Klop & van Goethem 2008) and may result from the patchy nature of burning (Sitters et al. 2015), grazing patterns (Kerby et al. 2006) or variation in floral composition (Numa et al. 2004) and habitat structure (Charles-Dominique et al., 2015). This fine-scale heterogeneity might contribute to the stability of large herbivore population densities across broad-scale resource gradients (e.g., pyrodiversity) in savanna systems (Owen-Smith, 2004).

Density of all species combined decreased with increasing extent of woody cover. Avoidance of high tree density areas may result from the selection of open area for improved grazing (Charles-Dominique et al. 2015) or enhanced predator detectability (Klop et al. 2007). The understorey conditions of savanna woodland can be unfavourable to C4 grasses leading to very little grazing in thickets and woodlands (Charles-Dominique et al. 2015). Thickets provide good foraging opportunities for browsers (Charles-Dominique et al. 2015) and yet no significant relationships were found between the extent of woody cover and browser density. Browser species may be responding to finer characteristics of woody habitat such as habitat type (e.g., thicket vs. woodland; Charles-Dominique et al., 2015) or woody

species composition (Bond et al. 2008). Dense thickets may be inaccessible to large browsers like giraffe and greater kudu. Given the high risk of extinction of some browser species (Courchamp et al. 2018), a better understanding of what drives browser densities and distributions will be important for the conservation of these species in African savannas. Furthermore, savanna systems are threatened by bush encroachment due to elevated CO₂ levels (Bond & Midgley 2000), inappropriate fire management (Skowno et al. 1999), and over-grazing (Roques et al. 2001). Therefore, knowledge of the local constraints on the relationships between fire regimes, woody vegetation and browser species will be important for planning fire management strategies.

In the present study, density surface models were used to explore the relationship between large mammal density and landscape variables. The low values of deviance explained by these models, especially for greater kudu and giraffe, suggest that important environmental variables influencing the density of large mammals in this system may have been missing. Habitat selection of large mammals varies by species and is influenced by many environmental variables (Eby et al. 2014; Pacifici et al. 2015) and as a result, a few environmental variables may not be robust at predicting large mammal densities across species and such a large spatial scale. The predictive capacity of these models might improve due to the inclusion of additional environmental covariates. This suggests further investigation of environmental factors that affect large mammal densities in the study area, particularly for browser species.

2.5.1 Implications for Management

Given that large, productive populations of savanna mammals has been a central management focus in southern African protected areas (Van Wilgen 2009), evaluating the effects of pyrodiversity on large mammal density is an important priority for conservation management. In addition, evaluating this relationship at a scale corresponding with fire prescription is important for exploring the relative effects of fire attributes and other environmental processes (Driscoll et al. 2010). The present study is part of a growing body of research (Ritchie et al. 2008; Pacifici et al. 2015) that suggests that resource selection by large herbivores on a burned savanna landscape is not uniform (Archibald 2004) or simply driven by the presence of burned and unburned habitat (Lemon et al. 1968) but is, in fact, influenced by multiple landscape features such as post-fire age, burn extent, proximity to water, and habitat type. Furthermore, these relationships are species-specific and most likely specific to the fire regime and a regionally

specific suite of environmental variables. The specificity of these relationships may explain the inconsistencies among previous studies and suggests that fire management practices that are not developed using local empirical evidence may be harmful to resident species (Taylor et al. 2012; Davies et al. 2018). The present study demonstrates that to best understand and disentangle the role of multivariate conditions requires modelling relationships with the incorporation of detection probabilities for count-based studies. Density surface models are a valuable tool for management practitioners and provide the opportunity to predict optimal fire management regimes for a protected area.

Although pyrodiversity does not promote large herbivore density, this does not obviate the use of patch mosaics for fire management. The findings outlined in this study demonstrate that densities respond to a fire successional gradient over a longer chronosequence than has previously been shown for large herbivores in African savanna. Short fire return intervals have been shown to have negative effects on large herbivores (Pacifi et al. 2015) and late seral-stage savanna can be important for preventing starvation during periods of drought (Owen-Smith 2004). To have new burns and fire return intervals greater than 1-year, it is necessary to have a range of fire age-classes. Furthermore, pyrodiversity may increase the availability of rare niches (Beale et al. 2018); thus, while low observation rates prevented us from assessing their response to fire, rarer species (e.g., common tsessebe, *Damaliscus lunatus*) may be positively associated with pyrodiversity. Roan antelope—a rare species of conservation concern—was shown to prefer unburned areas in Kruger National Park, South Africa (Pacifi et al. 2015). While regular burning appears to benefit the large herbivores in the present study, a population of small mammals at one of the study sites was found to have a negative response to burning and to prefer late-successional habitats (Yarnell et al. 2008). Similar strong negative relationships between small mammals and the extent of recently burnt habitats have been found in savannas elsewhere (Radford et al 2015). Providing a mosaic of fire age-classes may provide niches and resources for an array of mammal species. However, further research is needed to understand the effects of fire on a range of savanna mammal species and to inform the design of fire mosaics that are appropriate for early and late successional fire specialists.

National Parks and wildlife reserves benefit from tourism which can provide valuable revenues for conservation (Gray & Bond 2013; Pacifi et al. 2015). A primary reason tourists visit protected areas is to see large herbivores (Lindsey et al. 2007) which can provide additional incentives for burning to

facilitate visibility and to draw large herbivores to post-fire regrowth (Klop & van Goethem 2008). Visibility of animals in African savanna has been cited as a major determinant of tourist satisfaction and the probability of a tourist returning (Gray & Bond 2013). Peak season for visitors occurs between October and April in Pilanesberg National Park corresponding with the mammal densities and distributions from this study. These findings will allow park management to make important decisions about burning, species conservation, and meeting tourist and economic needs.

Chapter 3

The importance of unburned savanna for avian diversity and function in a pyrodiverse landscape



Secretarybird (*Sagittarius serpentarius*)

3.1 ABSTRACT

Prescribed fire is used throughout fire-prone landscapes to conserve biodiversity. Current best practice in managing savanna systems advocates methods based on the assumption that increased fire-mediated landscape heterogeneity (pyrodiversity) will promote biodiversity. However, significant knowledge gaps remain in our understanding of how savanna wildlife responds to pyrodiversity. The impact of pyrodiversity on functional diversity has rarely been quantified and assessing this relationship at a landscape scale which is commensurate with fire management is important for understanding mechanisms underlying ecosystem resilience. Here, I study the effects of three decades of fires on the spatial and temporal attributes of pyrodiversity and examine the consequences for avian diversity in North West Province, South Africa. I examined the response of (a) species richness and (b) indices of functional diversity (i.e., functional richness, functional evenness and functional dispersion) at two landscape scales (100 ha and 500 ha) to two measures of pyrodiversity, the extent of fire age-classes and habitat type. I then used null models to assess whether observed functional richness differed from expected. Pyrodiversity, measured by both fire age-class diversity and configuration, had little impact on species richness or functional diversity. Instead, the proportion of newly-burned (burned within one year of survey) and old, unburned (not burned for ≥ 10 years) habitat on the landscape were the best predictors of species richness and functional diversity. Both had a positive effect on species richness and functional richness, but the extent of old, unburned habitat was nearly three times more important than the extent of newly-burned habitat. Lower than expected levels of functional richness suggest that habitat filtering is occurring, resulting in functional redundancy across the study region. I demonstrate that evaluating functional diversity and redundancy is an important component of conservation planning as they may contribute to previously reported fire resilience. These findings suggest that to promote avian diversity and conserve ecological functions in savannas a management approach is needed that includes significant coverage of newly-burned and older, unburned grasslands; the latter, in particular, are inadequately represented under current burning practices.

3.2 INTRODUCTION

Savanna is the most fire-prone biome on earth (Chuvieco et al. 2016), with fire acting as an important driver of habitat structure and ecosystem function (Glover 1968). Prescribed burning has been widely used throughout savanna regions, often to enhance grazing opportunities for mammals (by encouraging palatable grasses), whilst also reducing bush encroachment and pre-empting wildfires by reducing fuel loads (Van Wilgen 2009). More recently, however, the focus of fire regimes has shifted towards burning as a means to conserve—and even promote—biodiversity through the introduction of landscape heterogeneity (Parr & Brockett 1999; Kelly & Brotons 2017).

Prevailing contemporary burning methods are rooted in the ecological theory that increased landscape heterogeneity will result in increased biodiversity (Parr & Brockett 1999). By applying fires that vary in time and space, land managers attempt to achieve some of the patchiness that is inherent to fire prone ecosystems (Brockett et al. 2001). These “patch-mosaic” burning methods are based on the idea that pyrodiversity promotes biodiversity (Martin & Sapsis 1991; Parr & Brockett 1999). Although initial developments of patch-mosaic burning methods were formalized in Pilanesberg National Park and Kruger National Park in South Africa (Brockett et al. 2001), variations of these methods are now employed worldwide, including Australia (Taylor et al. 2012; Sitters et al. 2014b), North America (Holcomb et al. 2014) and across southern Africa (Mulqueeney et al. 2010). While the effects of these methods on wildlife have mostly been studied in Australia, in shrub and forested habitats (Taylor et al. 2012; Sitters et al. 2014b; Farnsworth et al. 2014), relatively few studies have evaluated these methods in savannas (Davies et al. 2012). In South Africa, patch-mosaic burning is used in protected areas to achieve conservation goals (Brockett et al. 2001; Van Wilgen 2009) despite limited evidence that these regimes enhance local biodiversity.

Some work has questioned the generalities of the pyrodiversity promotes biodiversity (hereafter PPB) relationship (Parr & Andersen 2006; Taylor et al. 2012), with recent work demonstrating that this relationship is species-specific (Taylor et al. 2013a) and may be contingent on habitat type (e.g. forests; Ponisio et al., 2016; Tingley et al., 2016) or climate (Beale et al., 2018). Varied PPB findings may also result from how studies characterize and quantify pyrodiversity and biodiversity, and at what scale. Landscape heterogeneity has both temporal and spatial traits characterized by the type, shape and arrangement of habitat patches and can affect ecological systems and their functioning (Wiens 2000).

Most studies investigating the PPB paradigm have investigated the temporal attribute of fire age or 'time-since-fire' (Taylor et al. 2012; Haslem et al. 2012). Such a focus is justifiable because patch-mosaic methods emphasize the importance of fire patches burnt at different times (Brockett et al. 2001), and because temporal attributes may correspond with vegetation succession and changes in habitat structure following fire (Fox 1982). However, few studies have evaluated the impact of the spatial attributes of pyrodiversity (e.g. complexity and configuration) on animal communities (e.g. Sitters *et al.* 2014), despite the influence of spatial structure and scale on the diversity, composition and persistence of communities in heterogeneous landscapes (Pickett & Cadenasso 1995). A recent study revealed that pyrodiversity promotes avian and mammalian richness at a broad, continental scale (Beale et al. 2018). However, understanding this relationship at the landscape scale is important for defining and configuring key fire attributes for conservation planning and for predicting biodiversity change in response to local fire regimes. Therefore, the value of PPB research to land managers can be significantly increased when it is commensurate with the scale of fire prescription.

A topic often neglected in PPB research is the level of diversity affected. While species richness remains the most widely used measure of diversity in fire research, there is an emerging consensus on the importance of functional diversity, i.e. the abundance and distribution of species traits that affect ecosystem functions (Laliberté et al. 2010; Lindenmayer et al. 2015). Functional traits such as foraging strategy, nesting location, and habitat specialization are sensitive to the disturbance-induced changes in vegetation structure (Luck et al. 2012) that usually accompany fire. The PPB concept is based on the premise that species assemblages differ as a result of changes in patch characteristics and vegetation structure following fire (Parr & Brockett 1999). Understanding the relationship between environmental heterogeneity and functional diversity can illuminate processes contributing to the formation and maintenance of species assemblages (McGill et al. 2006) and processes driving ecosystem resilience in fire-prone landscapes (Oliver et al. 2015).

Resilience—the ability of a community to return to a pre-fire state—has been identified in savanna systems where the response of taxonomic diversity (i.e., species richness) to fire was investigated (Parr & Andersen 2008; Andersen et al. 2014). Ecosystem resilience depends on functional diversity and how functionally similar species respond to a particular disturbance (Laliberté et al. 2010). When an assemblage of species has significant overlap in functional traits (i.e. high functional

redundancy), ecosystem function is potentially safeguarded against environmental change and resulting species loss (Luck et al. 2013). In addition, landscape heterogeneity may increase resilience by supporting spill-over and a larger species-pool (Tschamtkke et al. 2012) and by providing resources and diverse niches that act as refugia to preserve species and their functions (Oliver et al. 2015). Spasojevic et al., (2016) found that functional diversity—unlike species richness—was a good predictor of community resilience and revealed mechanisms underlying fire resilience at the landscape scale. Understanding post-fire recovery and ecosystem resilience is vital for conserving biodiversity in fire-prone ecosystems.

Here, I present a study of the effects of fire-mediated, landscape-scale heterogeneity on avian diversity. I test for relationships between avian diversity and temporal and spatial characteristics of a fire regime at the landscape scale corresponding with the scale of fire prescription. Avian communities are known to respond to disturbance processes via changes in habitat structure and vegetation resources that alter food resources, foraging substrates, nest sites, predation, shelter and competition (Brawn et al. 2001). Furthermore, studies have shown that bird diversity responds rapidly to changes in vegetation structure following fire (Barton et al. 2014) and to landscape heterogeneity (Morelli et al. 2013). While the majority of studies investigating the effects of pyrodiverse fire regimes on birds have been conducted in shrublands and forests (Taylor et al. 2013b; Sitters et al. 2014b; Tingley et al. 2016; Prowse et al. 2017), very few have been conducted in savannas (*but see* Beale et al. 2018). The objective of this study was therefore to test the hypothesis that avian diversity increases with increasing pyrodiversity. I take a multifaceted approach, investigating the effects of multiple features of fire-mediated heterogeneity at two spatial scales on indices of avian diversity, including species richness and functional diversity.

3.3 METHODS

3.3.1 Study Area

The study was conducted at Pilanesberg National Park (PNP) and the nearby (5km) Mankwe Wildlife Reserve (hereafter Mankwe) in North West Province, South Africa (Figure 3.1). Both protected areas primarily comprise semi-arid savanna habitat, which falls primarily between November and March. Average annual rainfall at PNP was 637 mm (1999-2016; range 411-993 mm) and at Mankwe was 625

mm (2010–2016; range 352–835 mm). The vegetation is classified as sourish mixed bushveld and is a combination of grasslands and deciduous woodland dominated by *Acacia* and *Combretum* species (Acocks 1988). Most fires occur between May and August and, at both sites, are prescribed by land-managers, with occasional unplanned fires resulting from lightning or anthropogenic causes. At Mankwe a modified rotational block burning regime is used wherein established blocks of savanna habitat are burned every four to five years whilst maintaining some areas that burn more frequently, less frequently or not at all. The fire regime at PNP is based on the ‘patch-mosaic burning’ method and fires are ignited to vary in seasonality, space, and intensity (Brockett et al. 2001). Both protected areas sit within a matrix of human dominated landscapes and are immediately adjacent to developed areas, residential zones, and agriculture. The realities of this setting require an adaptive fire management regime, with decisions based on wildfire prevention or safety sometimes taking precedence over competing conservation priorities.

3.3.2 Bird Surveys

Survey points were located throughout the two study areas using a stratified-random sampling method, with points in all available fire age-classes (Figure 3.1). Points were spaced at least 250 m apart with a mean distance to the nearest neighbouring point of 409 m (range 251–2428 m). I surveyed points twice during two consecutive avian breeding seasons (October–March): once at the beginning of the season (October–November 2014 and 2015) and once towards the end of the season (January–March 2015 and 2016), resulting in four surveys per point. Surveys consisted of a 10-minute point count where all birds seen and/or heard within a 100-m radius were recorded. The observer used a laser rangefinder (Nikon Aculon-500m) to measure the distance to each detected bird. Point counts were conducted by the same experienced observer (TD) during the peak of vocal activity (sunrise until 10 am), and only during good weather conditions without rainfall or strong wind. The timing of repeat visits to points was varied to reduce sampling bias. Birds flying-over and not using the habitat or birds associated with water bodies were excluded from analyses. I visited 339 unique point count locations, with 302 of these points surveyed in the first season and 331 of these points surveyed in the second season (owing to access conditions), resulting in 1266 point counts.

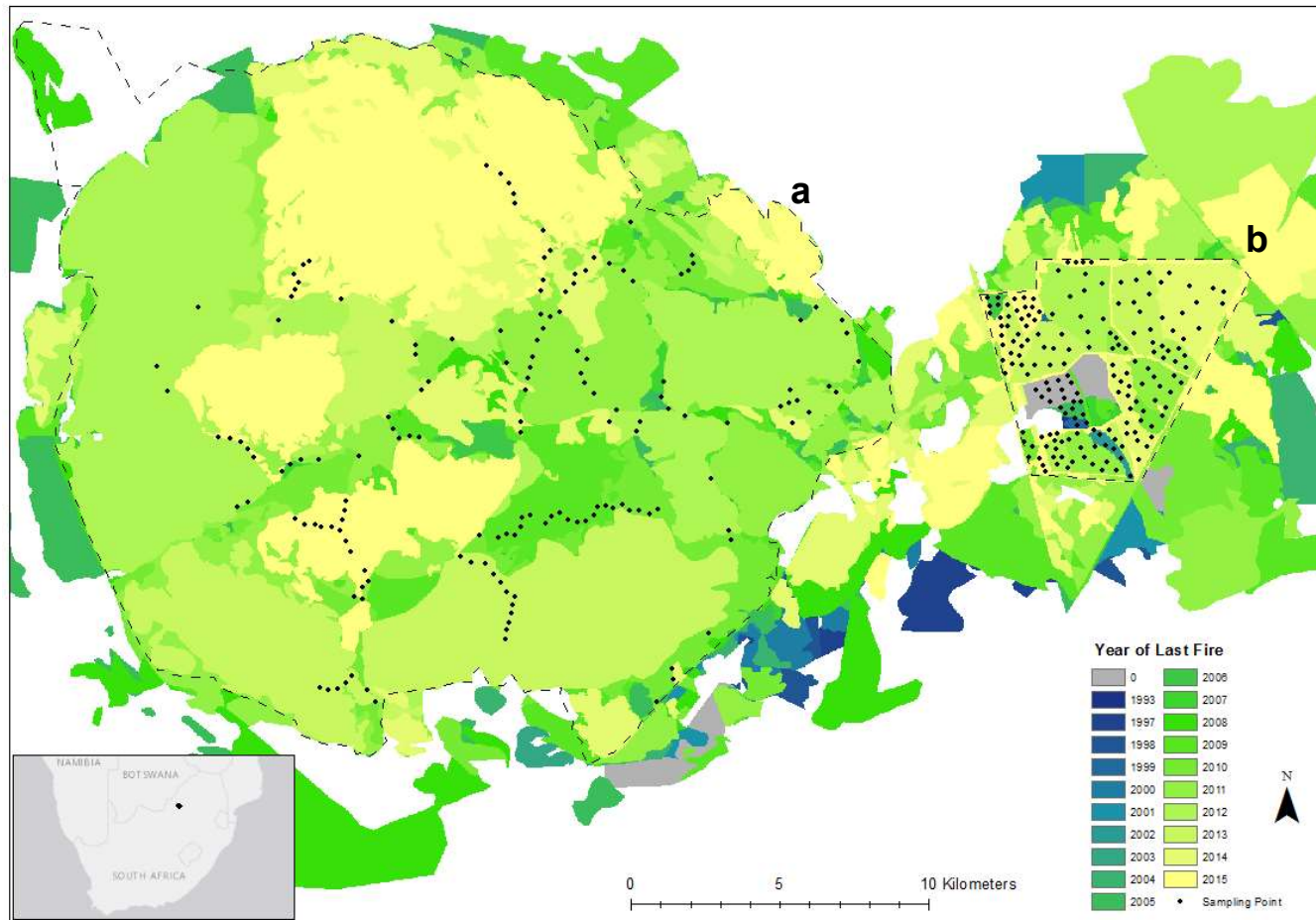


Figure 3.1 Location of the study area in South Africa. The map shows the avian sampling points and fire histories within the boundaries (dashed line) of (a) Pilanesberg National Park and (b) Mankwe Wildlife Reserve.

3.3.3 Avian Traits and Life History Characteristics

Qualitative and quantitative avian functional traits were compiled for all species detected, including life history traits and morphological characteristics. Trait data were extracted from Hockey et al. (2004) and comprised traits that may influence a species' response to fire (Sekercioglu 2006; Luck 2012). For traits that were highly correlated (Pearson correlation coefficient: $r > 0.7$), I retained only the trait considered most likely biologically relevant to the hypotheses; this resulted in 11 functional traits (Table 3.1). Many morphometric traits are correlated with body mass; I used the ratio of wing length to body mass to represent mass-independent morphology. Where necessary, data were normalised by square root (culmen length) or log- (clutch size and ratio of wing length to body mass) transformation.

3.3.4 Bird Species Richness and Functional Diversity

Bird species richness (hereafter SR)—the number of species recorded at each survey point—was calculated for each breeding season by compiling the total SR recorded across the two surveys. Shannon diversity was calculated for each breeding season as $\sum p_i \log(p_i)$, where p_i is the proportional abundance of a species at a point, using the 'vegan' package (Oksanen et al. 2015) in R (R Development Core Team 2016). For each species and each breeding season, the maximum count from the two surveys was used as the measure of abundance for a point. Avian functional diversity (hereafter FD) was quantified using the 11 functional traits and species abundances at points to produce a Gower dissimilarity coefficient, using the R package 'FD' (Laliberté & Legendre 2010; Laliberté et al. 2014). The Gower dissimilarity matrix was chosen because it allows mixed variable types (continuous, ordinal, and categorical) and missing values in the trait data (Laliberté & Legendre 2010). Three indices of FD were calculated for each survey point: 1) functional richness, 2) functional evenness, and 3) functional dispersion. Functional richness represents the "functional trait space" occupied by the community at a survey point (Villéger 2008). Functional evenness describes how regularly species abundances are distributed in functional trait space (Laliberté & Legendre 2010). Functional dispersion is a measure of how species are distributed in functional trait space; it estimates the mean distance of individual species to the centroid of this trait space, weighting these distances by species abundance (Laliberté & Legendre 2010). These measures of FD allow for the weighting of individual traits (Laliberté et al. 2014). For traits where an individual species can have more than one attribute (i.e. foraging behaviour), I

Table 3.1: Traits used to measure bird functional diversity indices.

Traits		Categories or Range	Data	Description and Functional Significance*
Life History	Foraging strategy	Carnivore, Insectivore, Omnivore, Frugivore, Nectarivore, Granivore, Scavenger	Factor	Diet or foraging strategy can affect all aspects of resource use, including seed dispersal, pollination, carcass and waste disposal, predation, nutrient cycling, and invertebrate populations. Birds with specialized diets are often more sensitive to disturbance.
	Foraging substrate	Ground, Off-ground, Air	Factor	Primary foraging location limits and concentrates a species' resource use. Foraging substrate is influenced by disturbance particularly when feeding is related to vegetation structure.
	Foraging behaviour	Ground, Aerial, Perch & Sally, Perch & Pounce, Glean, Hover, Dig, Probe	Binary	Species may have one or more method for foraging (e.g. catching prey in the air and on the ground). Species with specialized strategies are likely to be more affected by disturbance.
	Habitat use	Agriculture, Cliff or rocky outcropping, Forest, Grassland, Savanna, Wetland, Woodland	Factor	Primary habitat requirements constrain a species resource uses and other ecological processes such as nutrient cycling.
	Habitat breadth	1-13	Continuous	The number of unique habitats a species is known to inhabit or use. Species with low values are thought to be specialists increasing their sensitivity to disturbance.
	Mating behaviour	Pair, Facultative cooperative breeder, Obligate cooperative breeding, Brood parasite, Polyandrous, Polygynous	Factor	Habitat disturbance and change is known to influence or disrupt social behaviours such as pair forming or cooperative breeding.
	Clutch size	1.0-6.6 eggs	Continuous	Average number of eggs per nest attempt. Low clutch sizes may be more sensitive to disturbance.
	Nest site	Ground, Grass, Shrub, Tree, Cavity, Niche,	Factor	Nesting location or strategy can make a species vulnerable to disturbance and can concentrate resource use and nutrient cycling to one area. Cavity nesters are ecosystem engineers.

Traits		Categories or Range	Data	Description and Functional Significance*
	Migratory status	Resident, Resident with local movement, Nomad, Intra-African Migrant, Inter-Continental Migrant	Factor	Related to wing length to body mass ratio, metabolic rates and annual resource use and functional contributions to an ecosystem. Can influence broad scale nutrient cycling and resource use.
Morphological	Culmen length	5.0-111.2 mm	Continuous	Effects the type of food a bird consumes. Influences the manipulation of seeds and fruits, the size of seed or prey, as well as nectar or insect feeding.
	Wing length to body mass ratio	0.1-10.9 mm/g	Continuous	Length of wing (mm) divided by body mass (g). Large bodied species are often rarer and more sensitive to disturbance. Relates to life span, foraging behaviour, and home range size. Affects dispersal ability which affects nutrient cycling, seed dispersal and resource use. Species with limited mobility may be associated with more heterogeneous areas (which provide more diverse foraging and nesting opportunities) because their requirements need to be met within a small area.

*Functional significance from Sekercioglu 2006 and Luck et al. 2012

weighted binary attributes by the reciprocal of the number of attributes for each trait (Laliberté & Legendre 2010).

Shannon diversity was highly correlated with SR (Pearson correlation coefficient: $r = 0.84$). Consequently, and to simplify the interpretation of the results, I decided to use only SR as the measure of taxonomic diversity. The three indices of FD and SR were independent of one another ($r < 0.3$), except for functional richness and SR ($r = 0.72$). To examine changes in functional richness independent of SR a simulation analysis was used to create a null distribution of functional richness values (Pakeman 2011; Luck et al. 2013). I generated 1000 random assemblages at each survey point by maintaining the observed SR and randomly assigning species from the entire observed species pool. Functional richness was then calculated for each simulated community at each survey point in each season. Observed functional richness was considered significantly different from the expected functional richness if it fell outside of the central 950 ranked random values of the null distribution. This enabled us to determine if functional richness varied due to SR or if it varied due to the landscape variables.

3.3.5 Fire History and Vegetation Mapping

The vegetation and fire history within the study area was mapped separately using Landsat 5 and 8 surface reflectance imagery (30 m resolution) in Quantum GIS (QGIS 2016). To locate individual fire patches, Landsat data was displayed using the bands red, middle infrared, and near-infrared in blue, green, and red colours (Bowman et al. 2003; Jones et al. 2013). The boundary of every fire (including unburned interior areas) occurring between January 1989 and March 2016 was hand digitized at a constant scale (1:25,000). Each fire patch was assigned an age-class based on the calendar year in which it burned (Figure 3.1). To verify the dates of ignition derived from Landsat data, I used fire maps provided by the land managers for each study area. In a few cases where no ignition date data was available for old fires, I acquired the apparent month of ignition from Landsat imagery and set the ignition date as the 15th of that month. In addition, the vegetation at the study sites was mapped using Landsat 8 images. Vegetation was mapped as either tree covered (hereafter woodland) or open grassland with an object-based, segmentation resulting in discrete patches of woodland amongst open savanna grassland. The resulting vegetation raster was made up of discrete patches of woodland within a matrix of savanna grassland, with the latter including open grassland and grassland interspersed with shrubs and trees.

3.3.6 Landscape Variables

Landscape variables were derived from the previously described rasters using Fragstats 4.0 (Mcgarigal et al. 2012). Two pyrodiversity variables and three habitat variables were computed. To characterize the pyrodiversity I calculated metrics to describe the composition and configuration of the fire mosaic (Table 3.2). The composition of the fire mosaic was explained by the Shannon habitat diversity index (SHDI), which accounts for the number of age-classes in a landscape and their proportional area. The shape and configuration of the mosaic were described using the SHAPE variable in Fragstats, which quantifies the mean shape complexity of fire patches within a landscape, weighted by their area (Mcgarigal et al. 2012). In addition, the mean edge-contrast index (CONTRAST) was calculated, which describes the difference between adjacent patch types. I assigned contrast values (0–1) to each patch ranked by the degree of contrast between the burn age-class of the patch and that of neighbouring patches, with a value of 1 being maximum contrast and 0 being no difference.

The proportion of the landscape that had burned ≥ 10 years previously (OLD hereafter) and that had burned recently (burns occurred < 1 year prior to the survey, NEW hereafter; Table 3.2) were calculated. I included a variable quantifying the proportion of the landscape that is woodland (WOOD). I did not include a variable for savanna grassland cover as it was effectively the inverse of WOOD. These variables (OLD, NEW and WOOD) accounted for potential habitat-specific drivers of avian diversity that may not be related to spatial properties of fire age-class heterogeneity.

Spatial scale was considered by measuring the landscape metrics at several different circular spatial extents (25 ha, 50 ha, 100 ha, 250 ha, 500 ha, 750 ha, 1000 ha, 1250 ha, and 1500 ha) centred on each survey point. However, preliminary exploratory analyses suggested that relationships between SR and the explanatory variables were strongest at the 100-ha and 500-ha scales and that these two scales encompass the range of existing variation for each explanatory variable. These two spatial extents are also comparable to the scale of application of fires in this study area. Consequently, in subsequent analyses, I used only landscape metrics derived at the 100-ha and 500-ha scales.

Table 3.2. Landscape variables used to characterize the landscape. Subscripts denote the scale at which the metric was measured (100 ha or 500 ha)

Variable	Description	Abbreviation
Fire Age-Class Diversity*	Shannon's diversity index measures landscape diversity by the number of patch types and the proportional area distribution among patch types	SHDI ₁₀₀ SHDI ₅₀₀
Fire Shape Complexity*	Area-weighted mean shape index measures the complexity of patch shape compared to a square of the same size with a square having the minimum value of one.	SHAPE ₁₀₀ SHAPE ₅₀₀
New Habitat	Proportion of landscape that was recently burned (<1 year).	NEW ₁₀₀ NEW ₅₀₀
Old Habitat	Proportion of landscape that has not burned in ≥10 years	OLD ₁₀₀ OLD ₅₀₀
Woodland Habitat	Proportion of landscape that is tree covered	WOOD ₁₀₀ WOOD ₅₀₀
Site	Pilanesberg National Park or Mankwe Wildlife Reserve	SITE

*For a more detailed description of these variables see Mcgarigal, Cushman & Ene (2012).

3.3.7 Statistical Analyses

Linear mixed models with a Gaussian error were used to model the relationship between avian diversity (i.e., SR and the three indices of FD) and the landscape variables at two spatial scales. Preliminary data exploration was conducted following Zuur, Ieno & Elphick (2010). The variance inflation factor (VIF) was used to check for multi-collinearity among all explanatory variables; variables with a VIF > 3 were considered collinear (Zuur et al. 2010). The variable CONTRAST was highly collinear (VIF > 10) with the extent of old, unburned habitat at both scales and was therefore excluded from further analyses. High collinearity was observed between variables at the two focal spatial scales (100-ha and 500-ha); because of this, I did not fit any multi-scale models. Survey point was included as a random effect to account for repeated surveys across sampling seasons while all other variables were treated as fixed effects.

