



THE UNIVERSITY OF QUEENSLAND  
AUSTRALIA

**DRIVERS OF DIVERSITY AT THE LOCAL- AND LANDSCAPE-SCALE IN A FIRE-  
PRONE LANDSCAPE**

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## ABSTRACT

Determining the factors that generate and maintain patterns of biodiversity is a challenge central to ecology. To effectively manage heterogeneous landscapes for biodiversity conservation there is a need to understand the mechanisms driving the relationship between spatial heterogeneity and species richness at multiple scales. Disturbances such as fire affect landscape heterogeneity and are important influences on the distribution and abundance of biota across a range of scales. A key challenge for biodiversity conservation in fire-prone ecosystems is thus to understand the influence of fire on biotic communities.

Contemporary ecological fire management resounds with the term 'pyrodiversity'. Efforts to achieve pyrodiversity are usually motivated by the rationale that increasing gamma diversity relies upon maintaining a mosaic of patches of different fire histories. From a global review of literature, this thesis revealed that despite widespread acceptance of this paradigm, the evidence supporting it is extremely sparse. This dearth of knowledge of how heterogeneity affects biota limits effective application of the mosaic burning approach. Studies that consider the spatial and temporal attributes of the fire regime mosaic, and investigate the relationship between these and multiple taxa at different spatial scales, are urgently required.

To respond to this knowledge gap, this thesis investigated the effects of fire history and habitat heterogeneity on structure and composition of floral and avifaunal communities. This thesis tests hypotheses about the importance of variable fire regimes, spatial heterogeneity, extent of habitat, and local- and landscape-responses on birds and their habitat in the fire-prone sub-tropical woodlands of central Queensland. Two methods were used to collect the data: i) digital mapping and characterisation of the fire regime mosaic; and ii) surveys of woody vegetation and avifaunal communities.

The post-fire response of vegetation reflects not only a single fire event but is the result of cumulative effects of previous fires in the landscape. Fire history categories based on unique combinations of time since last burn, fire frequency and season of last burn were developed and used to map the fire regime mosaic of the study area. This thesis establishes that fire history category strongly influences richness and abundance of mid-storey trees and of individual plants currently comprising the mid-level strata. The particular elements of fire history, time since fire and fire frequency, had the strongest influence on vegetation structure. A longer time since fire (> 4 years since last burn) combined with infrequent fires (< 2 fires in 12 year period) appeared to

promote a dense mid-storey with the opposite conditions promoting more-open woodlands. This is of particular relevance for conservation management of woodland birds that have been shown to respond strongly to habitat structural variables in the study area.

Landscape heterogeneity and extent of habitat are each expected to contribute to species richness at intermediate- or landscape-scales (~1-100s km<sup>2</sup>) through elevating beta and mean alpha diversity, respectively. Understanding of their relative importance, however, is limited. I investigated the relative importance of diversity of habitat types (both natural and fire-mediated vegetation types), extent of habitat and indices of landscape configuration on landscape-scale (1 km<sup>2</sup>) bird richness. At this scale, species richness was most strongly associated (positively) with measures of landscape heterogeneity, in particular topographic complexity and diversity of vegetation types. Despite being relevant to management, fire-mediated diversity was of limited importance at this scale. Total estimated richness (Chao2) and richness of small passerines, a group of conservation concern, were also negatively associated with the mean abundance of noisy miners (*Manorina melanocephala*), a hyper-aggressive native species. Despite the relationship between heterogeneity and species richness, mean alpha diversity made a greater contribution to landscape-scale bird species richness than did beta diversity. These findings support environmental heterogeneity as a primary driver of species richness at the landscape-scale, and imply that it acts through increasing both turnover and mean alpha diversity.

Taxa respond to their environment at a variety of scales. An increasing number of studies have considered the impact of heterogeneity measured across spatial scales. Few studies, however have considered how the response of fauna to landscape elements varies when the response variable was measured at different scales. I investigated the relationship between properties of the fire regime mosaic, and the structure and composition of avian assemblages measured at both the site- (1 ha) and the landscape-scale (1 km<sup>2</sup>). I found topographic complexity was consistently important for bird species richness and composition; however, its explanatory power varied with spatial scale and the component of diversity under investigation. For foraging guilds different correlates of richness became evident depending on the scale at which the response was measured. The extent of unburnt habitat was the most important variable for the landscape-level richness of frugivores, insectivores and canopy feeders, whereas environmental heterogeneity was most important for site-level richness of these foraging guilds. These findings suggest that depending on the scale at which a biodiversity conservation goal is conceptualised – maximising richness at a site, or across a landscape – different landscape management approaches would be considered optimal.

The thesis outcomes have important implications for our understanding of the drivers of patterns of biodiversity and for conservation management in fire-prone landscapes. The main findings are: (i) a variable fire regime will maintain a heterogeneous vegetation mosaic through its influence on species in the mid-level strata in sub-tropical woodlands; (ii) environmental heterogeneity is an important driver of landscape-scale bird richness and acts through increasing both turnover and mean alpha diversity; (iii) the extent of unburnt habitat is also important, particularly influencing species composition and assemblage structure at the landscape scale; (iv) higher fire-mediated diversity of vegetation does not increase species richness at spatial scales of 1 km<sup>2</sup>; (v) landscapes with a higher abundance of noisy miners had fewer bird species, particularly small passerines; and (vi) landscape elements driving bird assemblages vary depending on the scale at which the response is measured and the foraging guild considered.

## **DECLARATION BY AUTHOR**

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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## **PUBLICATIONS DURING CANDIDATURE**

### **Published papers:**

Chapter 3: Burgess, E.E., Moss, P., Haseler, M. and Maron, M. 2014. The influence of a variable fire regime on woodland structure and composition. *International Journal of Wildland Fire*, 24 (1): 59-69.

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<b>Contributor</b>	<b>Statement of contribution</b>
Emma Burgess (Candidate)	Designed study (80%) Field Surveys (100%) Statistical analyses (100%) Wrote the paper (100%) Editing (70%)
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Murray Haseler	Designed study (10%) Edited paper (10%)
Patrick Moss	Edited paper (10%)

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Martine Maron	Designed study (15%) Edited paper (20%)



## **CONTRIBUTIONS BY OTHERS TO THIS THESIS**

Four jointly published or submitted papers form part of this thesis (chapters 2-5). I undertook the majority of the work for these articles, including generating ideas, data collection and analysis, interpretation and drafting of manuscripts. Martine Maron and Murray Haseler contributed to generating ideas for research, gave statistical advice, and reviewed and commented on draft manuscripts. Patrick Moss reviewed and commented on draft manuscripts.

### **Statement of parts of the thesis submitted to qualify for the award of another degree**

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*‘Knowledge is the key that unlocks all the doors’*- Ben Carson, Think Big: Unleashing Your Potential for Excellence.

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Fire management, mosaic burning, fire regimes, heterogeneity, avifauna, functional diversity, sub-tropical woodlands, conservation management, landscape pattern

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## CHAPTER 1:

### INTRODUCTION

#### 1.1 BACKGROUND TO THE PROBLEM

The 20<sup>th</sup> century marked a period of rapid growth in human population and consequent transformation of natural ecosystems and loss of biological diversity globally (Soule 1991; Kerr and Currie 1995; Forester and Machlis 1996; Fahrig 2003). Biological diversity, or biodiversity, can be defined simply as the variety of life on earth and the natural patterns it forms (CBD 2000). The consequences of loss of biodiversity are not only ecological but also economic, sociological, ethical, and aesthetic. This is because of the many resources and services biodiversity provides, from protection against natural disasters to provision of food, shelter and medicines.

The persistence of much of the world's biodiversity is now dependent on protected areas and nature reserves (Parr et al. 2009). Protected areas are legally or effectively managed areas of land or sea dedicated to the protection and maintenance of biological diversity (Chape et al. 2003). These protected areas, however, are coming under increasing internal and external pressures from human population growth and development (Soule 1991; Balmford et al. 2001; Jackson and Gatson 2008). The success of protected areas in conserving biodiversity will depend largely on how they are managed (Parr et al. 2009). To ensure effective management, a clear understanding of the key drivers and threats to diversity at multiple spatial and temporal scales is required.

##### *1.1.1 Drivers of diversity*

###### *Landscape structure*

Determining the factors that generate and maintain patterns of biodiversity is central to ecology (MacArthur and MacArthur 1969; Gaston 2000; Williams et al. 2002). Landscape ecology represents a rapidly-growing field within ecology that aims to explain the reciprocal interactions between spatial pattern and ecological processes, scale and hierarchy (Pickett and Cadenasso 1995; Turner 2005). A 'landscape' can be defined as a heterogeneous area, comprised of several interacting ecosystems, repeated in similar form across regions (Forman and Godron 1986). A key application of landscape ecology is an understanding of the consequences of spatial heterogeneity on species occurrence, and distribution and how this varies with scale (Pickett and Cadenasso 1995;

Turner 2005). As a result, landscape ecology generates important information for management of both natural and human-dominated landscapes (Turner 2005).

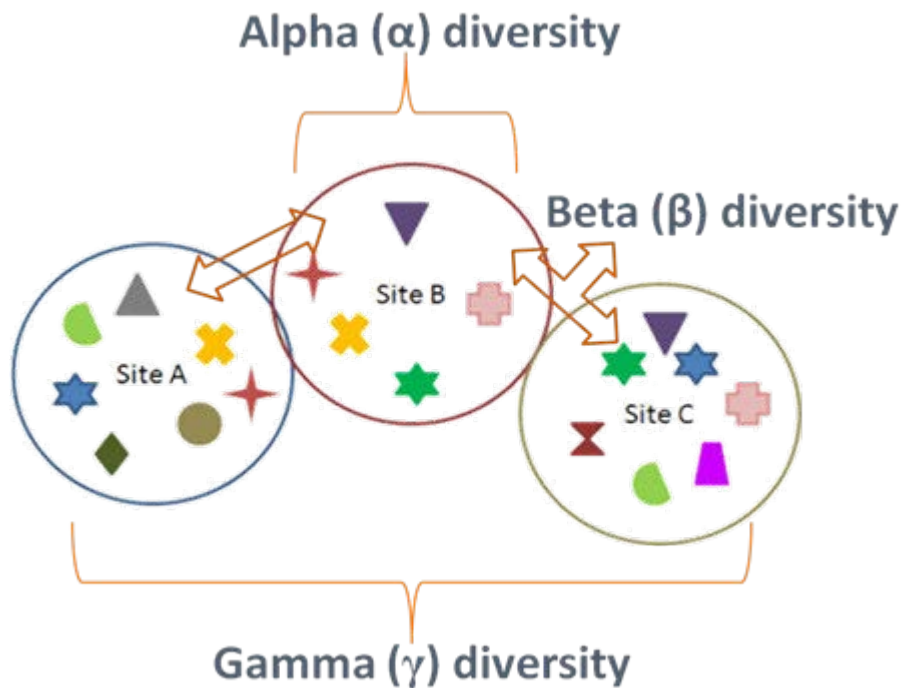
A key question in landscape ecology relates to how landscape structure is generated (Pickett and Cadenasso 1995). From an organism's perspective, landscape structure refers to the temporal and spatial heterogeneity of habitat and resources (Wiens 1989; Williams et al. 2002; Fischer et al. 2008). This heterogeneity in landscape pattern is driven by both stochastic and anthropogenic processes (Bennett et al. 2006). These processes range from abiotic factors such as climate and topography, to biotic interactions such as competition and predation (Turner 2005). Other drivers of landscape pattern include disturbance, both natural and anthropogenic, and human land use (Turner 2005). Whilst the causes of landscape pattern are widely understood, quantification of their interactions and resulting effects on biodiversity can be difficult.

Multiple metrics that describe landscape pattern have been developed to help elucidate the relationship between spatial heterogeneity and ecological processes. The metrics are largely based around two categories: landscape composition (e.g. the amount and type of habitat present) and landscape configuration (how habitat or resources are arranged spatially) (McGarigal and McComb 1995; Turner 2005; Bennett et al. 2006). Recent research has also highlighted the extent of habitat as an important landscape property driving species diversity and assemblage composition (Radford et al. 2005; Bennett et al. 2006; Kelly et al. 2012; Taylor et al. 2012). Questions remain however, regarding the relative influence of the different landscape properties on the persistence of biodiversity at multiple scales.

### *Diversity and scale*

Typically, ecologists have focused on local mechanisms to explain assemblage structure (Williams et al. 2002; Tschardtke et al. 2012). However, differences in autecology among species such as home range size, foraging behaviour and nesting requirements mean that taxa respond to their environment at a variety of scales (Williams et al. 2002; Flesch and Steidl 2010; Tschardtke et al. 2012; Cunningham et al. 2014). To effectively manage heterogeneous landscapes for biodiversity conservation there is therefore a need to understand the mechanisms driving the relationship between spatial heterogeneity and species richness at scales from the stand and site to those of the patch and the landscape (Fahrig et al. 2011).

Exploring how species diversity responds to spatial heterogeneity requires consideration of different elements of diversity (Fig. 1). Alpha diversity is the number or diversity of species within a habitat unit, such as a site or a patch. Beta diversity (or species turnover) is a measure of the difference in species identities between sites or samples. Gamma diversity refers to the total number of different species within a landscape, and is therefore a consequence of both alpha and beta diversity (Whittaker 1972; Wilson and Shmida 1984) (Fig. 1).



**Figure 1** Diagram of the relationship between alpha, beta and gamma diversity. Each of the different symbols represents a different species (adapted from the University of Idaho 2009).

Much research has been carried out at small scales ( $m^2$  to hectares), revealing factors such as productivity to be important drivers of alpha diversity (Huston, 1994; Burel et al., 2004; Willig, 2011). Richness at larger or macro-scales, such as across regions, is driven not only by productivity, but also by compositional turnover or spatial heterogeneity (Tuomisto et al., 2003; Chase, 2010). While considerable research attention has been focussed on correlates of richness at small and very large scales, there remains a limited understanding of the drivers of richness at intermediate or meso-scales—the scales at which management decisions are most often made (Heikkinen and Birks, 1996; Niemelä, 1999; Koivula, 2001; Estrada, 2007).

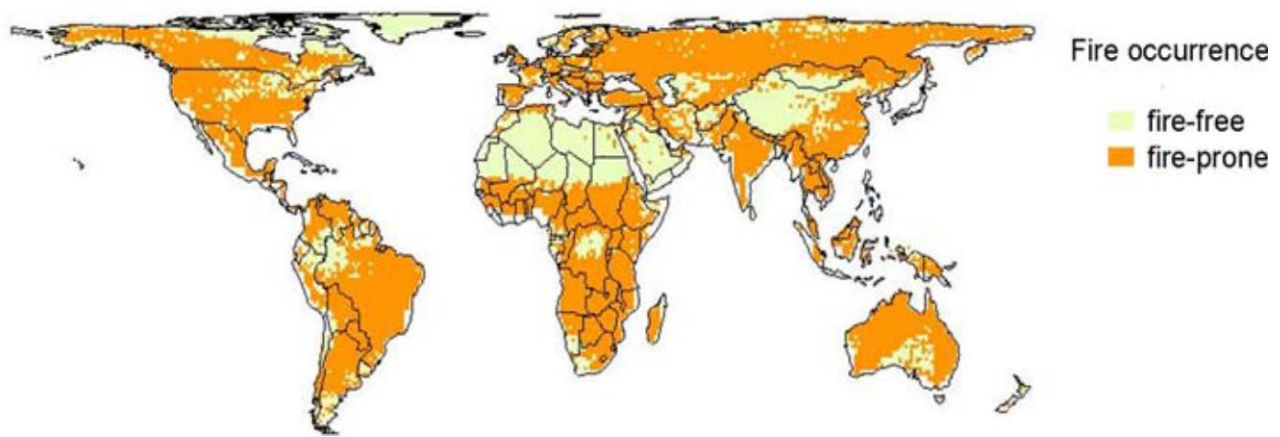
Disturbances such as fire affect landscape heterogeneity over a range of spatial and temporal scales (Bond and Keeley 2005; Bradstock 2008). Fire-mediated heterogeneity can be generated through (1) a single fire event, which causes variation in burn severity and patch size; and (2) repeated fires over time, which result in a distribution of patches with different seral stages and fire histories in a landscape (Bradstock et al. 2005; Falk et al. 2007). Much research in fire ecology to date has focused on the response of biota to temporal aspects of the fire mosaic, such as changes in biota with time since last fire (Zammit and Zedler 1988; Morgan and Lunt 1999; Keeley et al. 2005; Watson et al. 2012). However, there has been increasing interest in how spatial patterns of fire impact on biota (Bradstock et al. 2005; Parr and Andersen 2006).

In the study region covered by this thesis, spatial heterogeneity is driven by multiple factors. These factors include disturbance history (fire), vegetation type, and altitude (Howes and Maron 2009; Howes et al. 2010). This thesis applies the principles of landscape ecology to investigate the relationship between disturbance history, spatial heterogeneity, and the biota at multiple spatial scales.

### ***1.1.2 Fire***

#### *Fire - an ecological process*

Fire is both a natural disturbance mechanism and a tool utilised for land management that has been present in global ecosystems for hundreds of millennia (Bowman et al 2009). Since that time, fire has played a key role in shaping the structure and function of many ecosystems worldwide (Hallam 1979; Goldammer 1993; Archibold 1995; Adams and Attiwill 2009). It is currently estimated that sixty-nine percent of the Earth's terrestrial ecosystems are fire-prone (Fig. 2) (Krawchuk et al. 2009), from tropical forests to arid environments (Letnic 2003; Langner and Siegert 2009).

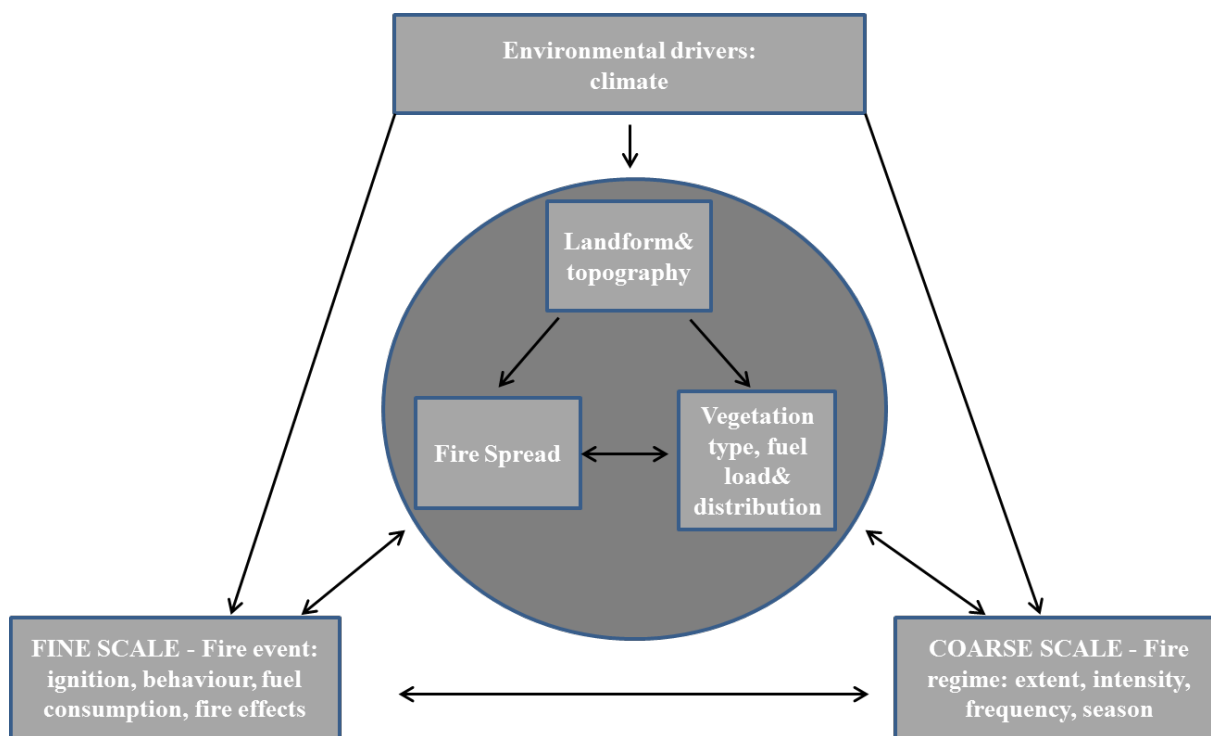


**Figure 2** Map showing fire-prone (orange) and fire-free (yellow) parts of the world. This is based on counts of fire activity detected by Along Track Scanning Radiometer (ATSR) around the world at a resolution of 100 km over 10 years (Krawchuk et al. 2009).

Fire influences the distribution and abundance of biota across sites and landscapes, as well as through time. The process by which fire affects biota relate to the properties of both individual fire events and sequence of fires (Bradstock et al. 2005). The term ‘fire regime’ is most commonly used in the fire management literature to define the attributes of fire at a particular site over time (Whelan 1995). The attributes of a fire regime are composed of the time between fires (fire frequency), the time since the last fire, the season in which the fire occurs, the fire extent (or patchiness), the fire intensity (the heat produced) and the type of fuel burnt (Gill 1975; Gill 1981 ; Gill et al. 2002).

No two fire events will have the same ecological impact. This will be determined by the interaction among the fire regime attributes, the organisms in question, the landscape and the climatic characteristics (Johnson 1992; Johnson and Miyanishi 2001; Watson 2001; Catchpole 2002; Whelan et al. 2002; van Wilgen et al. 2003; Falk et al. 2007; O’Connor et al. 2011). This complex interplay of various biotic and abiotic attributes operates at multiple scales, influencing the spatiotemporal configuration of the landscape fire mosaic (Fig. 3) (Clark 1983; Gill et al. 2002; Gill and Bradstock 2002; Bradstock et al. 2005; Kerby et al. 2007). As illustrated in Figure 3, the interactions are hierarchical, with a process at one scale being influenced by a process or processes operating at another scale (Falk et al. 2007).





**Figure 3** Feedback between landscape patterns and ecological processes are scale-dependent. Here, the pattern and process in fire regimes are influenced by interactions between individual fire events, abiotic elements of the landscape such as prevailing climate and topography, vegetation type, and past fire regime characteristics of the landscape (modified from Falk et al. 2007).