A Mantel test was used to test for spatial autocorrelation in the R package *ade4* (Dray & Dufour 2007). This test showed significant autocorrelation in the data ($r = 0.18$, $P=0.02$); however, this was

because points from PNP were more similar to each other than to points from Mankwe. No spatial autocorrelation was present (PNP: $r = -0.028$, $P=0.798$, Mankwe: $r = -0.001$, $P=0.497$) when separate Mantel tests were run for each site. Consequently, site (i.e., PNP and Mankwe) was included in all candidate models to account for this spatial variation. Spline correlograms (produced with 1000 permutations using the 'ncf' package in R; Bjornstad 2016) of the Pearson residuals were used to confirm no spatial structure remained.

An information theoretic approach to model selection was taken and *a priori* models were ranked using Akaike's Information Criterion (AICc), which includes a correction for small sample size (Burnham & Anderson 2002). I built a candidate model set ($n = 188$) with both additive and interactive combinations of the explanatory variables. Candidate models were single-scale models where all explanatory variables were included in a model at the same spatial scale. Models with a ΔAICc of ≤ 6 and less than the ΔAICc of all its simpler nested models were included in the top model set (Richards 2008). I model averaged across all models in this top set and computed 95% confidence intervals. All estimates of effect sizes are given as means ± 1 standard error. Model selection and model averaging were conducted using the 'nlme' (Pinheiro et al., 2014) and 'MuMIn' packages (Barton, 2016) in R (R Development Core Team 2016).

3.4 RESULTS

A total of 32,880 birds of 213 species were detected during surveys over two sampling seasons. Mean SR across all points was 23.4 (range = 8–50, SD = 6.72). Mean values of FD were: functional richness 0.18 (range = 0.01–0.48, SD = 0.08), functional evenness 0.85 (range = 0.67–0.96, SD = 0.04), and functional dispersion 0.31 (range = 0.09–0.38, SD = 0.03). Levels of observed SR and functional richness were higher at PNP than at Mankwe.

3.4.1 Species Richness Response to Landscape Variables

Variation in avian SR was not explained by pyrodiversity complexity and configuration, as SR was not associated with SHDI or SHAPE at either spatial scale (Figure 3.2). In contrast, SR was positively associated with the proportion of NEW and OLD at both spatial scales (Figure 3.2). The strongest predictor of SR was the proportion of OLD at the 100-ha scale (Figure 3.2a). SR was also positively associated with WOOD at the 100-ha scale (Figure 3.2a). Thus, sites surrounded by greater proportions

of newly-burned, old burn, and woodland cover had higher overall SR. The four top models for SR were all at the 100-ha spatial scale and all contained a significant interaction between NEW and WOOD ($\beta = 7.1 \pm 2.9$; Table A3.1); the effect of NEW on SR was greater when the landscape contained more woodland and this effect was greater at PNP (Figure 3.3a).

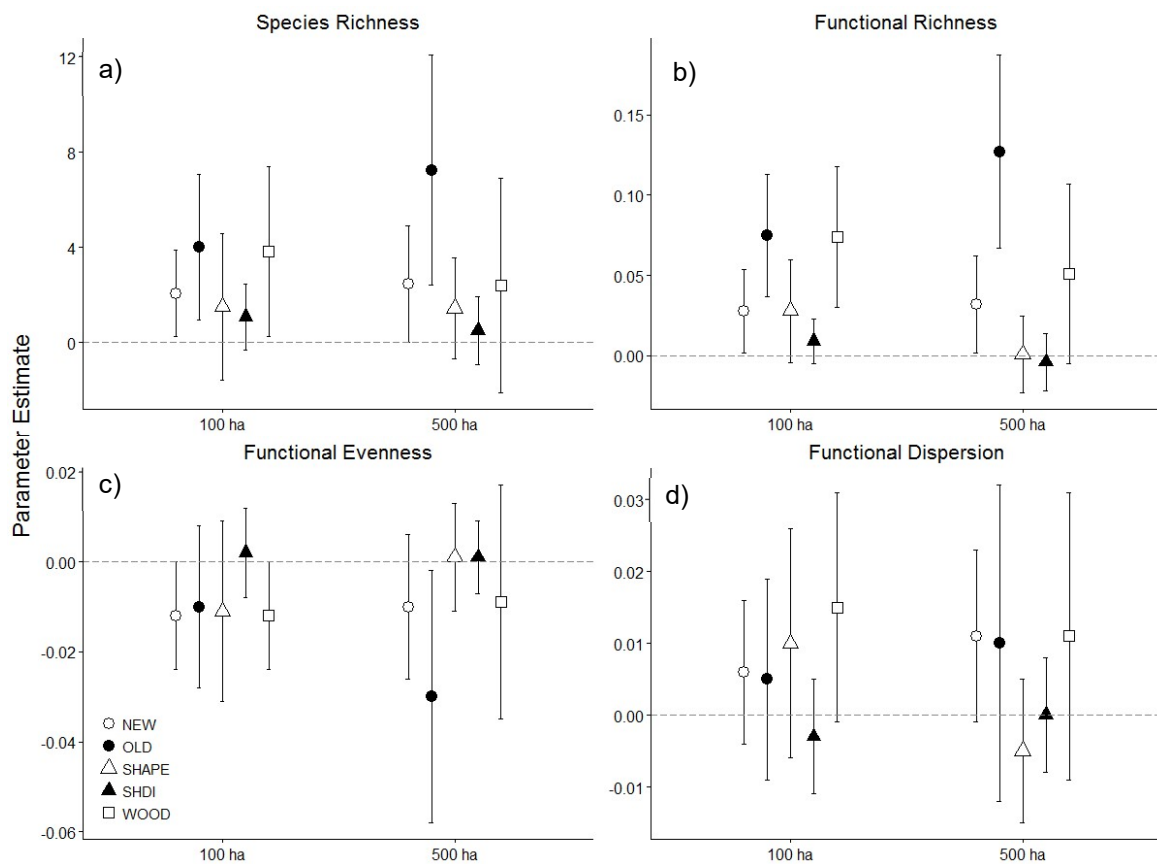


Figure 3.2 Model-averaged parameter estimates and 95% confidence intervals for landscape variables in the candidate set of models; effects of each landscape variable on species richness, functional richness, functional evenness and functional dispersion at the 100-ha and 500-ha scales.

3.4.2 Functional Diversity Response to Landscape Variables

None of the FD indices (i.e. functional richness, evenness and dispersion) were related to SHDI or SHAPE at either spatial scale, indicating that functional diversity did not vary with the diversity or composition of fire patches in the surrounding landscape. In contrast, functional richness significantly increased with increases in NEW, OLD, and WOOD within the 100-ha landscape and with increases in NEW and OLD within the 500-ha landscape (Figure 3.2b), indicating the number of functional traits was highest in landscapes with both newly-burned and old burn habitat. Functional evenness had a significant negative relationship with the amount of OLD at the 500-ha scale (Figure 3.2c). Functional evenness was best explained by a model that included an interaction between the extent of NEW and OLD at 500-ha (Table A3.1; $\beta = -0.66 \pm 0.17$). This relationship was only significant at Mankwe (Figure 3.3b). When the proportion of OLD was low, functional evenness was unaffected by greater amounts

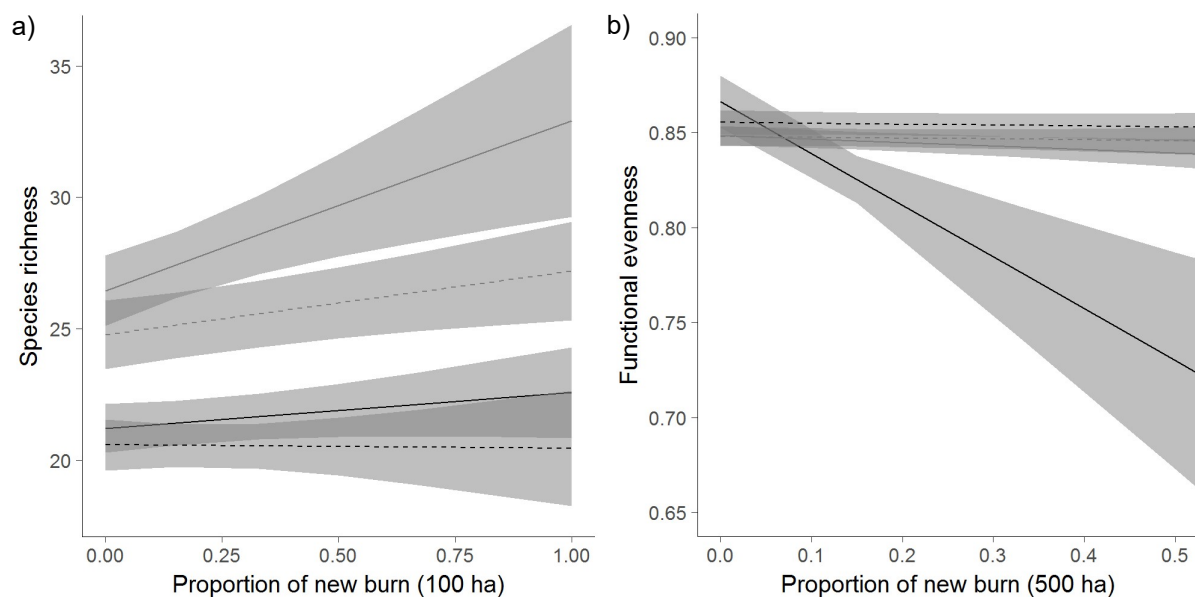


Figure 3.3 (a) Modelled avian species richness in relation to the proportion of newly-burned habitat, in areas of low (dashed line) and high (solid line) woodland cover. Modelled effects are shown for Pilanesberg National Park (grey lines) and Mankwe (black lines). (b) Functional evenness in relation to the proportion of new burn at the 500-ha scale; lines and colours are as in (a). Modelled effects in both plots are from the highest-ranking model. Low woodland cover is represented in these models as the 10th percentile of recorded woodland cover and high woodland cover as the 90th percentile. Shading around lines show 95% confidence intervals. The observed data are not displayed here in order to improve the visibility of the predicted relationships (lines).

of NEW. In contrast, when the extent of OLD was high, functional evenness declined significantly with increases in NEW at Mankwe (Figure 3.3b). Functional dispersion did not relate to any of the main predictors at either scale (Figure 3.2d).

3.4.3 Differences in Functional Richness from Random

Values of observed functional richness were positively related to values of SR (Figure 3.4). Thus, species rich sites are functionally rich sites (Figure 3.4). The comparison of observed functional richness to that of simulated communities indicated that the majority (88%) of survey points had lower than expected functional richness and 17% of survey points were significantly lower ($\alpha = 0.05$) than the null distribution (Figure 3.4). However, the distribution of lower than expected values were distributed evenly across gradients of landscape variables (Figure S3.1), indicating that differences between observed and expected values of functional richness were unrelated to any of the landscape variables at either spatial scale.

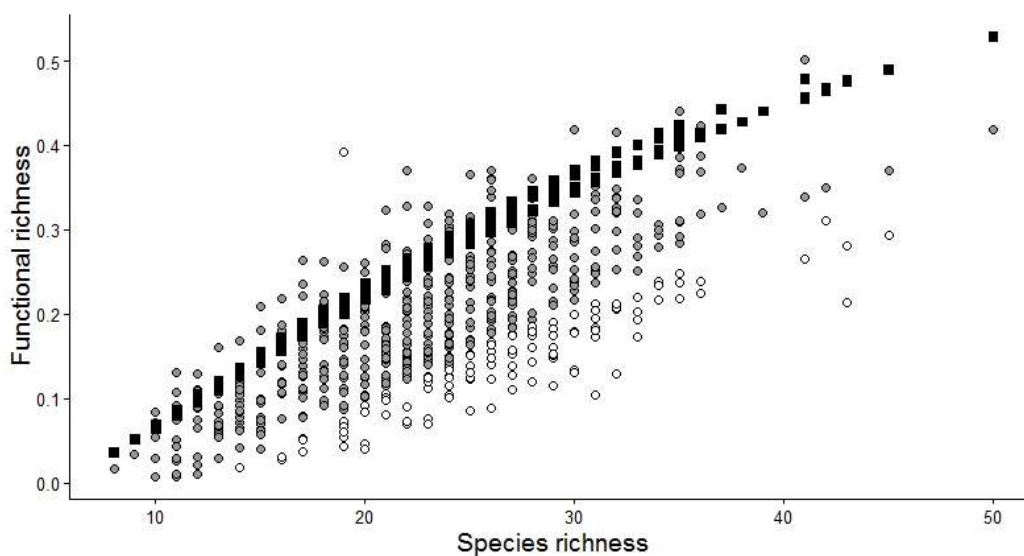


Figure 3.4 The observed (circles) and expected (black squares) functional richness values against the observed species richness. Open circles denote communities for which the observed functional richness differed significantly ($\alpha = 0.05$) from expected at a given level of species richness.

3.5 DISCUSSION

Fire age-class diversity (SHDI) and configuration (SHAPE) did not affect avian diversity at the taxonomic or functional level, providing very little support for the PPB hypothesis. Moreover, the extent of the extremes of the fire regime, i.e. the amount of newly-burned and old burn areas, best predicted both avian SR and measures of FD. These relationships are discussed below, in relation to avian habitat preferences, habitat filtering and functional redundancy, and the implications for fire management practices for conservation.

Newly-burned habitat was positively associated with species richness, consistent with previous empirical studies of birds (Nkwabi et al. 2011), mammals (Klop & Prins 2008), and other taxa (Moretti et al. 2010). Such associations are recognized as the result of temporary changes in post-fire resources that benefit particular early-successional species (Hutto 1995). However, it also implies that the influx of post-fire specialists was not matched by an efflux of post-fire evaders. Some species, including disturbance-adapted species, large birds, ground-breeding birds and ground-feeding insectivores preferentially utilize recently burned grassland in South Africa (Bouwman & Hoffman 2007). Many species were far commoner on the newly-burned habitats than elsewhere and some species, such as Temminck's courser (*Cursorius temminckii*) and buffy pipit (*Anthus vaalensis*), occurred exclusively in such areas, suggesting that a suite of species rely on annual burns in the study area. The positive relationship between species richness and newly-burned habitat was greater when the landscape contained a greater proportion of woodland cover. This indicates that locations where new burn and woodland overlap are important for maintaining savanna biodiversity, and is consistent with suggestions that habitat type and vegetation structure are important predictors of how species respond to fire (Barton et al. 2014).

Species richness was best predicted by the extent of old, unburned habitat (no fire in ≥ 10 years); for perspective, an increase of just 100 ha of this habitat across the study sites would increase species richness by approximately four species (Figure 3.2a, Table A3.2). This implies that species richness is positively associated with late-seral stage vegetation, greater woody biomass, and more structurally complex habitats, which are characteristic of long-unburned savanna systems (Higgins et al. 2007; Levick et al. 2012). These results correspond with other ecosystems, where the proportion of older, unburned vegetation was deemed an important predictor of avian diversity (Watson et al. 2012a; Taylor et al. 2012). Protecting large extents of late-seral habitat is important because unburned sites

may provide refuge for fire-sensitive species and, furthermore, may facilitate rapid post-fire recovery of species assemblages in a patchy landscape (Watson et al. 2012a).

Indices of functional diversity did not relate to the composition (SHDI) or configuration (SHAPE) of fire-mediated heterogeneity. Functional richness increased with the extent of old, unburned savanna, which is characterized by increased woody biomass and vegetation complexity (Higgins et al. 2007). Increases in tree and canopy cover can provide increases in foraging and nesting opportunities (Barton et al., 2014), ultimately providing greater resources for a range of species and functions. The positive relationship between functional richness and newly-burned habitat was unexpected, owing to existing evidence that functional richness declines with increasing disturbances that simplify habitat structure (Laliberté et al. 2010; Pakeman 2011; Edwards et al. 2013b). Newly-burned savannas are characterized by bare ground, a simplified herbaceous layer, and early-seral vegetation (Andersen 2003). Yet, as functional richness is sensitive to inflation by rare species with unique traits (Laliberté & Legendre 2010), the increase in functional richness in newly-burned habitats is most likely due to an increase in species exploiting post-fire changes in resources and habitat structure. In a study of the effects of time-since-fire on functional diversity in Australian birds, Sitters *et al.* (2016) also found that functional richness was high in recently-burned habitat. They attribute this relationship to the patchy nature of fires, resulting in altered vegetation structure, enhanced fine-scale heterogeneity, and increased resource availability.

Functional evenness describes how regularly abundance is distributed in the trait space of a community. Low levels of evenness occur when there is an irregular spread of species and abundance in occupied trait space (Villéger 2008) or an increase in species abundances within part of the functional trait space (Pakeman 2011). These findings show that low levels of evenness occur at sites with large extents of newly-burned and old burn habitat. This relationship was only significant at Mankwe (Figure 3.3b). Loss of functional evenness can occur when new species are added to the community and cause greater unevenness in the abundances across species (Luck et al. 2013). In this system, it is likely that this decrease in evenness resulted from the addition of rare or specialist species (e.g. disturbance-adapted, fire-sensitive species or late-seral species) associated with the newly-burned or the old, unburned savanna. Barbaro *et al.* (2014) identified a positive relationship between landscape diversity in fragmented forests and functional dispersion, but I did not find an association between functional dispersion and any of the landscape variables. Unlike functional richness, functional dispersion is not influenced by species richness but is influenced by species abundance (Laliberté et al. 2010). As

heterogeneous habitats offer an increased number of niches, I expected to find enhanced functional dispersion associated with pyrodiversity.

The positive relationship between functional richness and species richness suggests that functional richness is largely driven by changes in species richness (Figure 3.4). This relationship is expected because a larger number of species will fill a larger functional trait space; the relationship indicates that new species are adding functionally-unique traits (Villéger 2008). Most of the study sites had avian assemblages that occupied less functional trait space than would be expected due to chance (Figure 3.4). This general decrease in trait space was observed across study sites and landscape variables (Figure A3.1) and suggests that habitat filtering is occurring (Cornwell et al. 2006). Habitat filtering occurs when ecological conditions select for species that have similar traits (i.e., a reduction in functional richness) that are suitable for a given site (Cornwell et al. 2006), resulting in the non-random co-occurrence of species that are functionally redundant (Laliberté et al. 2010). It is plausible that a fire-prone environment like the present study area, with relatively frequent fires occurring across an ever-changing burn mosaic, has, over time, excluded species lacking fire-adapted traits. However, the environmental filters affecting functional diversity in savanna habitat require further investigation.

Functional redundancy has been identified as an important factor affecting resilience and stability in response to disturbance (Luck et al. 2013). The results of this chapter demonstrated that functional diversity was not significantly reduced by any of the fire landscape variables, although functional richness was lower than expected across all sites. Studies have noted that the biota in fire-prone landscapes such as savanna (Parr & Andersen, 2008; Andersen et al., 2014) and Mediterranean woodland (Jacquet & Prodon, 2009) can demonstrate a remarkable degree of resilience to burning. Functional redundancy may represent resilience against the loss of ecosystem functions within a species assemblage in the event that species with overlapping traits respond differently to disturbance (Laliberté et al. 2010). However, it is important that confidence in resilience to conserve ecological functions does not neglect the importance of rare traits and their contributions to ecological functions. Understanding the mechanisms contributing to resilience may assist in identifying thresholds and regime shifts beyond which savanna systems may not return to pre-fire states (Spasojevic et al. 2016).

3.5.1 Implications for Conservation and Management

The lack of support in this study for the PPB paradigm is troubling because, not only are predominant burning methods (i.e., patch-mosaic burning) in South Africa and elsewhere based on this paradigm, but I also tested it at a site where these methods were formalized (Brockett et al. 2001). However, while the results for avian diversity did not support the PPB hypothesis, this does not preclude the use of fire mosaics. Landscapes attempting to recover or protect late-seral habitat, while also undergoing regular fire prescriptions, are expected to have a range of post-fire successional stages. Yet, care must be taken when implementing a mosaic of fire age-classes. Studies have demonstrated that fire mosaics may not protect late-seral habitat leading to the regional extinction of avian species (Brown et al. 2009). At Pilanesberg National Park, the fire regime has resulted in the limited extent of late-seral savanna, suggesting that patch-mosaic burning methods inadequately protect this habitat. For example, the maximum amount of unburned habitat within 100 ha of a survey point was 38 ha for PNP (96 ha for Mankwe). Therefore, land managers may have to find a balance between new fire prescriptions, maintaining unburned savanna and mitigating wildfire risk due to increased fuel loads. This challenge is compounded by a changing South African climate where wildfires are predicted to increase in size and frequency (Archibald 2016). These conditions may necessitate an adaptive approach to burning and wildfire prevention, possibly requiring the careful use of infrastructure such as fire-breaks and roads. While the present study only focused on birds, the maintenance of early- and late-seral state as well as intermediate stages of savanna will likely support the habitat requirements of a range of taxa. However, as the habitat requirements of savanna taxa vary (Klop & Prins 2008; Davies et al. 2012), empirical data for other taxa would further contribute to the development of functional fire management for savanna systems.

Here, I demonstrated that both taxonomic and functional diversity responded to landscape predictors at multiple spatial scales and at scales commensurate with fire prescription. I identified that birds are most responsive to habitat mosaics generated by burn management at a 100-ha scale. In addition, the finding that the extremes of the fire regimes—newly-burned and unburned habitat—both had significant positive effects on taxonomic and functional diversity provides land managers with valuable insight for conserving avian diversity in this study regions. Most notably, an increase of 100 ha of old, unburned habitat can add 4 avian species to the landscape. The results at the landscape scale translate directly to easily defined fire prescriptions. I emphasize the importance of empirical landscape-

scale fire studies as they provide results at scales that are relevant to conservation management, thus supporting the incorporation of biodiversity data into the development of robust fire management practices.

Chapter 4

The response of invertebrates to fire is contingent on rainfall in
an African savanna



Familiar chat (*Oenanthe familiaris*)

4.1 ABSTRACT

Fire is a vital natural disturbance and an important conservation management tool in savanna systems. By altering vegetation structure and the availability of resources, fire regimes play a dynamic role in structuring biological communities. However, the evaluation of fire effects on savanna invertebrate fauna worldwide have produced inconsistent findings. Here I investigate, for the first time, the simultaneous and interactive effects of time-since-fire and fire frequency on invertebrate fauna. I also evaluate interactions between fire attributes and rainfall. Working in semi-arid savanna in South Africa, I evaluated the effects of long-term fire regimes, habitat structure and rainfall on order richness, abundance and biomass. I reveal that these two fire attributes have opposing influences on grass-layer and ground-layer invertebrate communities, and that impacts of fire are strongly mediated by seasonal rainfall, which might explain inconsistencies across previous studies. In grass-layer communities, dominated (in biomass terms) by Orthoptera, high rainfall in recently burnt areas resulted in increases in invertebrate biomass that were four times greater than increases seen in similar areas during low rainfall periods. However, in long-unburnt areas biomass was equally high, regardless of rain. This suggests that in drought periods, avoiding burning will maximise grass-layer insects. This strategy would also maximise insect order richness in the grass layer, regardless of rainfall events. By contrast, ground layer invertebrates were abundant in areas that had recently and frequently burned, regardless of rainfall, but declined in areas that had not been burned for longer periods. Areas left unburned for long periods maintained higher levels of ground invertebrate abundance in wet periods than in dry periods. This suggests that to maximise ground-level invertebrate abundance, areas can be burned regularly regardless of rainfall events; this approach would also maximise ground layer order richness across different rainfall regimes. The findings demonstrate that, despite the key role of rainfall in shaping invertebrate abundance patterns in savanna systems, burn strategies can be designed that would promote invertebrate numbers regardless of annual rainfall regimes. Management strategies can be designed to maximise ground or grass layer insect numbers, but not both. Integrating these findings with our insights into fire return intervals will inform burn management planning for different invertebrate groups and the species that depend upon them.

4.2 INTRODUCTION

Fire is an important natural disturbance and a major driver of ecosystem composition and function. Anthropogenic factors such as fire suppression, human encroachment, agricultural expansion and climate change alter natural fire regimes (Driscoll et al. 2010; Midgley & Bond 2015) with long-term impacts on ecosystem dynamics (Bowman et al. 2009). The individual spatial and temporal fire attributes (e.g. size, intensity, frequency, and seasonality) that comprise a fire regime may each have a significant independent or combined effect on biological communities (Archibald 2016). Given the importance of these disturbance regimes, management plans in many fire prone habitats include prescribed fire regimes to support the conservation of biodiversity (Kelly & Brotons 2017). However, ecological evidence to support and evaluate fire management in fire-prone ecosystems is limited (Driscoll et al. 2010). This is particularly true for evidence of invertebrate fire responses.

Invertebrates are sensitive to changes in disturbance regimes, habitat, and climate partially owing to their specialized microhabitat requirements, host-interactions, and vulnerable life history stages (Evans 1984). Given their essential roles as prey, pollinators, seed dispersers, herbivores and detritivores (Lavelle et al. 1997; Losey & Vaughn 2006), understanding how invertebrates respond to variation in fire regimes is important for the conservation of savanna ecosystems. A range of invertebrate responses to fire have been documented among habitats including a positive response by some groups (ants: Andersen 1991; York 1999; Sackmann & Farji Brener 2006; spiders: Haugaasen et al. 2003; Teasdale et al. 2013), a negative response by other groups (Hemiptera: Radford & Andersen 2012; Lepidoptera: Akite 2008; Little et al. 2013) and mixed responses for other groups in different studies (beetles: Muona & Rutanen 1994; Orgeas & Andersen 2001; Sackmann & Farji Brener 2006; grasshoppers: Bock & Bock 1991; Teasdale et al. 2013; Little et al. 2013). Most savanna invertebrate studies have focused on a single taxonomic group, particularly ants (Izhaki et al. 2003; Parr et al. 2004; Barrow et al. 2007; Parr & Andersen 2008; Andersen et al. 2014; Calcaterra et al. 2014; Kone et al. 2018). Studies in savanna have revealed that ants are remarkably resilient to variation in a fire regime (Izhaki et al. 2003; Barrow et al. 2007; Parr & Andersen 2008; Andersen et al. 2014). However, evidence from a small number of invertebrate taxa prevents our understanding of a full range of fire responses and constrains our ability to make generalisations and predictions of invertebrate response to changing fire regimes in savanna systems.

Evidence of how fauna respond to long-term fire regimes can support the development of ecologically sustainable fire management (Driscoll et al. 2010). However, for invertebrates this evidence is constrained by the short-term nature of studies of fire response (Orgeas & Andersen 2001; Farji Brener et al. 2002; Haugaasen et al. 2003; Andersen et al. 2006; Sackmann & Farji Brener 2006; Barrow et al. 2007; Vasconcelos et al. 2009; Pryke & Samways 2012b; Calcaterra et al. 2014; Kone et al. 2018). The response of invertebrates to fire can be direct and immediate (i.e., mortality and emigration; Swengel 2001). However, in the long-term invertebrates may respond to fire indirectly via changes in habitat structure and resource availability, related to post-fire successional processes and varied fire frequencies (Briani & Palma 2004; Davies et al. 2012; Radford & Andersen 2012; Griffiths et al. 2015). In savanna systems, fire regimes influence habitat structure by altering grass height (Bond & Keeley 2005) and leaf litter depth (Vasconcelos et al. 2009) in the short-term, while limiting tree recruitment (Higgins et al. 2000) and modifying woody vegetation cover (Sankaran et al. 2008; Case & Staver 2017) in the long-term. In addition, the repetition of fires over decades can alter the composition of soil nutrients in savanna habitat (Pellegrini et al. 2018), with effects on invertebrates (Bastias et al. 2006). A study that examined a long-term fire regime in Australian shrubland found that some invertebrate Orders were most abundant 40 years post-fire (Friend & Williams 1996). Evidence of how fauna responds to the extent of variation in a fire regime can guide fire management on the upper and lower limits of fire frequencies that best protect at-risk fauna (Griffiths et al. 2015).

While most studies have investigated the effects of fire regime attributes (e.g. fire frequency or time-since-fire) separately; these fire attributes do not operate in isolation, but rather interact with each other to shape habitat structure in the long-term (Morrison et al. 1995). For example, in conifer forest in California, where fire severity is an important attribute influencing forest structure, Tingley et al. (2016) discovered important interactions between time-since-fire and burn severity and determined that severity had a greater impact on avian diversity 10-years post-fire than 1-year post-fire. Furthermore, fire regime attributes interact with other environmental processes such as climatic drivers (Archibald et al. 2010). Rainfall has been identified as the main driver of the spatial and temporal variation in fire regimes in African savannas, particularly in arid regions (i.e. rainfall < 650 mm yr⁻¹; Hempson et al. 2017). Furthermore, rainfall is an important predictor of fire response in savanna fauna (Blanche et al. 2001; Vasconcelos et al. 2009; Beale et al. 2018), most likely due to the interactive effects of fire and rainfall on vegetation structure (Sankaran et al. 2005; D'Onofrio et al. 2018). Understanding the

interactions that underpin fire responses is important for conservation management (Driscoll et al. 2010). Changes in disturbance regimes and environmental drivers, have already led to alarming losses of invertebrate diversity and abundance worldwide (Dirzo et al. 2014; Lister & Garcia 2018). Given predictions of increasing fire frequencies and shifting climatic drivers (e.g., rainfall and temperature) in southern Africa (Pricope & Binford 2012; Conway et al. 2015), knowledge of how invertebrates respond to variable fire regimes in the long-term is important for making predictions about the ecological effects of emergent fire regimes and developing fire management strategies.

In this chapter I investigate the effects of fire regimes on two invertebrate communities in semi-arid savanna in South Africa. The objective of this study was to evaluate how invertebrates respond to the long-term effects of fire management and how climatic drivers (i.e., rainfall) effect this response. To elucidate the long-term effects of fire regimes on savanna communities I evaluate variation in fire attributes over approximately three decades. Here, I take a community-wide approach and investigate the response of richness, abundance and biomass of invertebrates in the ground-layer and grass-layer to time-since-fire, fire frequency, and rainfall. I also evaluate the response of invertebrates to habitat structure features which are known to impact savanna biota. Lastly, I discuss the results in terms of their implications for the conservation and management of savanna fauna.

4.3 METHODS

4.3.1 Study Area

This study was conducted at Mankwe Wildlife Reserve (*hereafter* Mankwe), a 4760-ha private reserve in North West Province, South Africa (Figure 4.1). The habitat is sourish mixed bushveld and consists of grasslands interspersed with thickets and deciduous woodland (Acocks 1988). Dominant shrub and woody cover species include acacias (e.g. *Acacia tortilis*, *A. mellifera*, and *A. karroo*) and combretums (*Combretum* sp.) and dominant grasses include *Hyparrhenia hirta*, *Loudetia simplex*, *Themeda triandra*, and *Heteropogon contortus*. The fire regime at Mankwe is a modified rotational block burning method, where established blocks of savanna habitat are burned every four or five years whilst maintaining some areas that burn more frequently, less frequently or not at all. Most fires occur between May–August and are prescribed by land-managers, with occasional unplanned fires resulting from anthropogenic causes. Average annual rainfall at Mankwe is approximately 600 mm (2010–2016; range 352–835mm), with more than 90% of rainfall occurring between September/October and March/April.

4.3.2 *Invertebrate Sampling*

To sample a chronosequence of fire age-classes I used a stratified random method to select sampling sites across a gradient of fire ages (Figure 4.1). Sites were located more than 250m apart and at least 100m from the fire edge. Invertebrates were sampled at 178 unique sites over four sampling periods which coincided with the start (October–November 2014; October–November 2015) and the end (January–February 2015; February–March 2016) of the rainy season. I sampled 164 of the sites in the first and second sampling period and 176 of the sites in the third and fourth sampling periods, comprising 680 site visits in total (differences in sites sampled between years 1 and 2 resulted from site accessibility issues).

Terrestrial invertebrate samples were collected from the grass layer and from the ground-layer at each site. Sweep netting was used to sample the grass layer along two transects that began at a distance of 50 m in opposite directions from the centre of each site on an east-west axis. Each sample consisted of 50 swings of a 37-cm diameter muslin net while walking a steady pace toward the site centre. The two samples at each site were combined for the subsequent analysis. Sweep net samples were not collected in windy or rainy conditions or if the grass was wet.

To sample the ground-layer I used wet pitfall traps. Trapping only occurred during two of the four sampling seasons (October 2014 and October 2015) because I could not control for capture success during the wettest months (January to March) due to erratic rainfall and flooding. Two pitfall traps were placed 10 m apart on opposite sides of the site centre on a north–south axis. Traps consisted of dark-green plastic cups, each 10 cm in height and 7 cm in diameter. Traps were filled with 100 ml of water (traps were approximately one-third filled) and included a drop of detergent to decrease the surface tension. A brown, waxed-cardboard cover (14 cm diameter) was placed 3 cm above the top of each pitfall trap. Such covers have been shown not to affect capture rate or efficiency of invertebrates in dry grassland habitats (Buchholz & Hannig 2009) but to be effective in limiting rain and debris ingress, reducing evaporation of the solution, and minimising vertebrates disturbance (Hohbein & Conway 2018). Traps were collected 72 hours after deployment (i.e. 23,616 total trap hours in year 1 and 25,344 total trap hours in year 2). The invertebrate catches were transferred to a propylene glycol solution (30% concentration) in the field. For analytical purposes, each pitfall trap was considered an independent sample (Andersen & Müller 2000; Parr et al. 2004).

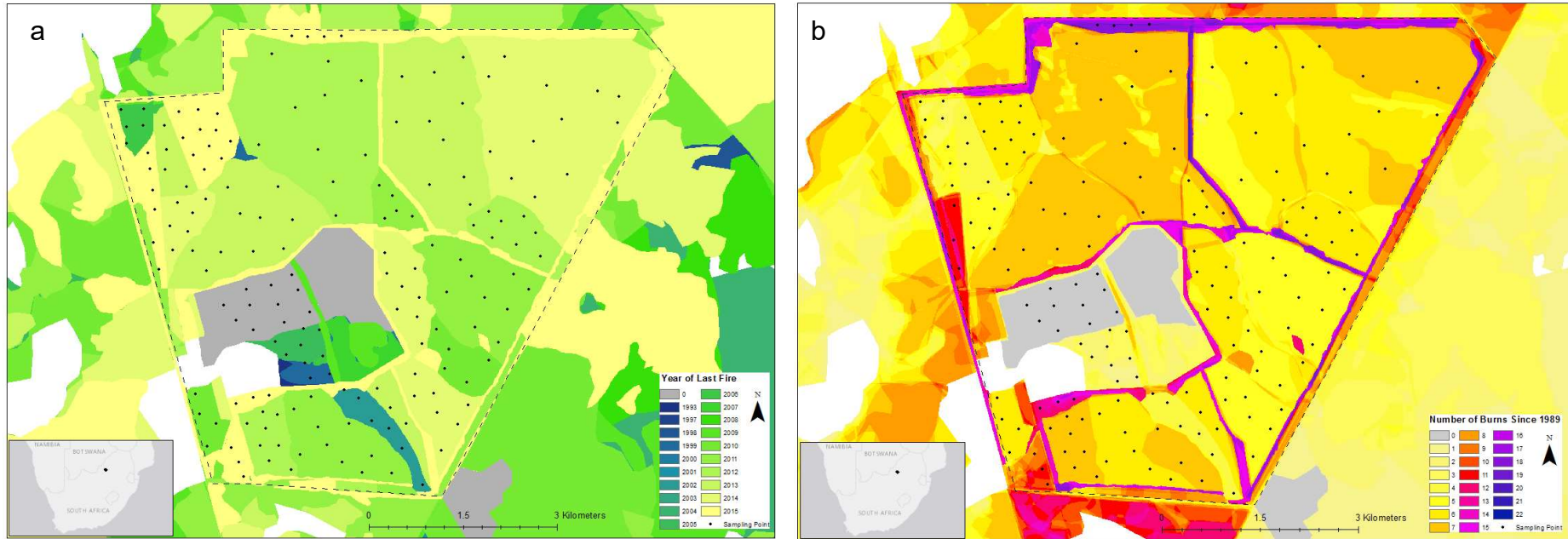


Figure 4.1 Location of study area in South Africa. Maps show the invertebrate sampling points and fire history at Mankwe Wildlife Reserve (dashed line). Fire history is represented by (a) year of last fire and (b) fire frequency.

All invertebrates were identified to order; this taxonomic level has been demonstrated to be effective for detecting invertebrate community response to land-use changes or environmental disturbance in an array of habitat types (Andersen & Müller 2000; Biaggini et al. 2007; Dennis et al. 2008; Engle et al. 2013; Little et al. 2013). Because different life-stages of some Orders (e.g. Lepidoptera) vary greatly in their resource requirements, the feeding guild they occupy, and their body length/biomass relationship (Stoner & Joern 2014), I assessed the life-stages of some Orders separately (see Table A4.1 and A4.2). I excluded the tiny (less than 1mm in length) larval stage of the tick *Acarid* *Ixodidae* from the grass-layer data as on multiple occasions I captured thousands of individuals due to the presence of a ‘nest’. In addition, for the grass-layer samples, I directly measured the length of each individual and estimated individual mass using available taxon specific length-regression relationships (Table A4.1; Hodar 1996; Benke et al. 1999; Wardhaugh 2013). Biomass was not estimated for the ground-layer samples.

4.3.3 Vegetation Sampling

Vegetation structure was measured at each invertebrate sampling site and included measures of grass length, shrub density, and tree density. Sampling was performed by placing a 50-m long transect at each site. Each transect started at the centre of the sampling site and radiated out in a randomly selected direction. Grass length (GrL) was measured using a 7-mm diameter vegetation pole which was placed on the ground, held vertically at every 1 m along the transect (Wiens & Rotenberry 1981). I recorded the maximum height (in mm) of contact of any plant in the grass layer that touched the pole. Density of shrub cover (ShD), defined as all woody plants with a height < 3m and a stem/trunk diameter at breast height (dbh) <10 cm, was estimated as the number of shrubs within 1 m on either side of the 50-m transect. Tree density (TrD) was estimated for all woody plants ≥ 3 meters in height or with a dbh ≥ 10 cm using the point-centred quarter method (PQM; Cottam & Curtis 1956). PQM is a “plotless” sampling method that performs well in open habitats when the vegetation of interest is relatively sparse (Pilliod & Arkle 2013; Khan et al. 2016). The distances to the nearest two trees from the central sampling point were measured in each of four quadrants which were delineated by the four cardinal compass points (8 distances per site). Mean distance \bar{d} (m) was used to calculate the density ($\hat{\lambda}$) of trees at each site using the following equation:

$$\hat{\lambda} = \frac{1}{\bar{d}^2} \quad (2)$$

4.3.4 Explanatory Variables

In addition to variables describing vegetation structure, I estimated environmental variables to represent variation in the fire regime, rainfall and season. A fire history within the study area was mapped using Landsat 5 and 8 surface reflectance imagery (30 m resolution) in Quantum GIS (QGIS 2016) (Figure 4.1). To locate individual fire patches, Landsat data was displayed on a computer screen using the bands red, middle infrared, and near-infrared in blue, green, and red colours (Bowman et al. 2003; Jones et al. 2013). The boundary of every fire (including unburned interior areas) occurring between January 1989 and March 2016 was hand digitized at a constant scale (1:25,000). Each fire patch was assigned an age-class based on the calendar year in which it burned. Mankwe has long-term fire records that were used to confirm ignition dates. In a few cases where no ignition date data was available for early fires, I acquired the apparent month of ignition from Landsat imagery and set the ignition date as the 15th of that month. Time-since-fire (*hereafter* TSF) represents the number of months since a site had last burned. Whereas, fire return interval (*hereafter* FRI), which is a common measure of fire frequency, represents the average number of months between recorded fire events at each site (Archibald et al. 2013).

Average daily rainfall was obtained from six stations across the reserve and was used to calculate two indices of local precipitation. A 30-day rainfall and a seasonal rainfall index were respectively quantified by (1) summing daily rainfall for the 30 days prior to an invertebrate sampling date and (2) summing daily rainfall from 1 September of one year to 31 May of the next year (Moeletsi et al. 2011). Finally, I assessed the effect of seasonal conditions by including a variable 'season' (0 for sampling conducted early in the rainy season and 1 for sampling conducted late in the rainy season) to account for seasonal variation in habitat structure and the invertebrate community.

4.3.5 Statistical Analyses

Generalised linear mixed models (GLMMs) and an information theoretic approach were used to assess the effects of environmental variables on (1) grass-layer order richness (number of orders, *hereafter* richness), (2) grass-layer abundance (sum of all individuals), and (3) grass-layer biomass (sum of biomass of all individuals), (4) ground-layer richness, and (5) ground-layer abundance. In addition, I evaluated the effects of the environmental variables on the abundance and biomass of the most

common individual orders in the grass- and ground-layer. Common Orders were determined to be those Orders that made up the top 75% of abundance or biomass.

Prior to modelling I tested for multicollinearity among the explanatory variables using variance inflation factors (VIFs). I found that the variables 'season' (i.e., early or late in rainy season) and 30-day rainfall were correlated with seasonal rainfall and exceeded my pre-selected threshold ($VIF > 3$). The variables season and 30-day rainfall were subsequently dropped from the analyses. The six explanatory variables included in the models were: (1) TSF, (2) FRI, (3) grass length, (4) shrub density, (5) tree density, and (6) seasonal rainfall (*hereafter* rainfall). The data for the variables time-since-fire and tree density were log-transformed because of skewed distributions. Modelling began by entering all predictor variables (centred and scaled to one standard deviation) and selected interactions into a full generalized linear mixed model (*hereafter* global model) for each response variable. I included two-way interactions among TSF, FRI and rainfall.

Richness linear mixed models were implemented with Gaussian errors. Biomass was modelled using a log-Normal linear mixed model, which is a simpler alternative to the Gamma distribution for continuous, skewed distributions (Bolker 2015). For the biomass global model, the log-Normal had a lower AIC than a Gamma model and had better residual fit. I investigated invertebrate abundance in the grass- and ground-layers by fitting Poisson mixed models. Typical of ecological count data I detected strong overdispersion in the abundance model residuals (Richards 2008). As a result I included an observation-level random effect (OLRE) to deal with overdispersion following Harrison (2014). An OLRE uses a unique level of a random effect for each observation in the data to model extra-Poisson variation present in the data (Harrison 2014). When compared to the overdispersed Poisson model and a negative binomial model, the OLRE model had the best model fit (i.e. lowest AIC_c). I assessed the distributions of model residuals to confirm that models did not violate assumptions of normality. I considered and compared full-models for each response variable with fire (i.e. burn patch) and site as individual and nested random effects (Zuur et al 2009). The nested random effect of site within fire—included to account for the hierarchical nature of the survey design—consistently resulted in singular fit (random effect variance estimated as zero) suggesting that its effect was negligible (Pasch, Bolker, and Phelps 2013). The full-models with the random effect site consistently resulted in the lowest AIC_c . Accordingly, I specified site as the only random effect, which accounted for the

repeated measures design of the sampling regime. Consequently, the two ground-layer samples at each site were analysed as subsamples rather than true replicates (Bolker et al. 2009).

Next, I analysed all subsets of the full model for each response variable. Explanatory variables (including interactions) were chosen based on *a priori* hypotheses and existing knowledge of the ecology of my study system. I considered all possible combinations of the explanatory variables to be reasonable candidate models for the data (Whittingham et al. 2006). The models were ranked using Akaike's information criterion (AIC_c) with a small sample size adjustment. All models with a ΔAIC_c of ≤ 6 and less than the ΔAIC_c of all simpler nested models were retained in the top model set (Richards 2008). I computed model-averaged parameter estimates and 95% confidence intervals using the top model set. To assess GLMM fit I calculated the marginal R^2 (variance explained only by fixed effects) and the conditional R^2 (variance explained by both fixed and random effects; Nakagawa & Schielzeth 2013). All statistical analyses were conducted in R (R Development Core Team 2016) using the packages 'lme4' (Bates et al. 2015) and 'MuMIn' (Barton 2018). All estimates of effect sizes are given as means \pm 1 standard error.

Lastly, I checked for spatial autocorrelation in the residuals of the top ranked model for each response variable using spline-correlograms from 1000 bootstrapped permutations in the package *ncf* (Bjornstad 2016). I found no evidence of spatial autocorrelation between sites (correlation values were < 0.1) confirming that model residuals were spatially independent.

4.4 RESULTS

In the grass-layer I sampled 49,741 individuals of 21 Orders and in the ground-layer I sampled 63,456 individuals of 24 Orders (see Table A4.1 & A4.2 for a full description of invertebrate Orders captured). In the grass layer the most abundant groups were Hemiptera (true bugs and leafhoppers; 31% total individuals), Diptera (flies; 14%) and Coleoptera (beetles; 11%). However, the orders with the greatest biomass were Orthoptera (grasshoppers and crickets; 59% of total biomass), Hemiptera (19%) and Mantodea (praying mantids; 4%). In the ground-layer the most abundant groups overall were Formicidae (Hymenoptera: ants; 59% total individuals) and Collembola (springtails; 31%), with these two groups representing 90% of all individuals caught. Due to the dominance of these two orders, I modelled total community abundance in the ground-layer without ants and springtails (see Table A4.4 for more details).

4.4.1 *Invertebrate Order Richness*

Mean order richness across all sampling sites in the grass-layer was 9.8 (range 0-18, SD = 3.5) and in the ground-layer was 6.5 (range 1-15, SD = 2.2). In the grass-layer, richness was positively associated with TSF, seasonal rainfall and grass length and negatively associated with FRI (Table 4.1). In addition, richness was associated with an interaction between TSF and rainfall that revealed that as TSF increased, richness increased when rainfall is both low and high (Figure 4.2a). However, richness was lowest when TSF and rainfall were low (Figure 4.2a). Although richness was highest when TSF and rainfall were high, richness was almost as high when TSF was high and rainfall was low (Figure 4.2a). In the ground layer, richness was positively associated with tree density and negatively associated with FRI (Table 4.2). However, the response of ground-layer richness to TSF was mediated by rainfall. As TSF increased, ground-layer richness increased when rainfall was high and decreased when rainfall was low (Figure 4.2g). In addition, when TSF increased, ground-layer richness decreased when FRI was low, suggesting that richness of ground-active invertebrates is highest in recently and frequently burned areas (Figure 4.3a). However, when rainfall was high, ground-layer richness did not change with increasing TSF (Figure 4.3a).

4.4.2 *Invertebrate Abundance*

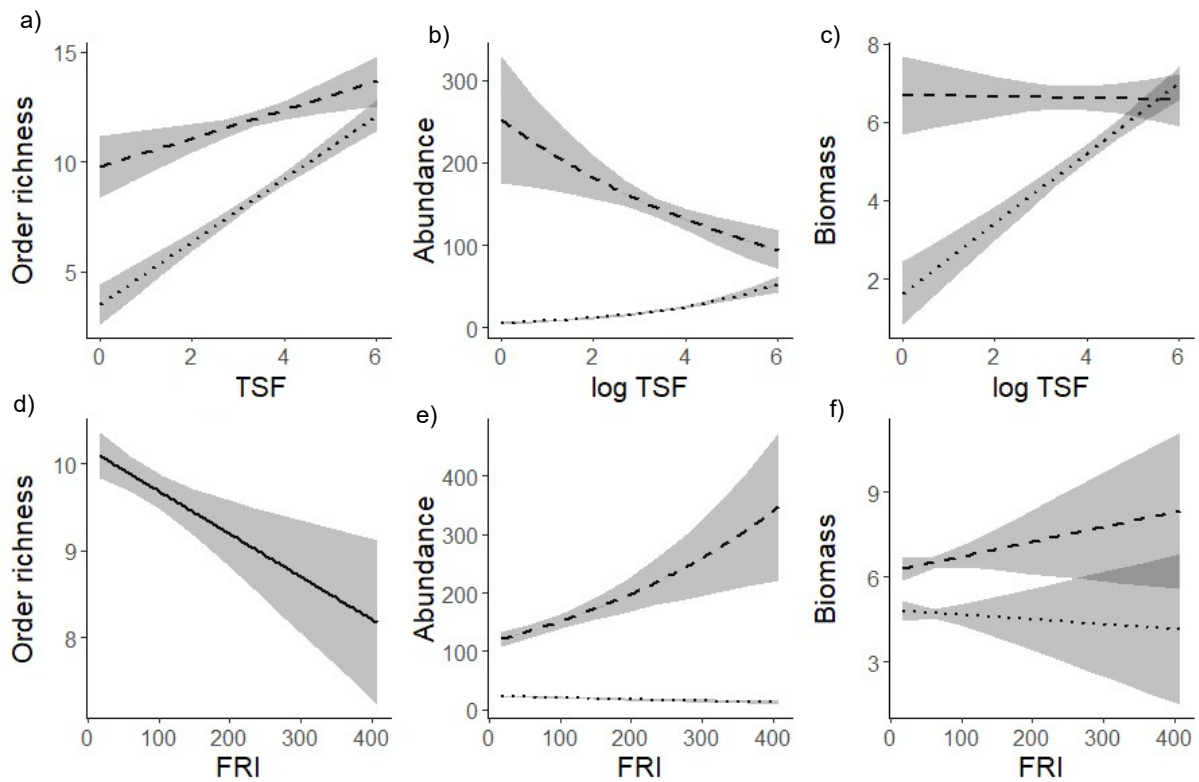
Mean invertebrate abundance was 73.1 (range 0-427, SD = 78.0) invertebrates per sample in the grass-layer. Mean ground-layer abundance was 9.4 (range 0-58, SD = 6.7) invertebrates per sample. In the grass-layer, TSF, rainfall and grass length had positive effects on invertebrate abundance (Table 4.1). Model-averaging revealed multiple significant interactions that influenced grass-layer abundance. Grass-layer abundance was influenced by an interaction between TSF and rainfall, which revealed that as TSF increased, abundance decreased when rainfall was high and increased when rainfall was low (Figure 4.2b). Therefore, contrary to richness in the grass-layer, abundance is highest in recently burned areas when rainfall is high. Grass-layer abundance was also influenced by an interaction between FRI and rainfall, which demonstrated that as FRI increased, abundance increased when rainfall was high and decreased when rainfall was low (Figure 4.2e). This interaction reveals that abundance in the grass-layer was highest in areas with high FRI (i.e. infrequent burning) and high rainfall (Figure 4.2e).

Table 4.1 Model-averaged parameter estimates ($\beta \pm SE$) predicting arthropod community richness, abundance and biomass in the grass-layer and ground-layer. Parameter estimates with 95% confidence intervals that did not include zero are indicated in bold. Predictor variables include times-since-fire (TSF), fire return interval (FRI), seasonal rainfall (Rain), grass length (GrL), shrub density (ShD), tree density (TrD) and interactions between them.

Model	TSF	FRI	Rain	GrL	ShD	TrD	TSF x FRI	TSF x RAIN	FRI x RAIN
<i>Grass-layer</i>									
Total Order richness	1.411 ± 0.146	-0.431 ± 0.127	1.333 ± 0.084	1.100 ± 0.097		-0.147 ± 0.121		-0.363 ± 0.111	0.192 ± 0.122
Total abundance	0.203 ± 0.037	0.005 ± 0.031	0.725 ± 0.020	0.268 ± 0.027		-0.058 ± 0.029		-0.246 ± 0.025	0.140 ± 0.023
Total biomass	0.678 ± 0.114	0.090 ± 0.334	0.720 ± 0.053	0.487 ± 0.070	0.047 ± 0.066	-0.122 ± 0.072	-0.146 ± 0.164	-0.423 ± 0.062	0.222 ± 0.061
Hemiptera abundance	-0.210 ± 0.049	0.230 ± 0.039	0.504 ± 0.029	0.386 ± 0.038				-0.144 ± 0.034	0.172 ± 0.032
Diptera abundance	0.444 ± 0.053	-0.170 ± 0.038	0.424 ± 0.028	0.060 ± 0.041				-0.260 ± 0.038	0.072 ± 0.035
Coleoptera adult abundance	0.360 ± 0.059	-0.057 ± 0.052	0.717 ± 0.036	0.003 ± 0.017		-0.054 ± 0.046		-0.065 ± 0.045	-0.006 ± 0.020
Tick abundance	0.375 ± 0.095	-0.371 ± 0.076	0.083 ± 0.052	0.281 ± 0.067		0.039 ± 0.053		-0.280 ± 0.068	0.261 ± 0.062
Araneae abundance	0.187 ± 0.068	0.128 ± 0.178	0.607 ± 0.030	0.250 ± 0.037	0.023 ± 0.030	-0.065 ± 0.036	-0.078 ± 0.087	-0.247 ± 0.039	0.107 ± 0.032
Orthoptera abundance	0.450 ± 0.073	-0.05 ± 0.058	0.631 ± 0.039	0.362 ± 0.051		-0.140 ± 0.041		-0.129 ± 0.035	
Orthoptera biomass	1.379 ± 0.242	-0.289 ± 0.215	1.289 ± 0.145	0.957 ± 0.190	0.167 ± 0.168	-0.481 ± 0.148		-0.608 ± 0.176	0.137 ± 0.184
Hemiptera biomass	0.017 ± 0.185	1.184 ± 0.542	0.829 ± 0.086	0.674 ± 0.115		-0.084 ± 0.105	-0.603 ± 0.266	-0.201 ± 0.123	0.090 ± 0.112
<i>Ground-layer</i>									
Total Order richness	-0.196 ± 0.109	-3.276 ± 0.974	-0.094 ± 0.201			0.233 ± 0.067	0.592 ± 0.164	0.299 ± 0.056	
Total abundance	-0.208 ± 0.072	-0.229 ± 0.158	0.287 ± 0.023	0.052 ± 0.047		0.097 ± 0.026	0.186 ± 0.077	0.118 ± 0.024	
Formicidae abundance	-0.012 ± 0.093	-0.072 ± 0.076		-0.031 ± 0.055	0.044 ± 0.050	0.057 ± 0.054			
Collembola abundance	0.349 ± 0.240	-0.841 ± 0.479	0.402 ± 0.067	0.059 ± 0.117	-0.079 ± 0.102		0.099 ± 0.230		0.202 ± 0.071

Blank spaces indicate a parameter that was not included in the top model set for model averaging

Grass-layer



Ground-layer

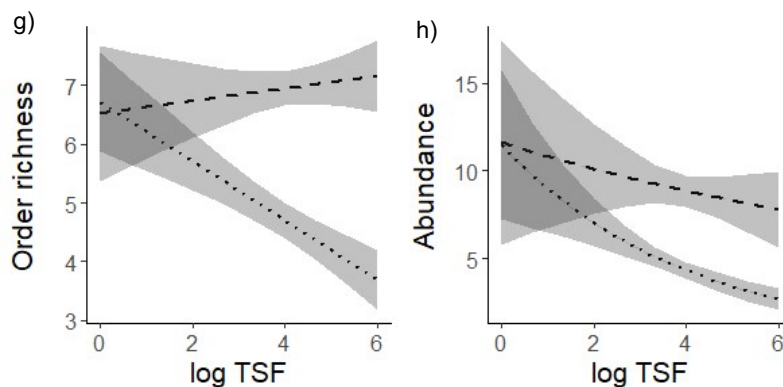


Figure 4.2 Modelled order richness, abundance, and biomass (mg) in the grass-layer and ground-layer in relation to log-transformed time-since-fire (TSF; months) and fire return interval (FRI; months). Predictions are from model averaging and grey shading represents 95% confidence intervals. Responses are for low rainfall (dotted line; 10th percentile of recorded seasonal rainfall) and high rainfall (dashed line; 90th percentile of recorded seasonal rainfall). Note that for order richness as a function of fire return interval (panel d) there was no evidence of an interaction with rainfall. Hence, the response is shown for mean seasonal rainfall (solid line; mm) only. The observed data are not displayed here in order to improve the visibility of the predicted relationships (lines).

In the ground-layer, abundance was negatively associated with TSF and positively associated with rainfall and tree density (Table 4.1). Therefore, in contrast to the grass-layer, in the ground layer abundance was highest in recently burned habitats. Ground-layer abundance responded to an interaction between TSF and rainfall, revealing that as TSF increased, abundance decreased; however, this decrease in abundance was greater when rainfall was low (Figure 4.2h). In addition, an interaction between TSF and FRI demonstrated that as TSF increased, ground-layer abundance decreased; however, this decrease was greater when FRI was low (Figure 4.2e). This relationship revealed that ground-layer abundance was highest in recently and frequently burned areas (Figure 4.3b).

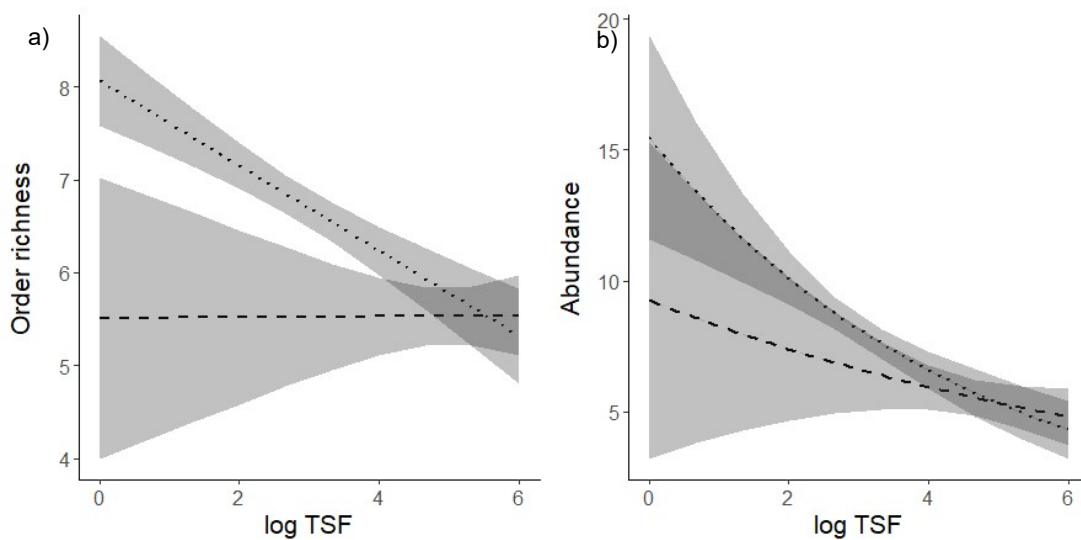


Figure 4.3 Modelled a) order richness and b) abundance (excluding ants and springtails) in the ground-layer in relation to log-transformed time-since-fire (TSF), in areas of short (dotted line) and long (dashed line) fire-return-interval (FRI). Predictions are from model-averaging and grey shading represents 95% confidence intervals. Low FRI is the 10th percentile of recorded FRI and high FRI is the 90th percentile. The observed data are not displayed here in order to improve the visibility of the predicted relationships (lines).

4.4.3 Invertebrate Biomass

In the grass-layer, biomass was positively associated with TSF, seasonal rainfall and grass length (Table 4.1). Biomass was influenced by an interaction between TSF and rainfall. This interaction revealed that as TSF increased, biomass increased when rainfall was low; however, when rainfall was

high, biomass exhibited no change with increasing TSF (Figure 4.2c). Furthermore, biomass in the grass-layer responded to an interaction between FRI and rainfall (Figure 4.2d). As FRI increased, biomass increased when rainfall was high and decreased when rainfall was low (Figure 4.2d).

The individual Orders responded differently to fire attributes. Orthoptera which contributed to 59% of grass-layer biomass, was positively associated with TSF, rainfall and grass length and negatively associated with tree density (Table 4.2). Community-level abundance and biomass fire responses in the grass-layer were similar, likely due to high correlation between these indices (Pearson correlation coefficient = 0.68). However, at the Order-level, Hemiptera abundance and biomass responded differently to predictor variables (Table 4.2) possibly due to a weaker abundance biomass correlation within this Order (Pearson correlation coefficient = 0.51).

4.5 DISCUSSION

In this chapter I found that community richness, abundance and biomass varied significantly with fire characteristics, habitat structure and rainfall and that effects of fire attributes on the ground-layer and the grass-layer invertebrate communities often differed. I found that fire responses are rainfall contingent, with significant interactions between rainfall and fire return intervals and time-since-fire. To the best of my knowledge, this study is the first to investigate the simultaneous and interactive long-term effects of time-since-fire and fire return intervals on fauna. These results reveal that these two fire attributes have opposing influences on grass-and ground-layer communities, and interactive effects on ground-active invertebrate diversity and abundance. Below I discuss these findings and their implications for conservation management.

Low invertebrate diversity and abundance in recently burned grassland have been previously reported and are attributed to mortality and emigration, as well as to changes in habitat structure including the loss of ground-layer vegetation, leaf-litter and in some cases shrub and tree canopies (Swengel 2001; Radford & Andersen 2012). Many studies have reported post-fire recovery of savanna invertebrate communities to have occurred within a few months (Parr et al. 2004; Underwood & Quinn 2010; Calcaterra et al. 2014) or a year (Vasconcelos et al. 2009; Radford & Andersen 2012). Here I demonstrate long-term responses to a multi-decade chronosequence of TSF, often dependent on rainfall. Long-term, post-fire successional responses have been recorded in Australian shrubland for foliage-active invertebrate species, many of which peaked in abundance 9 to 40 years after fire

(Teasdale et al. 2013). Post-fire recovery of many invertebrate taxa is likely to be slow, particularly those limited by mobility or host plant species (Swengel 2001), and can be influenced by population growth rates, the distance to unburned habitat for recolonization, and post-fire vegetation suitability (Panzer 2003; Mutz et al. 2017). The positive effect I observed of TSF on grass-layer invertebrate richness and biomass highlights the importance of maintaining long-unburned areas in a savanna fire regime.

Contrary to the grass-layer, the response of ground-layer community richness and abundance to TSF was negative; however, these relationships were dependent on fire return interval and rainfall. These findings suggest that ground-active invertebrates tend to be more diverse and abundant in recently and frequently burned savanna. Other studies have found a similar positive association between ground-active invertebrates and burning (Muona & Rutanen 1994; Driessen & Kirkpatrick 2017) and support suggestions of a high degree resistance in such communities to fire in grassland (Bock & Bock 1991; Gunawardene & Majer 2005), savanna (Parr et al. 2004; Parr & Andersen 2008; Davies et al. 2012), and shrubland (Friend & Williams 1996) habitats. This resistance is primarily attributed to individuals surviving fire below ground (Cook & Holt 2006; Pryke & Samways 2012b; Mutz et al. 2017) or using specific microhabitats (Uys et al. 2006) or refuge sites (e.g. retained logs; Andrew et al. 2000) to escape fire.