Inconsistencies in the ecological impacts of fire make it difficult for land managers to predict species and community responses (Whelan et al. 2001). Response to a single fire event can vary among different species (Letnic et al. 2003), and the same species may respond differently to fires occurring at different times or locations (Lindenmayer et al. 2009). For example, some species have been shown to respond positively (e.g. increased abundance) to a particular fire regime (e.g. Masters 1993; Fuhlendorf et al. 2006; Wilgers and Horne 2006; Churchwell et al. 2008), whilst others show a negative response (e.g. Woinarski and Recher 1997; Woinarski et al. 1999; Kelly et al. 2010), or no response (neither positive nor negative) (Short and Turner 1994; Uys et al. 2004; Wittkuhn et al. 2011). The variation in responses can be attributed, in part, to the different scales at which studies are conducted (Schwilk et al. 1997; Uys et al. 2004; Faivre et al. 2011).

Factors such as livestock grazing, introduction of exotic species, timber harvesting practices, fire suppression and other human activities continue to alter fuel loads and fire regimes in many parts of the world (Dombeck et al. 2004). These altered fire regimes are recognised as a threatening process for many species and communities (e.g. Russell-Smith and Bowman 1992; Bowman and Panton

1993; Price and Bowman 1994; Bradstock et al. 1995; Woinarski and Recher 1997; Biggs and Pottgieter 1999; Franklin 1999). This is further confounded by the uncertainty imposed by future climate change, with an increase in fire frequency, fire severity and fire extent predicted to occur in many parts of the world in the near future (Flannigan et al. 2005; Hennessy et al. 2005; Kasischke and Turetsky 2006; Williams et al. 2009). This highlights the need for a better understanding of the complex interactions among climate, fire, biodiversity, fuel management and land use change in order to mitigate their impacts (Williams et al. 2009).

### *Fire - a land management tool*

With an increase in frequency and extent of fires predicted under a changing climate (Flannigan et al. 2005; Hennessy et al. 2005; Kasischke and Turetsky, 2006; Krawchuk et al. 2009; Williams et al. 2009), there is a greater need to better understand their behaviour and how to mitigate their occurrence (Pastro et al. 2011). The purposeful application of fire is widely referred to as prescribed burning (Penman et al. 2011). Modern prescribed burning is used as a management tool in many fire-prone ecosystems globally (e.g. North America e.g. Bailey and Anderson 1978; McCullough et al. 1998 and South Africa e.g. van Wilgen et al. 1994; Brockett et al. 2001). Small scale, controlled burns are increasingly being prescribed for fuel hazard reduction, pasture improvement, vegetation clearing and more recently, biodiversity conservation (Parr and Brockett 1999; Valentine and Schwarzkopf 2008; Boer et al. 2009; Mulqueeny et al. 2010; Pastro et al. 2011). The adoption of fire management to support biodiversity conservation objectives has evolved in keeping with the following principles:

1) Conservation of biodiversity is now a guiding principle in natural resource management (Keith et al. 2002); and

2) Ecological systems exist in a state of flux (Illius and O'Connor 1999; Mentis and Bailey 1990; Parr and Andersen 2006; van Wilgen et al. 1998) as opposed to a state of balance.

This has resulted in a move from prescribed fire with fixed intervals, rotated over a fixed area, to one which introduces variability to the fire regime, often termed patch mosaic burning, or PMB (Bond and Archibald 2003; Van Wilgen et al. 2011). PMB introduces variability into the fire regime by varying the fire regime attributes of adjacent patches (e.g. Brockett et al. 2001; Saxon 1984; van Wilgen et al. 1998). The main aim is to produce a fire-created habitat mosaic composed

of different seral stages, vegetation structures, vegetation densities and functions (Smucker et al. 2005). This landscape heterogeneity is expected to support higher levels of biodiversity than a more homogeneous landscape (Bradstock et al. 1995; Pickett 1998 taken from Pickett et al. 2003; Edwards et al. 2001; Fuhlendorf and Engle 2001; Keith et al. 2002; Burrows and Wardell-Johnson 2003; Turner et al. 2003). This fire-created mosaic or fire-regime mosaic (FRM) also has potential to reduce the extent of major wildfires by breaking up the pattern of fuels in a landscape (Moral and Walker 2007; Boer et al. 2009).

Patch Mosaic Burning aims to produce and maintain a heterogeneous mosaic based on the 'pyrodiversity begets biodiversity' paradigm (Parr and Brockett 1999; Fuhlendorf and Engle 2001; Clarke 2008). Landscape pyrodiversity refers to the range or variability in fire regime patterns or mosaics across space and time in that landscape (Martin and Sapsis 1991; Parr and Andersen 2006; Faivre et al. 2011). Site- or local-level studies have repeatedly shown that different species or communities utilise different post-fire seral stages (Masters 1993; Woinarski and Recher 1997; Woinarski et al. 1999; Fuhlendorf et al. 2006; Wilgers and Horne 2006; Churchwell et al. 2008; Kelly et al. 2010). As no one type of fire regime is optimal for all biota present in a landscape (Bradstock et al. 2005; Burrows 2008), maintaining a mosaic with a diversity of fire histories has been advocated to promote high biodiversity at the landscape scale through increased beta-diversity (Parr and Andersen 2006; Faivre et al. 2011). This approach to burning for biodiversity, however, remains a contentious issue due to a lack of empirical studies directly addressing the relationship between pyrodiversity and biodiversity at the landscape scale (Van Wilgen et al. 2004; Parr and Andersen 2006; Oliveras and Bell 2008; Edwards and Russell-Smith 2009; Driscoll et al. 2010).

## *Spatial influences of fire*

Fire affects landscape heterogeneity over a range of spatial and temporal scales (Bond and Keeley 2005; Bradstock 2008). At the local scale, species distribution and abundance across different spatial properties of the fire mosaic will be influenced by landscape context. Species perceive the landscape as a mosaic composed of different patch types with differing habitat quality and suitability.

For fire management to be effective, however, we need to better understand the relative roles of FRM properties at a scale that coincides with those over which land management regimes apply, such as protected areas or programs of landscape restoration. At this scale (1–100s km<sup>2</sup>), there is a need to consider the response of biota to a range of emergent landscape properties (Faivre et al. 2011). These properties include landscape composition and configuration (Dufour et al. 2009; Duflot et al. 2014). Fire-mediated landscape composition incorporates the diversity of seral stages or habitat types. A greater number of habitat types are expected to increase resource availability and species diversity, in particular, species turnover or beta diversity among the different habitat types (Tuomisto 2010). Spatial configuration can be measured by patch shape complexity, the distance between a burnt patch and an unburnt patch, or by the total length of edge (Radford et al. 2005; Duflot et al. 2014). Landscape configuration affects species dynamics by influencing such things as dispersal and competitive interactions (McGarigal and McComb 1995; Dufour et al. 2009; Duflot et al. 2014).

The PMB paradigm does not account for the extent of particular habitat elements in the landscape; rather, its focus is on the diversity of elements. Recent work however, has identified the extent of most suitable or preferred habitat in a landscape as an important determinant of species occurrence and richness (Bennett and Ford 1997; Radford et al. 2005; Kelly et al. 2012; Taylor et al. 2012). A high proportion of species-rich habitat in a landscape would be expected to support high average alpha or within-patch diversity (Wilson and Shmida, 1984). In a fire-prone landscape, species may require a particular post-fire seral stage; for birds for example, the presence of unburnt patches has been shown to support post-fire recolonization of recently-burnt patches (Watson et al. 2012; Robinson et al. 2014), whilst a higher diversity of reptiles in semi-arid Australia was found in mid-successional post-fire vegetation compared with early- or late-successional vegetation (Nimmo et al. 2013).

Under the PMB approach, pyrodiversity is expected to influence species diversity through increasing turnover or beta diversity (Farnsworth et al., 2014). However, much research to date has focused on local or alpha diversity response to a particular fire event or to particular fire regime attributes (e.g. Turner et al. 1997; Andersen et al. 1998; Benwell 1998; Tran and Wild 2000; Setterfield 2002; Kashian et al. 2004; Parr and Andersen 2006; Penman 2009).

At the landscape level, greater gamma diversity is related to spatial turnover in species composition, or beta diversity. Beta diversity is relatively seldom-studied in ecological literature, compared with alpha diversity (Harrison et al. 1992; Uys et al. 2004). Yet achieving high beta, and thus gamma, diversity is a core goal of PMB approaches. Uncertainty in ecologically-motivated fire management plans remains due to this dearth of empirical studies on the relationship between landscape diversity and the patterns or degree of fire-mediated habitat heterogeneity (e.g. Abbott and Loneragan 1983; Brooker and Rowley 1991; Friend 1999; Catling et al. 2001; Barlow et al. 2002; Bradstock and Cohn 2002; Russell et al. 2003; NPWS 2004; Parr and Andersen 2006; Pausas and Lloret 2007; Clarke 2008; Faivre et al. 2011; Taylor et al. 2012).

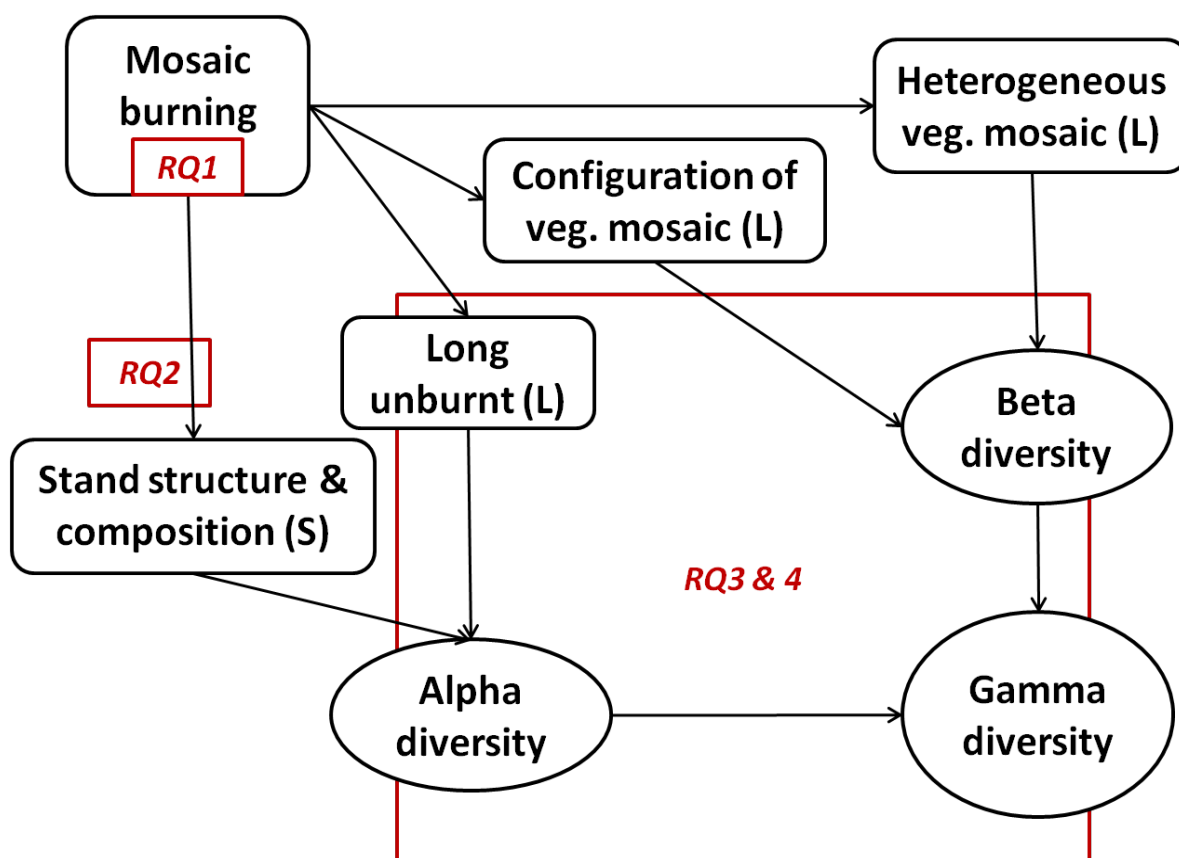
Whilst there is widespread support for the implementation of PMB to create a fire-mediated mosaic of habitats, empirical studies on the relationship between this heterogeneity and biodiversity are lacking (Parr and Andersen 2006; Faivre et al. 2011; Taylor *et al.* 2012). Many questions remain on the impact of the fire regime on the biota of landscapes, and what level of pyrodiversity achieves the best outcomes for biodiversity conservation (Parr and Andersen 2006).

## **1.2 THE PROBLEM**

Increasingly severe wildfires and altered fire regimes continue to threaten biodiversity in many regions globally. This has stimulated much research into the ecological impacts of fire and effective means of burning to maintain biodiversity. Much of this work has been carried out at the local scale, examining how alpha diversity responds to a fire event or particular fire regime attributes. Yet uncertainty remains regarding the landscape properties that maintain species rich assemblages at multiple spatial scales, including across landscapes. Controlled burning for biodiversity conservation thus remains a controversial topic as the particular spatial and temporal patterns of fire that maintain or threaten biodiversity are poorly understood.

### 1.3 THESIS AIMS AND OBJECTIVES

The overall aim of this thesis is to gain a better understanding of the relative effects of prescribed burning and other environmental factors on the structure and composition of floral and faunal communities at multiple spatial scales. To achieve this, the thesis examines the effect of accumulating fire scars on spatial patterning of vegetation structure and composition, and impacts of this pattern on woodland bird species assemblages, at the local- and landscape- scale within subtropical woodlands. This project links the different fire histories of sites (100 x 100 m) and landscapes (1000 x 1000 m) to conservation outcomes and explores the implications for nature conservation objectives in subtropical woodlands (Fig. 3).



**Figure 4** Potential drivers of bird species assemblages under a mosaic burning approach in subtropical woodlands. L = landscape property; S = site-level property; RQ= research question.

The specific research questions addressed in this thesis are:

1. What is the global evidence base for patch mosaic burning as a biodiversity management tool?

2. How does a variable fire regime influence stand structure and composition in subtropical woodlands?
3. What drives bird species richness in a fire-prone landscape: landscape heterogeneity or extent of habitat?
4. How do the spatial properties of the fire mosaic influence the composition of avifaunal assemblages at the local-level compared with the landscape level?

#### **1.4 THESIS APPROACH**

This thesis incorporates two key methodological elements. The first element involves quantifying fire regimes through a retrospective study of the fire history and investigating the influence of the fire regime on stand structure and composition. The second element applies a landscape ecology approach to gain a better understanding of the relationship among spatial properties of the fire regime mosaic, and bird assemblage structure and composition. Site- and landscape-level influences beyond those linked to fire were also investigated to gain a holistic understanding of the ecological drivers of bird assemblages within the study area.

#### **1.5 STRUCTURE OF THESIS**

This thesis consists of six chapters: an Introduction (this chapter) that introduces the background to the problem and aims and research questions, followed by four core chapters that address the aims and research questions listed above; and finally, a synthesis chapter that explores the key findings that emerged from the research described in the thesis and includes recommendations for ecological fire management in the study region. Chapters 2 to 5 are presented as a series of manuscripts, which have been published, submitted or assembled in preparation for submission to peer-reviewed journals. These chapters are presented according to the style required by the relevant journal. The core chapters therefore contain some repetition in their published and submitted forms, particularly in the description of the methods used.

The thesis chapters, in sequence, cover the following topics:

**Chapter 1:** *Introduction and background.* This chapter is a general introduction and overview of the problem, with the aims and research questions of the study.

**Chapter 2:** *Burning for biodiversity: a global review of mosaic burning research.* This systematic review delves further into the literature to investigate the evidence base for the ‘pyrodiversity begets biodiversity’ paradigm in fire ecology research. The gaps highlighted in this global review of mosaic burning research laid the foundations for the following three chapters of the thesis. This chapter has been prepared for submission to *The Rangeland Journal*.

**Chapter 3:** *The influence of a variable fire regime on woodland structure and composition.* In this chapter I introduce a method of characterising the fire regime mosaic based on unique combinations of season of fire, fire frequency and time since last burn; and investigate its influence on woody vegetation structure and composition. This laid the foundations for extracting spatial metrics of the fire regime mosaic which were investigated further in the following two chapters. This chapter is published in *The International Journal of Wildland Fire* (Burgess et al. 2014).

**Chapter 4:** *Landscape heterogeneity versus extent of habitat as determinants of bird species richness.* In Chapter 3, a variable fire regime was found to significantly influence woodland structure and composition. In this chapter, I investigate how this influences fauna assemblages. I evaluate the relative importance of landscape heterogeneity and extent of habitat as drivers of bird species richness at the intermediate or landscape scale (1 km<sup>2</sup>) in the context of a fire prone ecosystem. This chapter has been submitted to *PLoS ONE*.

**Chapter 5:** *Does the response of bird species richness to fire mosaic properties vary among spatial scales and foraging guilds.* While Chapter 4 explored the relative importance of different processes of habitat heterogeneity generation in driving species richness, this chapter compares the importance of the spatial properties of the fire mosaic on the composition of avifaunal assemblages measured at the landscape- and local-scale. This is to determine the scale at which birds respond most strongly to spatial properties of the fire regime mosaic. This chapter has been accepted for publication in *Landscape Ecology*.

**Chapter 6:** *Synthesis and conclusion.* In this final chapter I discuss how each of my four research questions was addressed and how the findings support or reject a range of hypotheses and concepts drawn from landscape ecology and conservation biology. I outline the importance of the findings for international and Australian approaches to ecological fire management. Finally, I discuss priorities for future research based on the findings of this work.



## **1.6 STUDY AREA – CARNARVON STATION RESERVE**

The study area is Carnarvon Station Reserve, a 59,000 ha conservation reserve located within the Carnarvon Ranges province of the Brigalow Belt Bioregion of Queensland. The Brigalow Belt Bioregion has previously experienced some of the highest rates of land clearing in Queensland, with more than 90% of previously forested land already cleared (Wilson et al. 2002; Bowen et al. 2009). The importance of protecting remaining tracts of remnant vegetation within the Brigalow Belt Bioregion was recognised by Bush Heritage Australia, a non-government conservation organisation, motivating them to purchase Carnarvon Station Reserve in 2001.

Prior to Bush Heritage ownership the key processes impacting the biota on Carnarvon Station were principally grazing of cattle (and, before that, sheep), clearing, dam construction, timber extraction, baiting of dingoes, introduction of exotic plant species, and cultivation (Bush Heritage Australia 2011a). The management of Carnarvon Station, principally for grazing purposes, motivated particular fire regimes in favour of others, because the amount and patterning of fuel was affected by grazing. The primary aim of Bush Heritage is to restore the condition, functioning and dynamics of the assemblages of species that would have been present on Carnarvon Station prior to its use as a cattle station (Bush Heritage Australia 2011a).

Fire is an important management tool on the reserve. To maintain representation of the different ecosystem types requires a fire management plan that considers the needs of each vegetation community. On Carnarvon Station, a mosaic burn approach has been implemented since 2001. This involves small-scale fires ignited throughout the year, usually during the late dry season (September – October) and early wet season (December-January). Timing is dependent on fuel loads, rainfall and temperature. The anticipated fire return interval is four to five years. The consequent fire scars from each burn season have been recorded and mapped in ArcGIS 10.

## CHAPTER 2

### BURNING FOR BIODIVERSITY: A REVIEW OF MOSAIC BURNING RESEARCH

TO BE SUBMITTED TO THE RANGELAND JOURNAL



**Plate 1:** Vegetation communities present on Carnarvon Station Reserve. The boundaries between the different vegetation communities are maintained by a combination of fire and underlying edaphic factors.

## 2.1 ABSTRACT

Contemporary ecological fire management resounds with the term ‘pyrodiversity’. A major goal of pyrodiversity is to increase gamma diversity through maintaining a mosaic of patches of different fire histories. With the widespread implementation of mosaic burning for ecological fire management, we ask, is there sufficient evidence to support this approach. We provide a global review of published literature on mosaic burning to examine whether (i) approaches are consistent among geographic regions; and (ii) reported fire-response of biota supports the ‘pyrodiversity begets biodiversity’ paradigm. The majority of studies originate from savanna and grassland biomes of Australia, South Africa and, more recently, the USA. Research on fire response of biota is focused on a limited number of taxa, in particular vascular plants and invertebrates. Further, despite the purported aim of mosaic burning being to increase spatial turnover, publications on fire response of biota continue to focus on the alpha diversity response to particular fire regime attributes. The dearth of investigation of the effects of heterogeneity on biota limits effective application of the mosaic burning approach. Studies that consider the spatial and temporal attributes of the fire regime mosaic, and investigate the interaction between these and multiple taxa across scales, are urgently required.

## 2.2 INTRODUCTION

In many fire-prone ecosystems globally, land managers manipulate the fire regime in attempts to mitigate wildfire and conserve biodiversity (Biggs and Potgeiter 1999; Clarke 2008; Faivre et al. 2011). Much controlled burning for the purpose of biodiversity conservation is informed by the ‘pyrodiversity begets biodiversity’ paradigm (Clarke 2008; Fuhlendorf and Engle 2001; Parr and Brockett 1999; Taylor et al. 2012). Pyrodiversity refers to the variation in the characteristics of the fire regime within a particular landscape (Parr and Andersen 2006). These characteristics include fire intensity, season, and frequency (Gill 1975).

Fire has been manipulated by people for many centuries (Hallam 1979; Kemp 1981; Kershaw et al. 2002; Singh et al. 1981). The cumulative ecological effects of natural and anthropogenic burning over many centuries, along with changes in climatic conditions, are now widely believed to have had a major influence on the evolution and patterning of fire-prone ecosystems (Bowman 1998; Pyne 1991; Singh et al. 1981). Evidence from traditional fire management suggests mosaic burning has a long history (e.g. Bowman 1998; Laris 2002; Yibarbuk et al. 2001). For example, traditional practice in the savanna of northern Australia involves the ignition of frequent, small fires throughout the year that result in a mosaic of patches of variable time since fire (Yibarbuk et al.