Little data exists on the long-term effects of varied fire frequency on invertebrates, with studies overwhelmingly examining the impacts of short fire return intervals (e.g. ≤ 3 years; Orgeas & Andersen 2001; Parr et al. 2004; Davies et al. 2012; Radford & Andersen 2012; Little et al. 2013). Furthermore, many studies compare an unburnt control area to frequently burnt areas without controlling for TSF (York 1999; Orgeas & Andersen 2001; Hanula & Wade 2003; Moretti et al. 2004; Andersen et al. 2006; Cook & Holt 2006; Uys & Hamer 2007; Maravalhas & Vasconcelos 2014) which in many cases is essentially comparing short TSF to long TSF (Wittkuhn et al. 2011). The effects of fire frequency are best demonstrated through long-term studies where sites are distributed across a gradient of both TSF and FRI or through experiments where sites with varying return intervals have a common TSF (e.g. Parr & Andersen, 2008; Wittkuhn et al., 2011). The different responses to fire return interval I observed between communities and among orders demonstrates that variability in fire return interval on the landscape is important for the persistence of a full complement of taxonomic groups. For ground-active invertebrates, I found that richness and abundance were highest in areas with a fire history characterised by a long time since last fire and infrequent burning. However, I found that the influence

of fire return interval decreased with time-since-fire. Morrison et al., (1995) found evidence of similar interactive effects on a dry sclerophyll plant community in Australia and determined that the effect of fire return interval on plant species composition decreased with increasing time-since-fire. Understanding this interaction reconciles what are otherwise seemingly contradicting fire disturbance results.

Semi-arid savannas are characterised by seasonal and annual variation in rainfall which is known to interact with fire to drive changes in vegetation structure (Sankaran et al. 2005). Rainfall had a dominant, positive effect on invertebrate richness, abundance and biomass in this study, yet demonstrated complex interactive effects with fire. In both the grass- and ground-layer the detection of a fire response was dependent on the inclusion of rainfall data. Notably, I found that the strength and direction of the TSF effect was conditional on rainfall. Furthermore, the interactive effects of fire and rainfall were different between the two communities. Similarly, a previous study of termite assemblages in South African savanna found that differences in density and composition between fire frequencies were more pronounced with increasing rainfall (Davies et al. 2012). Coupled effects of fire and rainfall may result from dynamic changes in habitat structure, net primary productivity and soil desiccation (Suttle et al. 2007). Furthermore, rainfall contingent fire responses may explain the frequently reported but unexplained inter-seasonal or inter-annual variation in the response of fauna to fire (Izhaki et al. 2003; Litt & Steidl 2011) and support the inclusion of rainfall in fire studies, particularly in drier regions.

Changes in vegetation structure and floral diversity associated with post-fire succession are good predictors of invertebrate diversity and abundance in a range of habitats (Brown & Hyman 1986; Hobbs et al. 1991; Niemelä et al. 1993; Pöyry et al. 2006). Grass length had a positive effect on grass-layer richness, abundance and biomass, as observed in grassland and savanna studies elsewhere (Dennis et al. 1998; Gebeyehu & Samways 2003; van Klink et al. 2015). A positive association between invertebrates and long grass swards may be a response to increases in niche and food availability (Lawton 1983), reduced predation risk due to increased vegetation cover (Belovsky et al. 1990), and cooler temperature refuges (Willott 1997). Tree density had a positive influence on ground-layer richness and abundance but did not influence invertebrates in the grass-layer. This result is most likely a positive response to an increased leaf-litter layer. In tropical savannas, the deep leaf-litter layer associated with high tree densities has a positive effect on the abundance of ground-active and litter-dwelling invertebrates (Andersen 1991; Vasconcelos et al. 2009), as it provides food resources for

saprophagous invertebrates, acts as a microhabitat, and may even provide refuge sites during fire events (Campbell & Tanton 1981). In addition to the leaf-litter layer, other factors associated with woody cover such as decreases in the presence of C4 grasses (Charles-Dominique et al. 2015) and increases in the availability of resources such as nutrients and water (Ludwig et al. 2004) may be important for the ground-active invertebrate community.

The approach used in this chapter of investigating a multi-decade, post-fire chronosequence provides valuable insight into the complex way in which fire affects invertebrate communities and the long-time frame over which these impacts operate. The findings reveal variable Order-specific responses to fire attributes over the long-term. I recognize the limitation of having evaluated changes in the invertebrate community at the ordinal level, thus potentially overlooking changes in species composition along a successional gradient resulting from the increase or decrease of species according to their habitat and resource requirements (Andersen et al. 2006; Driessen & Kirkpatrick 2017). For example, Jackson & Fox (1996) found that the composition of ant species and functional groups continued to change from 1 to 18 years post-fire in dry sclerophyll forest in Australia. Yet, despite a coarser taxonomic resolution, the present findings along with those from previous studies demonstrate that higher taxonomic resolution can provide a valuable assessment of invertebrate communities to fire for habitat management practices (Andersen & Müller 2000; Orgeas & Andersen 2001; Brennan et al. 2006; Biaggini et al. 2007; Engle et al. 2013) whilst overcoming taxonomic obstacles (e.g. skills, funding, time) common in invertebrate studies (Brennan et al. 2006). While I suggest that investigations of savanna invertebrate response to fire should be pursued at finer taxonomic resolutions to identify fire-sensitive species or traits, I conclude that ordinal level empirical evidence can provide valuable information for management such as the complex interactions demonstrated in this study.

The results of this study underscore the importance of considering multiple communities when assessing the response of invertebrates to disturbance (Teasdale et al. 2013; Driessen & Kirkpatrick 2017). In addition, this study reveals that fire response is order specific, highlighting the importance of multi-taxon studies for a comprehensive understanding of the effects of fire regimes on invertebrates. Fire-invertebrate research has overwhelmingly been conducted on ants; however, not only did I find that ants respond very differently to environmental variables than other invertebrate taxa, but I also found that ants can obscure community-level fire responses (see Table A4.4). In the present study and elsewhere ants demonstrate a remarkable degree of resistance to fire regimes (Parr & Andersen 2008;

Andersen et al. 2014; Kone et al. 2018) and are therefore unlikely to represent more fire-sensitive taxa. Consequentially, caution should be taken when making management recommendations (e.g. fire return interval; Brand, 2002) based on one taxonomic group as they may be harmful to others.

4.5.1 Implications for conservation management

Order- and community-specific responses to fire found in this study defy simple generalisations about optimal savanna management; however, important management recommendations can be made. The dominant positive effect of time-since-fire on the grass-layer community highlights the importance of maintaining long-unburned savanna areas for the conservation of savanna invertebrate diversity, biomass and abundance. Fire management that benefits invertebrate communities will likely have direct impacts on other savanna taxa through trophic interactions and the many important ecosystem services invertebrates provide. Key species that eat grass-layer insects (and particularly the most dominant Orthoptera) in semi-arid African savanna systems include numerous endemic bustards such as the Northern black bustard (*Afrotis afraoides*), declining grassland specialists such as the secretarybird (*Sagittarius serpentarius*), as well as numerous mammalian species such as the bat-eared fox (*Otocyon megalotis*; Kok & Louw 2000). To promote numbers of such species and their prey items I recommend burning during years of high rainfall to maximize richness and biomass in the grass-layer. Fire management that avoids burning during drought years will also benefit savanna taxa such as small (Yarnell et al. 2007) and large (Pacifci et al. 2015) mammals. By contrast, higher taxa that rely upon ground dwelling invertebrates include many crepuscular and nocturnal foraging charadrii, such as thick-knees, coursers and lapwings (Kok & Kok 2002) and ground-active passerines such as pipits (Kopij et al. 2002). Management to promote such species may require frequent burning. Meeting the contrasting fire management outcomes for these two communities may require a mosaic of burn ages that includes areas of long-unburned and areas of frequently burned habitat; however, fire management decisions will have to incorporate rainfall. Such a management programme will need to be adaptive and supported by long-term biodiversity monitoring.

Integrating invertebrates into fire management monitoring and planning in South Africa is important because of their vital roles in ecosystem function and process (McGeoch et al. 2011), including their potentially harmful roles as invasive or outbreak species (Graham 1994) and disease vectors (e.g. ticks; Fyumagwa et al., 2007). These results reveal that fire responses are diverse among

invertebrate taxa and therefore I recommend that a range of taxa, especially those groups that are sensitive to fire, are used to monitor fire management. Where invertebrates are used to monitor the effects of a fire regime on savanna systems, rainfall will need to be integrated into monitoring programmes to prevent significant fire impacts from being overlooked (Blanche et al. 2001). Furthermore, practitioners will have to incorporate plans for dry conditions and future climate scenarios into fire management strategies. This may require 'adaptive' burning strategies that integrate annual changes in community dynamics and potential interactive effects of climate conditions into more general conservation planning (Archibald et al. 2010).

Chapter 5

Indirect effects of fire and climate on birds: the role of food availability, vegetation structure and niche breadth



Common Hoopoe (*Upupa epops*)

5.1 ABSTRACT

Fire is an important natural disturbance that acts as a major driver of community dynamics and ecosystem function. While fire is increasingly used as a management tool to conserve and manage biodiversity in fire-prone systems, key gaps remain in our understanding of how biological communities respond to fire and the mechanisms that drive community structure in such systems. I sampled plant, invertebrate and avian communities across a long chronosequence of fire age and frequency and calculated the diversity, density and functional trait identity (body mass and three measures of niche breadth) of the avian insectivore community. I used structural equation modelling (SEM) to evaluate relationships between fire, climate, vegetation, invertebrates and avian insectivores and to assess whether the indirect effects of fire on avian insectivores are mediated by vegetation structure or food availability (the invertebrate community) in a semi-arid savanna ecosystem. Relationships between the avian insectivore community and fire were indirectly mediated by vegetation structure and the invertebrate community. However, SEMs revealed some direct effects of fire on avian insectivores, which included a positive effect of time-since-fire on species richness. Rainfall had strong direct and indirect effects on avian insectivore community structure. In addition, the findings indicate that the response of avian insectivores to fire and climate is determined by functional traits. Here, I demonstrate that fire influences biological communities in multiple ways beyond the previously recognised indirect effects of vegetation structure. Consideration of the bottom-up and top-down effects of fire and climate will support a predictive understanding of biological communities in fire-prone ecosystems and the development of ecologically sustainable fire management.

5.2 INTRODUCTION

Fire is an important natural disturbance that affects ecosystem structure and function (Glover 1968). Prescribed fire regimes are used in many fire prone habitats to achieve multiple management objectives, including mitigating wildfires, altering vegetation succession, and conserving biodiversity (Van Wilgen 2009; Kelly et al. 2017). However, our understanding of how fauna responds to fire regimes remains limited. Given the sensitivity of fire-prone landscapes to environmental change (Pausas et al. 2017), projections that fires in these landscapes will increase in frequency and size due to changes in land-use and climate (Midgley & Bond 2015), and the fragility of trophic interactions (Bowman et al. 2016), an enhanced understanding of the effects of fire regimes on biological communities is essential. An improved understanding of the mechanisms governing fire-fauna relationships is necessary if we wish to predict how fauna will respond to changes in fire regimes and for the development of effective fire management practices (Driscoll et al. 2010).

Fire disturbance can influence species in multiple ways in fire-prone ecosystems. While fire can impact fauna directly via mortality and emigration (Swengel 2001), it can also impact fauna indirectly via changes in vegetation structure and resources (Fox 1982). Understanding the indirect relationships between fire and fauna is important because they influence community structure and function (Sitters et al. 2016), and they can operate over long temporal scales (Kelly et al. 2011; Taylor et al. 2012; Haslem et al. 2012). In savanna systems, fire can reduce grass phytomass and modify woody vegetation structure (Skowno & Bond 2003), as well as alter vegetation resources important to animals, such as breeding (Nappi et al. 2010), foraging (Moranz et al. 2014), and refuge (Robinson et al. 2013) sites. Fire disturbance can reset ecological succession and studies have used time-since-fire as a proxy for species and community succession in animals (Fox 1982; Watson et al. 2012b). Recent studies have shown that temporal fire attributes (i.e., time-since-fire) may be poor predictors of post-fire faunal succession compared to direct measures of habitat structure (di Stefano et al. 2011; Sitters et al. 2014a; Swan et al. 2015). This suggests that there is a mismatch between time-since-fire and the temporal change in habitat structure and resource availability to which animals respond. This temporal mismatch between time-since-fire and faunal succession may result from the interactive effects of other fire attributes (e.g. severity and seasonality; Tingley et al. 2016), climate (e.g. drought; Crowther et al. 2018) and biotic interactions (e.g. trophic relationships; Ponisio et al. 2016 or herbivory; Moranz et al. 2014) on successional processes. The interaction of fire and water availability is a major driver of savanna

vegetation structure, particularly in arid savannas where low (<650 mm yr⁻¹) and seasonally variable rainfall conditions, coupled with frequent fire, greatly influence vegetation growth rates (Sankaran et al. 2005). In sub-Saharan Africa, the interaction between rainfall and fire largely determines the equilibrium among grass biomass, tree sapling density, and adult tree cover in savanna systems (Staver et al. 2011).

Aside from changes to habitat structure, disturbance can also alter the structure of food webs via changes in trophic interactions (Tylianakis et al. 2007; Ledger et al. 2013). Studies in savanna of large grazing mammals have investigated post-fire changes in nutrient quality of grasses (e.g., Parrini and Owen-Smith 2009, Eby et al. 2014), which underlie patterns of resource selection. However, few studies worldwide have linked the post-fire response of non-mammalian animals to changes in food availability, which include changes in seed crops for granivores and floral resources for pollinators (Poniso et al. 2016; Mola & Williams 2018). Those that have, demonstrate that fire can alter food resources with bottom-up effects on many foragers. (Crowley & Garnett 1999; Thibault & Prodon 2006). Moreover, disturbance-induced shifts in the diversity and density of lower trophic levels can drive the diversity or density of higher trophic levels (Scherber et al. 2010; Albrecht et al. 2014; Vollstädt et al. 2017). Therefore, food availability is likely an important mechanism driving relationships between fire and animal communities of higher trophic levels.

Organisms vary in their vulnerability to disturbance and environmental change (Bregman et al. 2014; Howard et al. 2018). Given current global rates of species loss, changing climate, and the increase of disturbance events (Dirzo et al. 2014; Lister & Garcia 2018), it is important to identify taxa that are particularly vulnerable to disturbance. Amongst birds, insectivores are highly susceptible to disturbance and land-use change due to their complex trophic relationships with invertebrates and vegetation structure (Hutto 1995; Hamer et al. 2014). Yet, studies of fire disturbance have reported varied insectivore responses, including both positive (Hutto 1995; Meehan & George 2003) and negative (Mestre et al. 2013; Burgess & Maron 2016) associations with burned habitat. Varied disturbance responses may result from within-guild variability in morphology, trophic position, and niche-breadth (Edwards et al. 2013a; Hamer et al. 2014). The niche-breadth hypothesis suggests that species that can exploit a wide variety of habitats and food types should be less susceptible to environmental change (Swihart et al. 2003). Habitat and dietary generalists are more likely to exploit disturbed or early-successional areas (Devictor et al. 2008) and are less vulnerable to changes in the

availability of native food resources (Laurance 1991; Swihart et al. 2003). Some species have flexibility in their foraging strategy or behaviour (Macdonald et al. 2012), which may be an adaptive response to variability in food resources and habitat structure. For many species, behavioural flexibility and a wide niche breadth enable persistence in disturbance prone habitats and changing environments (Wright et al. 2010), which may explain resilience in fire-prone communities (Jacquet & Prodon 2009; Podgaiski et al. 2013).

Body size affects energy, nutrient and water requirements of species and is correlated with life-history characteristics such as dispersal ability and home-range size (Swihart et al. 2003; Gardner et al. 2011). Studies have observed changes in mean body mass of a community in response to environmental change and disturbance (Senior et al. 2013; Hamer et al. 2014; Bregman et al. 2014). The ability to move within a larger home-range, recolonize habitat patches, access burned and unburned patches, and track resources at a larger scale can affect a species persistence in a structurally diverse landscape (Wiens et al. 1993; Cromsigt et al. 2009; Nimmo et al. 2018). Body mass also has implications for predation risk and habitat selection on burned landscapes, where heightened predation risk is associated with short-grass or open habitat (Belovsky et al. 1990; Valeix et al. 2009; Eby et al. 2014) and larger bodied animals are less vulnerable to predation. Functional traits such as niche breadth and body mass, can be used to link species to their functions in an ecosystem (Luck et al. 2012; Vollstädt et al. 2017). Functional identity—measured as a community weighted mean of a single trait—can be used to summarise the frequency of a trait across a community (Gagic et al. 2015). In comparison to species richness and abundance, functional trait-based metrics tend to better reflect ecosystem functions (Mokany et al. 2008; Gagic et al. 2015) and mechanistic responses to disturbance (Vollstädt et al. 2017). Although the response of plant functional traits to fire is well-studied (e.g., Cianciaruso et al. 2012; Spasojevic et al. 2016), the response of bird functional traits to fire has rarely been studied (Azeria et al. 2011).

In this study, I investigate indirect pathways by which fire may influence avian insectivore communities in South African semi-arid savanna, a habitat where changes in vegetation structure is thought to be the dominant causal pathway between fire and animal communities (Skowno & Bond 2003; Beale et al. 2018). I use long-term fire data (27-years) from a history of prescribed fire and shorter-term data (2-years) of rainfall, vegetation structure, invertebrates and avian insectivores. Structural equation modelling (SEM) was used to investigate support for two hypothesised indirect causal

pathways mediated by 1) vegetation structure and 2) food availability between fire and avian insectivores. I predicted that avian insectivore diversity and density will increase with the complexity and density of habitat structure, and in response to richer invertebrate communities associated with late successional and infrequently burned savanna. Furthermore, I expected (i) interactions between fire and rainfall would have moderating effects on the two hypothesised pathways and (ii) that insectivore response to the indirect effects of fire is related to niche breadth (i.e. habitat breadth, diet breadth and foraging flexibility) and body size. This study was designed to evaluate some of the mechanisms underlying the response of savanna communities to fire. Such a mechanistic understanding is important for making predictions about the response of fauna to changing disturbance regimes and for informing conservation policy.

5.3 METHODS

5.3.1 Study Area and Design

This study was conducted at Mankwe Wildlife Reserve (*hereafter* Mankwe), a 4760-ha private reserve in North West Province, South Africa (Figure 4.1). The habitat is sourish mixed bushveld and consists of grasslands interspersed with thickets and deciduous woodland (Acocks 1988). Dominant shrub and woody cover species include acacias (e.g. *Acacia tortilis*, *A. mellifera*, and *A. karroo*) and combretums (*Combretum* sp.) and dominant grasses include *Hyparrhenia hirta*, *Loudetia simplex*, *Themeda triandra*, and *Heteropogon contortus*. The fire regime at Mankwe is a modified rotational block-burn, where burning occurs from May to August and established habitat blocks are burned every four or five years whilst maintaining some areas that burn more frequently, less frequently or not at all. Land managers decide where to burn in a given year based on factors that include fire history, rainfall, fuel loads, and grazing mammal populations. Average annual rainfall at Mankwe is approximately 600 mm (2010–2016; range 352–835mm), with most rain falling between October and March. Mean daily precipitation was derived from six rain gauges across the reserve.

The 28-year fire history from 1989–2016 was digitized using Landsat 5 and 8 surface reflectance imagery (30 m resolution) in Quantum GIS (QGIS 2016) (Figure 4.1). To locate individual fire patches, Landsat data was displayed on a computer screen using the bands red, middle infrared, and near-infrared in blue, green, and red colours (Bowman et al. 2003; Jones et al. 2013). The boundary of every fire (including unburned interior areas) occurring between January 1989 and March 2016 was

hand digitized at a constant scale (1:25,000). Each fire patch was assigned an age-class based on the calendar year in which it burned. Paper records of fire events from across the entire period were used to confirm ignition dates. In a few cases where no ignition date data were available for old fires, I recorded the month of ignition based on the first detection of the event from Landsat imagery and set the ignition date as the 15th of that month.

To sample the variability in the fire regime I used a stratified-random method to select sampling sites across a gradient of fire ages and fire frequencies in the study area (Figure 4.1). Sites were located more than 250 m apart and at least 100 m from a fire edge. At each site I sampled the vegetation, invertebrates, and birds twice during two consecutive rainy seasons (October–March). To account for seasonal variability, each site was sampled early (October–November 2014 and 2015) and late (January–March 2015 and 2016) in the rainy season, resulting in four surveys per site. I visited 178 unique point count locations, with 164 of these points surveyed in the first season and 176 of these points surveyed in the second season, resulting in a total of 680 sampling events. The small differences in sites sampled between seasons arose due to occasional inaccessibility of some sites.

5.3.2 Vegetation Sampling

Vegetation structure was measured at each site and included measures of tree density, shrub density, shrub height, and grass length. A 50-m transect, centred on the sampling site and radiating out from the site in a randomly selected direction was used to collect vegetation structural data. Mean grass length (GrL) was measured using a 7-mm diameter vegetation pole which was held vertically at every 1 m along the transect. I recorded the maximum height of the grass layer touching the pole and calculated the mean of the 50 recorded grass lengths for each site. Density of shrub cover (ShD), defined as all woody plants with a height < 3m and a diameter at breast height (dbh) <10 cm, was estimated as the number of shrubs within 1 m on either side of the 50-m transect. In addition, I estimated the height of each recorded shrub and calculated the mean of all shrub heights (ShHt) for each site. Tree density (TrD) was estimated for all woody plants ≥ 3 meters in height or with a dbh ≥ 10 cm at each site using the point-centred quarter method (PQM; Cottam & Curtis 1956). PQM is a “plotless” sampling method that performs well in open habitats when the vegetation of interest is relatively sparse (Pilliod & Arkle 2013). The distances to the nearest two trees were measured in each of four quadrants radiating from the sampling site and delineated by the cardinal compass directions (8 distances per

site). The mean of the 8 distances was used to determine the density of trees per unit area (Cottam & Curtis 1956). Tree density was calculated using equation 2 (see section 4.3.3).

5.3.3 Invertebrate Sampling

Terrestrial invertebrate samples were collected from the grass layer using sweep netting. Sampling was conducted along two transects that began at a distance of 50 m in opposite directions from the centre of each site on an east-west axis. Each sample consisted of 50 swings of a 37-cm diameter muslin net while walking a steady pace toward the site centre. The two samples at each site were combined for the subsequent analysis. Sweep netting was not conducted in windy or rainy conditions or if the grass was wet. All invertebrates were identified to order; this taxonomic level has been demonstrated to be effective for detecting invertebrate community response to fire regimes (Andersen & Müller 2000; Engle et al. 2013). Because different life-stages of some Orders (e.g. Lepidoptera) vary greatly in their resource requirements, feeding guilds, and body length/biomass relationship (Stoner & Joern 2014), I decided also to collect life-stage data for some Orders separately (see Table A4.1). I excluded the larval stage of ticks (*Acar*i *Ixodidae*) from the data as on multiple occasions I captured thousands of individuals due to the presence of a nest. For all other taxa, we measured the length of each individual captured, subsequently estimating individual mass using available taxon specific length-regression relationships (Table A4.1; Hodar 1996; Benke et al. 1999; Wardhaugh 2013). I calculated total invertebrate biomass at each site visit because it can provide a more accurate interpretation of resource availability than abundance (Saint-Germain et al. 2007).

5.3.4 Avian Sampling

Bird surveys consisted of a 10-minute point count where all birds seen and/or heard within a 100-m radius were recorded. The observer used a laser rangefinder (Nikon Aculon-500m) to measure the radial distance to each detected bird or cluster of birds (i.e. pair or flock). When a bird was detected (i.e. visually or aurally) the distance to the first detected location of the bird was recorded. Point counts were conducted by the same experienced observer (TD) during the peak of vocal activity (sunrise until 10 am), and the timing of repeat visits to points was varied to reduce sampling bias. Point counts were only conducted during good weather conditions without rainfall or strong wind. Birds flying-over and not using the habitat, and birds associated with water bodies were excluded from analyses. In addition, I removed

two highly-mobile (nomadic) species that formed very large flocks (wattled starlings, *Creatophora cinerea* and red-billed queleas, *Quelea quelea*) from the data as their rare occurrence during counts was never associated with them settling to use an area.

5.3.5 Avian Traits

I identified insectivores as those species whose primary food resource was invertebrates, using trait data from Hockey et al. (2004). For all such species that were detected during surveys, I estimated the value of four further traits from Hockey et al. (2004). First, I defined 'foraging strategies' as the number of foraging methods a species uses (e.g. glean, perch & pounce, aerial, etc.). Second, I calculated 'diet breadth' as the total number of food resources a species uses (e.g. terrestrial invertebrates, seeds, fruits, nectar, etc.). Third, 'habitat breadth' was calculated as the number of habitats a species is known to use (e.g. savanna, agricultural, forest, etc.). And fourth, I estimated individual body mass as the mean of the male and female body mass for that species. Species specific trait data is shown in Table A5.3.

5.3.6 Statistical Analyses

The density (\hat{D}) of insectivores at each site was estimated using equation 1 (see section 2.3.4). To evaluate detection probability (\hat{P}_a), multiple covariate distance sampling (MCDS) was conducted in R (version 3.5.0; R Core Team 2018) using the package Distance (Miller 2017). I compared a suite of *a priori* candidate models and selected a top model based on the Akaike's information criterion corrected for small sample sizes (AIC_c), while taking into account chi-square goodness-of-fit tests and visual inspections of density and detection probability plots (Table A5.1; Buckland et al., 2015; Burnham & Anderson, 2002). Conventional distance sampling (CDS) models with no covariates were fitted as the null model. I used CDS to evaluate half-normal and hazard-rate key functions with no adjustment terms. The half-normal key function had the best fit and consequently I used this key function for the MCDS models. Next, four covariates that were anticipated to influence detectability and selected *a priori* were used included in MCDS models to singly and additively. These covariates included: (1) time-since-fire, (2) cluster size (flock size), (3) time since sunrise (hours), and (4) detection cues (i.e. aural or visual). Testing the effects of time-since-fire (months) on the probability of detecting birds is important because post-fire changes in vegetation cover may inflate abundance estimates in the more open burned habitats (Kotliar et al. 2007).

The community-weighted mean (CWM) was estimated for each of the four traits (i.e. foraging strategies, habitat breadth, diet breadth and body mass) in the R package 'FD' (Laliberté et al. 2014). The CWM was calculated as the mean trait value in the community weighted by the relative abundance of the respective species (Laliberté et al. 2014). Seasonal rainfall was estimated as the cumulative amount of precipitation since the beginning of the rainy season. I used 1st September as the beginning date for the rainy season (no rain fell between 1st May and 1st September in either sampling year). Time-since-fire (*hereafter* TSF) was estimated as the number of months since a site had last burned. I estimated fire frequency by calculating the fire return interval (*hereafter* FRI), which I estimated as the mean number of months between recorded fire events at each site. I assessed the effect of seasonal conditions within the rainy season by including a variable 'season' (0 for early season and 1 for late season).

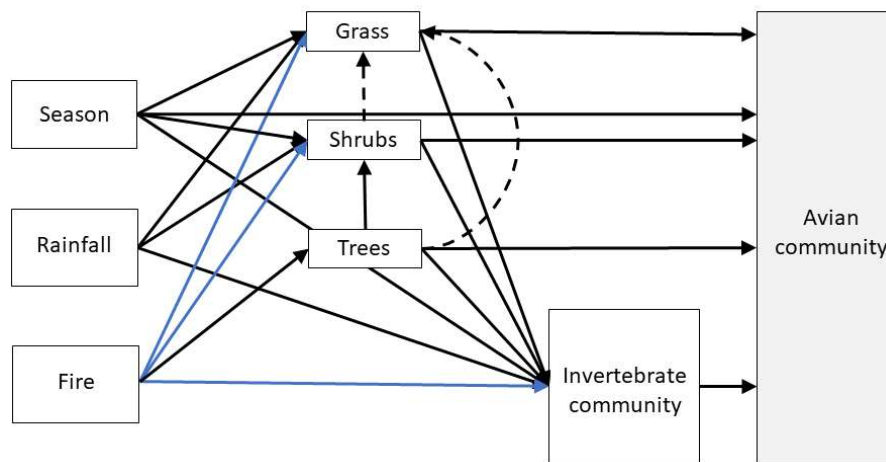


Figure 5.1 Hypothesised causal relationships in an *a priori* structural equation model (SEM), showing the hypothesised pathways between fire (time-since-fire and fire return interval), rainfall, season (beginning or end of rainy season), grass (grass length), shrubs (shrub height and density), trees (tree density), the invertebrate community (Order richness and biomass) and the avian community (insectivore richness and density). Black arrows represent positive relationships, dashed arrows represent negative relationships, and blue arrows represent interactions with rainfall.

In order to evaluate the indirect influences of fire on the avian insectivore community, I performed piecewise structural equation modelling (SEM) using packages 'nlme' (Pinheiro et al. 2018) and 'piecewiseSEM' (Lefcheck 2015). This method combines the information from multiple linear models into a single causal network and incorporate random effects and hierarchical structures (Lefcheck 2015). SEMs were built following recommendations from Grace (2006). Based on knowledge

of this study system and causal pathways of interest I built a conceptual model (Figure 5.1) that included all *a priori* determined relationships between variables. Variables can be included in the SEM as both predictors and responses and I fit linear mixed effects models for each component of the SEM (i.e. vegetation structure, invertebrate community, insectivore community). All models were fit with the variables 'fire' (i.e. burn patch) and 'site' (i.e. sampling point) as nested random effects to account for the hierarchical nature of the survey design (Zuur et al 2009). To evaluate whether the effect of fire varied with rainfall I included interaction terms between the two fire attributes and rainfall (i.e. TSF x Rain and FRI x Rain). Prior to modelling I scaled variables (by mean and variance) to achieve standardized parameter estimates. The data for the variables TSF, tree density, invertebrate biomass, and avian body mass were log-transformed to better meet assumptions of normality.

Candidate component models were fitted with all possible combinations of predictor variables and assessed model parsimony using a corrected Akaike's Information Criterion (AICc). I built component models that included only those predictor variables that were included in candidate models for the respective response variable with a ΔAIC of ≤ 6 and less than the ΔAIC of all simpler nested models (Richards 2008). I assessed model assumptions, including normality and homogeneity of variance, graphically. I tested for spatial autocorrelation in the component model residuals for each response variable using spline-correlograms from 1000 bootstrapped permutations using the package 'ncf' (Bjornstad 2016). No spatial autocorrelation was evident between sites (correlation values were < 0.1) verifying spatial independence of the model residuals. Six separate SEMs were fitted by substituting insectivore richness, density, habitat breadth, diet breadth, foraging strategies, and body mass. To assess the overall fit for each SEM I used directional separation test (Shiple 2009), which evaluates whether model fit would be improved by the inclusion of significant missing pathways among unconnected variables (Lefcheck 2015). The directional separation test can be used to obtain the Fisher's C test statistic (the hypothesized relationships represent the underlying data when $P > 0.05$) to evaluate the overall SEM fit and to produce an AICc value for model selection (Shiple 2009; Lefcheck 2015). I produced partial effects plots to examine the relationship between a response variable and a predictor variable, while accounting for the effects of the other covariates in the component model (Lefcheck 2015).

Table 5.1 Description of variables used to describe the fire regime, vegetation structure, rainfall invertebrate community and insectivore community

Variable	Abbreviation	Data range	Description
Time-since-fire	TSF	1-409	Months since last fire
Fire return interval	FRI	17-409	Mean number of months between fire events
Grass length	GrL	0-87 cm	Mean grass length resulting from maximum height of contact of grass-layer with a vertical pole recorded at 50 points along a 50-m transect
Shrub density	ShD	0-25,200 ha ⁻¹	Density per hectare of woody plants with a height < 3 m and a diameter at breast height (dbh) <10 cm derived the number recorded within 1 m on either side of a 50-m transect
Shrub height	ShHt	0-142.25 cm	Mean height of all woody plants defined as shrubs (with a height < 3 m and a diameter at breast height (dbh) <10 cm) recorded within 1 m on either side of a 50-m transect
Tree density	TrD	0.5-400 ha ⁻¹	Density per hectare of woody plants with a height ≥ 3 m or a diameter at breast height (dbh) ≥10 cm derived from the point-centred quarter method (PQM; Cottam & Curtis 1956)
Seasonal rainfall	Rain	0-414 mm	Mean cumulative precipitation since the beginning of the rainy season (September 1) recorded at six local rain gauges
Invertebrate richness	InvRich	0-19	Number of invertebrate Orders captured at each site
Invertebrate biomass	InvBiomass	0-4370.94 mg	Total biomass of all individuals captured at each site derived from Order specific length/weight equations see Appendix Table A4.1 for more information
Insectivore richness	AvianRich	0-19	Number of avian insectivore species recorded at each site
Insectivore density	AvianDens	0-35 ha ⁻¹	Density of avian insectivore species at each site estimated from multi-covariate distance sampling
Insectivore body mass	AvianBM	8.6-478.31 g	Community weighted mean (CWM) of the body mass of each individual insectivore recorded at each site*
Insectivore foraging strategies	AvianFS	1.0-3.50	CWM of the number of foraging strategies used by each insectivore recorded at each site*
Insectivore diet breadth	AvianDB	1.0-4.86	CWM of the number of diet types strategies used by each insectivore recorded at each site*
Insectivore habitat breadth	AvianHB	1.0-11.61	CWM of the number of habitat types used by each insectivore species recorded at each site*

*trait data compiled from Hockey et al. (2004)

5.4 RESULTS

In total, the surveys of 680 sites over two years recorded 8,582 avian insectivores of 109 species and sampled 49,741 invertebrates of 21 Orders (see Appendix Table A4.1 and A5.4 for a full list of avian species and invertebrate Orders respectively). Avian insectivore richness varied between 0 and 19 (mean \pm SE; 7.1 ± 0.13) among sampling sites. The distance-sampling model of best fit for the estimation of avian density used a half normal key function and included the covariate 'cues', demonstrating that detectability declined more rapidly for birds observed visually than for birds observed aurally. The detection function and density model selection summaries are provided in the appendix (Figure A5.1 and Table A5.1). Avian insectivore density varied between 0 and 35 (5.6 ± 0.19) among sampling sites. The results from structural equation modelling are described below.

5.4.1 Insectivore richness and density

The best-fit SEMs for insectivore richness and density adequately fit the data (in both cases: $P > 0.05$). Compared to the hypothesized initial SEMs, the directional separation tests identified three path additions were required, which revealed the importance of the direct effects of TSF and rainfall for the avian insectivore community (Fig. 5.2; missing pathways and SEM model selection are described in Table A5.4). There was a strong positive direct effect of TSF on grass-length, shrub density and invertebrate richness and biomass (Figure 5.2). There was a weaker direct positive effect of TSF on avian insectivore richness (Figure 5.2a). FRI had a direct positive effect on tree density and a weak negative effect on invertebrate biomass (Figure 5.2). There is evidence of strong positive direct effects of season on grass-length, shrub height and insectivore richness (Figure 5.2a), suggesting that there is an increase in these variables over the rainy season. Rainfall had strong positive direct effects on multiple components of this network which included a direct effect on insectivore density (Figure 5.2b). There is also evidence of interactions between rainfall and both fire attributes (TSF and FRI) that directly affect invertebrate richness and biomass (Figure 5.2). Insectivore richness was influenced by a positive relationship with invertebrate Order richness (Figure 5.4a) and a negative relationship with grass-length (Figure 5.4b). There is evidence that the positive indirect effect of FRI on avian insectivores is mediated by tree density (Figure 5.2) suggesting that areas with longer fire return intervals (i.e., less frequent fires) have higher tree density and higher insectivore richness and density (Figure 5.4c & d). The results of modelling reveal that insectivore richness responded indirectly to TSF, FRI and rainfall via vegetation

structure and the invertebrate community; however, the cumulative indirect effects of vegetation were stronger (Table 5.2). Moreover, the SEM for insectivore density reveals that the indirect effects of time-since-fire and rainfall were mediated by food availability (i.e., invertebrate biomass) and not by vegetation structure (Table 5.2).

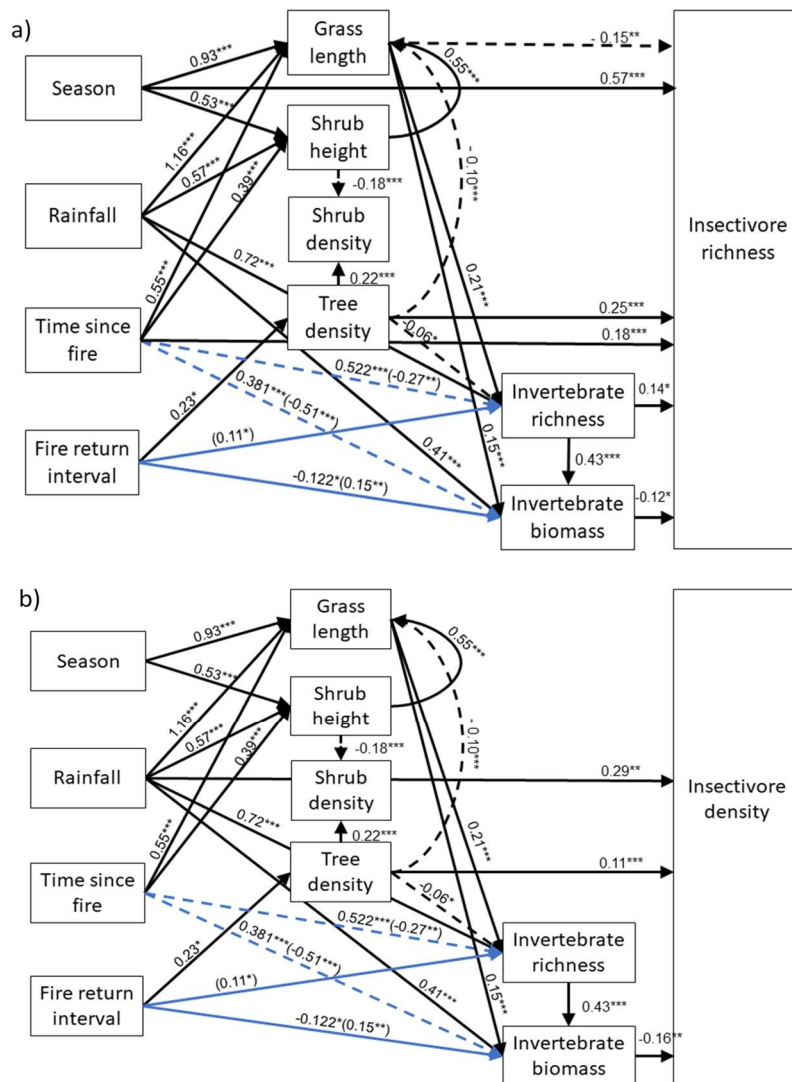


Figure 5.2 Structural equation models (SEMs) of the relationships between fire, rainfall, vegetation structure, invertebrates and the avian insectivore community. Diagrams represent the best fit models for insectivore a) richness and b) density. Black arrows represent positive relationships, dashed arrows represent negative relationships, and blue arrows represent interactions with rainfall. Standardized effect sizes are reported as path coefficients (*P < 0.05; **P < 0.01; ***P < 0.001). All non-significant paths are excluded, and interaction coefficients values are shown in parentheses.

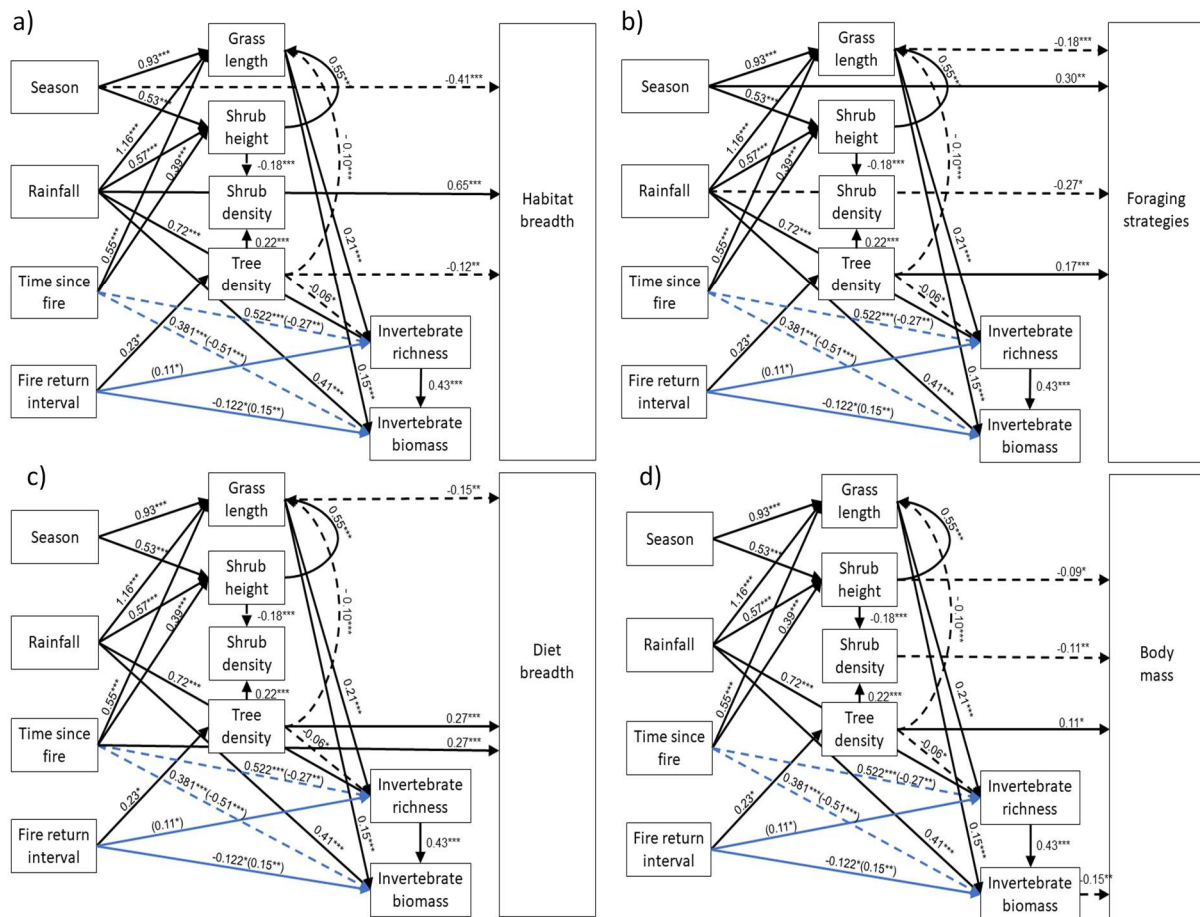


Figure 5.3 Structural equation models (SEMs) of the relationships between fire, rainfall, vegetation structure, invertebrates and avian insectivore functional identity. Diagrams represent the best fit models for the community weighted mean (CWM) of the insectivore traits a) habitat breadth, b) foraging strategies, c) diet breadth, and d) body mass (a more detailed description of these traits can be found in Table 1). Black arrows represent positive relationships, dashed arrows represent negative relationships, and blue arrows represent interactions with rainfall. Standardized effect sizes are reported as path coefficients (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). All non-significant paths are excluded, and interaction coefficients values are shown in parentheses.

5.4.2 Insectivore functional traits

The best-fit SEMs for habitat breadth, foraging strategies, diet breadth, and body mass adequately fit the data (in all cases: $P > 0.05$). Compared to the hypothesized initial SEMs, the directional separation tests identified multiple path additions were required (Fig. 5.3; see Table A5.4). Habitat breadth had a strong negative direct effect of season (Fig. 5.3a), suggesting that species late in the rainy season use less habitat types and are more likely to be habitat specialists. Avian habitat breadth was the only

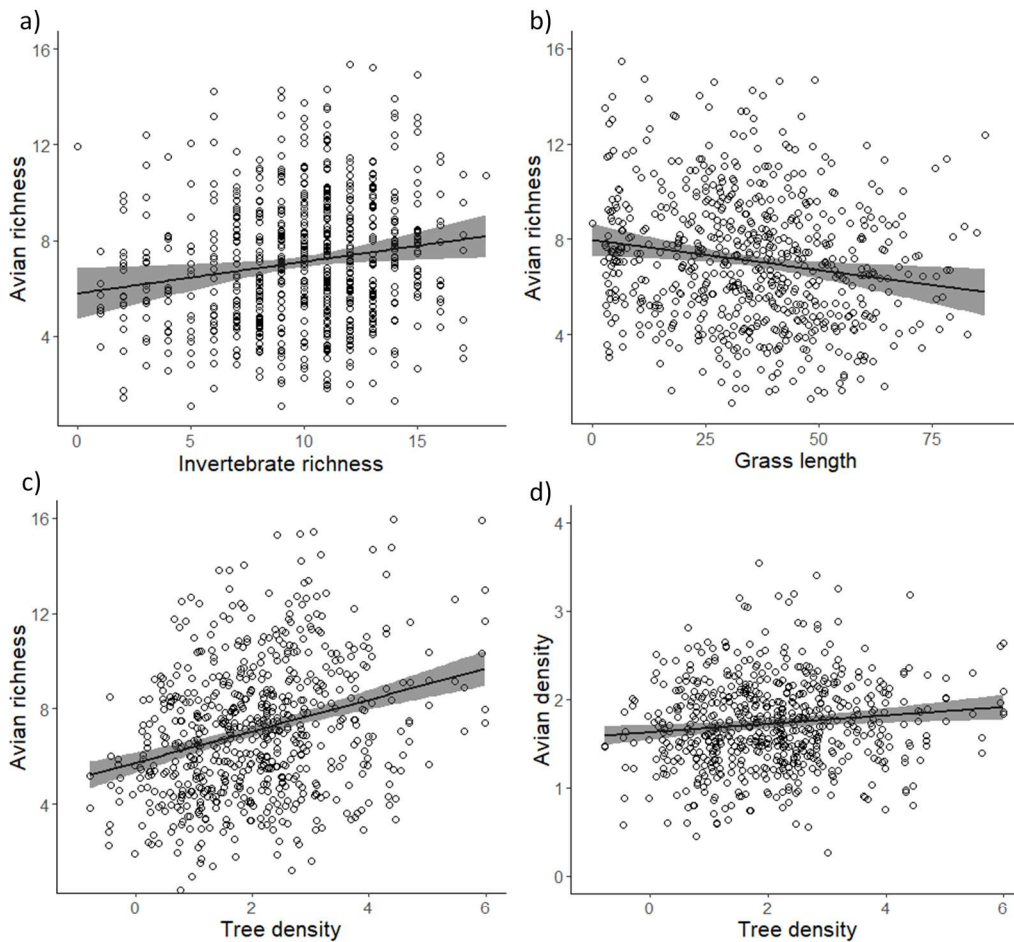


Figure 5.4 Partial residuals, partial effects and 95% confidence bands showing effect of a) invertebrate Order richness on avian insectivore species richness, b) grass length (cm) on avian insectivore species richness, c) log-transformed tree density (trees ha⁻¹) on avian insectivore species richness, and d) log-transformed tree density (trees ha⁻¹) on log-transformed avian insectivore density (individuals ha⁻¹).

functional trait to respond negatively to tree density (Fig. 5.3) and the only trait that did not respond (directly or indirectly) to TSF (Table 5.2). There was evidence of a negative relationship between grass-length and avian insectivore foraging strategies and diet breadth (Fig. 5.3b & c), suggesting that species in short grass are more likely to be foraging and dietary generalists (many foraging strategies and diet flexibility). Notably, diet breadth was the only functional trait that had a direct relationship with fire (Table 5.2), revealing that as TSF increases so does diet flexibility. Body mass showed a weak negative response to invertebrate biomass (Figure 5.3d). Moreover, body mass was the only response variable that responded to shrub density or height, revealing a negative relationship with both (Figure 5.3d). This relationship suggests that areas with denser and taller shrubs have smaller avian insectivores. The SEMs for functional traits reveal that the indirect effects of fire and rainfall on indices of niche width

(habitat breadth, foraging strategies, diet breadth) are mediated by vegetation structure only, while the indirect effects of fire and rainfall on body mass are mediated by vegetation structure and invertebrates (Table 5.2).

Table 5.2 Standardized direct and indirect effects of time-since-fire, fire return interval and rainfall on the insectivore community and functional traits. Indirect effects include i) pathways that are mediated by plants only and ii) pathways that are mediated by the invertebrate community.

Response	Time-since-fire effect			Fire return interval effect			Rainfall effect		
	Direct	Indirect (plant mediated)	Indirect (invertebrate mediated)	Direct	Indirect (plant mediated)	Indirect (invertebrate mediated)	Direct	Indirect (plant mediated)	Indirect (invertebrate mediated)
Richness	0.18	-0.115	-0.022	na	0.061	0.021	0	-0.221	0.011
Density	na	0	-0.126	na	0.025	0.17	0.29	0	-0.149
Foraging strategies	na	-0.138	0	na	0.043	0	-0.27	-0.056	0
Habitat breadth	na	0	0	na	-0.028	0	0.65	0	0
Diet breadth	0.27	-0.115	0	na	0.066	0	na	-0.221	0
Body mass	na	-0.027	-0.028	na	0.020	0.018	na	-0.040	-0.161

na = effects that were not included in the hypothesized structural equation model (SEM) and not identified as a missing link by directional separation tests and added during modelling. Effects with a value of zero were deemed to be insignificant or not included in the final SEM. Displayed are the direct and indirect effects obtained from the final SEMs shown in Figure 5.2 a-b and Figure 5.3 a-d.

5.5 DISCUSSION

In this chapter, I explored the relationships between fire, rainfall, vegetation, invertebrates and avian insectivores in semi-arid savanna habitat. Despite the frequent assertions that the impacts of fire on savanna biodiversity are mediated by vegetation structure (Monamy & Fox 2000; Watson et al. 2012b; Sitters et al. 2014a; Beale et al. 2018), causal pathways mediated by other animals have rarely been examined. Here, I demonstrate that fire and rainfall influence avian insectivores via changes in vegetation structure and invertebrate food supply. In addition, the results of this chapter indicate that the mechanisms underlying fire response are determined by functional trait identity. Furthermore, structural equation modelling showed that fire, rainfall and season had both direct and indirect effects on the structure of invertebrate and insectivore communities, revealing that fire and climate exert top-

down and bottom-up effects on animal communities in savanna systems. I discuss these effects below in relation to community dynamics and their implications for conservation management.

The effects of vegetation mediated pathways on richness were stronger than invertebrate mediated pathways. Despite the prediction that insectivore richness and density would increase with the structural complexity of late successional or infrequently burned habitats, I found contrasting causal pathways through which fire affects insectivores. Fire return interval had a positive effect on avian richness and density via tree density, whereas time-since-fire had a negative effect on avian richness via grass length. Both richness and density increased with tree density, but this relationship was strongest for insectivore richness (Figure 5.4 c & d). The relationship between fire frequency and tree density is well supported (Roques et al. 2001; Case & Staver 2017) and the positive effect of tree density on avian species has been documented in African savanna (Sirami & Monadjem 2012; Péron & Altwegg 2015). This relationship is likely due to increases in species that specialize in closed savanna habitats (Péron and Altwegg 2015). The result that species richness is highest in areas with short grass may similarly result from increases in specialist species such as short-grass specialists (e.g. African pipit, *Anthus cinnamomeus* and crowned lapwing, *Vanellus coronatus*; Krook et al. 2007), ground nesters (Wilson et al. 1995), and post-fire specialists (species that were only observed within 6 months of burning e.g., capped wheatear, *Oenanthe pileata*; buffy pipit, *Anthus vaalensis*; and Temminck's courser, *Cursorius temminckii*). In addition to these specialists, studies have documented species that select short-grass, post-fire habitats such as generalist, open-habitat, and early successional species (Davis & Peterson 2000; Pons & Bas 2005; Reidy et al. 2014). Lastly, many insectivores are selecting habitat based on multiple vegetation characteristics (e.g. grass length and tree density) such as red-backed shrikes (*Lanius collurio*) that are associated with trees and short grass to accommodate their 'perch and pounce' foraging strategy (Vanhinsbergh & Evans 2002).

Invertebrate food availability increased with grass length and was influenced by interactions between rainfall and fire. The positive association between avian richness and invertebrate richness suggests that species diverse communities depend on diverse prey communities (Figure 5.4a) consistent with evidence from other African ecosystems where the diversity of higher trophic levels is driven by the diversity of lower trophic levels through bottom-up relationships (Kissling et al. 2007; Vollstädt et al. 2017). Both avian richness and density were negatively associated with invertebrate biomass. This may result from decreases in foraging efficiency that accompanies long grass. Birds

consider trade-offs between prey abundance and accessibility when selecting where to forage (Whittingham & Evans 2004). Grassland studies demonstrate that avian insectivores select accessibility and detectability (e.g., short vegetation height and open ground surface) over increases in arthropod abundance in longer and denser grass swards (Martinez et al. 2010; Oosten et al. 2014). Avian species may also forage in shorter vegetation to decrease their predation risk (Whittingham & Evans 2004). Furthermore, the Ordinal level of the invertebrate data might be masking avian responses to variation in prey abundance of a particular species or group of invertebrates. For example, evidence suggests that the abundance of flying insects may drive insectivore densities in open grassland areas in Africa (López-Calderón et al., 2017).

Insectivore traits revealed varied indirect relationships with fire attributes, suggesting that fire response depends on functional identity. The effects of fire on niche width were mediated by changes in vegetation structure only. The identification of traits that respond to changes in vegetation structure is a critical step in the conservation of savanna species. Broad-scale increases in woody cover in savanna habitats across southern Africa, linked to global drivers such as climate and CO₂ and local drivers such as declines in fire and herbivory (Venter et al. 2018), have been implicated in the loss of avian species (Sirami & Monadjem 2012; Péron & Altwegg 2015). I found that species with narrow niche widths (specialists) were associated with low tree densities and short grassland, except in the case of habitat breadth. This is likely due to an influx of specialist species such as large-bodied, ground foragers (Engelbrecht 2001; Little et al. 2013) and aerial insectivores (López-Calderón et al. 2017) associated with open and burned grasslands. The positive link between tree density, diet breadth and foraging strategies may result from increases in foraging locations, perch sites, and food resources (e.g. fruits, seeds, nectar, vegetation). In contrast, I found that insectivore habitat breadth had an indirect, negative relationship with fire return interval mediated tree density. This relationship reveals that birds with a narrow habitat breadth (habitat specialists) were associated with areas that had more trees. This is likely due to a positive relationship between tree density and closed-savanna specialists such as crimson-breasted shrike (*Laniarius atrococcineus*), brubru (*Nilaus afer*), white-browed scrub-robin (*Cercotrichas leucophrys*), and Kalahari scrub-robin (*Cercotrichas paena*). These species have narrow niche breadths (are typically only associated with savanna and/or woodland habitat), are positively associated with tree density, and are increasing across South African savanna due to widespread bush encroachment (Péron & Altwegg 2015).

Body mass was the only response variable that responded to shrub density or shrub height, revealing a negative association with both. This suggests that larger birds were associated with open habitat and a less dense shrub-layer resulting from recent and frequent fires. Due to increased mobility and home-range size, larger birds may be able to support their resource needs by exploiting resources in these early successional habitats and elsewhere (Reif et al. 2016). Empirical evidence shows that both body mass and bird movement increase with disturbance in South Africa (Neuschulz et al. 2013). Furthermore, associations between large-bodied birds and burned grassland have been previously identified in South African grassland and are attributed to the selection of open habitat and bare ground by large ground-foraging insectivores (Engelbrecht 2001; Little et al. 2013). Avian body mass had a negative relationship with invertebrate biomass. This relationship may result from a lack of correlation between invertebrate biomass and nutritional value, palatability, or prey selection preference (Kaspari & Joern 1993). However, it may also result from trade-offs between food supply and foraging efficiency that are influenced by body size (Whittingham & Evans 2004). Large species may not be selecting the enhanced food supply in long grass due to reductions in prey detectability and accessibility as well as increases in energetic demands and predation risk of foraging in closed habitat (Devereux et al. 2006).

Seasonal and interannual variation in rainfall in African savannas has a strong impact on plant productivity (Rishmawi et al. 2016), invertebrate abundance (Denlinger 1980), and the distribution of birds (Beale et al. 2018). At large spatial scales, abiotic factors driving the distribution and diversity of species such as climate are thought to be stronger than biotic factors (Wisz et al. 2013). I demonstrated that direct climatic effects (i.e., rainfall and season) were stronger local drivers than vegetation and invertebrate food supply for avian density, foraging strategies and habitat breadth (see Table 5.2). Consistent with previous studies, rainfall had a greater effect on avian density than avian richness (Albright et al. 2010), likely resulting from numerical responses to increases in vegetation productivity (Macías-Duarte et al. 2018), increased reproductive success (Mares et al. 2017), or habitat selection by nomads and migrants (Albright et al. 2010). Given that migrant species are more likely to be habitat generalists (i.e., wide habitat breadth; Reif et al. 2016) and to select habitat based on high rainfall, this may explain the direct links between habitat breadth and rainfall. The strong indirect effects of rainfall and season were exhibited through their dominant effect on vegetation height (i.e. grass length and shrub height) and invertebrates (i.e. biomass and Order richness). These results, along with the rainfall-contingent fire effects on invertebrates, identify the key role of rainfall in this savanna system.

In addition to the direct effects of rainfall and season, I identified direct effects of fire on birds revealing potential top-down effects of fire. While the direct effects of fire through mortality, emigration and survivorship have been documented in invertebrates (Chambers & Samways 1998; Vasconcelos et al. 2009) with lasting demographics consequences (Broza & Izhaki 1997; Mutz et al. 2017), the direct effects of fire on birds are less well understood. Species such as the fork-tailed drongo (*Dicrurus adsimilis*) and Temminck's courser (*Cursorius temminckii*) in South Africa, may be nomadic during fire season, tracking recently burned habitats across a large region (Dean 1987; Dean & Siegfried 1997; Bouwman & Hoffman 2007). Additional direct effects on birds could result from changes in territorial behaviour (Dean 1987), reproduction (Robertson 2009), and survival (Fontaine & Kennedy 2012). However, I recognize that these direct effects could also result from the absence from the SEM of an important pathway or mediating process, such as plant productivity (Albright et al. 2010) or composition (Ponisio et al. 2016).

5.5.1 Conclusions and implications for conservation management

The findings of this study demonstrate that indirect effects of fire on the avian insectivore community are mediated by both vegetation structure and invertebrate food supply. However, the strength of these indirect relationships is dependent on avian functional trait identity. The identification of traits that respond to variation in disturbance is a powerful tool for conservation management because it can help to identify species sensitivity to disturbance regimes (Vollstädt et al. 2017), reveal the component of a disturbance regime that has caused a shift in a biological community (Bregman et al. 2016), and predict the potential loss of ecosystem function and services (Gagic et al. 2015). I found that small-bodied, foraging and dietary specialists were negatively affected by recent fires, while habitat specialists were negatively affected by frequent fires. Furthermore, dry conditions (low rainfall) had negative consequences for small-bodied, specialist species and interacted with fire to affect food availability. Given the combined projections that fire frequency will increase (Pricope & Binford 2012) and rainfall in this region will decrease by as much as 20% by the 2080s (Conway et al. 2015), the results of this chapter suggest that this will have significant implications for avian insectivores and their food supply. This may include declines in savanna species such as zitting cisticola (*Cisticola juncidis*), desert cisticola (*Cisticola aridula*) and bushveld pipit (*Anthus caffer*), which have small body size and narrow niche widths.

An improved understanding of the effects of fire on trophic processes and whole-ecosystems is needed for the development of sustainable management in fire-prone systems (Bowman et al. 2016). Such an understanding requires that we account for trophic interactions, top-down and bottom-up processes, predator-prey relationships, and the mediating effects of animal populations (Geary et al. 2018). In the present study, I was able to evaluate the relative support for multiple mediating pathways between fire, climate, vegetation structure, invertebrates and the avian community using SEMs. The identification of important environmental drivers, biotic interactions, and critical resources within disturbance-prone trophic networks can improve understanding of community assembly and dynamics (Ponisio et al. 2016) and ecosystem resilience (Bregman et al. 2016), and can enable predictions of community changes when disturbance regimes shift (Perry et al. 2015). Fire research that ignores the biotic interactions that mediate fire effects will have weak predictive power (Swan et al. 2015) and is unlikely to contribute to ecologically sustainable management practices.

Identifying key pathways in this trophic network that may change (e.g. increases in fire frequency or decreases in rainfall) is important for management. Changes to fire regimes due to management interventions, land-use alteration, or climate change will have significant bottom-up and top-down effects on wildlife. Fire management practices used extensively in savanna systems in South Africa and elsewhere alter time-since-fire and fire frequency (Brockett et al. 2001; Parr et al. 2009) and the results of this chapter predict how changes to these fire attributes would affect this trophic network in a piecewise manner. Furthermore, the findings of this chapter reveal that the direct effects of rainfall on many components of this trophic network were stronger than fire. The large inter-annual and inter-seasonal variation in southern African rainfall (Conway et al. 2009; Kane 2009), along with projected increases in fire frequency and size (Midgley & Bond 2015) will have significant consequences for savanna communities. Therefore, the conservation of savanna communities will benefit from fire management that incorporates climatic variables (i.e., inter-annual rainfall forecasts) and long-term fire histories into decision making.

Chapter 6

General Discussion



Prescribed burning, Mankwe Wildlife Reserve, South Africa

6.1 SYNTHESIS

In this thesis I assessed the effects of long-term fire regimes on mammal, bird and invertebrate community structure in semi-arid savanna. This thesis demonstrates that animal communities respond to fire regimes in many complex ways; however, important general conclusions can be drawn. I have shown that savanna community structure responds to nearly three decades of variation in fire regimes at the landscape-scale. Throughout this thesis, I demonstrate that a trait-based approach to community structure provides an enhanced mechanistic understanding of fire-fauna relationships. Further, this study highlights the importance of considering the interactive effects of climatic processes and biotic drivers on these relationships. These results demonstrate that fire and climate have direct and indirect effects on savanna fauna, with evidence that indirect effects are mediated by vegetation and animals. This thesis emphasises the relevance of studies of fire-fauna relationships from a cross-section of taxa and scales for informing fire management and conservation planning.

Below, I summarise and discuss the key findings of this thesis within the wider context of our current understanding of disturbance ecology and applied conservation. Specifically, I discuss the results of this thesis in relation to: 1) the importance of empirical evidence for conservation planning, 2) the importance of scale, and 3) the influence of climate on disturbance ecology. I go on to outline the application of these results to savanna conservation and future ecological studies.