2001). Maintenance of biodiversity in fire-prone ecosystems will require fire management based on the principles of traditional landscape burning (Bowman 1998; Laris 2002; Yibarbuk et al. 2001).

The pyrodiversity paradigm holds that temporal and spatial heterogeneity in fire regimes will promote biological diversity (Bradstock et al. 1995; Edwards et al. 2001; Fuhlendorf and Engle 2001; Keith et al. 2002; Parr and Andersen 2006; Taylor et al. 2012) by ensuring species that require different fire regimes can coexist (see Thuiller et al. 2007; Tozer and Bradstock 2002). Approaches that promote pyrodiversity contrast with approaches employing prescribed burns with fixed fire intervals and season of burn (Bond and Archibald 2003), or a focus on minimum and maximum fire return intervals that promote variability but within pre-determined bounds (Burrows 2008; Clarke 2008; Van Wilgen et al. 2011). These approaches to fire management are assumed to reduce diversity in a landscape by homogenising vegetation structure and composition across large areas (Van Wilgen et al. 1994). Fire management strategies that aim to introduce spatial and temporal variation into the fire regime of a landscape are commonly referred to as mosaic burning or patch-mosaic burning (PMB) approaches (Mulqueeny et al. 2010; Parr and Andersen 2006; Parr and Brockett 1999; Pastro et al. 2011). These strategies aim to create mosaics with variable patches whose boundaries overlap through time.

Mosaic burning is achieved by varying the application of fires over successive fire seasons (i.e. the weather and fuel conditions under which fire is ignited) (Brockett et al. 2001). This in turn can influence fire extent, fire intensity, post-fire recovery of vegetation and fire return interval (Brockett et al. 2001). In addition to the temporal or physical attributes of fire, spatial factors, such as the size, shape, age and configuration of different fire-created patches will also influence species responses (Bradstock et al. 2005; Di Stefano et al. 2013; Driscoll et al. 2010).

Much research has focused on local-scale or alpha diversity response to a particular fire event or to particular fire regime attributes (e.g. Andersen et al. 1998; Benwell 1998; Kashian et al. 2004; Parr and Andersen 2006; Penman et al. 2011; Setterfield 2002; Tran and Wild 2000; Turner et al. 1997). Alpha diversity refers to the number of species per compositionally distinct sampling unit (Tuomisto 2010; Wilson and Shmida 1984). Pyrodiversity aims to create heterogeneity in a landscape through greater representation of different successional stages of vegetation. Fire-mediated heterogeneity is therefore expected to achieve greater beta diversity: differentiation in compositional diversity or species turnover among the different fire-mediated patches (Anderson et

al. 2011; Barton et al. 2013; Harrison et al. 1992; Uys et al. 2004). This in turn is expected to support greater regional diversity.

Recent concerns over altered fire regimes as a threat to biodiversity have increased interest in the effectiveness of ecologically-motivated fire management (Clarke 2008; Faivre et al. 2011; Langlands et al. 2012; Parr and Andersen 2006; Pryke and Samways 2012; Taylor et al. 2012). However, there has been limited critical analysis of the approach to, and ecological impacts of, mosaic burning (Driscoll et al. 2010; Edwards and Russell-Smith 2009; Langlands et al. 2012; Oliveras and Bell 2008; Van Wilgen et al. 2004). Despite this, the mosaic burning approach continues to be adopted in many fire-prone regions of the world including savanna ecosystems (e.g. Brockett et al. 2001; Saxon 1985); sub-tropical woodlands (e.g. James and Bulley 2004); and temperate forests (e.g. Burrows 2006).

In Parr and Andersen's (2006) review of PMB in tropical Australia and South Africa, the authors highlighted a gap in knowledge on the appropriate level of pyrodiversity to support biodiversity (e.g. Abbott and Loneragan 1983; Barlow et al. 2002; Bradstock and Cohn 2002; Brooker and Rowley 1991; Catling et al. 2001; Clarke 2008; Faivre et al. 2011; Friend 1999; Pausas and Lloret 2007; Russell et al. 2003; Taylor et al. 2012). Lack of clarity on the relationship between fire mosaic characteristics and biodiversity conservation renders implementation of mosaic burning problematic. In addition, effective implementation is hindered by inconsistencies in the definition of terms relating to the mosaic burning approach both within and across regions (Driscoll and Lindenmayer 2012; Parr and Andersen 2006; Pastro et al. 2011; Taylor et al. 2012). With increased interest in mosaic burning as an approach to ecological fire management, has a common methodology emerged to define and monitor pyrodiversity?

This paper aims to examine: (1) how the approaches and objectives of mosaic burning differ across the world; (2) how these approaches evolved; and (3) do these practices result in better biodiversity outcomes?

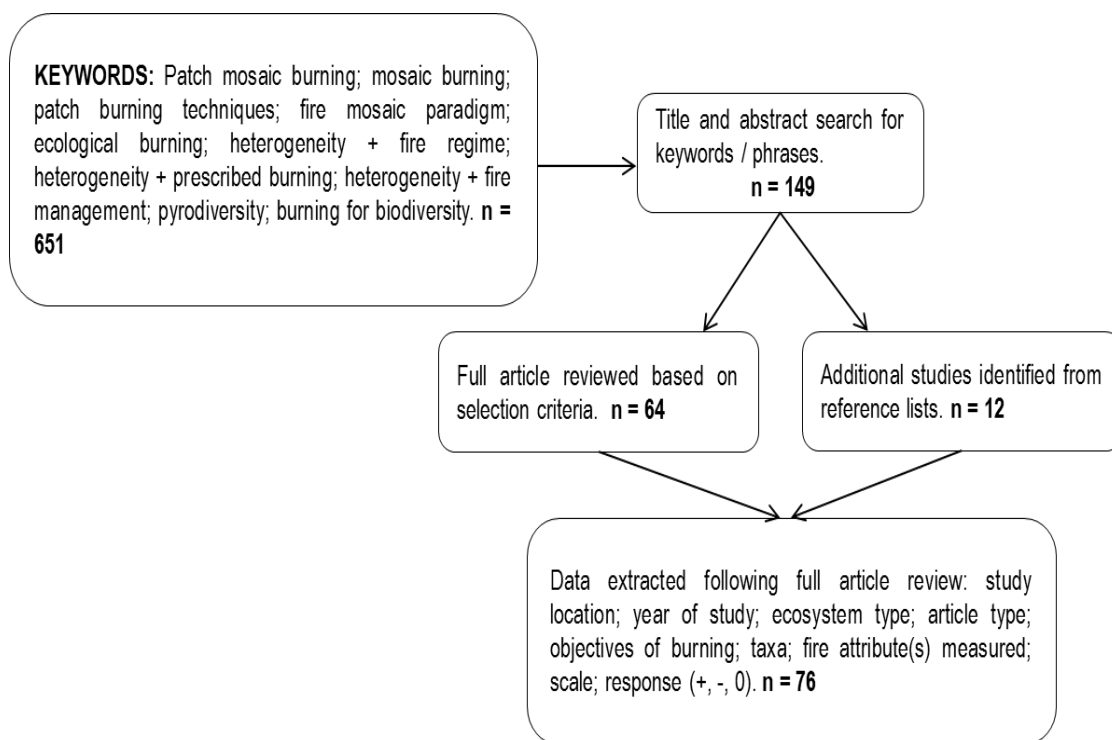
## **2.3 METHODS**

To extract information on the approach to and ecological impact of mosaic burning across geographic regions we undertook a detailed search of peer-reviewed literature. A variety of terms are used to refer to the mosaic burning or PMB method (Figure 5). These were entered into ISI Web of Knowledge, BioOne and Google Scholar during the 3<sup>rd</sup> - 5<sup>th</sup> April, 2012 and again on the 30<sup>th</sup>

October, 2012 to search for relevant scientific and technical literature. This produced a list of 651 publications, of which the title, keywords and abstract were examined to determine if they were relevant to the review (Figure 5). Publications were retained if they: defined the approach taken towards mosaic burning; documented plant or animal response to a mosaic burning regime; described the objectives for implementing mosaic burning; and/or compared the mosaic burning approach with other forms of fire management. Additional studies encountered during the examination of the reference lists of all relevant publications were also included.

For each of the 76 publications that met the selection criteria a variety of information was extracted and entered into a database (Figure 5). We summarised the proportion of studies originating from each of the major biogeographic regions (see Table 1). This was to allow comparison of geographical differences in (i) objectives; (ii) approach; (iii) fire regime attributes; (iv) focal biota; and (v) conclusions on mosaic burning. A common reason for excluding publications from the review was lack of clarity on the fire management methodology under investigation. Some papers focused on a variety of taxa or objectives; therefore, the number of studies ranges from 76 to 90.

The literature on mosaic burning is very heterogeneous in the approach to and methods of analysing fire response of biota. This limited our ability to extract comparable effect sizes to conduct a formal meta-analysis. We explored taxonomic and geographical bias using chi square tests in R version 2.15.2 (<http://www.r-project.org>).



**Figure 5** Flowchart detailing the preliminary steps of data access, exploration, and extraction for publications included in the systematic review.

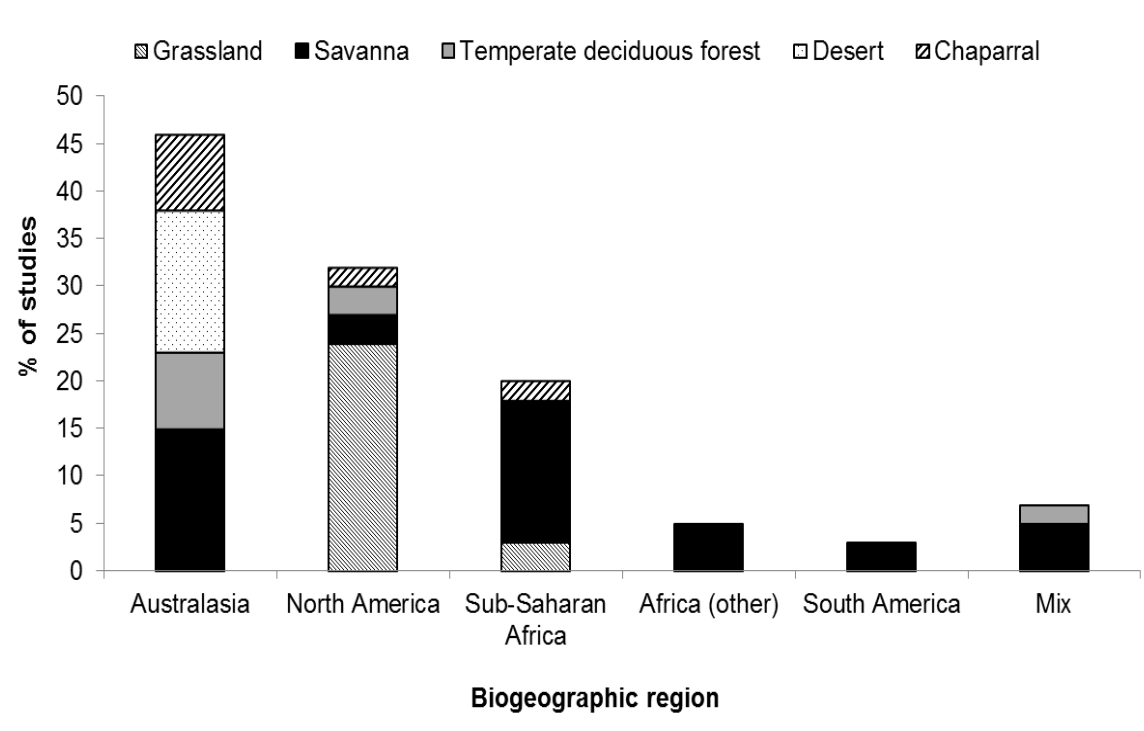
## 2.4 RESULTS

The studies included in this review were predominantly empirical in nature (71%). The remaining studies (29%) consisted of reviews of different fire management approaches.

### 2.4.1 Biogeographic focus and biome coverage

The vast majority of publications on mosaic burning (83.5%) have been since 2000. Most studies originate from Australia, followed by North America (mostly the USA) and Sub-Saharan Africa (mostly South Africa) (Figure 6).

Based on our review, the most studied biome is tropical savanna, followed by grassland (Figure 6). When assessed by biogeographic region, the majority of research in tropical savanna has originated from Australia and Sub-Saharan Africa, whereas in North America, there is a strong focus on the grassland biome (Figure 6). The biome in which studies were focussed varied among biogeographic regions ( $\chi^2 = 57.7$ ,  $p < 0.001$ ).



**Figure 6** Percentage of publications on mosaic burning by study location. Mix refers to publications that included results from more than one biogeographic region.

#### **2.4.2 Objectives of burning**

In ecosystem management, it is crucial to have clearly defined, measurable objectives at the outset in order to guide future activities (Du Toit et al. 2003; Parr and Chown 2003; Penman et al. 2011). The frequency of different stated objectives for mosaic burning differed among biogeographic regions ( $\chi^2 = 34.7$ ,  $p < 0.05$ ). Of the studies assessing the effects of fire, the most commonly cited objective for mosaic burning was biodiversity maintenance (43%) over all biogeographic regions (Table 1). The specific biodiversity outcomes sought were generally not defined in the publications reviewed. The publications that cited biodiversity maintenance as a key objective, only 35% described their desired outcomes.

After biodiversity conservation or management, mitigation of wildfires was the next most commonly-cited objective in all biogeographic regions with the exception of North America (Table 1). Despite mitigation of wildfire being a common objective of mosaic burning, only one study directly measured its effectiveness at achieving this (Boer et al. 2009).



In North America, habitat restoration was the second most commonly-cited objective, mostly in conjunction with biodiversity maintenance (e.g. Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006) (Table 1). Habitat restoration and maintenance for wildlife is expected to result from a landscape with a diversity of fire-age classes, as opposed to a homogeneous landscape (Fuhlendorf and Engle 2001). Other objectives reported include control of exotic species and to improve forage (Table 1) through a fire-grazing mosaic (Cummings et al. 2007). Animals preferentially graze recently burnt patches (Cummings et al. 2007). Therefore, a shifting mosaic of patches with different time since fire can be used to control selective grazing (Cummings et al. 2007).

**Table 1** Objectives of mosaic burning by biogeographic region (%). Number in parentheses is proportion of studies per biogeographic region.

<b>Objectives</b>	<b>Australia (40)</b>	<b>North America (25)</b>	<b>Sub- Saharan Africa (20)</b>	<b>Africa (other) (4)</b>	<b>South America (4)</b>	<b>Mix (7)</b>
Biodiversity conservation	19	16	6	0	2	4
Wildfire mitigation	11	3	3	3	1	0
Habitat restoration	0	10	2	0	0	0
Control of exotic species	1	2	0	2	0	0
Improve forage	2	1	0	2	1	0
Cultural (restoration of traditional burning techniques)	2	0	0	0	0	0
Protection of lives and property	1	1	0	0	0	0
Hunting	1	0	0	0	1	0

### ***2.4.3 Approaches to mosaic burning***

The original goals of mosaic burning remain the main motivation for current ecological fire management. Nevertheless, we found that the approach to mosaic burning varies both geographically and among biomes.

The mosaic burning approach in the grasslands of North America involves the application of fire to selected patches, typically on a 3-year rotation (e.g. Churchwell et al. 2008; Cook and Holt 2006; Doxon et al. 2011; Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006). The patches are fixed through time and form a portion of a larger pasture or landscape, of which managers aim to burn approximately 30% each year. The season of application varies between patches, with burns ignited either in spring or summer-autumn (e.g. Churchwell et al. 2008; Cook and Holt 2006; Doxon et al. 2011; Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006). Another layer of heterogeneity can be added through selective grazing of recently burned areas by large ungulates (see Cummings et al. 2007; Fuhlendorf and Engle 2001). Parallels can be drawn between the approach to mosaic burning reported for North America and the less flexible, block burning approach to prescribed fires (see Biggs and Potgieter 1999; Mulqueeny et al. 2010; Van Wilgen et al. 1998; Van Wilgen et al. 2004).

In Sub-Saharan Africa, in particular South Africa, mosaic burning is less precisely defined as compared with North America. Fire is ignited at random locations within pre-selected target areas. These are applied across seasons (winter and spring or early dry season to late dry season) and are allowed to burn out naturally (Biggs and Potgieter 1999; Brockett et al. 2001; Mentis and Bailey 1990; Mulqueeny et al. 2010; Van Wilgen 1998). Fuel loads are assessed annually in conjunction with rainfall predictions to determine the thresholds or upper and lower proportion of area to be burnt in a particular fire season (Biggs and Potgieter 1999; Brockett et al. 2001; Mulqueeny et al. 2010; Van Wilgen 1998). The proportion of area burnt is monitored on a monthly basis and compared to the pre-determined thresholds. Fires ignited early in the fire season tend to be smaller as they are applied under conditions that would not lead to extensive fires (e.g. Mulqueeny et al. 2010; Van Wilgen 1998; Van Wilgen et al. 2004). The fires applied later in the fire season are expected to burn out against these earlier burns, creating a fire regime mosaic of habitat burnt under different conditions in a given year (e.g. Mulqueeny et al. 2010; Van Wilgen 1998; Van Wilgen et al. 2004). Point ignitions are also thought to burn under a variety of intensities within a single fire as compared with other methods such as perimeter ignitions (see Mulqueeny et al. 2010; Van Wilgen et al. 2011).

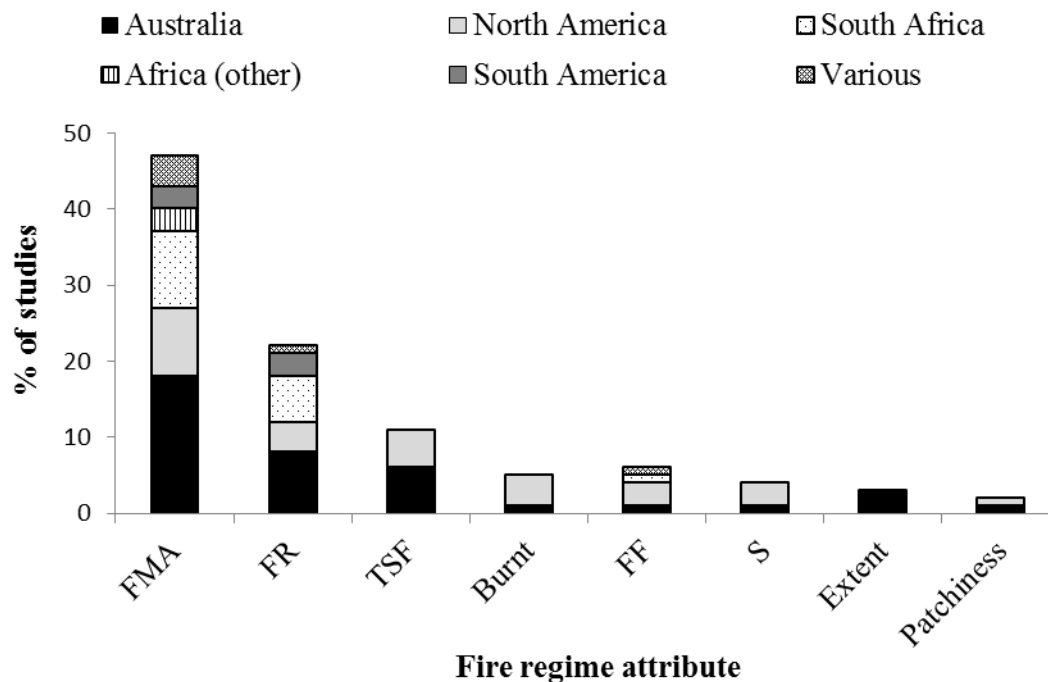
In Australia, particularly in the north, mosaic burning is broadly based on indigenous fire regimes (Bird et al. 2008; Whitehead et al. 2003; Yibarbuk et al. 2001). From the reviewed literature, the most common approach is the application of point ignitions throughout the fire season, at various times since last fire to create a mosaic of different seral stages, burnt under variable conditions (Saxon 1984; Taylor et al. 2012). This best describes the approach in savanna landscapes. In the temperate and arid landscapes of Australia, planned ignitions are generally avoided at the peak of the fire season when conditions are conducive to large fires. When determining target areas to apply fire not only is time since fire considered, but also fuel conditions, amount of precipitation received, and habitat type (Burrows 2006; Saxon 1984).

#### ***2.4.4 Recorded fire regime attributes***

The term ‘fire regime’ refers to the attributes of fire at a particular site over time (Gill 1975; Whelan 1995). The attributes of a fire regime include the fire frequency, time since the last fire, and the season in which the fire occurs (Gill 1975). Other attributes of fire that can influence the fire response of biota include fire extent (or patchiness), fire intensity (the heat produced) and type of fuel burnt (Gill 1981; Gill et al. 2002). There was no significant variation among biogeographic regions in the fire regime attributes recorded in publications on mosaic burning ( $\chi^2 = 22.4$ ,  $p > 0.05$ ). Time since fire and fire frequency were the most commonly investigated attributes of the fire regime across all publications (Figure 7) (e.g. Churchwell et al. 2008; Doxon et al. 2011; Fuhlendorf et al. 2006; Pastro et al. 2011). Time since fire was measured in years since last fire. Fire frequency was measured as the number of fires in a landscape over a defined period of time. Extent of burn, intensity and patchiness within a burn all contribute to maintaining heterogeneity in the fire regime mosaic but have seldom been measured (Figure 7). Several authors, however, did use season of burn as an indication of low and high intensities (e.g. Andersen et al. 2005; Davies et al. 2012; Parr et al. 2004).

Fewer than a quarter of the publications examined analysed the fire response of biota to a combination of fire regime attributes (22%) (Figure 7). Almost half of these (46%) looked at a combination of fire frequency, time since fire and season of burn (e.g. Andersen et al. 2005; Cook and Holt 2006; Davies et al. 2012). Those that included a combination of attributes tended to investigate their impact individually. Almost half (47%) (Figure 7) of all the publications examined compared the effectiveness of particular fire management approaches to achieve conservation outcomes e.g. patch mosaic burning, block burning, and annual burning (Biggs and Potgieter 1999;

Boer et al. 2009; Engle et al. 2008). This did not provide insights into what particular attribute and spatial pattern most influenced the response of biota.