6.1.1 The importance of empirical evidence for conservation planning

Evaluating the ecological impacts of management interventions is a critical component of conservation policy and practice, particularly in protected areas (PAs) (Baylis et al. 2016). However, lack of ecological monitoring and a paucity of evaluation of national park policy and management have been identified as factors inhibiting the effective governance of protected areas in southern Africa (Novellie et al. 2016). In this thesis, I tested the hypothesis that pyrodiversity promotes biodiversity, which underpins widely used fire management practices (i.e., patch mosaic burning), using large mammals (Chapter 2) and birds (Chapter 3). This study, to the best of my knowledge, is the first to evaluate the effects of pyrodiversity on multi-trait functional diversity in animals (Chapter 3). Moreover, it is one of the first studies to evaluate the relationship between pyrodiversity and vertebrate densities. Understanding the relationship between fire management and density is particularly relevant for large mammals because their densities remains an important priority for conservation and tourism in South African Protected

Areas. Furthermore, understanding how variability in fire regimes affects indices of population size (i.e., density) is important, because these indices are the best correlates of extinction risk (O'Grady et al. 2004) and ecosystem service delivery (Winfree et al. 2015).

This study is part of a growing body of research that has found no effect of pyrodiversity on birds (Taylor et al. 2012, 2013a; Kelly et al. 2014; Burgess & Maron 2016; Prowse et al. 2017) and mammals (Kelly et al. 2012; Davies et al. 2018). Instead, I found that the extents of single fire age-classes (i.e., ≤ 1 year and ≥ 10 years post-fire) were better predictors of avian species richness and functional diversity (Chapter 3) and large mammal density (Chapter 2). Throughout this thesis, I have demonstrated that savanna biodiversity responds to the temporal fire attribute time-since-fire (TSF) at the trait, species and community level. Understanding how animals respond to the extent of burned areas is important because data from National Parks in southern Africa has shown that while fire managers can control the configuration of burn patches on the landscape they have less control over the total burned area (Pricope & Binford 2012; Van Wilgen et al. 2014). A major finding of this study is the importance of long-unburned savanna (≥ 10 years post-fire) for avian richness and functional diversity (Chapter 3). I also demonstrated that areas of increasing TSF were important for grass-layer invertebrate richness and biomass (Chapter 4). Elsewhere, in Australian shrubland and woodland, long-unburned areas have been shown to be important for birds and small mammals (Kelly et al. 2011; Taylor et al. 2012; Berry et al. 2015). Such areas are important for rare species (Taylor et al. 2012) and critical resources that support species persistence on the landscape (Haslem et al. 2012). In Chapter 3, I found that functional evenness decreased with the increasing extent of long-unburned area on the landscape, suggesting that rare bird species were associated with these areas. Long-unburned areas may act as important temporary refuge sites and may be important areas for species that cannot persist in early-successional or burnt habitat (Yarnell et al. 2008; Robinson et al. 2014). While the results of this thesis reveal that the extent of these late successional habitats is important, how this habitat is configured on the landscape will need to be further examined; this is discussed in more detail below.

In this thesis, I have found considerable evidence of resistance to high fire frequency among communities. In Chapter 2, fire frequency was not a good predictor of large mammal density, suggesting that large mammals can tolerate a range of fire frequencies. In Chapter 4, invertebrate (ground- and grass-layers) Order richness increased with increasing fire frequency, and invertebrate abundance (ground-layer) was highest in frequently and recently burned habitat. I demonstrated that invertebrate

response to fire frequency is Order specific, which supports previous studies in semi-arid savanna that suggest that response to fire frequency is Order, guild, or species specific (Andersen & Müller 2000; Davies et al. 2012). These taxon or species-specific responses to fire frequency may be the result of fire-tolerant functional traits or life-history strategies (Charles-Dominique et al. 2017). This was demonstrated in Chapter 5 where I showed that the response of avian insectivores to fire frequency was determined by life-history traits, a relationship that was mediated by vegetation structure. For example, habitat generalists increased with increasing fire frequency. A recent study of savanna plants, demonstrated that high fire frequency can act as an environmental filter on species by selecting for fire tolerant traits over time (Charles-Dominique et al. 2017). This may explain why in Chapter 3 avian communities had lower than expected functional richness. High disturbance frequencies over long time periods may deplete populations of species with disturbance-sensitive traits, reducing overall community functional richness (Mouillot et al. 2013). Thus, high fire frequencies operating through history may have filtered out species with fire sensitive traits across this study region. This result has broader implications for global semi-arid savanna regions, where average fire return intervals can be as low as 1 to 3 years (Archibald et al. 2013). However, knowledge of fire resistance and fire-adaptive traits in animals is poorly understood and developing this knowledge is important for fire management in fire-prone habitats (Pausas & Parr 2018).

This thesis has revealed that fire regimes affect savanna biodiversity at the trait, species, functional guild, and community level. Notably, I demonstrated that fire regimes affect trophic interactions and food webs, with evidence of top-down and bottom-up effects of long-term fire history on savanna animals (Chapter 5). Moreover, I demonstrated that the indirect effects of fire, that are generally attributed to changes in vegetation structure, are much more complex than previously understood and are often mediated by other animals. Recognition that fire alters many components of trophic networks directly and indirectly suggests that trophic ecology should be incorporated into fire research and has important implications for habitat restoration (Bowman et al. 2016). Recently, researchers in Australia found that fire history at the landscape scale altered the activity of an apex predator which had important consequences for the suppression of an invasive mesopredator and native small mammal populations (Geary et al. 2018). This thesis serves as further evidence that the indirect effects of fire regimes should be considered when managing fire for biodiversity conservation.

6.1.2 *The importance of scale*

Throughout this thesis, I have demonstrated the importance of spatial and temporal scale on fire-fauna relationships. Further, the findings of this study reveal that evaluating the effects of prescribed fire regimes is best conducted at the scale of fire management. In Chapter 2, I used landscape-scale density surface models to evaluate the relative effects of fire regimes and landscape variables on large mammal density and distribution. These results provide spatially-explicit information to guide fire management, such as optimal distance to artificial water sources and extent of habitat patches. In Chapter 3, I demonstrated that species richness and functional diversity were driven by fire variables at multiple spatial scales, thus supporting the idea that species perform functions across multiple spatial scales and respond to scale-specific disturbance in different ways (Peterson et al. 1998). Studies which examine functional diversity at the landscape scale can reveal important patterns that can assist in our understanding of community assembly processes (Petchey & Gaston 2006), ecosystem resilience (Spasojevic et al. 2016), and the conservation of critical functions and resources (Robinson et al. 2014). Furthermore, landscape-scale fire studies are increasingly valuable as they provide ecological evidence that can be explicitly incorporated into fire management and policy (Driscoll et al. 2010).

A primary objective of this thesis was to explore the ecological effects of fire history across long temporal scales. Throughout this thesis I have shown that mammals, birds and invertebrates are responding to long-term variation in a fire regime. In Chapter 2, I demonstrated that large mammal densities respond to a longer post-fire chronosequence than has previously been shown in savanna ecosystems. These results conflict with previous claims that large mammal fire response lasts up to one year post-fire in African savanna (Green et al. 2015). Without the evaluation of a long-term fire regime, this thesis would not have revealed the importance of long-unburned habitat for avian diversity and function (Chapter 3) or the interactive effects of climatic and biotic drivers on fire response (Chapter 4 and 5). In Chapter 4 and 5, I revealed that short-term variation in rainfall interacts with long-term variation in fire regimes to alter invertebrate and avian communities. This result suggests that sensitivity of savanna communities to interannual variability in climate depends on long-term context of disturbance. Thus, the present study of long-term fire histories, can provide a context for studies of short-term variation in fire regimes. This thesis demonstrates the importance of investigating long-term fire regimes for: i) understanding postfire successional processes, ii) identifying critical resources that support a species persistence in fire-prone landscapes, iii) predicting a species' occurrence on a

landscape, and iv) identifying the upper limit of fire response. Information on how savanna fauna respond to a full range of fire and successional variation will allow for proactive rather than reactive management approaches and can help us to predict how communities will respond to altered successional trajectories resulting from shifting disturbance and environmental drivers (Péron & Altwegg 2015). For example, drought can favour vegetation that typically dominates late successional habitats (Uriarte et al. 2016). In addition, woody vegetation encroachment into grassy biomes is increasing in southern Africa due to changing fire regimes, farming practices and atmospheric CO₂ concentrations (Péron & Altwegg 2015).

6.1.3 The influence of climate on disturbance ecology

This thesis highlights the dominant effect that climatic drivers, particularly rainfall, have on savanna communities. Results from Chapter 5 illustrate that rainfall was the strongest driver (stronger than fire) of habitat structure, invertebrate biomass and richness, and avian insectivore density. In Chapter 4 and 5, I found significant interactions between rainfall and fire regimes, revealing that the effects of fire on invertebrate communities were contingent on rainfall. For example, grass-layer richness and biomass were positively associated with TSF; however, the strength of these relationships increased with rainfall. These results highlight the importance of short-term variation in rainfall on fire response, likely leading to inter-annual variability in fire response, and have important implications for fire research. Rainfall-moderated effects of fire may explain the variable fire responses observed among studies, particularly for invertebrates. Furthermore, given projections that rainfall will decrease and inter-annual variability will increase in southern Africa (Conway et al. 2015), the findings of this thesis suggest that future changes to rainfall will have important implications for fire management. Given the combined projections that fire frequency will increase (Pricope & Binford 2012) and rainfall in this region will decrease by as much as 20% by the 2080s (Conway et al. 2015), the results of this thesis suggest that this will have significant negative effects on invertebrate and avian communities.

Comparing the relative effects of environmental drivers and fire can provide valuable information for conservation management. The findings of this thesis reveal that water availability was a stronger driver of community and species abundance than fire. In Chapter 2, I found that large mammal density (particularly grazing species) was highest in areas closest to water bodies. Furthermore, rainfall was the strongest predictor of invertebrate abundance (Chapter 4) and avian

density (Chapter 5). These results reveal that fluctuations in climate will have significant consequences for populations in this region and fire management should be adapted to consider rainfall. Data from long-term drought events reveal significant declines in animal populations, including common species, which can put considerable stress on food webs (Gandiwa et al. 2016; Prugh et al. 2018)

A limitation of this study is that sampling was not conducted during the dry season. Limited water resources (Kimanzi et al. 2014) and winter malnutrition (Oliver 1978) can be critical population-limiting factors, particularly for animals in arid savanna. Sampling during the dry season may be important because: i) this is the time of year when fires are typically applied in this study region, ii) quantifying the critical resources required by target species may be best understood during critical periods (Du Toit 2003), iii) some species demonstrate seasonal variation in their relationship with TSF (Mentis & Bigalke 1979; Parrini & Owen-Smith 2009), and iv) species can switch their resource use or interspecific interactions during the dry season (Traill 2004; Kimanzi et al. 2014). Given the interactions found in this thesis between climate, water availability and fire, developing an understanding of how savanna communities respond to a fire regime during the dry season will be important for conservation management.

6.2 APPLICATIONS TO CONSERVATION MANAGEMENT

Findings from this thesis, and elsewhere, demonstrate that fire management needs to progress away from policy based on vague definitions of pyrodiversity towards clearly defined fire regimes based on local empirical evidence (McGregor et al. 2014; Berry et al. 2015; Ponisio et al. 2016; Davies et al. 2018). This thesis demonstrates that ecological evidence can lead to the characterisation of fire regimes that support local biodiversity conservation. In this thesis, I highlight the importance of habitat that represents a long chronosequence of post-fire succession for multiple animal communities and that areas of recently burnt (<1-year post-fire) and long-unburnt (≥ 10 -years post-fire) habitat were particularly important for the conservation of savanna biodiversity. Current patch-mosaic burning methods at PNP have resulted in an insufficient extent of late-seral savanna and efforts should be taken to increase the amount of this habitat on the landscape. Given that reducing the annual burned area in protected areas in semi-arid South Africa is likely unachievable (Pricope & Binford 2012), a burning regime that increases the amount of unburned habitat on the landscape is needed. Studies in arid regions of Australia have demonstrated that strategic burning can be used to achieve greater extents

of unburned habitat (Andersen et al. 2005; Murphy et al. 2015). These studies suggest a decrease in the 'randomness' of burning and to target prescribed burning strategically. Based on the findings from this thesis, I recommend the following:

- 1) targeting a large portion of annual burning in recently burned habitats (<5 years),
- 2) burning across a full range of fire frequencies,
- 3) increasing the total area of long-unburned habitat (>10 years) by actively avoiding burning in these areas,
- 4) incorporating rainfall into prescribed burn planning, and
- 5) planning burning strategically through an adaptive framework (see Table 6.1).

Strategically burning in recently burned habitat is likely to have multiple benefits for Pilanesberg and Mankwe. First, it would maintain a large extent of early-seral habitat on the landscape with positive implications for the density of large grazing mammals (Chapter 2), taxonomic and functional diversity of birds (Chapter 3), ground-layer invertebrates (Chapter 4), and specialist bird species (e.g., short-grass specialists; Chapter 5). Targeting burning in recently burned areas (<5 years post-fire) will shift prescribed burning away from unburned areas (>10 years post-fire). This will be particularly important at Pilanesberg, where unburned areas are limited. Murphy et al. (2015) found that burning in recently burned areas, whilst maintaining the extent of annual fires, led to an increase in the extent of unburned habitat in Australian heathland. Burning in early-seral state habitat may lead to a decrease in fire return intervals in a portion of the landscape. Evidence suggests short fire return intervals are likely to benefit ground-layer invertebrates (Chapter 4) and have no effect on large mammals (Chapter 2). However, short fire return intervals may cause shifts in the vegetation composition (Bond et al. 2008), as well as having some negative consequences for avian insectivores (Chapter 5) and soil nutrients (Pellegrini et al. 2018).

While I propose that burning should occur in recently burned habitat (<5 years), burning should also occur across a range of fire frequencies. This strategy can lead to a more even distribution of fire age- and frequency-classes on the landscape, with larger amounts of both frequently and infrequently burned habitat (Murphy et al. 2015). This method is currently being used at Mankwe where most areas are burned every 4 to 5 years, while some areas are burned more or less frequently, and some areas are not burned at all. This has resulted in a greater overall proportion of unburned habitat on the landscape compared to Pilanesberg where fires are largely located randomly. A larger extent of recently

and unburned habitat will lead to increases in the taxonomic and functional diversity of birds (Chapter 3). Furthermore, a range of fire return intervals will support both ground-layer and grass-layer communities (Chapter 4), as well as avian insectivores (Chapter 5) and small mammals (Yarnell et al. 2008). However, strategic planning of burning locations on the landscape will require maintenance of local, long-term spatial fire data, as well as continuous development and adaptation of burning plans.

Conserving long-unburned habitat on the landscape may contribute significantly to ecosystem resilience by conserving ecosystem functions in fire-prone landscapes (Haslem et al. 2012), providing colonists for recovering post-fire habitats (Nimmo et al. 2015), and offering temporary refuge sites (Gandar 1982). However, an increase in the extent of late seral habitat on the landscape may present extra challenges for management. Late-seral habitats have higher fuel loads (greater grass biomass) and are more likely to lead to wildfires (Brockett et al. 2001). Protecting late-seral habitat and limiting the spread of uncontrolled fires may require the reduction of fuel loads through the mechanical removal of fuels or the use of infrastructure such as dirt roads and fire-breaks. While recent work suggests that the use of this fire breaks does not impact the diversity or composition of savanna invertebrates (Salles et al. 2018), further research on other taxa is required. In addition, natural features on the landscape such as watercourses or rocky outcrops can be used as natural fire-breaks (Murphy et al. 2015). Removing fire from sections of the landscape may lead to increased woody vegetation encroachment and the loss of open savanna grassland, which can be difficult to reverse (Case & Staver 2016) and can lead to shifts in wildlife communities (Péron & Altwegg 2015), reduced grazing opportunities (Venter et al. 2014), altered hydrological processes (Honda & Durigan 2016) and the spread of native and alien invasive woody plants (Case & Staver 2016). In addition, dense vegetation in late-seral savanna habitat may provide cover for and facilitate poaching activity (Shaffer & Bishop 2016) and may reduce visibility and viewing opportunities for tourists throughout the reserve (Gray & Bond 2013). Expanding late-seral habitat therefore may have unforeseen or negative conservation consequences and further research and monitoring should accompany this management decision.

In addition to burning strategically, an adaptive fire management strategy should incorporate inter-annual and seasonal rainfall data. South Africa has highly variable, seasonal, and unpredictable annual rainfall, along with an increasing trend in climate-related extreme events such as droughts and heat waves (Kupika et al. 2018). With increases in the frequency of dry and warm conditions, flexible strategies that improve the capacity to burn during suitable conditions and limit burning during

Table 6.1 Summary of burning recommendations with the objective, approach, situation, and considerations for implementation.

Objective	Approach	Situation	Considerations
Burning in areas that have recently burned	Burn in areas that have burned in the last 5 years.	Average to high rainfall	<ul style="list-style-type: none"> • The timing, amount and location of burning in these areas will depend on the amount of rainfall, time-since-fire and fire return interval. • During high rainfall years consider burning in areas with lower fire return intervals and time-since-fire as this will benefit grass- and ground-layer invertebrates. • Will improve visibility for tourists who want to see large mammals and other open habitat species. Consider having some of these areas next to roads.
		Below average rainfall	<ul style="list-style-type: none"> • Limit burning in low rainfall years. • Consider burning only in areas with higher fire return intervals and higher time-since-fire (e.g., 4-5 years) as this will benefit grass-layer invertebrates.
Burning across a range of fire frequencies	Attempt to burn across a range of fire frequencies	Average to high rainfall	<ul style="list-style-type: none"> • Burn across a range of fire frequencies. This will require a long-term burning plan to manage for current and future fire frequencies on the landscape.
		Below average rainfall	<ul style="list-style-type: none"> • Limit burning in low rainfall years particularly in areas with longer time-since-fire (>5 years) as these areas are important for grass-layer invertebrates during dry conditions.
Protecting long-unburned areas from fire	Actively avoid burning in areas that have not experienced fire in 10 or more years. Increase the amount of this habitat on the landscape.	Average to high rainfall	<ul style="list-style-type: none"> • May require use of fire-breaks, roads and natural features to keep fire from spreading into these areas. • Will reduce visibility for tourists who want to see large mammals. Consider having these areas farther from roads. • Unburned areas may attract birding tourists so consider having some of these zones near hides, quiet roads or viewing areas.
		Below average rainfall	<ul style="list-style-type: none"> • Unburned areas have large fuel loads and will have high fire risk particularly in dry years when fuel is cured. May require use of fire-breaks, roads and natural features to keep fire from spreading into these areas. May also require occasional fire suppression.

unsuitable conditions will be valuable going forward. I recommend that practitioners attempt to limit the amount of burning during dry conditions and periods of low rainfall. This action will benefit grass-layer invertebrates and the insectivores that rely on them, and is likely to benefit other taxa including small and large mammals (Yarnell et al. 2007, Pacifici et al. 2015). However, it can be difficult to limit burning in drought conditions due to wildfires when conditions are dry, and fuels are cured. This may necessitate the use of fire-breaks, natural features and occasional fire suppression. Furthermore, the challenges associated with forecasting seasonal rainfall can hinder the planning process and will require adapting plans throughout the year. This may also require burning early in the dry season if conditions are suitable and limiting late season burning if conditions become drier (Murphy et al. 2015). The complexity of incorporating rainfall into fire management suggests that management efforts will increase as climate variability and risk increases. Furthermore, the integration of rainfall data into fire management planning will need to be supported by further research into the effects of fire-rainfall interactions on wildlife, particularly from low and high rainfall years, as well as predicting the impacts of climate change on fire regimes and wildlife.

Fire management has important implications for ecotourism and conservation management in South African PAs. Recent studies in South Africa suggest that practitioners should consider tourism when planning fire management (Gray & Bond 2013; Pacifici et al. 2015). For many PAs in South Africa, ecotourism and wildlife viewing generate revenue that is vital for funding conservation and park management (Lindsey et al. 2007; Van Wilgen et al. 2014). To generate these funds, PAs must attract visitors, preferably returning visitors, which depends on wildlife viewing opportunities and tourist satisfaction (Gray & Bond 2013). Large mammals are the most popular species attracting tourists to South African PAs (Lindsey et al. 2007). Increased visibility of animals (i.e., reduced vegetation cover) has been cited as a major determinant of tourist satisfaction and the probability of a tourist returning to African PAs (Gray & Bond 2013). However, more recently, studies in South Africa highlight an emerging sector of tourists interested in a diverse range of species, including birds, plants and rarer mammals (Lindsey et al. 2007; Di Minin et al. 2013). This thesis demonstrates that fire can be managed to benefit biodiversity within the constraints of tourism and economic needs and may even offer mechanisms to promote ecotourism. Findings from this thesis reveal that new burns have high densities of large mammals (Chapter 2) and high diversity of birds (Chapter 3). Furthermore, this thesis demonstrates that managing newly burned and long-unburned areas can provide high bird diversity on the landscape,

which may be an increasingly important factor for birdwatching and ecotourism in South Africa (Lindsey et al. 2007). Increases in fire frequency can reduce woody vegetation cover for improved wildlife viewing and the results from this thesis suggest that such changes would not negatively affect the density of large mammals. However, increases in fire frequency may have negative consequences for avian insectivores (Chapter 5) and care should be taken when administering frequent fires to enhance wildlife viewing.

Fire management in arid systems may best be achieved through an adaptive management framework which offers a flexible approach to managing complex disturbance processes, climate dynamics, and uncertainty (Allen et al. 2011). For National Parks, an adaptive management strategy can integrate multiple social and ecological objectives such as tourism and visitor experience, biodiversity and nature conservation, and fire management (Jacobs et al. 2018; see Table 6.1). Evidence suggests that prescribed fire strategies are more cost-efficient if they are planned and presented to have multiple objectives (Duane et al. 2019). An adaptive fire management strategy must outline ecological outcomes against which to evaluate management (Van Wilgen et al. 2014). Outcomes are monitored and evaluated using long-term data collection and research; and management is developed and updated regularly (Lindenmayer and Likens 2009). Therefore, Pilanesberg and Mankwe will need to develop well-defined conservation objectives and management outcomes to direct and evaluate fire management.

An adaptive management strategy that incorporates biological data represents a shift in current management and policy at Pilanesberg National Park (Brockett et al. 2001). However, the complexity associated with the delineation of an adaptive management strategy required to deliver the multiple objectives and functions of protected areas in semi-arid or arid environments, coupled with the uncertainty surrounding the local impacts of climate change and variability, is considerable. While this thesis is a first step towards the development fire management strategies based on ecological evidence across multiple taxa, additional research is needed. Evidence suggests that while short term studies and experiments can provide invaluable knowledge regarding the relationship between fire regimes and wildlife, long-term, large-scale monitoring is important for meeting the complex information requirements of fire management in savanna systems (Russell-Smith et al. 2003). This type of effort will likely require collaborative partnerships among regional managers, fire practitioners, researchers

and stakeholders to expand the spatio-temporal extent of data collection (Russell-Smith et al. 2003, Davies et al. 2016, Jacobs et al. 2018)

Globally, protected areas (PAs) are important sites for the conservation of savanna species diversity and abundance (Gray et al. 2016). In South Africa, a recent study has revealed that PAs are also important for the conservation of ecological function (Duckworth & Altwegg 2018). Currently, only 6.2 per cent of South Africa's land area is designated as protected (Secretariat of the Convention on Biological Diversity 2012). As a party to the Convention on Biological Diversity, South Africa is a long way from meeting its conservation commitments to expand formal protection to at least 17 per cent of terrestrial and inland water areas by 2020 (Aichi Biodiversity Target 11; Secretariat of the Convention on Biological Diversity 2012). Given this failure to meet targets, it is important that conservation management within current PAs is optimised to effectively conserve native habitats and species. It is important to note that an additional 30 per cent of South Africa's land is designated as private protected areas (Bingham et al. 2017). However, while these areas are of increasing importance for the conservation of biodiversity, little is known about their capacity for that function. Furthermore, prescribed burning is increasing in PAs and private landholdings in southern Africa (Pricope & Binford 2012). This highlights the importance of developing evidence-based guidelines for fire and ecosystem management to support biodiversity conservation in formal and private PAs (Bingham et al. 2017). This thesis serves as an example of a study that was designed to evaluate fire regimes and develop management recommendations to forward conservation in reserves with different governance strategies.

6.3 FUTURE WORK

This thesis has demonstrated the importance of a deeper, mechanistic understanding of fire-fauna relationships for conservation. Developing an understanding of how fire affects animal demographic vital rates, such as reproduction, survival, and movement, will be important for broadening this mechanistic understanding of fire-fauna relationships and for designing ecologically sustainable fire management (Nimmo et al. 2018). Disturbance can alter demographic vital rates resulting in a species' local extinction; however, it can also result in temporary changes in species richness and abundance (Cosset et al. 2019). While there is considerable research on how species diversity and abundance respond to fire across taxa and regions, there is a paucity of research on demography. In Chapter 5, I observed direct effects of fire on birds and invertebrates, suggesting that fire altered vital rates. While

the direct effects of fire on invertebrates include mortality, dispersal and changes to survivorship (Chambers & Samways 1998; Vasconcelos et al. 2009) with lasting demographic consequences (Broza & Izhaki 1997; Mutz et al. 2017); the direct effects of fire on bird demographic rates are less well understood. Fire can alter avian territorial behaviour (Dean 1987), survival (Fontaine & Kennedy 2012) and nest success (Robertson 2009). Moreover, predation of juvenile and adult birds is likely an important mechanism underlying fire response. Two studies in South African grassland have demonstrated that nest predation was positively associated with fire (Muchai & Plessis 2005; Maphisa et al. 2009). A study of radio-tracked small mammals in Australian savanna found that prescribed burning led to increased predation by native and non-native (i.e., feral cats) predators and was related to loss of vegetation cover (Leahy et al. 2015). Understanding demographic rates and how they relate to a burn regime is critical for the conservation of biodiversity, especially of threatened species (Brown et al. 2009).

Several findings from this thesis have important implications for animal movement and dispersal. Identifying patterns of movements is fundamental to understanding ecosystem dynamics and how communities respond to landscape structure (Wiens et al. 1993; Ims 1995). Dispersal can interact with patch size, patch isolation and other patch attributes to determine a species' distribution within a landscape mosaic (Ims 1995). Findings from this thesis demonstrate that the extent of recently burned habitat was an important predictor of mammal density (Chapter 2) and bird diversity (Chapter 3). Furthermore, this habitat is important for species with unique functional traits (Chapter 3) and specialist species (Chapter 5), suggesting that there is an influx of fire-specialist species following burning. Evidence from avian community functional evenness suggested that the dispersal of post-fire specialists with unique functional traits is occurring at a large spatial scale (i.e., 500-ha; Chapter 3). These findings suggest that processes related to post-fire habitat selection, such as colonisation or dispersal, respond to landscape spatial structure and have important implications for fire management. Species such as the fork-tailed drongo (*Dicrurus adsimilis*) and Temminck's courser (*Cursorius temminckii*) in South Africa, may be nomadic during fire season, tracking recently burned habitats across large regions (Dean 1987; Dean & Siegfried 1997; Bouwman & Hoffman 2007). Given this, the timing and extent of burning across much wider spatial extents may require consideration to ensure the long term viability of populations of such species. In boreal forests, genetic data have revealed that fire specialist bird species that disperse to find recently burned habitats locate this optimal habitat relatively

close to their natal territory (<110 km) which has important consequences for prescribed burning in this region where fires are on average 40 km apart (Pierson et al. 2013). Land managers will have to take into consideration the spatial context and the dispersal abilities of target species (e.g., specialist or threatened species) when making decisions regarding burning.

A key finding of this thesis was the importance of the extent of unburned habitat (Chapter 3). Long-unburned habitat is important in many fire-prone systems and may influence processes such as refuge seeking and dispersal (Gandar 1982; Yarnell et al. 2008) and post-fire recolonization (Uys et al. 2006), with implications for ecosystem resilience (Nimmo et al. 2015). Furthermore, as discussed above (section 6.2), the use of roads or fire breaks may be required to protect late-successional habitat. Fire breaks have distinct vegetation composition and structure and may act as habitat edge (Numa et al. 2004). Thus, evidence of how movement and dispersal patterns are influenced by the spatial configuration of unburned habitat, habitat edge, and fire breaks at multiple spatial scales is important for informing conservation management. Berry et al. (2015) found that large unburnt areas were more important than small unburnt patches for the conservation of avian diversity in semi-arid Australian woodland and that this relationship varied with distance between unburnt patches on the landscape. However, unlike birds, which are highly mobile species, invertebrates require much shorter distances to unburnt habitat (e.g., <300 m) to support post-fire recolonization (Uys et al. 2006). During conservation planning the spatial arrangement of fire regimes should be decided in relation to the habitat requirements and movement abilities of target species or faunal groups. While collecting data related to movement and dispersal remains a challenge for ecologists, new technologies (e.g., telemetry, camera-trapping and biologging) and genetic data can provide valuable information about animal movement and should be incorporated into fire research (Nimmo et al. 2018).

6.4 CONCLUSIONS

In this thesis, I have demonstrated the vital role that long-term fire histories have on multiple taxonomic communities (i.e., mammals, birds and invertebrates) at the landscape-scale. I have shown that the extent of recently burned (<1-year post-fire) and unburned (≥ 10 -years post-fire) habitat are important predictors of functional diversity, taxonomic diversity, and abundance of savanna species and communities. Notably, I did not find that landscape-level pyrodiversity promoted the diversity or density of savanna animals. Throughout this thesis, I have demonstrated the dominant effect rainfall has on

savanna biodiversity. In particular, I demonstrated the important influence that interactions between short-term variation in rainfall and long-term variation in fire regimes have on invertebrate diversity, abundance and biomass. I revealed that long-term variation in fire affects trophic networks, which include indirect effects of fire on fauna that are mediated by vegetation and animals. This study has demonstrated that fire management in savanna will be enhanced by the definition of clear fire regime guidelines, but also with an improved understanding of mechanistic drivers, trophic interactions, and climatic influences. Here, I recommend protecting large extents of unburned savanna and reducing burning during periods of drought. The findings of this thesis have important implications for demographic vital rates, such as dispersal and movement, and these should be considered for future work. This study serves as evidence that studying fire-fauna relationships over long-term fire regimes can provide valuable empirical evidence to support the conservation of biodiversity and ecosystem function, ecosystem resilience and the management of protected areas.

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Appendix

Table A1.1: List of studies investigating the effects of fire on large herbivorous mammals (ungulates) across habitat types with a description of the temporal and spatial scale of the fire regime studied, including the age-class (time-since-fire) of burned treatments, fire return interval, and fire age-class (time-since-fire) of the control treatment. Also included is the dominant habitat type and the number of species studied. Systematic search methods used to compile these studies are described below.

Reference [†]	Habitat	Country	Reserve area (Sampling area) ha*	Time-since-fire (years)	Fire return interval (years)	Control TSF	No. of Species
Rickbeil et al. 2016	Forest	Canada	70000000	<26			1
Kraaij and Novellie 2010	Fynbos	South Africa	2786	<4		>5	4
Watson et al. 2011	Fynbos	South Africa	3435	<3		>5	2
Lemon et al. 1968	Grassland	Malawi	194249	<2		3 or 10	4
Vogl and Beck 1970	Grassland	USA	8094	8		unknown	1
Oliver et al. 1978	Grassland	South Africa	4194	<2		unknown	3
Rowe-Rowe 1982	Grassland	South Africa	36000	<1		<2	5
Coppock and Detling 1986	Grassland	USA	(120)	<1		unknown	1
Everett et al. 1991	Grassland	South Africa	7 small reserves	< 1.5		>1.5	1
Hobbs et al. 1991	Grassland	USA	(104)	<1		unknown	1
Shackleton 1992	Grassland	South Africa	7760	<1		<2	10
Vinton et al. 1993	Grassland	USA	3487	<1		>1	1
Coppedge and Shaw 1998	Grassland	USA	15342 (1973)	<1		unknown	1
Vermeire et al. 2004	Grassland	USA	6507	<1		unknown	1
Allred et al. 2011	Grassland	USA	9532	<1		unknown	2
Augustine and Derner 2014	Grassland	USA	(195)	<1		unknown	1
Venter et al. 2014	Grassland	South Africa	7700	<4		unknown	2
Marshal et al. 2016	Grassland	South Africa	4500	<1		>1	1
Raynor et al. 2016	Grassland	USA	3487	<1		unknown	1
Sittler et al. 2015	Mixed	Canada	741000	<31			2
Proffitt et al. 2016	Mixed	USA	421400	<15		>15	1
Moe et al. 1990	Savanna	Tanzania	5950	<1		unknown	14
Mduma and Sinclair 1994	Savanna	Tanzania	40000	unknown (weeks)		unknown	1
Wilsey 1996	Savanna	Tanzania	unknown	<1		unknown	6
Dorgeloh 1998	Savanna	South Africa	4000	<1		unknown	1
Gureja and Owen-Smith 2002	Savanna	South Africa	2700	<1		unknown	5

Reference [†]	Habitat	Country	Reserve area (Sampling area) ha*	Time-since-fire (years)	Fire return interval (years)	Control TSF	No. of Species
Tomor and Owen-Smith 2002	Savanna	South Africa	3989	<1		unknown	4
Archibald and Bond 2004	Savanna	South Africa	90 000 (26 000)	<1		unknown	8
Traill 2004	Savanna	Zimbabwe	40000	<1		unknown	11
Archibald et al. 2005	Savanna	South Africa	90 000		2.1 to 13.3		?
Sankaran 2005	Savanna	India	(0.2)	<2	1 or 2	>3	
Zavala and Holdo 2005	Savanna	Kenya	20000(12)	<4		unknown	7
Klop et al. 2007	Savanna	Cameroon	180000	<1		unknown	11
Klop and van Goethem 2008	Savanna	Cameroon	180000	<1		unknown	11
Averbeck et al. 2009	Savanna	Uganda	26000	<1		unknown	11
Parrini and Owen-Smith 2009	Savanna	South Africa	4500	<2		unknown	1
Sensenig et al. 2010	Savanna	Kenya	(364)	<1.5			10
Gandiwa 2013	Savanna	Zimbabwe	505300		<5		7
Isaacs et al. 2013	Savanna	South Africa	36000	<1		unknown	5 +
Kimanzi et al. 2014	Savanna	Kenya	12000	<1		>1	1
Eby et al. 2014	Savanna	Tanzania	(14)	<1		unknown	7
Green et al. 2015	Savanna	Kenya	(<560)	<2		unknown	8
Hailu et al. 2015	Savanna	Ethiopia	5400 (<640)	unknown		unknown	1
Pacifici et al. 2015	Savanna	South Africa	(1948500)	<6	< 33		3
Anderson et al. 2016	Savanna	Tanzania	(112500)	<1 month		unknown	8
Cherry et al. 2017	Savanna	USA	12,000	<2	1 to 3		1
Kimuyu et al. 2017	Savanna	Kenya	60000 (465)	<7		unknown	9
M'soka et al. 2017	Savanna	Zambia	120000	<1		unknown	3
Odadi et al. 2017	Savanna	Kenya	20000 (72)	<1		unknown	5

Blanks represent information that was not part of the study. Unknowns represent information that was part of the study but was not described in the article.

*Sampled area included when available

[†]Literature search method: I searched the electronic database Web of Science using combinations of the following search terms: fire*, burn*, wildfire*, mammal*, ungulate*, antelope* and deer*. In addition, I also searched the lists of references from relevant papers. Only published, peer-reviewed journal articles were included in this table. Literature was included up until December 2017. Papers were included if they addressed the effect of fire on a measure of an ungulate species, community or population dynamics. Studies were excluded that reported the effects of fire on elephants only. Studies were also excluded that reported the effects of fire on domestic livestock.

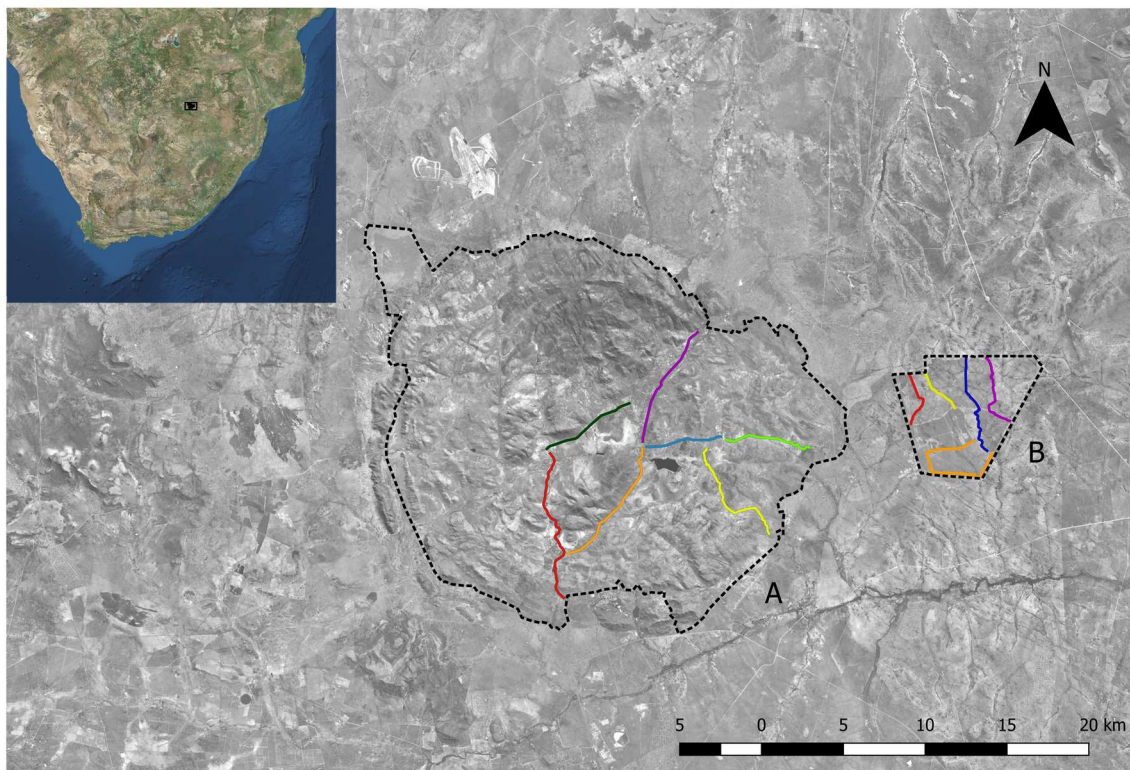


Figure A2.1: Map of the study area displaying the 12 transect lines (solid lines) and the reserve boundaries (dotted lines) for (A) Pilanesberg National Park and (B) Mankwe Wildlife Reserve, North West Province, South Africa

Table A2.2: Large herbivores detected during transect surveys at Pilanesberg National Park and Mankwe Wildlife Reserve. Data includes mean adult body mass in kilograms; diet: GRO = obligate grazer, GRV = variable grazer, BGI = browser-grazer intermediate, GEN = generalist browser, and BRW = browser; gut type; and water dependence and is collected from Hempson et al. (2015).

Common name	Species name	Number of groups (individuals)	Body mass	Diet	Gut type	Water dependence
Elephant	<i>Loxodonta africana</i>	35 (146)	4101.8	BGI	Non-ruminant	High
White rhino	<i>Ceratotherium simum</i>	49 (117)	2195.8	GRO	Non-ruminant	High
Black rhino	<i>Diceros bicornis</i>	3 (4)	999.9	BRW	Non-ruminant	High
Giraffe	<i>Giraffa camelopardalis</i>	61 (190)	1117.5	BRW	Ruminant	Low
Greater kudu	<i>Tragelaphus strepsiceros</i>	70 (251)	202.3	GEN	Ruminant	Low
Blue wildebeest	<i>Connochaetes taurinus</i>	351 (3133)	220.1	GRV	Ruminant	High
Plain's zebra	<i>Equus quagga burchellii</i>	266 (2097)	280.4	GRO	Non-ruminant	High
Hippopotamus	<i>Hippopotamus amphibius</i>	6 (14)	1866.9	GRV	Non-ruminant	High
Common tsessebe	<i>Damaliscus lunatus</i>	40 (152)	126.7	GRO	Ruminant	Low
Red hartebeest	<i>Alcelaphus buselaphus caama</i>	33 (151)	150.3	GRV	Ruminant	High
Blesbok	<i>Damaliscus pygargus phillipsi</i>	42 (267)	68.4	GRV	Ruminant	High
Common eland	<i>Tragelaphus oryx</i>	14 (87)	511.2	BGI	Ruminant	None
Gemsbok	<i>Oryx gazella</i>	16 (74)	203.7	GRV	Ruminant	None
Impala	<i>Aepyceros melampus</i>	265 (2683)	49.1	BGI	Ruminant	High
Springbok	<i>Antidorcas marsupialis</i>	20 (197)	35.3	BGI	Ruminant	Low

Common name	Species name	Number of groups (individuals)	Body mass	Diet	Gut type	Water dependence
Steenbok	<i>Raphicerus campestris</i>	22 (37)	11.2	BGI	Ruminant	None
Waterbuck	<i>Kobus ellipsiprymnus</i>	57 (223)	211.8	GRV	Ruminant	High
Common reedbuck	<i>Redunca arundinum</i>	1 (1)	53.5	GRO	Ruminant	High
Mountain reedbuck	<i>Redunca fulvorufula</i>	1 (4)	29.1	GRO	Ruminant	High
African buffalo	<i>Syncerus caffer</i>	1 (56)	486.3	GRV	Ruminant	High
Warthog	<i>Phacochoerus africanus</i>	95 (217)	75.9	GRO	Non-ruminant	High

Table A2.4: Parameters for density surface models (DSMs) of the relationship between mammal densities (animals km⁻²) and landscape variables including restricted maximum likelihood (REML) score, R² (adjusted), deviance explained, with the approximate *P* values and estimated degrees of freedom (edf) for each explanatory variable. Landscape variables include proportion of newly burned habitat (NEW), burn-age diversity (SHDI), proportion of woodland habitat (WOOD), distance to the nearest permanent waterbody (WATER), and fire frequency (FREQ). Only the five top models are presented for each species.

Model	edf	P	REML	R ²	Deviance explained (%)
All Species					
NEW + SHDI + WOOD + WATER + FREQ			870.186	0.310	34.18
NEW	1.000	<0.001			
SHDI	1.000	0.089			
WOOD	1.799	0.045			
WATER	2.696	<0.001			
FREQ	1.000	0.335			
NEW + SHDI + WOOD + WATER			868.985	0.301	33.94
NEW	1.000	<0.001			
SHDI	1.000	0.043			
WOOD	1.191	0.047			
WATER	2.654	<0.001			
NEW + WOOD + WATER + FREQ			870.062	0.29	33.29
NEW	1.000	<0.001			
WOOD	1.811	0.049			
WATER	2.643	<0.001			
FREQ	1.001	0.134			
NEW + WOOD + WATER			869.528	0.285	32.73
NEW	1.000	<0.001			
WOOD	1.155	0.037			
WATER	2.370	<0.001			
NEW + SHDI + WATER + FREQ			871.953	0.270	31.62
NEW	1.000	<0.001			
SHDI	1.000	0.103			
WATER	2.686	<0.001			
FREQ	1.000	0.367			
Impala					
NEW + SHDI + WOOD + WATER + FREQ			639.058	0.18	25.17
NEW	1.000	0.002			
SHDI	1.149	0.633			
WOOD	2.384	0.237			
WATER	1.000	<0.001			
FREQ	1.000	0.200			
NEW + SHDI + WOOD + WATER			638.829	0.17	25.07
NEW	1.000	0.002			
SHDI	1.406	0.468			
WOOD	2.493	0.193			
WATER	1.000	<0.001			
NEW + WOOD + WATER + FREQ			638.024	0.17	24.68
NEW	1.000	<0.001			
WATER	1.000	<0.001			
WOOD	2.336	0.270			
FREQ	1.000	0.122			
NEW + WOOD + WATER			638.264	0.17	24.16
NEW	1.000	<0.001			

Model	edf	P	REML	R ²	Deviance explained (%)
WATER	1.000	<0.001			
WOOD	2.451	0.236			
NEW + WATER + SHDI + FREQ			639.922	0.15	22.56
NEW	1.000	<0.001			
WATER	1.000	<0.001			
SHDI	1.000	0.742			
FREQ	1.000	0.119			
Blue wildebeest					
NEW + SHDI + WOOD + WATER + FREQ			743.570	0.40	39.18
NEW	1.367	0.021			
SHDI	1.001	0.071			
WOOD	2.081	0.198			
WATER	2.739	<0.001			
FREQ	1.487	0.751			
NEW + SHDI + WOOD + WATER			742.390	0.40	38.95
NEW	1.286	<0.001			
SHDI	1.002	0.062			
WOOD	2.044	0.200			
WATER	2.725	<0.001			
NEW + WOOD + WATER + FREQ			744.114	0.37	38.09
NEW	1.001	<0.001			
WATER	2.606	<0.001			
WOOD	2.298	0.192			
FREQ	1.365	0.661			
NEW + WOOD + WATER			743.074	0.37	37.80
NEW	1.001	<0.001			
WATER	2.449	<0.001			
WOOD	2.317	0.188			
NEW + WATER + SHDI + FREQ			744.691	0.36	37.60
NEW	1.007	0.001			
WATER	3.138	<0.001			
SHDI	1.001	0.071			
FREQ	1.286	0.818			
Plain's zebra					
WOOD + SHDI + WATER			697.392	0.18	25.06
WOOD	1.284	0.354			
SHDI	1.000	0.236			
WATER	5.370	0.004			
WOOD + WATER			696.783	0.17	24.62
WOOD	1.438	0.384			
WATER	5.378	0.005			
FREQ + SHDI + WATER			698.410	0.17	24.09
FREQ	1.000	0.668			
SHDI	1.000	0.292			
WATER	5.458	<0.001			
FREQ + WATER			697.647	0.17	23.70
FREQ	1.000	0.491			
WATER	5.491	<0.001			
NEW + SHDI + WATER + FREQ + WOOD			698.333	0.17	23.09
NEW	1.000	0.053			
SHDI	1.000	0.542			
WATER	2.132	0.006			
FREQ	1.000	0.450			
WOOD	1.429	0.557			

Model	edf	P	REML	R ²	Deviance explained (%)
Greater kudu					
NEW + SHDI + WATER + FREQ + WOOD			608.67	0.052	18.28
NEW	4.833	0.470			
SHDI	1.669	0.076			
WATER	2.680	0.314			
FREQ	2.443	0.300			
WOOD	1.037	0.566			
NEW + SHDI + WATER + WOOD			609.652	0.060	18.15
NEW	4.863	0.412			
SHDI	2.088	0.071			
WATER	2.849	0.251			
WOOD	1.667	0.767			
NEW + WATER + SHDI + FREQ			608.24	0.056	18.00
NEW	4.918	0.423			
WATER	2.771	0.275			
SHDI	1.816	0.074			
FREQ	2.350	0.323			
NEW + WATER + SHDI			609.04	0.059	17.69
NEW	4.993	0.348			
WATER	2.968	0.190			
SHDI	2.117	0.059			
NEW + WOOD + SHDI			611.33	0.054	16.30
NEW	4.802	0.444			
WOOD	2.306	0.570			
SHDI	1.914	0.109			
Giraffe					
SHDI + WATER + FREQ + WOOD			405.51	0.092	21.70
SHDI	1.003	0.939			
WATER	2.281	0.565			
FREQ	1.183	0.869			
WOOD	2.865	0.604			
NEW + SHDI + WATER + FREQ + WOOD			406.01	0.087	21.68
NEW	1.000	0.446			
SHDI	1.000	0.954			
WATER	2.262	0.558			
FREQ	1.138	0.872			
WOOD	2.884	0.585			
WATER + FREQ + WOOD			404.460	0.094	21.58
WATER	2.281	0.558			
FREQ	1.069	0.807			
WOOD	2.858	0.605			
NEW + WATER + FREQ + WOOD			404.961	0.089	21.58
NEW	1.000	0.443			
WATER	2.881	0.586			
FREQ	1.042	0.812			
WOOD	2.259	0.552			
NEW + WATER + SHDI + WOOD			404.906	0.089	21.58
NEW	1.000	0.442			
WATER	2.229	0.569			
SHDI	1.000	0.897			
WOOD	2.885	0.595			
Warthog					
SHDI + WATER + FREQ + WOOD			438.32	0.306	36.86
SHDI	2.264	0.596			

Model	edf	P	REML	R ²	Deviance explained (%)
WATER	2.023	0.012			
FREQ	3.607	0.595			
WOOD	7.220	0.001			
WATER + FREQ + WOOD			437.86	0.295	35.80
WATER	1.777	0.008			
FREQ	4.099	0.520			
WOOD	7.075	0.003			
NEW + SHDI + WATER + FREQ + WOOD			438.90	0.306	35.64
NEW	1.000	0.313			
SHDI	2.468	0.534			
WATER	1.235	0.010			
FREQ	1.000	0.366			
WOOD	7.291	0.002			
NEW + SHDI + WATER + WOOD			438.647	0.304	34.90
NEW	1.000	0.287			
SHDI	2.348	0.608			
WATER	7.251	0.003			
WOOD	1.000	0.006			
SHDI + WATER + WOOD			438.113	0.307	34.44
SHDI	2.108	0.690			
WATER	1.002	0.005			
WOOD	7.249	0.003			

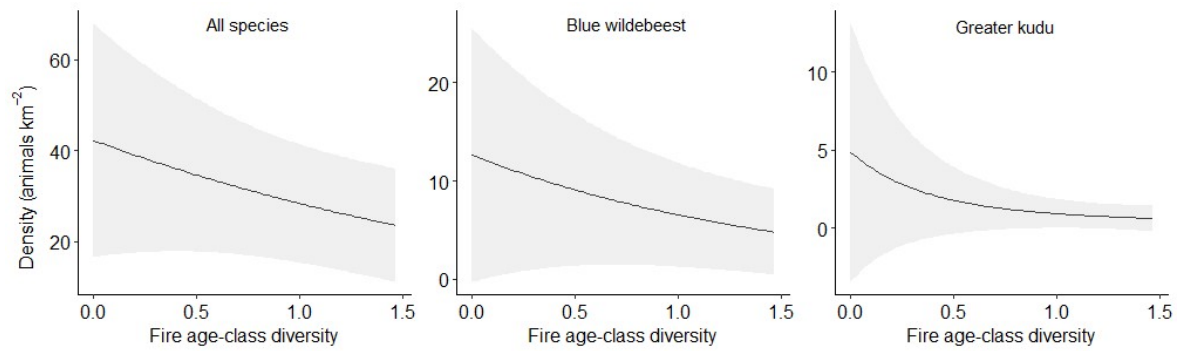


Figure A2.2: Responses of a) total mammal, b) blue wildebeest, and c) greater kudu density to the diversity of fire age-classes (pyrodiversity) on the landscape. Predictions and 95% confidence intervals from the top-ranked generalized additive mixed model are shown.

Table A3.1: Linear mixed models describing the relationship between the four response variables (i.e., species richness, functional richness, functional evenness and functional dispersion) and the landscape predictor variables. Predictor variables are described in Table 3.1. In addition to the predictor variables listed for each model, all models included the fixed effect 'site' and the random effect 'survey point'. The log-likelihood values are indicated by logL; k denotes the number of parameters in each model; ΔAIC_c is the difference in the Akaike's Information Criterion (AIC_c) values between a model and the model of best fit; and w is the Akaike weight which represents the weight of evidence in support of a model. Only models within 2 AIC_c of the best model are shown.

Model [†]	logL	k	ΔAIC_c	w
Species Richness				
OLD ₁₀₀ + SHDI ₁₀₀ + NEW ₁₀₀ * WOOD ₁₀₀	-2015.79	9	0	0.14
OLD ₁₀₀ + NEW ₁₀₀ *WOOD ₁₀₀	-2017.37	8	1.09	0.08
OLD ₁₀₀ + SHAPE ₁₀₀ + NEW ₁₀₀ * WOOD ₁₀₀	-2016.36	9	1.14	0.08
OLD ₁₀₀ + SHDI ₁₀₀ + SHAPE ₁₀₀ + NEW ₁₀₀ * WOOD ₁₀₀	-2015.74	10	1.96	0.05
Functional Richness				
NEW ₁₀₀ + OLD ₁₀₀ + SHAPE ₁₀₀ + WOOD ₁₀₀	694.61	8	0.00	0.09
NEW ₁₀₀ + OLD ₁₀₀ + WOOD ₁₀₀	693.16	7	0.85	0.06
Functional Evenness				
NEW ₅₀₀ * OLD ₅₀₀	1137.26	7	0.00	0.25
WOOD ₅₀₀ + NEW ₅₀₀ * OLD ₅₀₀	1137.56	8	1.46	0.12
OLD ₅₀₀ + NEW ₅₀₀ * SHDI ₅₀₀	1137.52	8	1.55	0.11
SHDI ₅₀₀ + NEW ₅₀₀ * OLD ₅₀₀	1137.32	8	1.94	0.09
Functional Dispersion				
NEW ₅₀₀ + SHDI ₅₀₀	1292.88	3	0.00	0.05
WOOD ₁₀₀	1294.47	5	0.88	0.03
NEW ₁₀₀ * WOOD ₁₀₀	1295.49	6	0.89	0.03
SHAPE ₁₀₀ + WOOD ₁₀₀	1295.33	6	1.19	0.03
WOOD ₁₀₀ + NEW ₁₀₀ * SHAPE ₁₀₀	1296.20	7	1.52	0.02
NEW ₅₀₀ + SHDI ₅₀₀ + SHAPE ₅₀₀	1294.14	5	1.54	0.02
SHDI ₁₀₀ + SHAPE ₁₀₀ + WOOD ₁₀₀	1296.09	7	1.72	0.02
SITE	1292.91	4	1.96	0.02

[†] Subscripts denote the scale at which the metric was measured (i.e., 100 ha or 500 ha)

Table A3.2: Model-averaged parameter estimates and standard errors for landscape variables in the candidate set of models; effects of each explanatory variable on species richness, functional richness, functional evenness and functional dispersion. Parameter estimates with 95% confidence intervals that did not include zero are indicated in bold.

Response Variable	Scale	SHDI	SHAPE	OLD	NEW	WOOD	SITE
Species Richness	100 ha	1.067 (0.686)	1.503 (1.548)	4.012 (1.536)	2.062 (0.912)	3.822 (1.787)	4.220 (1.420)
	500 ha	0.495 (0.712)	1.435 (1.070)	7.246 (2.414)	2.452 (1.228)	2.388 (2.251)	
Functional Richness	100 ha	0.009 (0.007)	0.028 (0.016)	0.075 (0.019)	0.028 (0.013)	0.074 (0.022)	0.010 (0.020)
	500 ha	-0.004 (0.009)	0.001 (0.012)	0.127 (0.030)	0.032 (0.015)	0.051 (0.028)	
Functional Evenness	100 ha	0.002 (0.005)	-0.011 (0.010)	-0.010 (0.009)	-0.012 (0.006)	-0.012 (0.006)	-0.010 (0.010)
	500 ha	0.001 (0.004)	0.001 (0.006)	-0.030 (0.014)	-0.010 (0.008)	-0.009 (0.013)	
Functional Dispersion	100 ha	-0.003 (0.004)	0.01 (0.008)	0.005 (0.007)	0.006 (0.005)	0.015 (0.008)	0.000 (0.010)
	500 ha	-0.0001 (0.004)	-0.005 (0.005)	0.010 (0.011)	0.011 (0.006)	0.011 (0.010)	

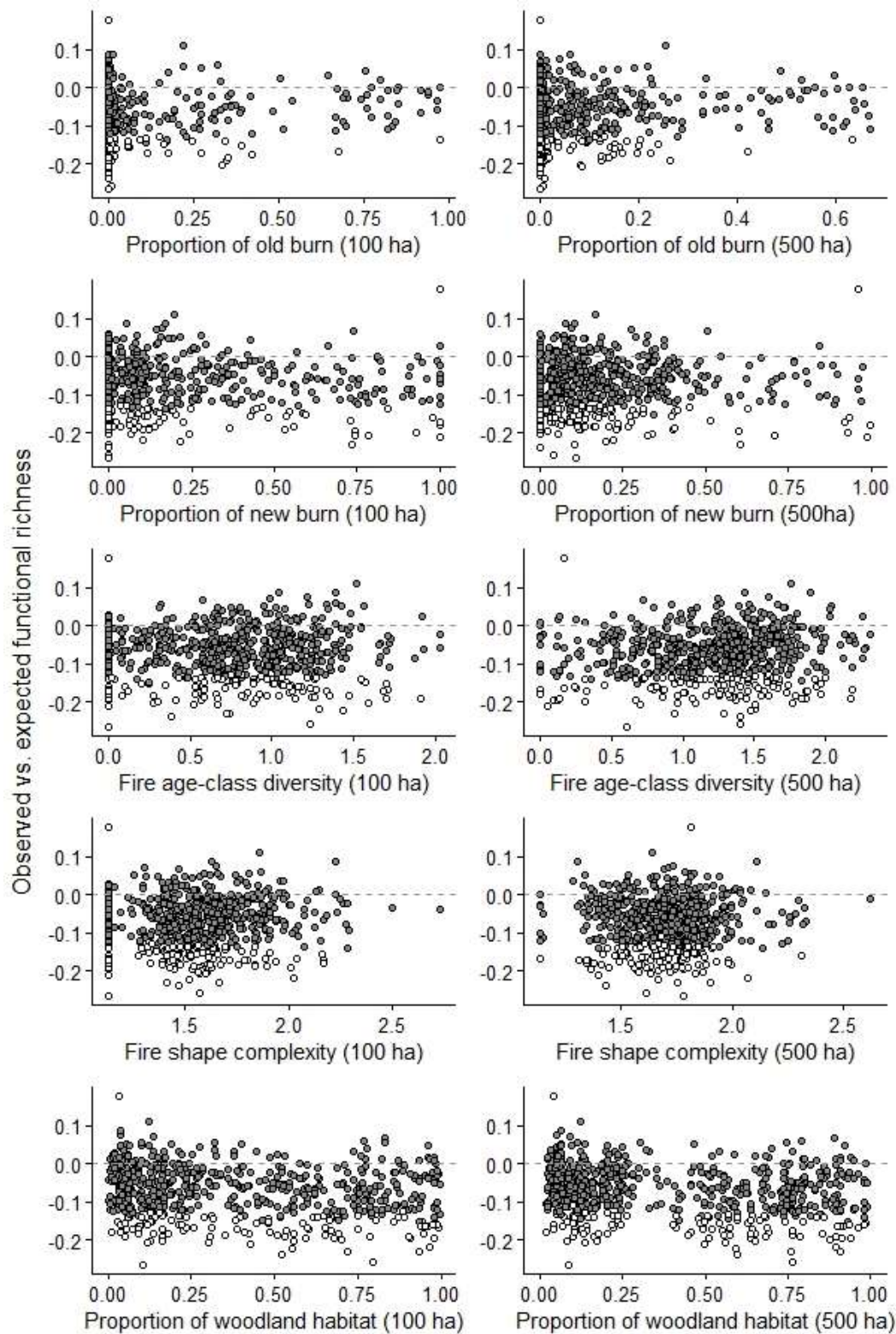


Figure A3.1: The difference between the observed and expected values for functional richness for the various landscape variables at both spatial scales. Open circles represent communities for which the observed functional richness was significantly different ($\alpha = 0.05$) than the expected functional richness.

Table A4.1: Parameters used for the regression of weight (mg) on body length (mm) for invertebrate taxonomic groups recorded in the grass layer. Also included are the number of individuals, size range (the extreme values of body length), and the percentage of the overall invertebrate abundance and biomass.

Taxonomic Group	n	Size range (mm)	a [†]	b [†]	% of abundance	% of biomass
Non-insect invertebrates						
Araneae (spiders)	3756	0.42-31.46	0.1044	2.296	7.139	2.157
Acarina (mites)	784	0.13-3.81	0.0530	2.494	1.490	0.014
Acarina (ticks)	3759	0.22-6.72	0.0530	2.494	7.145	0.215
Pseudoscorpiones (pseudoscorpions)	109	0.64-3.27	0.1044	2.296	0.207	0.018
Insecta						
Collembola (springtails)	78	0.22-1.91	0.0024	3.676	0.148	0.00004
Odonata (dragonflies, damselflies)	30	21.04-40.54	0.0078	2.792	0.057	0.806
Orthoptera (grasshoppers, crickets)	3650	1.30-83.74	0.0255	2.637	6.938	58.895
Phasmatodea (stick insects)	570	5.15-113.53	0.0027	2.310	1.083	2.528
Isoptera (termites)	301	0.48-5.16	0.0494	2.344	0.572	0.009
Mantodea (praying mantis)	483	1.42-78.23	0.0017	2.953	0.918	3.843
Blattodea (cockroaches)	74	0.95-8.99	0.0494	2.344	0.141	0.048
Hemiptera (bugs)	16538	0.40-26.42	0.0341	2.688	31.434	19.295
Thysanoptera (thrips)	3022	0.45-3.93	0.0071	2.537	5.744	0.019
Psocoptera (booklice)	16	0.20-2.01	0.0425	1.637	0.030	0.0002
Coleoptera adults (beetles)	5605	0.92-25.47	0.0408	2.560	10.653	3.290
Coleoptera larvae (beetles)	219	0.32-14.16	0.0238	2.730	0.416	0.101
Neuroptera (lacewings)	85	2.23-39.68	0.0814	1.530	0.162	0.074
Hymenoptera (non-ants)	1671	0.59-32.26	0.1636	1.900	3.176	0.749
Hymenoptera (ants)	3093	0.62-27.87	0.0104	2.763	5.879	0.693
Trichoptera (caddisflies)	49	1.15-22.80	0.0315	2.492	0.093	0.229
Lepidoptera imago (moths, butterflies)	422	1.95-103.51	0.0095	2.969	0.802	2.915
Lepidoptera larvae (caterpillars)	812	0.92-53.58	0.0110	2.571	1.543	2.813
Diptera (flies)	784	0.36-41.33	0.0312	2.392	14.225	1.292

[†]Values for a & b are from Hodar 1996; Benke et al. 1999; Wardhaugh 2013

Table A4.2: Taxonomic groups recorded in the ground layer, including the number of individuals and the percentage of the overall invertebrate abundance.