**Figure 7** Percentage of papers investigating particular fire regime attributes by location of study. FMA: fire management approach e.g. patch mosaic burning, block burning. FR: fire regime, and refers to studies which investigate a particular combination of fire regime attributes. TSF: time since last fire. Burnt: studies comparing burnt/unburnt areas. FF: fire frequency. S: season of burn. Extent: size of burnt area. Patchiness: studies investigating the presence of unburnt areas within a fire perimeter. Fire regime: studies investigating a combination of fire regime attributes.

#### 2.4.5 Focal biota

The majority of publications investigating the fire response of biota measured the response of plants (58%) to mosaic burning as compared with animals (42%). Most studies of the response of animals to mosaic burning have been concerned with invertebrates (36%) (e.g. Cook and Holt 2006; Davies et al. 2012; Engle et al. 2008; Parr et al. 2004) and birds (27%) (e.g. Fuhlendorf et al. 2006; Powell 2006). Publications investigating invertebrates examined a limited number of taxa including ants (Parr et al. 2004), termites (Davies et al. 2012) and beetles (Cook and Holt 2006). Few studies focused on the response of large mammals to mosaic burning (5%), and none investigated the fire

response of amphibians. The remaining fauna studies were on small mammals (18%) and reptiles (14%). Most publications on animal response to fire were focused at the species (74%) level.

#### ***2.4.6 Response to mosaic burning***

From the publications included in the review, just over half (54%) reached a positive conclusion on mosaic burning as a method to either create heterogeneity in the fire regime mosaic (e.g. Brockett et al. 2001; Mulqueeney et al. 2010); as an approach to mitigate wildfires (e.g. Boer et al. 2009); or as a management technique to conserve biodiversity (e.g. Churchwell et al. 2008; Engle et al. 2008). Heterogeneity, for example, was measured in terms of the number of fires and the percentage area burned over a fire season (Brockett et al. 2001). Higher heterogeneity scores were therefore obtained when a greater number of smaller fires were ignited over a fire season (Brockett et al. 2001). It is important to note that a variable fire regime may well be promoted by mosaic burning, but this may have no effect on biodiversity, or even a negative effect. Wildfire mitigation, for example, was measured as the lowest incidence and extent of unplanned fires in relation to the annual extent of control burns (Boer et al. 2009). Biodiversity conservation measures were predominantly based on comparisons of species-richness and/or abundance among sites with different fire histories (e.g. Churchwell et al. 2008; Fuhlendorf et al. 2006; Vigilante and Bowman 2004). Whether mosaic burning was concluded to be favourable or unfavourable did not vary significantly among biogeographic regions ( $\chi^2 = 8.2$ ,  $p > 0.05$ ).

Almost a third of the publications assessed did not reach a conclusion on the value of mosaic burning, particularly in relation to biota. Commonly-cited reasons were the inconsistencies in fire response of biota at the community level, whereby some species increased whilst others decreased or were unaffected (Fuhlendorf et al. 2006; Kelly et al. 2010; Wilgers and Horne 2006), the need for larger- (temporal and spatial) scale studies, more replication, and more empirical studies on animal response to mosaic burning (Beckage et al. 2000; Bond and Archibald 2003; Bradstock et al. 2005; Faivre et al. 2011; Pastro et al. 2011). Of the publications reaching a positive conclusion, there was a tendency to extrapolate from the variable fire response of a small number of species or particular taxa (e.g. Doxon et al. 2011; Letnic 2003; Powell 2006). Only three studies directly measured the response of biota to fire-mediated heterogeneity at the whole-of-landscape scale (Kelly et al. 2012; Nimmo et al. 2013; Taylor et al. 2012). Each of these studies was located in the Mallee shrubland of south-eastern Australia and investigated the landscape-scale response of animals (birds, reptiles and small mammals) to a measure of the diversity of fire age-classes in the study landscape (Kelly et al. 2012; Nimmo et al. 2013; Taylor et al. 2012). Greater diversity of fire age-classes was found to

have a limited effect on landscape-scale animal species richness in all three studies (Kelly et al. 2012; Nimmo et al. 2013; Taylor et al. 2012). The proportion of longer-unburnt habitat had the greatest influence on species richness (Kelly et al. 2012; Nimmo et al. 2013; Taylor et al. 2012).

## **2.5 DISCUSSION**

We found that despite widespread acceptance of the ‘pyrodiversity begets biodiversity’ paradigm, the actual approaches to and objectives of mosaic burning vary widely. Publications on the fire response of biota to mosaic burning are highly skewed geographically, with the majority of studies from just three countries: Australia, USA and South Africa. Importantly, we found that one of the main goals of the paradigm—greater landscape-scale diversity—was only directly examined in three studies, all of which originated from Australia.

### ***2.5.1 Does the evidence support mosaic burning for biodiversity?***

From the publications reviewed, there are two aspects to pyrodiversity: diversity of patches with different fire histories, and sufficient representation of preferred fire-mediated patches. The most common strategies to achieve these goals are a reduction in fire patch size with an increase in number of ignitions. These ignitions are spread across the fire season, with a variable fire return interval. However, despite an increase in publications investigating the response of biota to mosaic burning, many questions remain around practical application of pyrodiversity for biodiversity conservation and maintenance of biotic diversity. There is evidence to suggest that variability in the fire regime supports coexistence of vascular plant species (Cary and Morrison 1995; Thuiller et al. 2007; Tozer and Bradstock 2002), small mammals (Masters 1993) and reptiles (Masters 1996). However, these studies have been mostly based on variable fire frequency, and there is a need to consider the response of biota to other attributes of the fire regime. Importantly, these conclusions are drawn from extrapolation of site-level responses of taxa, rather than examination of what mosaic of different fire-mediated patches best accommodates multiple taxa (Bradstock et al. 2005; Di Stefano et al. 2013).

The majority of studies examined focussed on the response of biota to temporal pyrodiversity, for example, comparing biota at sites with different fire histories, reflecting diversity in fire histories over time at local scales (Fuhlendorf et al. 2006; Masters 1993; Masters 1996). In contrast, studies directly investigating response to spatial pyrodiversity – sampling a larger area comprising patches of different fire histories, to reflect diversity in fire histories over space – were less common (Kelly

et al. 2012; Nimmo et al. 2013; Taylor et al. 2012). Whilst the patch mosaic burning approach incorporates heterogeneity over both time and space, the latter is likely to be more closely aligned with the aims of managers, in terms of maintaining pyrodiversity within their reserves at a given point in time (Saxon 1984; James and Bulley 2004).

The few studies that did investigate landscape-scale responses found the proportion of a preferred fire age class in a landscape, not pyrodiversity, had the greatest influence on species richness (Kelly et al. 2012; Taylor et al. 2012) and on occurrence of individual species (Nimmo et al. 2013). This raises the question of representation of suitable habitat, in addition to diversity of habitat types. To determine the success of the mosaic burning approach for biodiversity maintenance there is a need to evaluate whether promoting pyrodiversity will result in a sufficient representation of a preferred fire-age class.

Only one study to date has assessed methods of determining the optimal mix of fire histories for maintaining multispecies diversity (see Di Stefano et al. 2013). Di Stefano et al. (2013) measured the abundance of vegetation age classes as a metric of fire mosaics (operational objective) and the geometric mean of species from several taxa (conservation outcome) to determine the age class distribution that maximises diversity (Di Stefano et al. 2013). Whilst their method provides a means of predicting the optimal mix of fire histories, it does not assess if pyrodiversity as a management approach can promote sufficient representation of a preferred fire age class. The authors highlight that other factors need to be considered in addition to optimal fire histories, such as finances and resources available, impact on human life and property, and the spatial attributes such as extent and configuration of fire age classes that influence species persistence in a landscape (Di Stefano et al. 2013).

### ***2.5.2 Geographic and taxonomic bias***

There is a strong geographical bias in the studies we located, with most originating from Australia, USA and South Africa. This could be due to several factors. Firstly, Australia and South Africa contain some of the most fire-prone ecosystems globally, and have a long history of fire management (Pyne 1991; Saxon 1984; Van Wilgen et al. 1994). The mosaic burning approach originated in Australia and South Africa, where non-indigenous management of fire for conservation outcomes has been most actively implemented over the last 30 years (Brockett et al. 2001; Parr and Andersen 2006; Parr and Brockett 1999; Saxon 1984). In North America, research on mosaic burning has only emerged during the last decade (e.g. Engle et al. 2008; Fuhlendorf and

Engle 2001; Fuhlendorf et al. 2006; Powell 2006). This could reflect the continued practice of active fire suppression as opposed to the purposeful application of fire for ecological outcomes in many biomes of North America (Keeley et al. 2009; Pyne 1991). Inconsistencies in the approach to, and objectives of, mosaic burning by geographic region hinder the ability to draw general conclusions about the benefits of the approach.

Increased interest in mosaic burning for biodiversity has stimulated a recent increase in publications measuring response of fauna to burning, although a larger proportion overall have measured the response of plants. This is consistent with the broader literature on fire ecology in which the responses of animals are often inferred from the fire response of plants (Clarke 2008; Driscoll and Henderson 2008; Driscoll et al. 2010; Parr and Andersen 2006; Penman et al. 2011).

Studies of the fire response of animals have been focused on a limited cross-section of taxa. Most work has been on invertebrates, for example, mostly ants, termites and beetles. The fire response of terrestrial vertebrates remains poorly understood, despite their frequent use as targets of conservation (e.g. Assunção-Albuquerque et al. 2012; Loyola et al. 2009; White et al. 1997). As highlighted by Pryke and Samways (2012a, 2012b), the impacts of burning on fire-sensitive taxa might not be represented accurately by the fire response of more tolerant taxa, such as ants. To conserve biodiversity in fire-prone environments there is a need for more multi-taxon studies to assist land managers predict both the direct and indirect impacts mosaic burning may have on different components of the biota (Di Stefano et al. 2013; Pastro et al. 2011).

### ***2.5.3 The way forward***

The planning and implementation of mosaic burning continues to be hindered by (i) insufficient data to predict the response of focal biota to the mosaic, particularly at the gamma and beta diversity level; and (ii) a lack of clarity on how to quantify and define an appropriate level of fire diversity e.g. spatial as well as temporal heterogeneity (Bradstock et al. 2005; Faivre et al. 2011, Parr and Anderson 2006; Uys et al. 2004).

We know that variation in fire age classes can maintain alpha diversity by supporting coexistence of different species. Evidence also suggests that pyrodiversity increases heterogeneity and can mitigate the risk of wildfires. However, in order to advance the science of ecologically-motivated fire management there remains a need for well-designed, replicable studies that consider the interaction



among biota, particularly animals, the fire regime mosaic across multiple scales and other environmental factors, in particular long-term climate data (Bradstock et al. 2005; Kelly et al. 2012; Parr and Andersen 2006). These studies should not only consider pyrodiversity in terms of the number of fire-mediated patches but also the proportional representation and configuration of different patches. The outcomes of these studies need to be translated into practical, on-ground actions under a framework of adaptive management with well-defined objectives. Information housed in grey literature also needs to be made more readily available and methods on the approach to and goals of mosaic burning clearly articulated.

## CHAPTER 3

### THE INFLUENCE OF A VARIABLE FIRE REGIME ON WOODLAND STRUCTURE AND COMPOSITION

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**Plate 2:** *Petalostigma pubescens* resprouting after fire on Carnarvon Station Reserve.

### 3.1 ABSTRACT

The post-fire response of vegetation reflects not only a single fire event but is the result of cumulative effects of previous fires in the landscape. For effective ecological fire management there is a need to better understand the relationship between different fire regimes and vegetation structure. The study investigated how different fire regimes affect stand structure and composition in subtropical eucalypt woodlands of central Queensland. We found that fire history category (i.e. specific combinations of time since fire, fire frequency and season of last burn) strongly influenced richness and abundance of species categorised as mid-storey trees and those individuals currently in the mid-level strata. Time since fire and fire frequency appeared to have the strongest influence. A longer time since fire (> 4 years since last burn), combined with infrequent fires (< 2 fires in 12 year period) appeared to promote a dense mid-storey with the opposite conditions (< 4 years since last burn; > 2 fires in 12 year period) promoting more-open woodlands. Consideration of these combined fire regime attributes will allow fire managers to plan for a particular range of fire-mediated patches to maintain the desired diversity of vegetation structures.

### 3.2 INTRODUCTION

Fire regimes and fuel loads are altered by factors such as livestock grazing, introduction of exotic species, cessation of traditional burning practices, and other human activities in many parts of the world (Bowman and Prior 2004; Dombeck et al. 2004). This alteration of fire regimes is recognised as a threatening process for many species and communities (e.g. Russell-Smith and Bowman 1992; Bowman and Panton 1993; Bradstock et al. 1995; Woinarski and Recher 1997; Bowman et al. 2013). Further compounding the threat of altered fire regimes is the uncertainty imposed by future climate change, with an increase in fire frequency, fire severity and fire extent predicted to occur in many parts of the world (Flannigan *et al.* 2005; Kasischke and Turetsky 2006; Hennessy et al. 2007; Williams et al. 2009).

The post-fire response of vegetation reflects not only a single fire event but is the result of cumulative effects of previous fires in the landscape, along with other biotic and abiotic factors (Bradstock et al. 2005). Therefore, it is not just the attributes of the last fire event (time since last fire, intensity, post-fire climatic conditions: the visible mosaic), but also the frequency of or intervals between previous fires, the intensity of those fires, and the season in which the fires were ignited (invisible mosaic) (Bradstock et al. 2005) that can influence vegetation structure and species composition. This invisible mosaic (history of fires with different intensity, season, frequency, extent etc.) at a particular point in the landscape is not immediately evident from the ground.

The term 'fire regime' refers to the combination of fire characteristics at a site over time (Gill 1975). Thus, the mosaic of patches with varying fire histories in a landscape could be referred to as the fire regime mosaic. Examination of the response of biota to particular fire events often focuses on the mosaic defined by the most recent burn (Bradstock et al. 2005). Few studies to date have considered the influence of combined attributes of the fire regime on biota. This limits our ability to answer questions on the appropriate fire regimes for conservation (Watson and Wardell-Johnson 2004; Bradstock et al. 2005).

The diversity and abundance of fauna populations is often profoundly affected by habitat structural variables. For example, bird species diversity and abundance have been shown to respond to the configuration of different vegetation layers, and availability of nesting sites and food resources (McArthur and McArthur 1961; Baker 1997; Woinarski and Recher 1997; Zhang et al. 2013); ground dwelling and arboreal mammals to availability of shelter and food resources (Sutherland and Dickman 1999; Banks et al. 2011; Arthur et al. 2012); and spider assemblages to vertical habitat complexity (Hemm and Höfer 2012). Different fire regimes will impact vegetation structure in different ways. At the local level, species may be suited to a particular fire regime or the vegetation structure and composition created (e.g. Higgins et al. 2007). At the landscape level, diversity may require a range of vegetation types to meet their resource requirements. Configuration of these habitat variables within the landscape will also influence fire response of fauna (Bradstock et al. 2005). Whilst there has been much research into the relationship between habitat structure and fauna, there remains a gap in understanding on the response of vegetation to spatial and temporal aspects of the fire mosaic. If we aim to implement fire management regimes that support species co-existence, there is a need to better understand the relationship between different fire regimes and vegetation structure (Spencer and Baxter 2006).

We employ 12 years of fire history data to expand consideration of the fire regime mosaic and its influence on vegetation structure. We aim to investigate how different combinations of time since fire, fire frequency, and season of last burn affect stand structure and composition. In particular, we examine (1) how plants belonging to different plant life history categories are influenced; and (2) which life history categories contribute to the differences in vegetation structure and composition among different fire regime categories.

### 3.3 METHODS

#### 3.3.1 Study area

The study was conducted in the private owned Carnarvon Station Reserve (59 000 ha), Carnarvon Ranges, Queensland, Australia. The region is located in the sub-humid to semi-arid zone (Cummings and Hardy, 2000). Average winter temperatures range from 3° to 22° and summer temperatures from 18° to 34°, with average annual rainfall of 500–750 mm (Bailey 1984; Bureau of Meteorology 2013). There is large variation in rainfall in response to both the El Niño Southern Oscillation (ENSO) (Risbey et al. 2003) and the Pacific Decadal Oscillation (PDO) cycle (Crimp and Day, 2003). ENSO operates on a sub-decadal scale (3 to 7 year cycles) and results in drier conditions during El Niño events (Risbey et al. 2003; Hill et al. 2009). La Niña periods observe a strengthening in the southeast trade winds bringing higher rainfall (Risbey et al. 2003; Hill et al. 2009). There are two PDO phases, with the ‘warm’ period associated with below average rainfall and the ‘cool’ mode linked to above average precipitation (Mantua and Hare 2002; McGowan et al. 2009). The bimodal nature of the rainfall regimes at the decadal scale can significantly influence fire regimes (Bush Heritage Australia 2013b).

The reserve is characterised by rugged sandstone hills, narrow valley floors and high (> 1000 m) escarpments (Bush Heritage 2013a). Open eucalypt woodland is the dominant vegetation type on the reserve, and is ecologically important in the Brigalow Belt Bioregion in which the study area is located. This vegetation type includes ecosystems dominated by poplar box (*Eucalyptus populnea*), silver-leaved ironbark (*E. melanophloia*), and mountain coolibah (*E. orgadophila*) (Sattler and Williams 1999). The wetter basalt slopes support now rare vegetation types such as vine thickets, brigalow (*Acacia harpophylla*) and belah (*Casuarina cristata*) woodland. Other distinctive vegetation types include Queensland bluegrass grasslands (*Dicanthium sericeum*) on basalt soils, white cypress pine (*Callitris glaucophylla*) and smooth-barked apple (*Angophora leiocarpa*) woodlands on the sandy plateaus (Bush Heritage 2013b).

Fire is an important management tool on the reserve. A mosaic burn approach has been implemented since 2001. This involves small-scale fires ignited throughout the year, with timing dependent on fuel loads, rainfall and temperature. The planned fire return interval in the grassy eucalypt woodlands is four to five years. The prescribed burning is intended to mitigate the spread of extensive, homogenising fires. The managers aim to create and maintain a diversity of vegetation structures across the reserve (Bush Heritage 2013b). This variation in vegetation structure is

expected to support a higher diversity of fauna, particularly birds (Law and Dickman 1998; Howes and Maron 2009).

### **3.3.2 Survey design**

To make the invisible fire mosaic visible, the first step was to re-classify the fire regime mosaic based on a combination of fire regime attributes (Table 2). The spatial fire history of the reserve was mapped from a combination of Landsat MSS satellite imagery and ground truthing by managers. The spatial and temporal variation in fire history was classified into fire history categories (FHCs) based on frequency, season of burn and time since last fire. These fire regime attributes were deemed most important for influencing vegetation structure and composition based on review of literature (e.g. Mentis and Bailey 1990; Bradstock et al. 1997; Vigilante and Bowman 2004; Bradstock et al. 2005).

Season is assumed to provide a measure of intensity, with more intense fires expected later in the dry season as compared with early dry season fires (Parr et al. 2004; Andersen et al. 2005; Govender et al. 2006; Radford et al. 2012). Early dry season relates to fires ignited during February to June. Late dry season relates to fires ignited during July to October. As few fires occurred outside of these dates it was decided to combine any outliers into one of the two categories: fires occurring during November to December were classed as late dry season, and fires occurring in January were classed as early dry season. Fire frequency was based on the number of times burnt since 2001, using the classification: infrequent = 1-2; frequent =  $\geq 3$  (Whelan 1995). Time since last burn was classified as recent if it occurred  $\leq 4$  years; not recent if  $> 4$  years; unburnt if  $> 10$  years i.e. last burn was pre-2001 (Table 2). The polygons resulting from the intersection of these three spatial datasets represented the fire regime mosaic for the study area.

The study area was then overlaid with a grid composed of 1 km<sup>2</sup> cells using ET GeoWizards 10.1 software (ET Spatial Techniques) in ESRI ArcGIS 10. The 1 km<sup>2</sup> cells are referred to as landscapes. Twenty-eight of these landscapes were selected as study landscapes to sample the range of FHCs represented in the study area Table 1. Landscapes were selected to ensure each had  $> 60\%$  cover of open eucalypt woodlands according to the Regional Ecosystem (RE) mapping (DEHP 2012). The number of FHCs present within each landscape varied from 2 to 7.

**Table 2** Attributes selected to categorise the fire regime mosaic of Carnarvon Station Reserve for study landscape selection. The first letter in the abbreviation refers to the season (early or late). The second letter refers to the fire frequency (frequent or infrequent). The last letter refers to the time since last fire (recent or old). UB = unburnt since at least 2001.

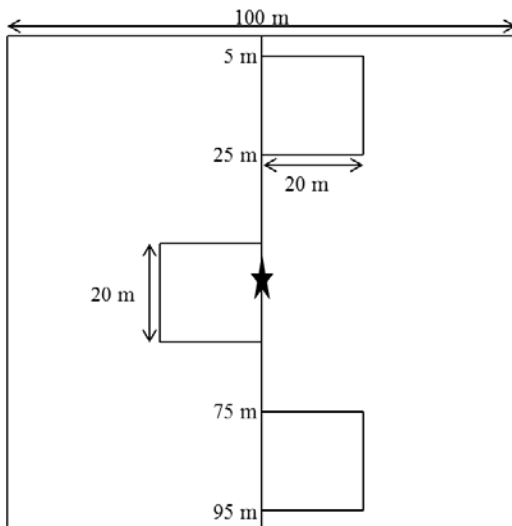
<b>Fire History</b>		<b>Category description</b>	
<b>Category</b>	<b>Season</b>	<b>Fire frequency</b>	<b>Time Since Last Burn (y)</b>
<b>(no. sites)</b>			
UB (10)	-	0	> 10
EIR (8)	Early Dry Season	Infrequent	≤ 4
LIR (7)	Late Dry Season	Infrequent	≤ 4
EIO (8)	Early Dry Season	Infrequent	> 4
LIO (7)	Late Dry Season	Infrequent	> 4
EFR (6)	Early Dry Season	Frequent	≤ 4
LFR (4)	Late Dry Season	Frequent	≤ 4
EFO (0)	Early Dry Season	Frequent	> 4
LFO (0)	Late Dry Season	Frequent	> 4

### 3.3.3 Study sites and vegetation data

Three 1 ha (100 x 100 m) sites were selected within each 1 km<sup>2</sup> study landscape, in approximate proportion to the representation of each FHC within that landscape, for a total of 84 sites. Thirty-four of the 1 ha sites were burnt by either prescribed burns in June 2012 or a wildfire that occurred during Jan – Feb 2013, and so were excluded from further consideration, leaving 50 sites from 18 landscapes.