Taxonomic Group	n	% of abundance
<i>Non-insect invertebrates</i>		
Araneae (spiders)	1090	1.72
Acarina (mites)	775	1.22
Acarina (ticks)	68	0.11
Solifugae (sun spiders)	337	0.53
Pseudoscorpiones (pseudoscorpions)	57	0.09
<i>Insecta</i>		
Isopoda (woodlice)	48	0.08
Chilopoda (centipedes)	32	0.05
Diplopoda (millipedes)	23	0.04
Collembola (springtails)	19618	30.92
Blattodea (cockroaches)	115	0.18
Isoptera (termites)	248	0.39
Mantodea (praying mantis)	11	0.02
Orthoptera (grasshoppers, crickets)	389	0.61
Hemiptera (bugs)	375	0.59
Thysanoptera (thrips)	182	0.29
Psocoptera (booklice)	7	0.01
Neuroptera (lacewings)	10	0.02
Hymenoptera (non-ants)	149	0.23
Hymenoptera (ants)	37480	59.06
Coleoptera adults (beetles)	299	0.47
Coleoptera larvae (beetles)	122	0.19
Trichoptera (caddisflies)	186	0.29
Lepidoptera imago (moths, butterflies)	476	0.75
Lepidoptera larvae (caterpillars)	39	0.06
Diptera (flies)	1114	1.76
Thysanura (silverfish)	206	0.32

Table A4.3: Generalised linear mixed models for the response of arthropod order richness, biomass and abundance in the grass- and ground-layers to predictor variables and interaction terms (predictor variables are described in Table 1). The Akaike's information criteria (AIC_c) adjusted for sample size was used to rank models; *w* is the Akaike weight and *k* is the number of model parameters. Two measures of model goodness-of-fit are shown; marginal R² (R²_m) is the variance explained by the fixed factors and conditional R² (R²_c) is the variance explained by the fixed and random factors. Models in the top model set are displayed. Top model sets for individual orders are displayed in Table S3.

Model	k	ΔAIC _c	w	R ² _m	R ² _c
Grass-layer					
Order richness					
TSF + FRI + GrL + TrD + Rain + TSF*Rain+ FRI* Rain	10	0.00	0.62	0.629	0.677
TSF + FRI + GrL + Rain + TSF*Rain+ FRI* Rain	9	2.06	0.22	0.626	0.676
TSF + FRI + GrL + TrD + Rain + TSF*Rain	9	3.30	0.12	0.627	0.674
TSF + FRI + GrL + Rain + TSF*Rain	8	5.51	0.04	0.624	0.674
Biomass					
TSF + FRI + GrL + Rain + ShD + TrD + TSF*FRI + TSF*Rain + FRI*Rain	12	0.00	0.28	0.559	0.600
TSF + FRI + GrL + Rain + TrD + TSF*FRI + TSF*Rain + FRI*Rain	11	0.26	0.25	0.557	0.600
TSF + FRI + GrL + Rain + ShD + TrD + TSF*Rain + FRI*Rain	11	0.76	0.19	0.557	0.599
TSF + FRI + GrL + Rain + TrD + TSF*Rain + FRI*Rain	10	1.23	0.15	0.555	0.599
TSF + FRI + GrL + Rain + TSF*FRI + TSF*Rain + FRI*Rain	10	2.95	0.07	0.553	0.600
TSF + FRI + GrL + Rain + TSF*Rain + FRI*Rain	9	3.37	0.05	0.552	0.599
Abundance					
TSF + FRI + GrL + Rain + TrD + TSF*Rain + FRI*Rain	10	0.00	0.91	0.785	0.819
TSF + FRI + GrL + Rain + TSF*Rain + FRI*Rain	9	4.61	0.09	0.782	0.819
Hemiptera abundance					
TSF + FRI + GrL + Rain + TSF*Rain + FRI*Rain	12	0.00	NA	0.546	0.903
Diptera abundance					
TSF + FRI + GrL + Rain + TSF*Rain + FRI*Rain	9	0.00	0.74	0.569	0.783
TSF + FRI + Rain + TSF*Rain + FRI*Rain	8	2.82	0.18	0.568	0.784
TSF + FRI + GrL + Rain + TSF*Rain	8	4.59	0.08	0.548	0.775
Coleoptera abundance					
TSF + FRI + GrL + Rain + ShD + TrD + TSF*Rain	9	0.00	0.25	0.524	0.813
TSF + Rain + TrD + ShD + TSF*Rain	8	1.42	0.12	0.522	0.813
TSF + FRI + Rain + ShD + TSF*Rain	8	1.45	0.12	0.519	0.812
TSF + FRI + Rain + TrD + TSF*Rain	8	1.59	0.11	0.514	0.810
TSF + Rain + TrD + TSF*Rain	7	2.22	0.08	0.514	0.810
TSF + FRI + Rain + ShD + TrD + FRI*Rain	9	2.82	0.06	0.509	0.808

Model	k	ΔAIC_c	w	R ² m	R ² c
TSF + GrL + Rain + ShD + TSF*Rain	8	3.45	0.04	0.510	0.809
TSF + Rain + ShD + TSF*Rain	7	3.72	0.04	0.509	0.809
TSF + FRI + Rain + ShD + TrD	8	3.72	0.04	0.502	0.807
TSF + FRI + Rain + ShD + FRI*Rain	8	4.31	0.03	0.505	0.808
TSF + FRI + Rain + TrD + FRI*Rain	8	4.45	0.03	0.507	0.808
TSF + FRI + Rain + TSF*Rain	7	4.92	0.02	0.516	0.812
TSF + FRI + Rain + ShD	7	5.11	0.02	0.499	0.807
TSF + Rain + ShD + TrD	7	5.39	0.02	0.495	0.805
TSF + FRI + Rain + TrD	7	5.64	0.01	0.499	0.807
Ticks abundance					
TSF + FRI + GrL + Rain + TrD + TSF*Rain + FRI*Rain	10	0.00	0.51	0.785	0.819
TSF + FRI + GrL + Rain + TSF*Rain + FRI*Rain	9	0.05	0.49	0.782	0.819
Araneae abundance					
TSF + FRI + GrL + Rain + ShD + TrD + TSF*FRI + TSF*Rain + FRI*Rain	12	0.00	0.31	0.608	0.624
TSF + FRI + GrL + Rain + TrD + TSF*FRI + TSF*Rain + FRI*Rain	11	0.57	0.24	0.606	0.621
TSF + FRI + GrL + Rain + ShD + TrD + TSF*Rain + FRI*Rain	11	0.89	0.20	0.608	0.624
TSF + FRI + GrL + Rain + TrD + TSF*Rain + FRI*Rain	10	1.45	0.15	0.605	0.622
TSF + FRI + GrL + Rain + TSF*FRI + TSF*Rain + FRI*Rain	10	3.60	0.05	0.601	0.619
TSF + FRI + GrL + Rain + TSF*Rain + FRI*Rain	9	4.01	0.04	0.600	0.620
Orthoptera abundance					
TSF + FRI + GrL + Rain + TrD + TSF*Rain	9	0.00	0.58	0.599	0.979
TSF + GrL + Rain + TrD + TSF*Rain	8	0.64	0.42	0.593	0.979
Orthoptera biomass					
TSF + FRI + GrL + Rain + ShD + TrD + TSF*Rain + FRI*Rain	11	0.00	0.31	0.382	0.392
TSF + FRI + GrL + Rain + ShD + TrD + TSF*Rain	10	0.65	0.22	0.379	0.390
TSF + FRI + GrL + Rain + TrD + TSF*Rain + FRI*Rain	10	1.08	0.18	0.379	0.393
TSF + FRI + GrL + Rain + TrD + TSF*Rain	9	1.77	0.13	0.376	0.390
TSF + GrL + Rain + ShD + TrD + TSF*Rain	9	1.90	0.12	0.376	0.386
TSF + GrL + Rain + TrD + TSF*Rain	8	3.89	0.04	0.373	0.387
Hemiptera biomass					
TSF + FRI + GrL + Rain + TrD + TSF*FRI + TSF*Rain + FRI*Rain	11	0.00	0.29	0.303	0.379
TSF + FRI + GrL + Rain + TSF*FRI + TSF*Rain + FRI*Rain	10	0.48	0.23	0.300	0.380
TSF + FRI + GrL + Rain + TrD + TSF*FRI + TSF*Rain	10	0.90	0.19	0.301	0.377
TSF + FRI + GrL + Rain + TSF*FRI + TSF*Rain	9	1.46	0.14	0.297	0.377
TSF + FRI + GrL + Rain + TrD + TSF*FRI	9	3.05	0.06	0.298	0.374
TSF + FRI + GrL + Rain + TSF*FRI	8	2.74	0.04	0.294	0.374
TSF + GrL + Rain + TSF*Rain	7	3.86	0.04	0.291	0.369

Model	k	$\Delta AICc$	w	R ² m	R ² c
Ground-layer					
Order richness					
TSF + FRI + Rain + TrD + TSF*FRI + TSF*Rain	9	0.00		0.273	0.348
Abundance (no collembola or ants)					
TSF + FRI + GrL + Rain + TrD + TSF*FRI + TSF*Rain	10	0.00	0.66	0.300	0.376
TSF + FRI + Rain + TrD + TSF*FRI + TSF*Rain	9	1.60	0.30	0.295	0.369
TSF + FRI + GrL + Rain + TrD + TSF*Rain	9	5.52	0.04	0.292	0.377
Abundance (with collembola and ants)					
TSF + FRI + Rain + TrD + TSF*FRI + TSF*Rain	9	0.00	0.38	0.088	0.190
TSF + FRI + Rain + TrD + TSF*Rain	8	0.89	0.25	0.083	0.190
TSF + FRI + Rain + TrD	7	2.35	0.12	0.079	0.181
TSF + GrL + Rain + TrD	7	3.32	0.07	0.075	0.186
TSF + FRI + Rain + TSF*FRI + TSF*Rain	8	4.03	0.05	0.075	0.187
TSF + FRI + Rain + TSF*Rain	7	4.16	0.05	0.075	0.188
TSF + Rain + TrD + TSF*Rain	7	5.35	0.03	0.070	0.191
TSF + FRI + Rain	6	5.45	0.03	0.070	0.178
TSF + Rain + TrD	6	5.45	0.03	0.068	0.185
Formicidae abundance					
TSF + FRI + ShD + TrD	7	0.00	0.15	0.048	0.984
TSF + ShD + TrD	6	0.11	0.14	0.043	0.984
TSF + FRI + TrD	6	0.22	0.14	0.044	0.984
TSF + ShD	5	0.34	0.13	0.039	0.984
TSF + TrD	5	0.89	0.10	0.038	0.984
FRI + GrL + ShD + TrD	7	1.25	0.08	0.046	0.984
FRI + GrL + TrD	6	1.35	0.08	0.042	0.984
FRI + GrL + ShD	6	1.38	0.08	0.042	0.984
TSF	4	2.34	0.05	0.032	0.984
FRI + GrL	5	2.62	0.04	0.037	0.984
FRI + ShD + TrD	6	5.37	0.01	0.036	0.984
ShD + TrD	5	5.60	0.01	0.033	0.984
FRI + ShD	5	5.80	0.01	0.032	0.984
Collembola abundance					
TSF + FRI + Rain + ShD + FRI*Rain	8	0.00	0.36	0.130	0.995
TSF + FRI + Rain + TSF*FRI + FRI*Rain	8	0.96	0.22	0.132	0.995
TSF + FRI + Rain + FRI*Rain	7	1.28	0.19	0.125	0.995
FRI + GrL + Rain + ShD + FRI*Rain	8	1.95	0.14	0.123	0.995
FRI + GrL + Rain + FRI*Rain	7	2.73	0.09	0.119	0.995

Table A4.4: Model-averaged parameter estimates ($\beta \pm SE$) predicting arthropod ground-layer richness and abundance. Parameter estimates with 95% confidence intervals that did not include zero are indicated in bold. Predictor variables include times-since-fire (TSF), fire return interval (FRI), seasonal rainfall (Rain), grass length (GRL), shrub density (ShD), tree density (TrD) and interactions.

Model	TSF	FRI	Rain	GrL	ShD	TrD	TSF x FRI	TSF x RAIN	FRI x RAIN
<i>Ground-layer</i>									
Total Order richness	-0.196 ± 0.109	-3.276 ± 0.974	-0.094 ± 0.201			0.233 ± 0.067	0.592 ± 0.164	0.299 ± 0.056	
Total abundance (with ants and Collembola)	-0.075 ± 0.093	-0.252 ± 0.232	0.148 ± 0.033	0.008 ± 0.031		0.079 ± 0.047	0.076 ± 0.110	0.053 ± 0.043	
Total abundance (no ants or Collembola) [†]	-0.208 ± 0.072	-0.229 ± 0.158	0.287 ± 0.023	0.052 ± 0.047		0.097 ± 0.026	0.186 ± 0.077	0.118 ± 0.024	
Formicidae abundance	-0.012 ± 0.093	-0.072 ± 0.076		-0.031 ± 0.055	0.044 ± 0.050	0.057 ± 0.054			
Collembola abundance	0.349 ± 0.240	-0.841 ± 0.479	0.402 ± 0.067	0.059 ± 0.117	-0.079 ± 0.102		0.099 ± 0.230		0.202 ± 0.071

Blank spaces indicate a parameter that was not included in the top model set for model averaging

[†]We calculated ground-layer abundance after removing the two most abundant groups (i.e. ants and Collembola). We removed these groups because of their dominance in the sample (90% total abundance) and because they have demonstrated resistance to fire elsewhere (Parr et al. 2004; Vasconcelos et al. 2009) and therefore may conceal the response of less abundant fire-sensitive groups.

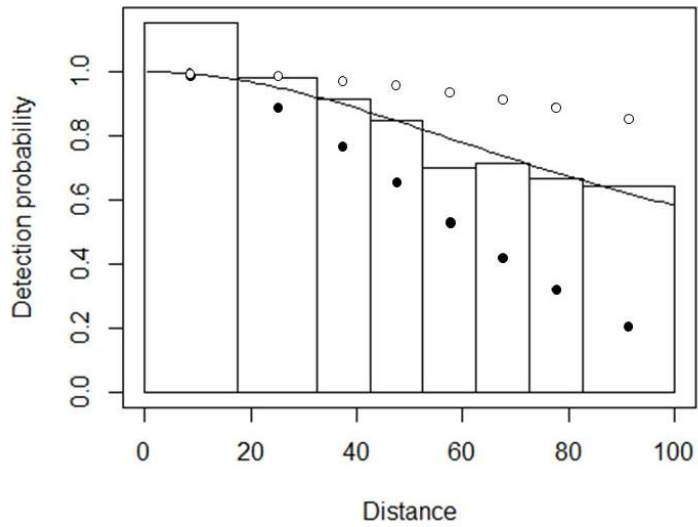


Figure A5.1: Histogram of detection distances (m) for avian insectivores with the fitted detection function displayed for the half-normal model of best fit. The model included the covariate 'cues' which identified if a bird was first detected visually (closed circles) or aurally (open circles). See Table S2 for further information about the detection function model.

Table A5.1: Summary of detection function models with covariates, AIC_c model fit scores, for combined avian insectivore species. Covariates included size: cluster size (e.g. single, pair or flock size), time: hours since sunrise, cues: bird cluster detected aurally or visually, TSF: time-since-fire (months). CDS (conventional distance sampling) includes no covariates. Key functions include the half-normal (hn) and hazard-rate (hr), P_a is the estimated proportion of bird clusters observed at the point.

Model	Covariates	Key function	AIC_c	Delta AIC_c	P_a
1	cues	hn	21807.61	0.00	0.744
2	cues + size	hn	21808.01	0.40	0.743
3	cues + TSF	hn	21812.16	4.55	0.742
4	cues + time	hn	21814.13	6.52	0.742
5	none (CDS)	hn	21989.04	181.43	0.772
6	size + time	hn	22006.47	198.86	0.766
7	size	hn	22007.12	199.51	0.768
8	size + TSF	hn	22011.15	203.54	0.767
9	time	hn	22011.69	204.08	0.770
10	TSF	hn	22014.30	206.69	0.771
11	time + TSF	hn	22016.16	208.55	0.769
12	none (CDS)	hr	22143.65	336.04	0.788

Table A5.2: Individual models for each node of the structural equation model. Site was included in each model as a random effect to account for repeated measures and was nested inside fire (burn patch) which was included to account for the hierarchical nature of the sampling design. R^2 values include the marginal (R^2_m), variance explained by fixed effects only, and the conditional (R^2_c), variance explained by fixed and random effects. See Table 5.1 for a description of the variables.

Model	R^2_m	R^2_c
Grass length GrL \leftarrow log(TrD) + log(TSF) + Rain + Season + ShHt + (Fire Site)	0.59	0.72
Tree density log(TrD) \leftarrow log(TSF) + FRI + (Fire Site)	0.04	0.96
Shrub density ShD \leftarrow log(TrD) + ShHt + (Fire Site)	0.07	0.38
Shrub height ShHt \leftarrow log(TSF) + FRI + Rain + Season + ShD + log(TSF):Rain + Rain:FRI + (Fire Site)	0.13	0.33
Invertebrate Order richness InvRich \leftarrow GrL + log(TrD) + logTSF + Rain + FRI + Season + ShrubHt + logTSF*Rain + Rain*FRI+ (Fire Site)	0.63	0.72
Invertebrate biomass InvBiomass \leftarrow GrL + InvRich + log(TSF) + Rain + FRI + Season + log(TSF):Rain + Rain:FRI + (Fire Site)	0.63	0.66
Avian insectivore species richness AvianRich \leftarrow GrL + InvRich + log(InvBiomass) + log(TrD) + Season + (Fire Site)	0.30	0.32
Avian insectivore density AvianDens \leftarrow GrL + InvRich + log(InvBiomass) + log(TrD) + Season + (Fire Site)	0.22	0.24
Avian insectivore body mass AvianBM \leftarrow log(InvBiomass) + log(TrD) + ShD + ShrubHt + GrassLength + (Fire Site)	0.06	0.12
Avian insectivore foraging strategies AvianFS \leftarrow GrL + log(TrD) + Season + (Fire Site)	0.10	0.11
Avian insectivore habitat breadth AvianHB \leftarrow GrL + log(TrD) + Season + (Fire Site)	0.11	0.18
Avian insectivore diet breadth AvianDB \leftarrow GrL + ShD + log(TrD) + Season + (Fire Site)	0.17	0.18

Table A5.3: Species list of all avian insectivores from all study sites including value of the functional traits i) body mass (g), ii) number of foraging strategies, iii) habitat breadth (number of habitat types used) and iv) diet breadth (number of food types used). Data was collated from Hockey et al. (2004).

Common Name	Scientific Name	Family	Adult body mass	Niche Breadth	Diet Breadth	Habitat Breadth
Flappet lark	<i>Mirafraga rufocinnamomea</i>	Alaudidae	25.7	2	2	4
Rufous-naped lark	<i>Mirafraga africana</i>	Alaudidae	44.0	3	2	6
African black swift	<i>Apus barbatus</i>	Apodidae	42.1	1	1	13
African palm-swift	<i>Cypsiurus parvus</i>	Apodidae	15.0	1	1	3
Common swift	<i>Apus apus</i>	Apodidae	36.9	1	1	8
Horus swift	<i>Apus horus</i>	Apodidae	26.2	1	1	12
Little swift	<i>Apus affinis</i>	Apodidae	24.5	1	1	10
White-rumped swift	<i>Apus caffer</i>	Apodidae	24.1	1	1	10
Cattle egret	<i>Bubulcus ibis</i>	Ardeidae	379.0	4	5	4
African grey hornbill	<i>Tockus nasutus</i>	Bucerotidae	167.0	5	7	3
Red-billed hornbill	<i>Tockus erythrorhynchus</i>	Bucerotidae	150.0	3	7	2
Southern yellow-billed hornbill	<i>Tockus leucomelas</i>	Bucerotidae	211.0	2	8	2
Black cuckooshrike	<i>Campephaga flava</i>	Campephagidae	32.0	2	1	3
Burchells coucal	<i>Centropus burchellii</i>	Centropodidae	179.5	1	4	8
Blacksmith lapwing	<i>Vanellus armatus</i>	Charadriidae	163.0	3	2	4
Crowned lapwing	<i>Vanellus coronatus</i>	Charadriidae	186.7	2	1	4
Barred wren-warbler	<i>Calamonastes fasciolatus</i>	Cisticolidae	13.1	1	1	2
Black-chested prinia	<i>Prinia flavicans</i>	Cisticolidae	8.8	2	2	5
Desert cisticola	<i>Cisticola aridulus</i>	Cisticolidae	8.0	1	1	3
Grey-backed camaroptera	<i>Camaroptera brevicaudata</i>	Cisticolidae	10.2	1	1	4
Lazy cisticola	<i>Cisticola aberrans</i>	Cisticolidae	12.6	1	1	6
Neddicky	<i>Cisticola fulvicapillus</i>	Cisticolidae	9.8	3	2	7
Rattling cisticola	<i>Cisticola chiniana</i>	Cisticolidae	17.9	2	2	3
Tawny-flanked prinia	<i>Prinia subflava</i>	Cisticolidae	9.0	3	2	5
Zitting cisticola	<i>Cisticola juncidis</i>	Cisticolidae	9.3	1	1	2
European roller	<i>Coracias garrulus</i>	Coraciidae	122.3	3	1	2
Lilac-breasted roller	<i>Coracias caudata</i>	Coraciidae	110.0	3	4	2
African cuckoo	<i>Cuculus gularis</i>	Cuculidae	103.0	2	1	3
Black cuckoo	<i>Cuculus clamosus</i>	Cuculidae	90.2	2	1	3
Diederik cuckoo	<i>Chrysococcyx caprius</i>	Cuculidae	34.3	3	2	6
Great spotted cuckoo	<i>Clamator glandarius</i>	Cuculidae	139.3	1	2	4
Jacobin cuckoo	<i>Oxylophus jacobinus</i>	Cuculidae	69.8	2	2	4
Levaillants cuckoo	<i>Clamator levaillantii</i>	Cuculidae	122.0	1	1	3
Red-chested cuckoo	<i>Cuculus solitarius</i>	Cuculidae	75.3	2	2	3
Brown-hooded kingfisher	<i>Halcyon albiventris</i>	Dacelonidae	60.1	2	5	5

Common Name	Scientific Name	Family	Adult body mass	Niche Breadth	Diet Breadth	Habitat Breadth
Striped kingfisher	<i>Halcyon chelicuti</i>	Dacelonidae	36.0	2	3	3
Fork-tailed drongo	<i>Dicrurus adsimilis</i>	Dicruridae	50.2	5	5	3
Amur falcon	<i>Falco amurensis</i>	Falconidae	136.0	3	2	4
Greater kestrel	<i>Falco rupicoloides</i>	Falconidae	265.0	3	4	5
Lesser kestrel	<i>Falco naumanni</i>	Falconidae	153.0	2	4	4
Temmincks courser	<i>Cursorius temminckii</i>	Glareolidae	69.3	3	2	5
Banded martin	<i>Riparia cincta</i>	Hirundinidae	26.2	1	1	7
Barn swallow	<i>Hirundo rustica</i>	Hirundinidae	20.4	2	2	9
Brown-throated martin	<i>Riparia paludicola</i>	Hirundinidae	13.15	1	1	8
Common house-martin	<i>Delichon urbicum</i>	Hirundinidae	13.3	1	1	7
Greater striped swallow	<i>Hirundo cucullata</i>	Hirundinidae	27.0	2	2	9
Lesser striped swallow	<i>Hirundo abyssinica</i>	Hirundinidae	17.5	2	2	6
Pearl-breasted swallow	<i>Hirundo dimidiata</i>	Hirundinidae	11.8	1	2	8
Red-breasted swallow	<i>Hirundo semirufa</i>	Hirundinidae	31.5	2	1	2
Rock martin	<i>Hirundo fuligula</i>	Hirundinidae	15.6	1	1	7
White-throated swallow	<i>Hirundo albigularis</i>	Hirundinidae	21.3	2	1	6
Brown-backed honeybird	<i>Prodotiscus regulus</i>	Indicatoridae	14.0	1	1	5
Greater honeyguide	<i>Indicator indicator</i>	Indicatoridae	49.5	1	1	3
Lesser honeyguide	<i>Indicator minor</i>	Indicatoridae	28.2	1	1	4
Common fiscal	<i>Lanius collaris</i>	Laniidae	41.8	3	6	6
Lesser grey shrike	<i>Lanius minor</i>	Laniidae	48.3	2	1	2
Magpie shrike	<i>Corvinella melanoleuca</i>	Laniidae	82.3	2	5	3
Red-backed shrike	<i>Lanius collurio</i>	Laniidae	29.5	2	3	3
Black-backed puffback	<i>Dryoscopus cubla</i>	Malaconotidae	27.1	2	3	4
Black-crowned tchagra	<i>Tchagra senegala</i>	Malaconotidae	51.5	2	2	4
Southern boubou	<i>Laniarius ferrugineus</i>	Malaconotidae	60.2	2	7	4
Brown-crowned tchagra	<i>Tchagra australis</i>	Malaconotidae	32.0	1	1	4
Brubru	<i>Nilaus afer</i>	Malaconotidae	24.1	2	1	3
Crimson-breasted shrike	<i>Laniarius atrococcineus</i>	Malaconotidae	48.3	2	2	1
Chinspot batis	<i>Batis molitor</i>	Malaconotidae	11.2	3	1	3
Grey-headed bush-shrike	<i>Malaconotus blanchoti</i>	Malaconotidae	78.5	2	4	4
Orange-breasted bush-shrike	<i>Telophorus sulfureopectus</i>	Malaconotidae	27.5	2	1	2
White-crested helmet-shrike	<i>Prionops plumatus</i>	Malaconotidae	32.7	2	2	3
European bee-eater	<i>Merops apiaster</i>	Meropidae	51.7	2	1	4
Little bee-eater	<i>Merops pusillus</i>	Meropidae	14.6	2	1	4
African paradise-flycatcher	<i>Terpsiphone viridis</i>	Monarchidae	14.6	3	2	4
African pipit	<i>Anthus cinnamomeus</i>	Motacillidae	25.4	3	3	3
Buffy pipit	<i>Anthus vaalensis</i>	Motacillidae	27.0	1	2	2

Common Name	Scientific Name	Family	Adult body mass	Niche Breadth	Diet Breadth	Habitat Breadth
Bushveld pipit	<i>Anthus caffer</i>	Motacillidae	17.5	1	1	2
Long-billed pipit	<i>Anthus similis</i>	Motacillidae	29.1	1	2	5
Plain-backed pipit	<i>Anthus leucophrys</i>	Motacillidae	23.9	1	2	4
Capped wheatear	<i>Oenanthe pileata</i>	Muscicapidae	27.8	3	3	4
Familiar chat	<i>Cercomela familiaris</i>	Muscicapidae	21.5	4	3	7
Fiscal flycatcher	<i>Sigelus silens</i>	Muscicapidae	26.2	4	4	7
Groundscraper thrush	<i>Psophocichla litsipsirupa</i>	Muscicapidae	75.5	1	1	3
Grey tit-flycatcher	<i>Myioparus plumbeus</i>	Muscicapidae	12.2	3	1	2
Kalahari scrub-robin	<i>Cercotrichas paena</i>	Muscicapidae	19.7	1	3	2
Kurrichane thrush	<i>Turdus libonyanus</i>	Muscicapidae	59.6	2	2	3
Marico flycatcher	<i>Bradornis mariquensis</i>	Muscicapidae	24.1	3	2	3
Southern black flycatcher	<i>Melaenornis pammelaina</i>	Muscicapidae	29.8	5	2	2
Spotted flycatcher	<i>Muscicapa striata</i>	Muscicapidae	15.58	3	2	8
White-browed scrub-robin	<i>Cercotrichas leucophrys</i>	Muscicapidae	20.1	2	3	2
White-bellied korhaan	<i>Eupodotis senegalensis</i>	Otididae	1400.0	2	5	2
Ashy tit	<i>Parus cinerascens</i>	Paridae	20.8	3	3	3
Cape penduline-tit	<i>Anthoscopus minutus</i>	Paridae	7.5	1	2	4
Southern black tit	<i>Parus niger</i>	Paridae	22.0	4	3	3
Green wood-hoopoe	<i>Phoeniculus purpureus</i>	Phoeniculidae	83.0	3	4	5
Bearded woodpecker	<i>Dendropicos namaquus</i>	Picidae	87.0	1	1	2
Bennetts woodpecker	<i>Campethera bennettii</i>	Picidae	70.0	1	1	2
Cardinal woodpecker	<i>Dendropicos fuscescens</i>	Picidae	33.0	1	1	3
Golden-tailed woodpecker	<i>Campethera abingoni</i>	Picidae	70.0	1	1	3
Lesser masked-weaver	<i>Ploceus intermedius</i>	Ploceidae	21.4	2	5	4
Pearl-spotted owlet	<i>Glaucidium perlatum</i>	Strigidae	98.0	3	5	2
Red-billed oxpecker	<i>Buphagus erythrorhynchus</i>	Sturnidae	51.0	2	1	3
Arrow-marked babbler	<i>Turdoides jardineii</i>	Sylviidae	72.2	2	5	4
Burnt-necked eremomela	<i>Eremomela usticolis</i>	Sylviidae	8.6	2	2	3
Garden warbler	<i>Sylvia borin</i>	Sylviidae	21.1	3	2	5
Icterine warbler	<i>Hippolais icterina</i>	Sylviidae	13.6	2	2	2
Long-billed crombec	<i>Sylvietta rufescens</i>	Sylviidae	11.6	2	4	5
Olive-tree warbler	<i>Hippolais olivetorum</i>	Sylviidae	17.5	1	1	3
Southern pied babbler	<i>Turdoides bicolor</i>	Sylviidae	77.9	4	3	2
Willow warbler	<i>Phylloscopus trochilus</i>	Sylviidae	9.0	2	1	4
Yellow-bellied eremomela	<i>Eremomela icteropygialis</i>	Sylviidae	8.3	1	4	5
African hoopoe	<i>Upupa africana</i>	Upupidae	51.3	4	1	3

Table A5.4: Hypothesised and final structural equation models (SEMs) of avian insectivore community structure. Directional separation tests revealed relationships with significant path coefficients that were missing from hypothesized models. These missing relationships were added to the hypothesized SEMs and these final models were compared with the hypothesised models using the Fisher's C statistic ($P > 0.05$ indicates no significant lack-of-fit between model and data) and Akaike information criterion corrected for small sample sizes (AIC_c).

Model	Missing relationships	Fisher's C	<i>P</i>	AIC_c
Species richness				
Hypothesised model	<i>insectivore richness ~ time-since-fire</i> <i>insectivore richness ~ rainfall</i>	52.68	0.012	170.39
Final model		26.96	0.52	164.96
Density				
Hypothesised model	<i>insectivore density ~ rainfall</i>	35.78	0.30	169.78
Final model		27.24	0.61	163.24
Habitat breadth				
Hypothesised model	<i>habitat breadth ~ rainfall</i>	73.86	<0.001	209.86
Final model		24.35	0.66	162.35
Foraging strategies				
Hypothesised model	<i>foraging strategies ~ rainfall</i>	26.65	0.76	159.82
Final model		29.82	0.81	158.65
Diet breadth				
Hypothesised model	<i>diet breadth ~ rainfall</i> <i>diet breadth ~ time-since-fire</i>	101.16	0.00	233.16
Final model		25.71	0.69	161.71
Body Mass				
Hypothesised model (final model)		26.71	0.73	160.71