Detailed vegetation surveys were conducted in three sub-plots (20 x 20 m) which were systematically located within each 1 ha site (Figure 8). We identified all woody plant species (using Carnarvon Station Reserve field herbarium where necessary) and counted the number of stems within each stratum for each sub-plot. Four strata, based on plant height were selected: understorey 0 – 1 m; shrub 1 – 2 m; mid-storey 2 – 6 m; and canopy > 6 m (modified from Spencer and Baxter 2006). Within each sub-plot, a single observer estimated plant height and all stems of each individual woody plant were counted and grouped according to the stratum within which they

occurred. Trees (> 6 m) that bifurcated at or below breast height were recorded as separate individuals. Saplings and shrubs were recorded as individuals if no physical connection was observed near the soil surface. This categorisation reflected the current structure of the vegetation in each site. Each site was sampled twice and the abundance of each species was averaged across the two sampling periods. Sampling was conducted in Sept – Oct 2012 and Feb – Mar 2013.



**Figure 8** Diagram of 1 ha site displaying systematic location of each 400 m<sup>2</sup> sub-plot. The star indicates the central point of the site at which a permanent pole was placed. The GPS location of the pole was recorded for relocation.

### 3.3.4 Response variables

The sub-plot count data for each species and height class were averaged for each 1 ha site (sum totals from each sub-plot / no. of sub-plots sampled). Total species richness for each site was aggregated across the three sub-plots. In addition to the four height classes, species were divided into three life-history categories: canopy trees (maximum height exceeding 6 m), mid-storey trees (maximum height less than 6 m), and shrubs/ sub-shrubs (species rarely exceeding 2 m, some with only a minor woody component) (PlantNET 2013; Vigilante and Bowman 2004). This categorisation reflected the potential structure of the site if all plants were to grow to maturity. A total of 58% of species were confidently assigned to one of two fire response groups based on their dominant fire response as reported in the literature: resprouter (have the ability to resprout after fire), seeder (regenerate from seed following fire or non-sprouters) (Land Manager 2011). The remaining 40% of woody plant species could not be assigned to a fire response group due to a lack



of definitive information in the published literature. The relative abundance and species richness within each life-history category and fire response group were calculated for each site. Evenness (Pielou's) was also calculated for each woody vegetation category.

### 3.3.5 Explanatory variables

Local environmental variables were averaged across each site and are detailed in Table 3. The dominant geology type was used for each site. Geology was derived from an ArcGIS map (Geoscience Australia 2013). Vegetation type was derived from the regional ecosystem map (DEHP 2012) and ground-truthed to represent the dominant canopy species. FHCs are likely confounded by vegetation type and geology as these cannot be fully controlled in a natural experiment. To control for this as far as possible, the study was limited to the four dominant eucalypt ecosystem types (Table 3), and sites were also selected to achieve replication of each FHC across each habitat and geology type.

**Table 3** Description of the explanatory variables for each study site (100 x 100 m).

<b>Factors</b>	<b>Categories</b>
Geology	pebbly quartz sandstone
	basaltic flows
	alluvium
FHC	Nine categories based on a combination of season of last burn, time since last fire and fire frequency (Table 1).
Vegetation type	Ironbark woodland
	Poplar box woodland
	Mountain Coolibah woodland
	Mixed eucalypt Woodland

### 3.3.6 *Statistical analysis*

A preliminary analysis using two-tailed Student t-tests revealed the average number of stems per site and the total plant species richness per site were not significantly different between the two sampling periods. The cumulative species richness was calculated and the number of stems was averaged across the two sampling periods for each site.

#### *Vegetation structure*

Preliminary graphical exploration of the relationship between response and predictor variables was carried out and Spearman's rank correlation was applied to test for collinearity between predictor variables. Only predictor variables that were not highly correlated (correlation coefficient  $< 0.5$ ) were included in final models. We modelled the relationship between the response and predictor variables using Type II analysis of variance (ANOVA) (Langsrud 2003) in the R statistical environment using the package 'car' (R Core Development Team 2012). To account for the variation due to the sites being nested within landscapes, landscape was included as a random factor. Abundance and richness data were fourth-root transformed prior to analysis to reduce the weighting of more abundant species while not losing information on relative abundance (Scogings et al. 2012). Post-hoc analyses using Tukey's honestly significant difference (HSD) test were done where ANOVA results were significant.

#### *Species composition*

Multivariate data analyses were employed to examine variation in the community composition of woody vegetation among FHCs, geology type and vegetation type. Floristic data were ordinated using non-metric multi-dimensional scaling (NMDS) based on the Bray-Curtis similarity matrix and the dimensionality of the result explored. We used nonparametric, permutational multivariate analysis of variance PERMANOVA (Anderson 2001) to test for differences among groups. Due to the unbalanced nature of the data we used type II PERMANOVA (Anderson et al. 2008). The analysis was based on Bray-Curtis dissimilarity measures from fourth-root transformed abundances to reduce the weight of common species. The test statistic for PERMANOVA is the pseudo F-ratio, where a large pseudo F-ratio indicates that sites in different FHCs, geology and/or vegetation types differed in woody vegetation community composition in multivariate space. Additional pairwise PERMANOVA tests were performed to explore the extent of differences in species composition

among FHCs, geology and vegetation types (Anderson *et al.* 2008). When we found significant differences in the composition of woody vegetation we also performed the similarity percentage (SIMPER) routine. This identifies the percentage contribution each species made to the dissimilarity between sites of different FHCs, geology and vegetation type (Clarke and Warwick 2001). Permutational analysis of multivariate dispersions (PERMDISP) was performed to compare multivariate dispersion among FHC, geology and vegetation type groups (Anderson *et al.* 2006). Pairwise tests followed significant results. Analyses were conducted using the PERMANOVA+ add-on package for PRIMER v6 (Anderson *et al.* 2008).

### 3.4 RESULTS

One hundred and seventeen native plant taxa were recorded across the 50 sites. Thirteen species were present in at least 30% of all sites surveyed, the majority of which are canopy species and classed as resprouters (Table 4).

**Table 4** Species that were present in at least 30% of the 50 sites included in analyses.

Species	No. of sites in which present	Functional group	Fire response
<i>Macrozamia moorei</i>	39	Mid-Storey	Resprouter
<i>Eucalyptus melanophloia</i>	36	Canopy	Resprouter
<i>Brachychiton populneus</i>	30	Canopy	Resprouter
<i>Jasminum simplicifolium</i>	30	Shrub / Vine	Resprouter
<i>Eucalyptus orgadophila</i>	21	Canopy	-
<i>Pittosporum spinescens</i>	21	Mid-Storey	-
<i>Corymbia erythrophloia</i>	18	Canopy	Resprouter
<i>Grewia latifolia</i>	17	Shrub/ sub-shrub	Resprouter
<i>Notelaea microcarpa</i>	16	Canopy	Resprouter
<i>Callitris glaucophylla</i>	16	Canopy	Seeder
<i>Solanum semiarmatum</i>	16	Mid-Storey	-
<i>Acacia leiocalyx</i>	15	Canopy	Resprouter
<i>Acacia muelleriana</i>	15	Mid-Storey	-

### ***3.4.1 Vegetation structure and life history categories***

A significant response to FHC was detected for the mean abundance of stems and total species richness (Table 5). The mean abundance and richness of species in the height classes 1–2 m and 2–6 m (Table 5), and those categorised as mid-storey trees and seeders (Table 6) were significantly different across FHCs. Evenness of species in the height classes 1–2 m and > 6 m (Table 5), and those categorised as mid-storey and canopy trees (Table 6) responded significantly to FHC. Post-hoc Tukey HSD tests revealed significant pairwise differences between sites with a fire history of less frequent fires, with a long time since last fire (UB, EIO and LIO) and those burnt frequently, with a short time since last fire (EFR, LFR and LIR) (all  $p < 0.05$ ) (Table 5 and 6). Sites with a fire history characterised by infrequent fire and last burnt in the early dry season had greater species evenness (Fig. 9b). The mean abundance and species richness in the height class > 6 m (Table 5), and those categorised as shrubs and resprouters (Table 6) did not respond to FHC.

A significant interaction between FHC and geology was detected for total species richness, species richness in the 0–1 m height class (Table 5) and species richness of mid-storey trees (Table 6). Sites of pebbly quartz sandstone with a fire history of less frequent fires, burnt in the early or late dry season and generally with a longer time since last burn had a higher abundance of stems and number of species (Fig. 9a and 9c). The mean abundance of shrubs was significantly influenced by interactions between FHC and vegetation type (Table 6).

Geology significantly influenced species richness across all life history categories except those categorised as shrubs (Table 6), and the species richness of the height classes 0–1 m and 2–6 m (Table 5). The mean abundance of species categorized as mid-storey trees and seeders (Table 6), and species evenness in the 0–1 m, 2–6 m and > 6m height classes was significantly different across geology types (Table 5). Vegetation type had a significant influence on the mean abundance of stems in the > 6 m height class (Table 5).

**Table 5** F-values and statistical significance ( $P < 0.05$  '\*',  $P < 0.01$  '\*\*',  $P < 0.001$  '\*\*\*') of ANOVA comparisons of abundance, species richness and evenness within vegetation structural groups among fire history categories (FHCs), geology type (geology) and vegetation type (vegetation). Significant factors are highlighted in bold. The greatest pair-wise differences from Tukey post-hoc tests for significant effects of FHC are presented in brackets. EFR = early frequent recent. LFR = late frequent recent. EIR = early infrequent recent. LIR = late infrequent recent. EIO = early infrequent old. LIO = late infrequent old. UB = long unburnt.

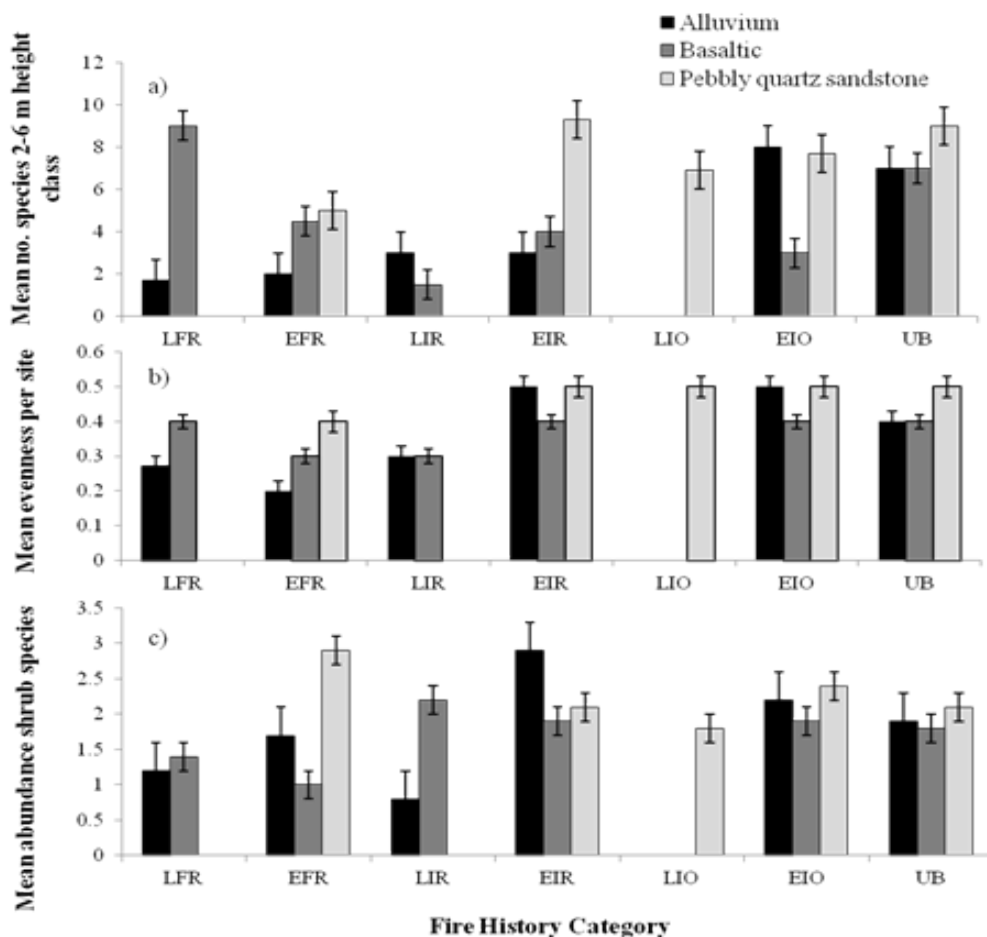
<i>Height class</i>	<i>FHC</i>	<i>Geology</i>	<i>Vegetation</i>	<i>FHC x Geology</i>	<i>FHC x Vegetation</i>	<i>Geology x Vegetation</i>
<i>Abundance</i>						
All categories	<b>8.5**</b> (UB > LFR)	3.3	0.4	1.7	3.5	1
0-1m	3.3	2	0.4	2	<b>5.4*</b>	3.6
1-2m	<b>5.4*</b> (EIO > LIR)	2	0.4	0.1	1.5	0.04
2-6m	<b>15.4***</b> (LIO > LIR)	3.7	0.1	2	1.1	1.1
>6m	0.5	0.9	<b>4.1*</b>	0.01	1.4	<b>6.2*</b>
<i>Species richness</i>						
Species richness	<b>9**</b> (UB > LFR)	<b>10.8**</b>	1.8	<b>4.2*</b>	1.7	1.9
0-1m	<b>7.8**</b> (LIO > LFR)	<b>19.4***</b>	0.3	<b>6.4*</b>	1	3.9
1-2m	<b>4.7*</b> (EIO > LIR)	2.7	0.01	0.8	1.9	0.3
2-6m	<b>6.7*</b> (UB > LIR)	<b>9.9**</b>	0.5	1.7	2	0.14

<i>Height class</i>	<i>FHC</i>	<i>Geology</i>	<i>Vegetation</i>	<i>FHC x Geology</i>	<i>FHC x Vegetation</i>	<i>Geology x Vegetation</i>
>6m	2.3	4	0.1	2.5	1.6	0.05
<i>Evenness</i>						
All categories	<b>11.6**</b> (EIO > EFR)	<b>6.2*</b>	0.04	1.6	2.8	1.6
0-1m	1.3	<b>5*</b>	0.7	2.1	0.4	0.5
1-2m	<b>7.2*</b> (EIO > LIR)	1.9	1.7	<b>5.6*</b>	0.2	1.5
2-6m	0.8	<b>10.9**</b>	0.5	1	0.2	2.4
>6m	<b>4.8*</b> (UB > EFR)	<b>9.3**</b>	3	<b>6.2*</b>	0.001	0.1

**Table 6** F-values and statistical significance ( $P < 0.05$  '\*',  $P < 0.01$  '\*\*',  $P < 0.001$  '\*\*\*') of ANOVA comparisons of mean abundance of stems, species richness and evenness within life history categories among fire history categories (FHC), geology type (geology) and vegetation type (vegetation). Significant factors are highlighted in bold. The greatest pair-wise differences from Tukey post-hoc tests for significant effects of FHC are presented in brackets. Shrubs = species rarely exceeding 2 m; mid-storey = tree species with maximum height  $< 6$  m; canopy = tree species with maximum height  $\geq 6$  m. EFR = early frequent recent. LFR = late frequent recent. EIR = early infrequent recent. LIR = late infrequent recent. EIO = early infrequent old. LIO = late infrequent old. UB = long unburnt.

<i>Veg. functional group</i>	<i>FHC</i>	<i>Geology</i>	<i>Vegetation</i>	<i>FHC x Geology</i>	<i>FHC x Vegetation</i>	<i>Geology x Vegetation</i>
<i>Abundance</i>						
Shrubs	2.7	0.1	1.4	1.2	<b>4.3*</b>	<b>4.3*</b>
Mid-storey	<b>23.6***</b> (UB > LFR)	<b>5.5*</b>	1	1.7	0.6	0.3
Canopy	2.4	0.2	3.8	1.4	0.4	0.7
Resprouter	2.8	1.9	0.05	2.8	2.2	0.03
Seeder	<b>7.1*</b> (LIO > EFR)	<b>9.8**</b>	0.5	2	3.8	0.1
<i>Species richness</i>						
Shrubs	2.8	2.6	1	0.8	<b>6.5*</b>	<b>5.8*</b>
Mid-storey	<b>7.6**</b> (UB > LFR)	<b>9.7**</b>	0.9	<b>6*</b>	0.02	0.6
Canopy	<b>5.5*</b> (UB > LFR)	<b>9.3**</b>	0.2	3.6	0.5	1.7
Resprouter	3	<b>6.9*</b>	<b>4.8*</b>	4.1	0.9	1.9
Seeder	1.3	<b>9.4**</b>	0.8	1.2	3	0.4
<i>Evenness</i>						
Shrubs	2.2	1.4	0.03	1	0.3	<b>7.3**</b>

<i>Veg. functional group</i>	<i>FHC</i>	<i>Geology</i>	<i>Vegetation</i>	<i>FHC x Geology</i>	<i>FHC x Vegetation</i>	<i>Geology x Vegetation</i>
Mid-storey	<b>4.5*</b> (LIO > LFR)	<b>17***</b>	1.3	<b>5.2*</b>	0.01	1.7
Canopy	<b>8.7**</b> (UB > EFR)	2.1	0.5	1	1	0.6



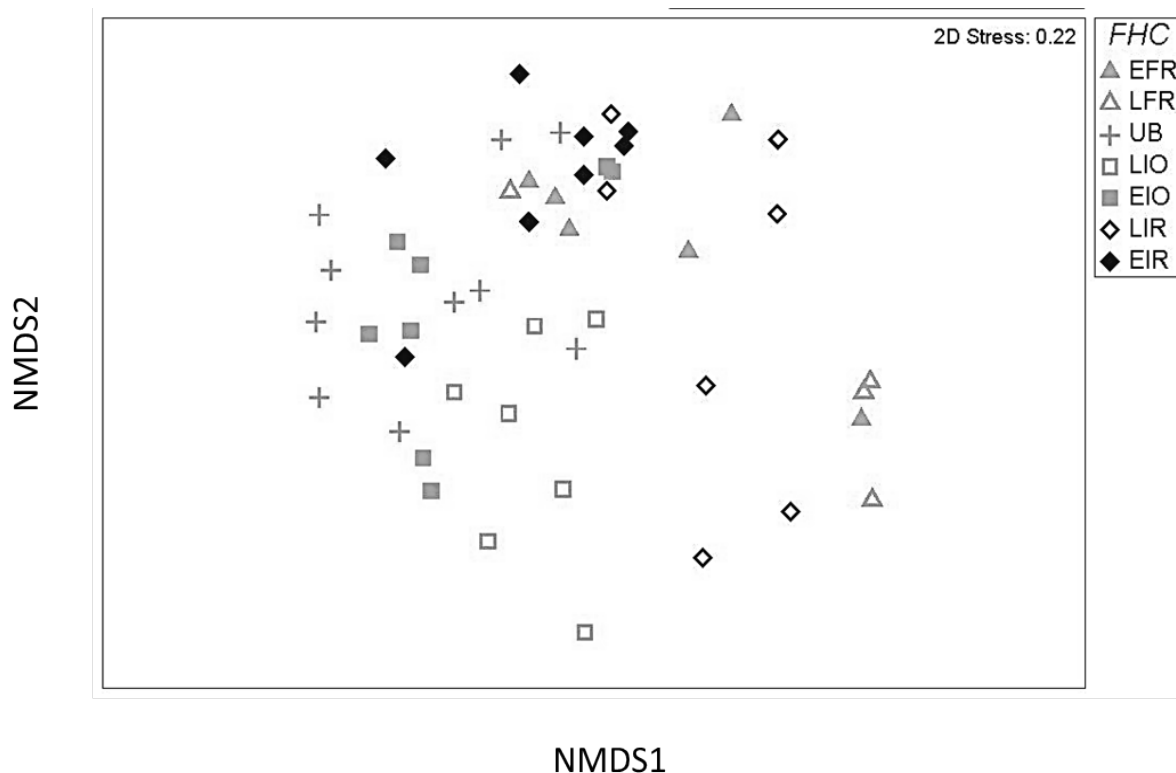
**Figure 9** Mean values for (a) species richness within height class 2-6 m; (b) evenness per site; and (c) abundance (fourth-root transformed) of shrub species for each geology type within each of the seven fire history categories. EFR = early frequent recent. LFR = late frequent recent. EIR = early infrequent recent. LIR = late infrequent recent. EIO = early infrequent old. LIO = late infrequent old. UB = long unburnt.



### 3.4.2 Species composition

Floristic composition of native, live woody vegetation (all height categories) displayed clustering of sites within the same FHC, and among sites characterised by similar FHCs (Fig. 10). Compositional differences among sites of different FHCs (PERMANOVA:  $F = 1.9$ ,  $P < 0.001$ ), geology type ( $F = 2.0$ ,  $P < 0.01$ ), and vegetation type (PERMANOVA:  $F = 2.2$ ,  $P < 0.0001$ ), were all significant. The PERMANOVA pairwise *a posteriori* comparison tests revealed the most pronounced separation among FHCs was observed between longer-unburnt sites and sites with a short time since fire ( $P < 0.05$ , Appendix 1). PERMDISP revealed no significant difference in multivariate dispersion among FHCs ( $F = 1.3$ ,  $P < 0.4$ ). The significant difference in community composition across sites of varying FHC from the PERMANOVA was thus due to differences in the location of sites in multivariate space rather than differences in dispersion around the mean composition within sites in the different FHCs. The greatest difference in community composition across geology types was between sites on alluvium and those on basaltic flows ( $P < 0.01$ , Appendix 1) and between sites on basaltic flows and pebbly quartz sandstone ( $P < 0.01$ , Appendix 1). PERMDISP analyses for the homogeneity of variances also showed significant differences in dispersion among geology types ( $F = 13.7$ ,  $P < 0.001$ ). For vegetation type PERMANOVA pairwise *a posteriori* comparison tests revealed the greatest difference in community composition was between sites dominated by mixed eucalypts and poplar box ( $P < 0.01$ , Appendix 1), and between poplar box and ironbark ( $P < 0.01$ , Appendix 1). PERMDISP analyses for the homogeneity of variances showed significant differences in dispersion among vegetation types ( $F = 4.4$ ,  $P < 0.05$ ). PERMANOVA did not reveal any significant differences in community composition due to interactions among FHC, geology and vegetation type ( $P > 0.05$ ).

SIMPER analyses identified *Acacia* species, in particular *A. muelleriana* and *A. leiocalyx*, as contributing to overall differences among sites of a recent time since fire and those with a longer time since fire, being more common in longer unburnt sites (Appendix 2). *Jasminum simplicifolium*, a rainforest associate, contributed to differences between sites of a recent time since fire and those with a longer time since fire, with a higher abundance in sites that were longer unburnt (Appendix 2). Those sites with a fire history characterised by frequent fires, and with a recent time since fire, tended to have a higher abundance of *Eucalyptus* and *Corymbia* species excepting *E. melanophloia* (Appendix 2).



**Figure 10** Sites positioned through a two-dimensional ordination space based on species composition data for all species, annotated by fire history category. EFR = early, frequent, recent. LFR = late, frequent, recent. EIR = early, infrequent, recent. LIR = late, infrequent, recent. EIO = early, infrequent, old. LIO = late, infrequent, old. UB = long unburnt

### 3.5 DISCUSSION

The fire regime (combinations of season, frequency and time since last fire) explained important differences in stand structure and composition of open eucalypt woodlands of Carnarvon Station Reserve. We found that FHC strongly influenced richness and abundance of species categorised as mid-storey trees and those individuals currently in the mid-level height classes 1-2 m and 2-6 m. Our study suggests successive fires, in particular fire return interval (combinations of frequency and time since last fire), have a strong influence on habitat structure and composition of sub-tropical woodlands. Simplification of woodland structure could result from fires that are too frequent, with a short time since last fire.

#### 3.5.1 Fire regimes and habitat structure

The FHCs defined in this study significantly influenced vegetation structure. Greater richness and abundance of stems in the 0-1 m, 1-2 m and 2-6 m height classes characterised patches of less

frequent fires, burnt in the early dry season, and with a longer time since last fire. This is consistent with previous studies in which less-frequently burnt or long-unburnt sites had a more complex structure and composition than sites burnt more frequently (Hoffman 1999; Williams et al. 1999; Woinarski et al. 2004; Radford et al. 2008; Lewis and Debuse 2012).

Individual plants currently in mid-storey strata responded most strongly to fire history, suggesting that the mid-storey may be particularly fire-sensitive. High fire frequency and/or high-intensity burns can prevent woody species from realising their height potential due to repeated scorching of their canopy and branches (Williams et al. 1999; Russell-Smith et al. 2003; Vigilante and Bowman 2004; Werner 2011). This can have population-level consequences. For example, a reduction in population growth of woody species was most strongly linked to the negative effect of frequent fires on individual plant size in the Brazilian Cerrado ecosystem (Hoffman 1999). Studies from the northern Australian savanna reported greater recruitment of stems into the mid-storey following periods of low fire frequency and/or intensity (Williams et al. 1999; Russell-Smith et al. 2003; Vigilante and Bowman 2004; Woinarski et al. 2004; Radford et al. 2008). Previous studies have demonstrated a positive relationship between a species' resilience to fire and plant height and age (Fensham and Fairfax 2006; Gignoux et al. 2009; Lewis and Debuse 2012). Low- to moderate-intensity and frequency of prescribed burns results in lower stem mortality and reduced scorching of foliage, and so plants do not have to restart shoot production from near the ground (Higgins et al. 2007).

Sites characterised by frequent burns, and a recent time since last fire (EFR, LFR, LIR), had fewer stems in the understorey and mid-layer strata belonging to fewer plant species. The simplification of habitat structure under a regime of frequent fire with a short fire return interval can have negative impacts for fauna (Catling 1991; Valentine and Schwarzkopf 2009; Valentine et al. 2012). For example, in this system, more structurally-open woodlands have been shown to support higher abundances of the colonial bird, the noisy miner (*Manorina melanocephala*) (Maron 2007; Maron and Kennedy 2007; Howes and Maron 2009; Kutt et al. 2012). The presence of this hyper-aggressive native bird depresses small passerine abundance and richness (Maron 2007; Maron and Kennedy 2007; Howes and Maron 2009; Kutt et al. 2012). Simplification of habitat structure associated with fire has also been implicated in altered trophic interactions among mammal fauna in savannas of northern Australia (Radford 2012). The combined effects of time since fire and fire frequency therefore both need to be considered when predicting fire response of both fauna and flora (Spencer and Baxter 2006).

### 3.5.2 Fire regimes and woody plant species composition

The composition of woodlands on the reserve varied among the different FHCs. Thus, to fully understand drivers of patterns in plant species composition we need to consider the fire regime mosaic (Cary and Morrison 1995; Bradstock et al. 2005). The fire response of plants is not only a response to the most recent fire event, but to the attributes of successive fires over time (Cary and Morrison 1995; Spencer and Baxter 2004; Gill et al. 2002; Bradstock et al. 2005). This underscored the need to consider the underlying or invisible characteristics of the fire regime, not just time since last fire (visible characteristic), over the long-term when developing ecological fire management guidelines (Cary and Morrison 1995; Spencer and Baxter 2004; Bradstock et al. 2005; Lewis and Debuse 2012).

The differences in composition among FHCs were driven largely by species classified as canopy and mid-storey trees. Mid-storey trees tended to have a greater abundance in sites with a fire history characterised by a longer time since last burn, burnt infrequently and in the early dry season. Season of burn can relate to intensity; fires in the early dry season are often of a lower intensity than those late in the dry season (Parr et al. 2004; Andersen et al. 2005; Radford 2012). Less-frequent fires allow sufficient time for mid-storey trees to reach reproductive maturity and for individuals to reach a sufficient height to avoid canopy scorch (Vigilante and Bowman 2004). One group of mid-storey trees that appear to exert an important influence on variation in assemblage structure among fire regimes, in particular time since fire, are *Acacia*. A thickening of some *Acacia* species in the mid-storey strata in sites burnt infrequently and with a longer time since last fire (> 4 years) was observed in the field. This supports the findings from an experimental fire study in savanna woodlands in north Queensland (see Radford et al. 2008).

Although the mix of canopy tree species varied among FHCs, the abundance of those categorised as canopy species and recorded in the > 6m height class did not. This may reflect the relatively greater resilience of canopy trees to prescribed burning, at least in the short term (Russell-Smith et al. 2003). The majority of canopy species on the reserve were classed as resprouters. The capacity to resprout following fire can reduce the likelihood of individual mortality (Noble and Slatyer 1980; Higgins et al. 2007; Allen 2008). However, our inability to assign 40% of plant species to a fire response group (resprouter or seeder) limited our ability to draw conclusions about the relative responses of these groups to fire management.

### ***3.5.3 Fire regimes and geology***

Vegetation patterns on Carnarvon Station are also strongly influenced by the major geology types in the region (Parker 1991), and the interaction between geology and fire history (Bowman et al. 1988; Vigilante and Bowman 2004; Spencer and Baxter 2006). The relationship among edaphic factors and fire history is complex, with fire history influencing soil properties, and edaphic factors potentially affecting fire behaviour through their effects on the type, configuration and amount of fuel (Vigilante and Bowman 2004). On Carnarvon Station, the relationship between abundance of woody plant species, species richness and geology differed across FHCs. Among sites with a history of infrequent fire with a longer time since last fire, abundance and richness tended to be higher when located on the less-fertile pebbly quartz sandstones. Conversely, sites with a fire history of frequent fire and a recent time since last fire have a higher abundance and richness of plant species when located on more-fertile basaltic flows. Vigilante and Bowman (2004) noted the greater frequency of fire on basalt substrate in northern Australia. The authors related this to the productivity of the grasslands found on nutrient-rich basaltic soils (Vigilante and Bowman 2004). Despite the potential confounding effects between fire history and geology, the effects of different FHCs on differences in woody species composition were still clear across geology types.

### ***3.5.4 Conservation and management implications***

Fire continues to be an important management tool in many fire-prone ecosystems. Prescribed burning has created a mosaic of patches with varying FHCs across the reserve. The mosaic of various FHCs produces important differences in stand structure and composition of open eucalypt woodland. This emphasizes the role of a variable fire regime in maintaining the diversity of vegetation types and structure across the landscape. Although plant species respond in different ways to fire history, generalisations about habitat structural responses, in particular the mid-storey, to specific fire regimes can be made.

At the landscape scale, a variable fire history will result in a mosaic of patches with varying vegetation structure and composition. Time since fire and fire frequency appeared to have the strongest influence on woody vegetation structure and composition. A longer time since fire (> 4 years since last burn), combined with infrequent fires (< 2 fires in a 12 year period), supported a dense mid-storey with the opposite regime (< 4 years since last burn; > 2 fires in a 12 year period) supporting open, eucalypt woodlands in central Queensland. Thus, rather than aiming for a single inter-fire interval, introducing spatial variation in multiple attributes of fire history is likely to assist

in maintaining a variety of vegetation and habitat structures. Consideration of these combined fire regime attributes will allow fire managers to plan for a mosaic of particular vegetation states that collectively will maintain habitat for a diversity of plant species that vary in their response to disturbance (Nieuwenhuis 1987; Roxburgh et al. 2004; Watson and Wardell-Johnson 2004; Thuiller et al. 2007).

Much research to date on ecological fire management has focussed on the fire-response of vascular plants (Clarke 2008). Relatively few studies, however, have considered the influence of multiple attributes of fire history on vegetation structure and composition. The results indicate that patches of less-frequently burnt vegetation with a long time since fire have a more complex vegetation structure. Habitat complexity is positively correlated with vertebrate and invertebrate fauna (e.g. Woinarski and Recher 1997; Arthur et al. 2012; Hemm and Höfer 2012; Zhang et al. 2013) though not all variations in vegetation structural elements associated with less frequent fire may be functional in terms of fauna assemblages (Parr and Anderson 2006; Radford et al. 2013). However, rather than aiming simply to maximise site-level vegetation complexity, the significant difference in plant species composition among FHCs indicates it may be appropriate to manage for a variety of fire regimes in relation to the specific management objectives.

## CHAPTER 4

### LANDSCAPE HETEROGENEITY VERSUS HABITAT EXTENT AS DETERMINANTS OF LANDSCAPE-LEVEL BIRD SPECIES RICHNESS

SUBMITTED TO PLoS ONE



**Plate 3:** Male and female red-winged parrots (*Aprosmictus erythropterus*) in a poplar box (*E. populnea*) woodland, Carnarvon Station Reserve.

## 4.1 ABSTRACT

Landscape heterogeneity and extent of habitat are each expected to contribute to species richness at intermediate- or landscape-scales (~1-100s km<sup>2</sup>) through elevating beta and mean alpha diversity, respectively. However, understanding of their relative importance, especially at scales at which land is often managed, is limited. We investigated the relative effects of different measures of landscape heterogeneity (describing variation in vegetation communities, elevation, and fire history), extent of preferred habitat (in this case, long-unburnt habitat favoured by small passerines) and landscape configuration on landscape-scale bird richness (in this case, 100 ha units), and its components: mean alpha (1-ha survey site) and beta diversity within landscapes in sub-tropical woodlands of central Queensland, Australia. We found observed species richness was most strongly associated (positively) with measures of landscape heterogeneity, particularly diversity of vegetation communities and range in elevation. However, fire-mediated heterogeneity and configuration were not important. Despite this, mean alpha diversity had a greater influence on landscape-scale bird species richness than did beta diversity. Surprisingly, landscape heterogeneity exerted more influence on landscape-level richness through increasing mean alpha diversity, rather than beta diversity, within landscapes. The observed richness of small passerines, a group of conservation concern, was also negatively associated with the mean abundance of noisy miners (*Manorina melanocephala*), a hyper-aggressive native species, and positively influenced by the extent of long-unburnt (preferred) habitat. Although conservation management strategies often aim to introduce heterogeneity to boost biodiversity, we found underlying variation (such as range in elevation) had much greater influence on species richness than manipulable factors such as fire-mediated heterogeneity. Heterogeneity acts to increase richness across landscapes not only through generating turnover, but also by increasing mean alpha diversity, at least for this mobile taxon.

## 4.2 INTRODUCTION

Drivers of species richness vary depending on the scale under consideration (Niemelä 1999). At small scales (m<sup>2</sup> to hectares), productivity is important (Huston 1994; Burel et al. 2004; Willig 2011), although the pattern and strength of this relationship is complex, being both species- and context- specific (Huston 1994; Willig 2011; Adler et al. 2011). At very large scales such as across regions, richness is driven not only by productivity, but also by compositional turnover, which in turn is related to both deterministic and stochastic processes (Tuomisto et al. 2003; Chase 2010). Deterministic processes driving regional richness include habitat heterogeneity and biogeography; stochastic processes can include ecological drift and dispersal limitations (Tuomisto et al. 2003; Chase 2010). Yet knowledge gaps remain on the relative importance of these different drivers of



species richness at intermediate or landscape scales—the scales at which management decisions are most often made (Heikkinen and Birks 1996; Niemelä 1999; Koivula 2001).

Determinants of species richness at such intermediate or landscape scales—defined here as one to hundreds of square kilometers (*sensu* Niemelä 1999; Koivula 2001)—have attracted increasing attention (Niemelä 1999; Koivula 2001; Estrada 2007). Although strictly, the ‘landscape’ from an ecological perspective is context and species-specific, such scales often coincide with units over which land management regimes apply, such as protected areas or programs of landscape restoration. These management regimes often aim to maximise the number of species the landscape can support (e.g. Elmes and Thomas 1992; Fuhlendorf and Engle 2001). It is therefore important to understand the relative roles of different landscape characteristics in determining landscape-scale species richness.

Intuitively, landscape-scale species richness ought to be related closely to landscape heterogeneity (Pickett and Cadenasso 1995; Pino et al. 2000; Weibull et al. 2000; Bennett et al. 2006; Dufour et al. 2006; Haslem and Bennett 2008). As landscape heterogeneity increases within a given area, the amount of between-habitat (beta) diversity of species within that area is likely to increase (Tews et al. 2004; Zhang et al. 2014). This is one common explanation for species-area relationships: as the area sampled increases, so does the number of different habitats (Williams 1964; McGuinness 1984; Boecklen 1986; Olszewski 2004). Recent work, however, has identified extent of a ‘preferred’ or more-suitable type of habitat to be of overriding importance in determining landscape-scale species richness: for example, woodland extent for woodland birds (Bennett and Ford 1997; Radford et al. 2005; Taylor et al. 2012); long-unburnt habitat for small mammals (Kelly et al. 2012); and mid-successional vegetation for certain reptile species (Nimmo et al. 2013). By definition, the mean alpha diversity (number of different species per site sampled) in landscapes with more preferred habitat is higher. A greater extent of the preferred habitat type will support more individuals, which through passive sampling will include more species (Osman 1977; Connor and McCoy 1979; McGuinness 1984; Maron et al. 2013; Zhang et al. 2014).

Here, we compare explicitly the relative importance of these two different processes of generation of landscape-scale species richness: landscape heterogeneity and extent of preferred habitat. We use woodland birds as our focal taxon in a region where spatial heterogeneity in habitat types—both composition and configuration—(Dufour et al. 2006; Tuomisto 2010; Dufort et al. 2014), and extent of preferred habitat are driven by multiple factors. These factors include disturbance history (fire),

vegetation community, and elevation (Howes and Maron 2009; Howes et al. 2010). Fire represents an important management tool in many regions. Two major objectives of ecological fire management are (1) to mitigate the spread of extensive, homogenising fires; and (2) to create and maintain a diversity of vegetation structures (Brockett et al. 2001; Parr and Andersen 2006; Burrows 2008). In this region, higher alpha diversity (i.e., measured in sites of 1- 2 ha) of bird species is associated with long-unburnt habitats with more-complex habitat structure. This pattern is, in turn, driven largely by the reduced suitability of such areas for the aggressive noisy miner (*Manorina melanocephala*) (Howes and Maron 2007; Howes et al. 2010; Maron and Kennedy 2007). Noisy miners are a major influence on bird assemblages across eastern Australia, as their presence markedly depresses the abundance and richness of other bird species (Major et al. 2001; Maron and Kennedy 2007; Kutt et al. 2012; Maron et al. 2013).

The principal aim of this research is to investigate the relationship between different spatial properties of landscapes (in this case, 100 ha units) and bird species richness of those landscapes. In particular, we examine the relative importance of heterogeneity in habitat types (based on both vegetation communities and fire history) and elevation, extent of preferred (long-unburnt) habitat and an index of landscape configuration on bird species richness in a relatively intact woodland system. If habitat heterogeneity is the primary driver of elevated species richness across landscapes, we expect that landscape-scale bird richness would be driven largely by species turnover among habitat elements within a landscape (beta diversity), whereas if the extent of preferred habitats within a landscape is more important, then we expect mean alpha diversity would contribute most to landscape-scale richness.

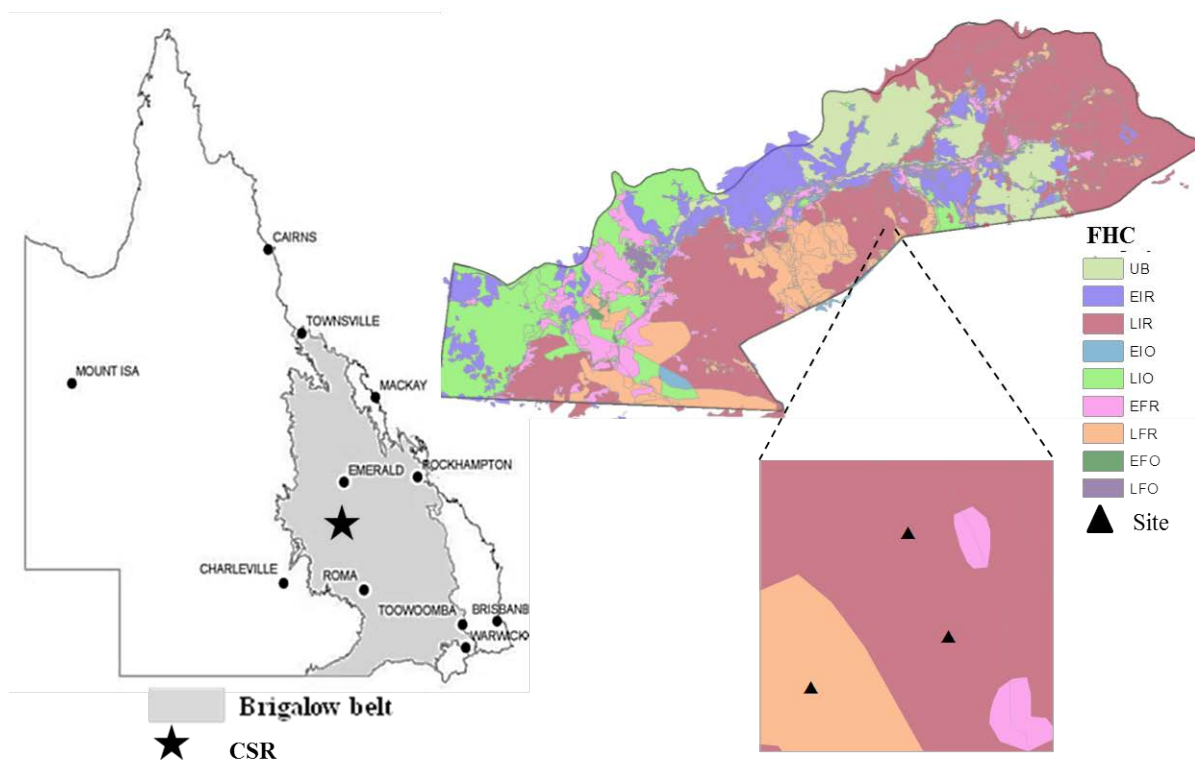
## **4.3 METHODS**

### ***4.3.1 Study area***

The study area covered a 59, 000 ha section of the Carnarvon Ranges (Carnarvon Station Reserve) in central Queensland, Australia (Fig. 11) where the climate is sub-humid to semi-arid (mean annual rainfall 500–750 mm, mean annual minimum and maximum temperatures are 3° and 34°) (Bailey 1984; Environment Australia 2000; Bureau of Meteorology 2013).

The reserve is characterised by rugged sandstone hills, narrow valley floors and high (> 1000 m) escarpments (Bush Heritage 2013). Open eucalypt woodland is the dominant vegetation type on the reserve, and is ecologically important in the Brigalow Belt Bioregion in which the study area is

located as habitat for threatened species (Ryan 2006; Richardson 2008). The vegetation structure of the eucalypt woodland varies from tall woodland in riparian zones to open woodland with a sparse mid-storey of shrubs and saplings and a grassy ground layer (QPWS 2013). The canopy height can range between 12 to 25 metres (QPWS 2013). This vegetation type includes several different ecological communities, dominated variously by poplar box (*Eucalyptus populnea*), silver-leaved ironbark (*E. melanophloia*), and mountain coolibah (*E. orgadophila*), (Sattler and Williams 1999). Planned burns in the open eucalypt woodland typically cover areas of ~100 ha and are implemented throughout the year, with timing dependent on fuel loads, rainfall and temperature (Bush Heritage 2013). The planned fire return interval in the grassy eucalypt woodlands is four to five years.



**Figure 11** Carnarvon Station Reserve in central Queensland, Australia. The enlarged detail shows a single study landscape containing 3 sites mapped by fire history category (FHC). UB = long unburnt; EIR = early, infrequent, recent; LIR = late, infrequent, recent; EIO = early, infrequent, old; LIO = late, infrequent, old; EFR = early, frequent, recent; LFR = late, frequent, recent.

#### 4.3.2 Study design

We selected landscape-scale sampling units (each 1 km<sup>2</sup>) based on mapping of vegetation types and fire history categories (hereafter, ‘FHC’; see Appendix 3 for description of fire history mapping). This extent was deemed suitable to encompass variation in landscape composition whilst allowing for sufficient replication (Haslem and Bennett 2008) as well as being an appropriate scale for fire management on the region. Twenty-eight study landscapes were selected in total to include a range of landscape compositions with respect to fire history, from uniform to highly heterogeneous (Fig. 11; Appendix 3). The number of fire history categories present within each landscape varied from two to seven (Fig. 1; Appendix 3), and the extent of long-unburnt habitat varied from 0 ha to 88 ha per study landscape. Long unburnt habitat is defined here as ‘preferred’ habitat for woodland birds; Howes and Maron (2009); and Howes et al. (2010) showed greater richness of woodland birds at survey sites in long-unburnt habitat in the same study area, and other work within the same bioregion has supported this finding (Maron and Kennedy 2007).

We used a systematic protocol to select three 1-ha (100 x 100 m) survey sites within each study landscape. A total of 84 sites were selected and located in FHCs in approximate proportion to the representation of each FHC within that landscape (Fig. 11). Each site was placed at least 250 m apart (mean = 478 m  $\pm$  210 m). Twelve of the sites were burnt by either prescribed burns in June 2012 or a wildfire that occurred during Jan – Feb 2013, and so landscapes in which these sites occurred were excluded from further consideration, leaving 72 sites from 24 landscapes.

#### **4.3.3 Bird species richness**

Bird surveys consisted of four 10 min counts following the active-timed search method (Loyn 1986) and were conducted by a single observer (EB). Surveys involved traversing the 100 m central line, recording all birds seen and heard during the sample period. Each site was surveyed during August (2012), September (2012) October (2012), and February–March (2013) (total survey effort per site = 40 mins). The bird surveys were conducted both in the morning (up to 4 hours after sunrise) and afternoon (3 hours prior to sunset) at each site. The sequence of site visitation was rotated between survey rounds such that each site was surveyed twice in the morning and twice in the afternoon. Surveys were carried out on days of fine weather (no strong wind or rain). Birds flying above the canopy were not included in analysis.

Bird survey data were pooled across all sites within each study landscape and bird species richness metrics for all bird species (observed richness) and small passerines were calculated. Small passerines were classified as those species whose body size is smaller than that of the noisy miner (< 27 cm head to tail length) and therefore most susceptible to interference competition from that species (Mac Nally et al. 2012). Observed species richness in a sample is generally lower than the actual species richness of an ecosystem (Hortal et al. 2006; Colwell 2013), and relative completeness of species inventories can be biased even when sample effort is equal (Watson 2010). We therefore also used the nonparametric species richness estimator Chao2 (predicted richness) to calculate estimated species richness for each study landscape. Nonparametric estimators attempt to estimate the true number of species based on abundance and/or incidence data in a given area based on observed values from multiple samples (Hortal et al. 2006; Colwell 2013). The calculation used the classic formula in the programme EstimateS 9.1.0 (Colwell, 2013).

We also calculated the mean site-level richness in a landscape (1-ha) as the total number of species per site averaged across all sites in that landscape; and the beta diversity (Sørensen index of

dissimilarity) of each landscape using the vegan package v.2.0-10 in R (R Core Development Team 2012).

#### ***4.3.4 Landscape variables***

Each study landscape was characterised by eight landscape variables (Table 7). Landscape heterogeneity was described by four variables: (i) the number of vegetation communities (regional ecosystems) present; (ii) the Shannon-Weaver diversity of vegetation communities; (iii) the Simpson diversity of fire histories; and (iv) range in elevation (m) (Table 7). Regional ecosystems are vegetation communities defined by their association with particular combinations of geology, landform and soil (Sattler and Williams 1999). Extent of habitat was described by two variables: (i) extent of long unburnt habitat (preferred habitat); and (ii) the mean abundance of noisy miners (Table 7), both factors known to relate to woodland bird richness at the site level. Landscape configuration was described by two variables: (i) total edge length of fire-mediated patches; and (ii) mean shape complexity of fire-mediated patches. We tested for collinearity among the explanatory variables using Spearman's correlation coefficient matrix (Zuur et al. 2009). Only uncorrelated explanatory variables (correlation coefficient < 0.5) were used in further analysis.

**Table 7** Summary of predictor variables used in analyses.

Variable	Abbreviation	Description
<i>Landscape heterogeneity</i>		
Diversity of fire histories †	DivFMP*	Diversity of fire histories using Simpson's diversity index, influenced by both richness (no. of different fire histories) and evenness (distribution of area among different fire histories).
Diversity of vegetation communities †	Veg*	Diversity of vegetation communities (defined by regional ecosystem mapping) based on both richness and evenness in a landscape using Shannon's diversity index.
Richness of vegetation communities	RichVeg	The raw number of different vegetation communities.
Range in elevation	ElvRange	The difference between the highest and lowest contour in landscape (m).
<i>Extent of habitat</i>		
Extent of unburnt	ExtUB	Area of long unburnt habitat per landscape, considered here as preferred habitat.
Abundance of noisy miners	AvgNM	The abundance of noisy miners was pooled across all sites within a landscape and across all surveys at each site, and the average calculated to give mean abundance of noisy miners per landscape.
<i>Landscape configuration</i>		
Total edge ( <i>area-edge</i> ) (m) †	Edge	Total length of edge of fire-mediated patches in each study landscape.
Patch-shape complexity †	Circle	Measure of fire-mediated patch shape complexity based on the ratio of patch area to the area of smallest circumscribing circle. This averaged for all fire-mediated patches within a landscape. Patches were clipped to the study landscape boundary. CIRCLE = 0 for intact circular patches;

as circle approaches 1 the patch becomes more irregular and elongated.

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† Calculated in FRAGSTATS

\* Based on proportional data

#### **4.3.5 Data analysis**

Preliminary graphical exploration of the relationship between each of the bird richness and the landscape predictor variables indicated some nonlinear responses. Univariate analyses using generalized linear models (GLMs) with untransformed and second-order polynomial terms were compared. Where the support for the polynomial model was notably higher than for the untransformed model ( $\Delta AIC > 2$ ) the polynomial term was retained (Burnham and Anderson 2002; Taylor et al. 2012).

We modelled the effect of six weakly correlated explanatory variables on three main response variables: total (observed) species richness, small passerine richness and Chao2 (predicted richness) for each landscape. The explanatory variables in these models included three measures of heterogeneity (the number of vegetation communities present, Simpson's diversity of fire histories, range in elevation), two measures of extent of preferred habitat (extent of long unburnt habitat and the mean abundance of noisy miners) and mean shape complexity of fire-mediated patches.

We modelled the relationship between these response and predictor variables using generalised linear models (GLMs) with a log-link function and a Poisson distribution (for total observed species richness and observed species richness of small passerines) using the lme4 package v.1.1-5 in R (R Core Development Team 2012). Each landscape represented a single sampling unit. All predictor variables were standardised to have a mean of zero and a standard deviation of 1 to allow direct comparisons of model parameter estimates (Quinn and Keough 2002). Exploratory analyses identified no clear nonlinear relationships therefore all explanatory variables were entered as linear fixed effects.

Based on analysis of model residuals, no evidence of over-dispersion was found for models of total observed species richness or richness of small passerines (following methods laid out in Zuur et al. 2009). Over dispersion was detected in the global model for Chao2 (estimated richness). To account for this we used a quasi-GLM that adds an over-dispersion parameter to all models (Quinn and



Keough 2002; Zuur et al. 2009). Applying model-selection processes such as an information theoretic approach requires full likelihood (Burnham and Anderson 2002; Nimmo et al. 2013) and cannot be applied when using penalised quasi-likelihood methods. For Chao2 (estimated richness) we used standardised effect sizes from the global model to assess the importance of each predictor variable (Gelman and Hill 2007). The predictor variables were considered to have a significant influence if the standard error of the variable's coefficient multiplied by 1.96 (i.e. 95% confidence interval) did not overlap zero (Gelman and Hill 2007; Nimmo et al. 2013).

We employed a model averaging approach to investigate the relative influence of the predictor variables on these response variables (Burnham and Anderson 2002). For each response, alternative models from all linear combinations of predictor variables and interactions were generated from the global model (Grueber et al. 2011). The models were ranked by their Akaike weights calculated from AICc values (Akaike's Information Criterion corrected for small sample size). A 95% confidence set of models was constructed by starting with the model with the highest Akaike weight and repeatedly adding the model with the next highest weight until the cumulative sum of weights exceeded 0.95 (Burnham and Anderson 2002). For each response variable, the model-averaged parameter estimates and the unconditional standard errors of each estimate were calculated across all models in the confidence set (Burnham and Anderson 2002). The relative importance of each explanatory variable was quantified by summing the Akaike weights for all models containing the variable (Burnham and Anderson 2002). We used the MuMIn package v1.9.5 in R (R Core Development Team, 2012) to conduct these analyses.

Model fit was assessed by calculating the deviance explained and plotting the residuals against the predicted values. Spline correlograms of the model residuals of full models for all response variables were constructed to test for spatial autocorrelation (Zuur et al. 2009) in the 'nfc' extension package v.1.1-4 for R (R Core Development Team, 2012). No effects of spatial autocorrelation were detected for response variables. Diagnostic plots of the residuals, and the residuals versus the fitted values of the global model, indicated the assumptions of normality, lack of bias and heterogeneity were met.

Finally, univariate linear regression was used to model separately the relationship between landscape-scale bird species richness (total observed species richness) and each of its components: mean alpha diversity (mean species richness per site) and beta diversity (Sørensen index of dissimilarity); as well as the effect of important explanatory variables from the models of

landscape-level richness (summed Akaike weight > 0.9) on mean alpha and beta diversity, using lme4 package v.1.1-5 in R (R Core Development Team 2012). We also used lme4 to quantify model fit ( $R^2$ ) for all regression models. The adjusted  $R^2$  is given. This is a modification of  $R^2$  that adjusts for the number of explanatory terms in a model.

## 4.4 RESULTS

A total of 83 species of bird were recorded during surveys across the 24 landscapes. Mean observed species richness per study landscape was 18.6 (range 8-31, SD = 7) compared to Chao2 richness of 29.4 (SD = 16). Mean richness of small passerines per study landscape was 4.4 (range 0–18, SD = 3.6).

There was some model uncertainty, with 3 to 4 models in the 95% confidence set (summed Akaike weights = 0.95) for the different responses. Model fit was generally good based on deviance values (Appendix 4).

### 4.4.1 Predictors of landscape-scale species richness

#### *Landscape heterogeneity*

Variables representing landscape heterogeneity were consistently included in the best models of total observed species richness (Appendix 4). Range in elevation had a high relative importance for total species richness, with study landscapes with a greater range in elevation supporting more species (Fig. 12a; Fig. 13a). These patterns were also evident in the best models for the species richness of small passerines (Appendix 4). The number of vegetation communities had a strong positive influence on the richness of small passerines and Chao2 richness (Appendix 5), with a high summed Akaike weight ( $\sum 0.99$ ) for the richness of small passerines (Fig. 12b). Range in elevation had a high relative importance for richness of small passerines (Fig. 12b). The diversity of fire histories had a weak, negative influence (Fig. 13d; Appendix 5) on all measures of species richness, with a low rank in summed Akaike weight (Fig. 12a and 12b).

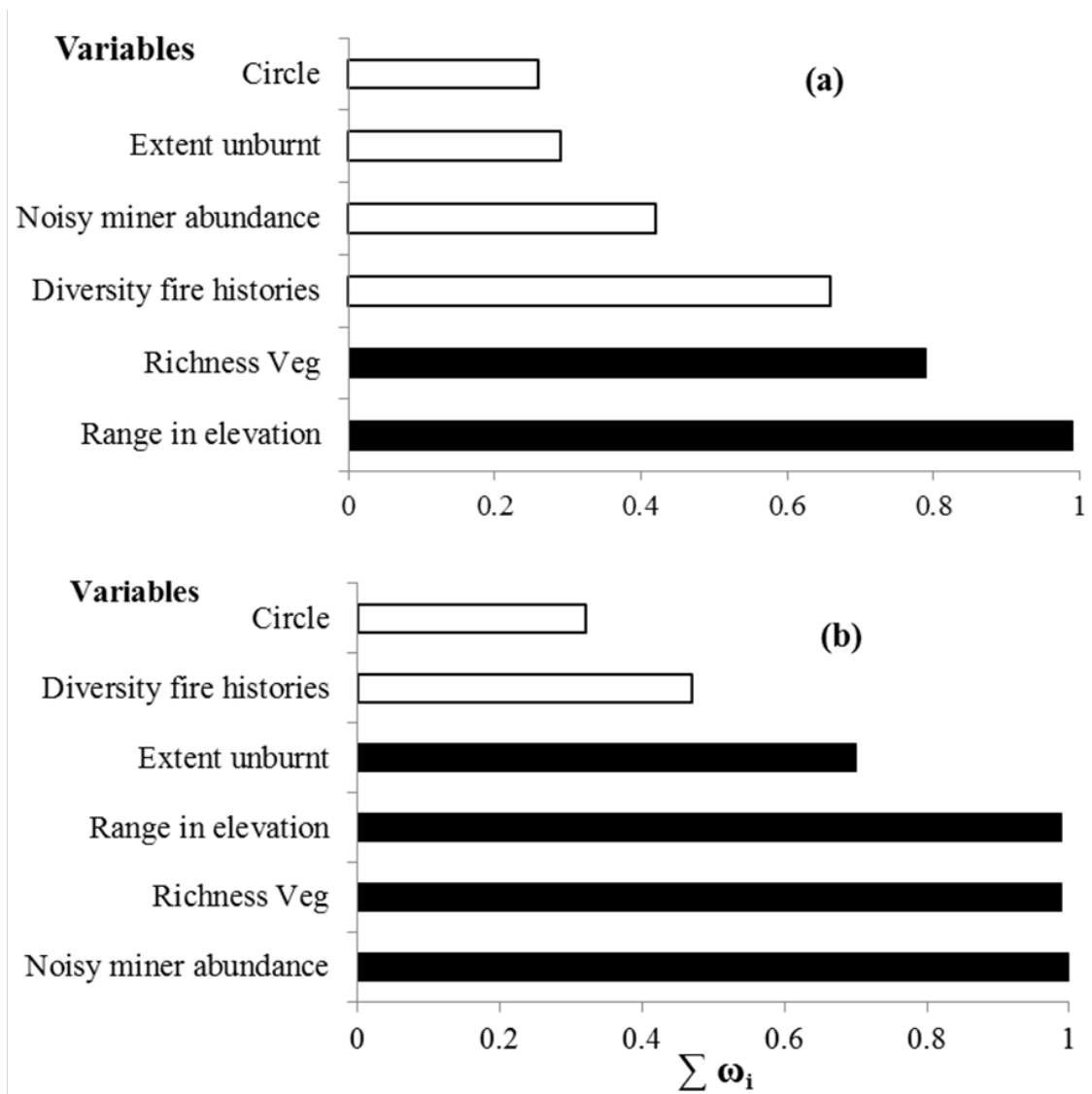
#### *Extent of habitat*

In contrast, the measures of extent of preferred habitat—extent of long-unburnt habitat and abundance of noisy miners—were consistently less important in explaining variation in the species

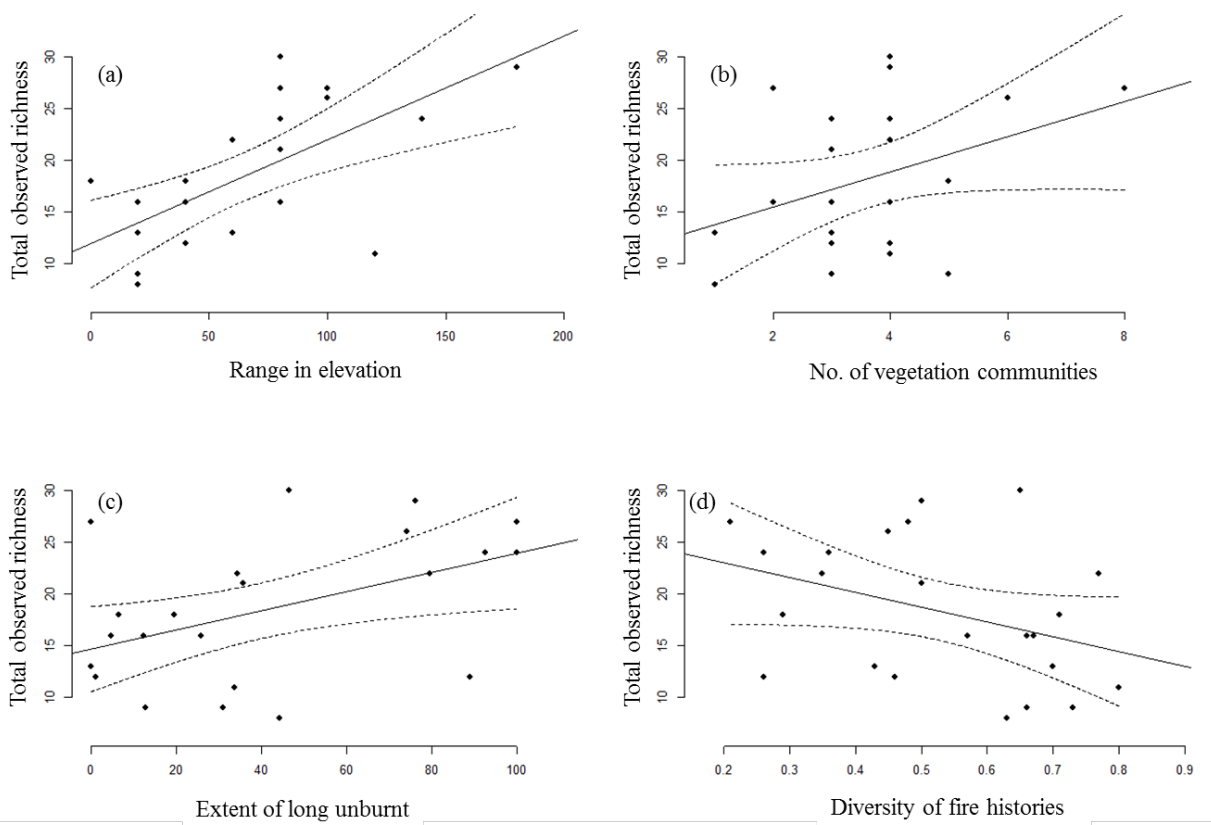
richness measures. However, for the richness of small passerines, there was a negative influence of noisy miners (Fig. 12b; Fig. 14a). The extent of unburnt habitat was included in three of the four best models for richness of small passerines (Appendix 4; Fig. 14b), although it had a low importance ranking based on summed Akaike weight (Fig. 12b).

### *Landscape configuration*

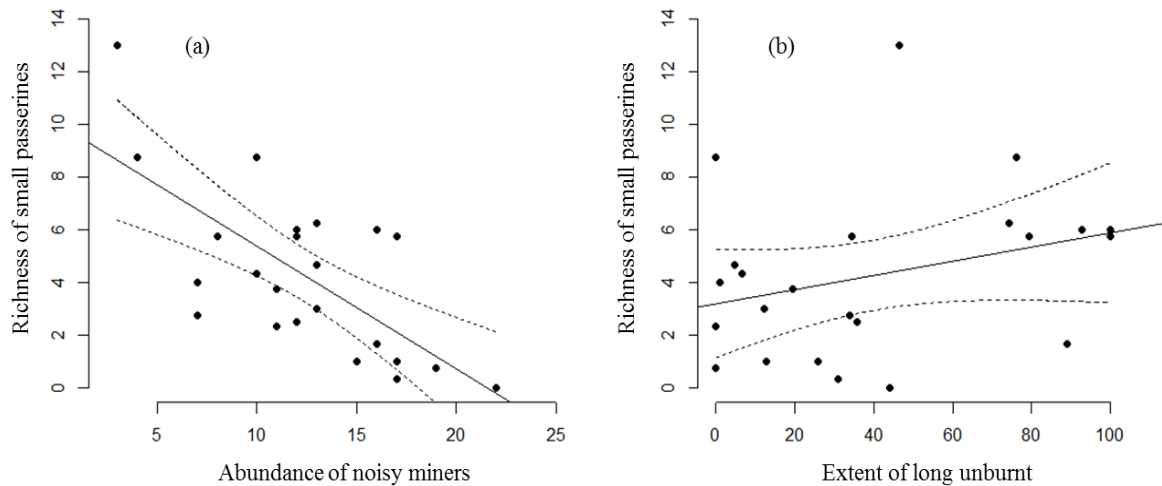
The index of landscape configuration—characterised by patch shape complexity—had a low relative importance, and did not substantially influence total observed species richness and small passerine richness (Fig. 12a-b; Appendix 5). A weak, positive relationship was detected between Chao2 richness and fire-mediated patch shape complexity (Appendix 5).



**Figure 12** Ranking of the variables according to the summed Akaike weights ( $\sum \omega_i$ ) for (a) total observed bird species richness; and (b) observed richness of small passerines per landscape. ‘Circle’= measure of fire-mediated patch shape complexity. Filled (black) bars indicate predictor variables for which the 95% confidence intervals of the model-averaged coefficients did not include zero.



**Figure 13** Scatterplots of total bird species richness against standardised a) range in elevation; b) number of vegetation communities per landscape; c) the extent of long unburnt habitat; and d) diversity of fire histories.



**Figure 14** Scatterplots of small passerine richness against a) the mean abundance of noisy miners; and b) the extent of long unburnt habitat per study landscape.

#### *Components of landscape-level species richness*

Despite measures of landscape heterogeneity being most influential on landscape-scale species richness, mean site level richness (alpha diversity) had a stronger influence ( $F_{70} = 167.2$ ,  $p < 0.0001$ ,  $R^2_{adj.} = 0.88$ ) on landscape-level species richness than did species turnover (beta diversity) ( $F_{70} = 18.1$ ,  $p < 0.001$ ,  $R^2_{adj.} = 0.44$ ) (Appendix 6). Mean site level richness was, in turn, influenced by range in elevation ( $F_{70} = 16.2$ ,  $p < 0.001$ ,  $R^2_{adj.} = 0.41$ ). The effect of this element of heterogeneity on mean alpha diversity was greater than on species turnover (beta diversity) ( $F_{70} = 7.8$ ,  $p < 0.05$ ,  $R^2_{adj.} = 0.24$ ) (Appendix 6).

## **4.5 DISCUSSION**

We found that more-heterogeneous landscapes were more species-rich, but that heterogeneity in elevation and diversity of vegetation communities drove this pattern, not diversity of fire histories. However, despite the importance of heterogeneity, landscape-level richness was more associated with high average site-level richness (alpha diversity) than turnover of species among sites (beta diversity). Thus, environmental heterogeneity resulted in elevated landscape-level richness primarily because of its influence on mean alpha diversity. In addition, landscapes with higher mean abundance of noisy miners had fewer bird species, particularly small passerines.

#### ***4.5.1 Landscape heterogeneity versus extent of preferred habitat***

Measures of landscape heterogeneity, rather than extent of preferred habitat or landscape configuration, were consistently stronger determinants of bird species richness. The number of vegetation communities and range in elevation both strongly and positively influenced total bird species richness. A greater number of vegetation communities provides an array of resources and niches to be exploited, thus supporting the coexistence of a greater number of animal species across the landscape (Miller et al. 1997; Aauri and Lucio 2001; Williams et al. 2002; Brose et al. 2004), and an increase in topographic complexity would be expected to support a greater diversity of vegetation types (Radford et al. 2005; Poulos and Camp 2010). Although intuitive, our finding is in contrast with those recent studies that have found the extent of habitat a stronger driver of woodland bird species richness as compared with environmental- (e.g. Bennett & Ford 1997; Radford et al. 2005) or fire-mediated heterogeneity (Taylor et al. 2012). It is important to note that some of these studies were conducted in fragmented systems which may partly explain the stronger influence of habitat extent as compared with habitat heterogeneity (Bennett & Ford 1997; Radford et al. 2005).

Nevertheless, the extent of long unburnt habitat within a landscape had a weak, positive relationship with richness of small passerines. This agrees with findings in south-east Australia that revealed a strong, positive relationship between extent of long unburnt vegetation and bird species richness (Taylor et al. 2012). Previous research in this system has shown small passerines to respond negatively to recent wildfire at a site level (2 ha) (Howes and Maron 2009; Howes et al. 2010). The site-level fire-response of small passerines suggests a need for prescribed burns to be strategically placed to allow, as far as possible, previously-unburnt areas to remain so. In sub-tropical woodlands at least, areas not burnt for at least 10 years could be expected to support a greater diversity of birds. However, it is important to consider that the most-preferred seral stage will vary both within and among taxonomic groups (Brotons et al. 2005; Di Stefano et al. 2013). Reptiles in semi-arid and arid Australia for example, had a higher richness in mid-successional vegetation as compared with early and late successional vegetation (Nimmo et al. 2013), whilst small mammals in the same system had a greater richness in older vegetation (Kelly et al. 2012).

#### ***4.5.2 Alpha diversity as a driver of landscape-scale richness***

We predicted that if habitat heterogeneity was the primary driver of elevated species richness across landscapes, landscape-scale bird richness would be driven largely by species turnover among habitat elements within a landscape (beta diversity). However, surprisingly, we found that

landscape-scale bird richness was related most strongly to mean alpha diversity, not to turnover, as might be expected where habitat heterogeneity is the key correlate of richness (Williams 1964; McGuinness 1984; Boecklen 1986; Olszewski 2004). The strong influence of habitat heterogeneity in our study landscape arose from the influence of spatial context on richness at the site-level, whereby sites in more heterogeneous landscapes were more species-rich. The greater numbers of vegetation communities may reflect the chance that particular vegetation types that support higher bird richness are present in a landscape. Landscapes with a higher proportion of, and in close proximity to, good-quality habitat have been shown to support greater species richness of, for example, micro-arthropods that inhabit moss in Canada (Chisholm et al. 2010); arthropods in agricultural landscapes in Europe (Hendrickx et al. 2007); and woodland-dependent birds in fragmented landscapes in south-eastern Australia (Polyakov et al. 2013).

The low turnover of species in our study landscape could also be an artefact of the prevailing fire management approach. In the study landscape, the majority of ignitions result from small-scale prescribed burns as compared with wildfires. The resultant fire mosaic would therefore allow for movement among the different fire history patches and thus species turnover among habitats would be low (Cleary et al. 2004; Pastro et al. 2014). Past research found greater spatial turnover of species in wildfire mosaics compared with mosaics generated by prescribed burns (Pastro et al. 2011; Pastro et al. 2014).

#### ***4.5.3 Heterogeneity in fire history***

Despite the important role of heterogeneity in vegetation types and elevation, there was little support for heterogeneity in fire history as a driver of bird species richness. Although achieving landscape pyrodiversity increasingly is a goal of fire management in fire-prone landscapes (Parr and Andersen 2006; Sitters et al. 2014), several recent studies have brought into question the empirical support for the hypothesis that pyrodiversity leads to greater species richness at the landscape level (Taylor et al. 2012; Kelly et al. 2013; Nimmo et al. 2013). This limited fire response could be due to several factors: 1) highly mobile taxa, such as birds, may respond to heterogeneity in fire history at scales larger than that of our study landscapes (100 ha); 2) the grain size at which the fire regime is applied is too coarse to induce the sort of heterogeneity that promotes increased bird diversity; 3) the fire regime classification we used does not capture the seral stages of vegetation that influence bird communities; and/or 4) birds respond more strongly to topographical and vegetation type differences than the short-term change in vegetation structure and composition caused by fire (Sitters et al. 2014).



### ***4.5.3 Interspecific competitors***

The abundance of noisy miners, summed across all sites in a landscape, was an important predictor of landscape-scale richness of small passerines. Sites dominated by noisy miners tend to support relatively few, ubiquitous species with a predictable composition and low turnover (Maron et al. 2011; Mac Nally et al. 2012; Howes et al. 2014). This pattern was evident in the study area, and as a result, landscapes with few noisy miners supported a higher richness of small passerines. Noisy miners prefer structurally more open woodlands which allow them to expend less energy defending their territories (Kath et al. 2009; Kutt et al. 2012), and so are less common in long-unburnt areas (Howes and Maron 2009, Howes et al. 2010, Maron and Kennedy 2007), an association that may partly explain the positive effect of extent of long-unburnt habitat on small passerines. It should be noted that our measure of landscape-level noisy miner abundance is imperfect, as it was based on surveys at few sites. It may be a variable with primarily local effects, which were propagated as the data were scaled-up to the landscape level. Nevertheless, although the strong effect of this species at the site-level is well-documented, the emergent effect of this for assemblages at the landscape-scale has not hitherto been explored. A focus on creating landscape heterogeneity to promote diversity without addressing key processes such as interspecific competition may therefore be unsuccessful.

### ***4.5.4 Conclusions***

Our results support environmental heterogeneity as the key driver of biodiversity at the intermediate or landscape-scale (100 ha) (Huston 1994; Tews et al. 2004). However, we found underlying variation (diversity of vegetation types, range in elevation) to be of much greater influence than potentially manipulable factors such as heterogeneity in fire history. Contrary to our expectations, landscape-scale richness was driven most strongly by alpha diversity, suggesting that alpha diversity itself was also influenced by a spatial context of greater heterogeneity. However, the influence of extent of preferred habitat, as measured by long unburnt woodland, on richness of one group of conservation interest—small passerines—highlights the importance of considering site-level processes, such as interference competition, that modify alpha diversity and, through this, landscape-scale diversity.

## CHAPTER 5

### DOES THE RESPONSE OF BIRD SPECIES RICHNESS TO FIRE MOSAIC PROPERTIES VARY AMONG SPATIAL SCALES AND FORAGING GUILDS?

ACCEPTED FOR PUBLICATION IN LANDSCAPE ECOLOGY

Emma E Burgess, Martine Maron



**Plate 4:** Control burn on Carnarvon Station Reserve, June 2012.

## **5.1 ABSTRACT**

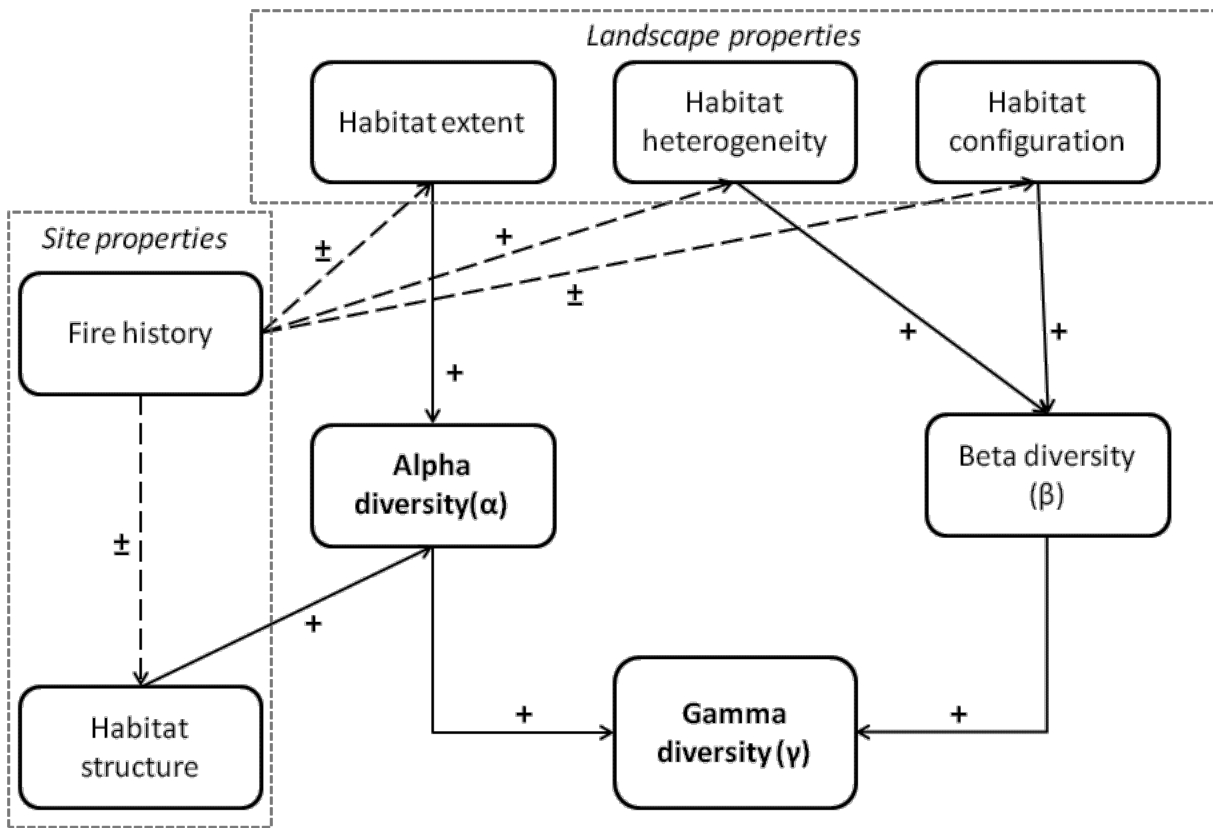
Scale is a key concept in ecology. An increasing number of studies have investigated the impact of environmental heterogeneity when measured at multiple spatial scales on faunal assemblages. Few studies, however, have considered how the effects of heterogeneity on fauna vary with the spatial scale at which the response variable is characterised. We investigated the relationship between landscape properties in a region characterised by diverse fire mosaics, and the structure and composition of avian assemblages measured at both the site scale (1 ha) and the landscape scale (100 ha) in relatively intact woodlands of central Queensland, Australia. Environmental heterogeneity, as measured by topographic complexity, was consistently important for bird species richness and composition. However, the explanatory power of topographic complexity varied depending on the spatial scale and the component of diversity under investigation. We found different correlates of richness within particular foraging guilds depending on the scale at which richness was measured. Extent of unburnt habitat was the most important variable for the landscape-level richness of frugivores, insectivores and canopy feeders, whereas environmental heterogeneity in the surrounding landscape was more important for site-level richness of these foraging guilds. The response of species richness to landscape characteristics varies among scales, and among components of diversity. Thus, depending on the scale at which a biodiversity conservation goal is conceptualised – maximising richness at a site, or across a landscape – different landscape management approaches should be preferred.

## **5.2 INTRODUCTION**

Understanding the factors that generate and maintain patterns of biodiversity is a central challenge in ecology (MacArthur and MacArthur 1961; Gaston 2000; Williams et al. 2002). Environmental heterogeneity is widely recognised as a key driver of patterns in assemblage structure and composition (Pickett and Cadenasso 1995; Pino et al. 2000; Weibull et al. 2000; Bennett et al. 2006; Dufour et al. 2006; Haslem and Bennett 2008). Heterogeneity reflects both the geographical characteristics of the study area, and the stochastic and anthropogenic processes that modify landscape structure (Hortal et al. 2009; Flesch and Steidl 2010; Bennett et al. 2006). The relative contribution of environmental heterogeneity to the distribution of organisms, their resources and habitat, however, can be scale-dependent (Milne et al. 1989; Pickett and Cadenasso 1995). Effective management of heterogeneous landscapes thus relies on understanding the processes that maintain species richness across different scales (Milne et al. 1989; Chave 2013).

Differences in autecology among species such as home range, foraging and nesting requirements mean different taxa respond to their environment at a variety of scales (Williams et al. 2002; Elmqvist et al. 2003; Flesch and Steidl 2010; Tschardt et al. 2012; Cunningham et al. 2014). For example, in south-east Australia, occurrence of the granivorous Superb Parrot responded negatively to the amount of native vegetation at a landscape scale, but positively to vegetation cover at the site level (Cunningham et al. 2014). It can therefore be difficult to identify the scale or scales at which assemblages respond to particular landscape properties (Flesch and Steidl 2010). Whilst many studies have investigated the influence of environmental characteristics measured at different scales (e.g. Fahr and Kalko 2010; Flesch and Steidl 2010; Butler et al. 2013) few have considered how the response of fauna varies depending on the scale at which that response is measured (but see Williams et al. 2002; Cunningham et al. 2014; Farnsworth et al. 2014).

In a fire-prone environment, fire history is a key driver of spatial heterogeneity, configuration and extent of habitat (Lloret et al. 2002; Faivre et al. 2011). Landscape heterogeneity and configuration incorporate the distribution and arrangement of vegetation of different seral stages, composition and structure (Lloret et al. 2002; Faivre et al. 2011). More habitat types are expected to mean greater diversity of resources and species, in particular through generating species turnover (beta diversity) among the different habitats (Fig. 15) (Tuomisto 2010). This greater spatial turnover contributes to increased total species across the landscape (gamma diversity). The extent of habitat in a landscape is also an important determinant of species occurrence (Niemelä 1999; Radford et al. 2005; Taylor et al. 2012). A high proportion of high-quality habitat in a landscape should support high average alpha, or within-patch, diversity (Fig. 15) (Wilson and Shmida, 1984). High-quality habitat for many taxa in fire-prone environments is often that which confers protection from the effects of fire on fauna at the site level, such as more structurally-complex, unburnt habitat (Barton et al. 2014; Sitters et al. 2014).



**Figure 15** Conceptual pathway diagram and predictions of drivers of bird species assemblages at the site (alpha) and landscape (gamma) scale in a fire-prone landscape. ('+' indicates a hypothesized positive influence and ' $\pm$ ' indicates a hypothesized positive or negative influence).

In addition to considerations of spatial scale, there are many different ways to categorise and measure biological diversity. Studies examining the effects of environmental heterogeneity on assemblages often focus on aggregate species richness or diversity indices (Huston 1994; Usher 1997; French and Picozzi 2002). However, without considering how different species and foraging guilds respond, important patterns can be obscured (Huston 1994; Usher 1997; French and Picozzi 2002). Considering the response of different components of biodiversity to landscape composition allows the identification of species traits associated with particular responses to landscape change (Andersen 1995; French and Picozzi 2002; Blondel 2003).

Here, we employ a multi-scale approach to assess the influence of landscape- and local-scale environmental characteristics on avian assemblages measured at different scales in relatively intact woodlands. In our study region, spatial heterogeneity is driven by variation in disturbance history (fire), vegetation type, and elevation (Howes and Maron 2009; Howes et al. 2010). Our aim was to investigate the relationship between landscape characteristics including the fire regime mosaic, and

the richness and composition of avian assemblages measured at two spatial scales: the site scale (1 ha) and the landscape scale (100 ha). In particular, we ask: (1) when the bird assemblage is characterised at different scales, do the different landscape properties that most strongly influence them differ? and (2) how do bird foraging guilds vary in their response to landscape properties, including when the assemblage measures relate to different scales? We predicted greater structural complexity and extent of suitable habitat would increase mean richness at a site, or alpha diversity, but that landscape heterogeneity would be the main driver of species turnover (Fig. 15) and thus be a more important contributor to richness at the landscape scale.

## 5.3 METHODS

### 5.3.1 Study area

The study was conducted in the privately-managed conservation reserve Carnarvon Station Reserve (59 000 ha), Carnarvon Ranges, Queensland, Australia. The region is located in the sub-humid to semi-arid zone (Environment Australia 2000). Average winter temperatures range from 3°C to 22°C; and summer temperatures from 18°C to 34°C, with average annual rainfall of 500–750 mm (Bailey 1984; Bureau of Meteorology 2013).

Open eucalypt woodland is the dominant vegetation type on the reserve, and is ecologically important in the Brigalow Belt Bioregion in which the study area is located as habitat for threatened species (Ryan 2006; Richardson 2008). Fire is an important ecological management tool in the study region. Two major objectives of ecological fire management are (1) to mitigate the spread of extensive, homogenising fires; and (2) to create and maintain a diversity of vegetation structures (Brockett et al. 2001; Parr and Andersen 2006; Burrows 2008). Fire management in the open eucalypt woodland involves small-scale (~100 ha) fires ignited throughout the year, with timing dependent on fuel loads, rainfall and temperature. The planned fire return interval in the grassy eucalypt woodlands is four to five years. This vegetation type includes ecosystems dominated by poplar box (*Eucalyptus populnea*), silver-leaved ironbark (*E. melanophloia*), and mountain coolibah (*E. orgadophila*), (Sattler and Williams 1999). The wetter basalt slopes support now rare vegetation types such as semi-evergreen vine thickets, brigalow (*Acacia harpophylla*) and belah (*Casuarina cristata*) woodland (Bush Heritage 2013).

### **5.3.2 Study design**

The study area was overlain with a grid composed of 1 km<sup>2</sup> (100 ha) cells using ET GeoWizards 10.1 software (ET Spatial Techniques) in ESRI ArcGIS 10. This extent was deemed suitable to encompass variation in landscape composition whilst allowing for sufficient replication (Haslem and Bennett 2008). Initial selection of study landscapes was based on mapping of vegetation types and fire history categories (see Appendix 3 for description of fire history mapping). Twenty-eight of these cells were selected to include a range of landscape compositions with respect to fire history, from uniform to highly heterogeneous (Appendix 3). The number of fire history categories present within each landscape varied from two to seven (Appendix 3), and the extent of long-unburnt habitat ranged from 0 ha to 88 ha per study landscape.

Three 1 ha (100 x 100 m) survey sites were selected within each study landscape, and located in fire history categories in approximate proportion to the representation of each fire history category within that landscape, for a total of 84 sites. Twelve of the sites were burnt by either prescribed burns in June 2012 or a wildfire that occurred during Jan – Feb 2013, and so landscapes in which these sites occurred were excluded from further consideration, leaving 72 sites from 24 landscapes.

### **5.3.3 Bird species richness**

Four repeat bird surveys were completed per 1 ha site, with each site surveyed during August (2012), September (2012) October (2012), and February–March (2013). All bird surveys were conducted by a single observer (EB) and followed the active-timed search method (Loyn, 1986). This involved traversing the 100 m central line, recording all birds seen and heard during a 10 minute sample period. The bird surveys were conducted both in the morning (up to 4 hours after sunrise) and afternoon (3 hours prior to sunset) at each site. The sequence of site visitation was rotated between survey rounds such that no site was surveyed more than twice in the morning or afternoon. Surveys were not conducted during periods of strong wind or rain. Birds flying above the canopy were not included in analysis.

### **5.3.4 Response variables**

Two sets of response variables were generated, corresponding to site-level and landscape-level responses. For the site-level bird response variables, bird survey data were pooled across all samples for each site. For the landscape-level response variables, the data were pooled across all

sites within each study landscape. For both levels of scale, bird species richness was calculated for total species, and for each foraging guild. We identified guilds based on food type and primary foraging zones. This resulted in five foraging guilds: nectarivore, frugivore, insectivore, carnivore, granivore; and five foraging zones: ground, shrub, canopy, bark, aerial. Dietary categories were not mutually exclusive and species that frequently consumed both nectar and insects, for example, were assigned to both relevant foraging guilds. Data on food types and foraging zones were obtained from Mac Nally (1994) and Garnett et al. (2013), and were checked and adjusted using the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB 2006).

### **5.3.5 Predictor variables**

Landscape spatial pattern metrics were calculated using FRAGSTATS version 4 from fire and vegetation mapping data (McGarigal et al. 2012). Three variables described environmental heterogeneity at the landscape scale (Table 8): (1) fire-mediated heterogeneity, characterised by the Simpson's diversity index of fire history categories in each study landscape; (2) diversity of vegetation types, characterised by the number of regional ecosystems; and (3) topographic complexity, measured as the range in elevation across each study landscape. Landscape configuration was measured by patch complexity relative to a standard shape for each of the different fire-mediated patches within each study landscape (Table 8). Two variables measured extent of habitat elements within study landscapes (Table 8): (1) the proportion of long unburnt habitat in a landscape; and (2) the proportion of recently burnt habitat in a landscape. For habitat structure we used the density of woody stems in the mid-storey. This variable was measured at each site, and the values averaged across all sites in a landscape yielded a landscape-scale estimate of habitat structure (Table 8) (for details on vegetation survey methods see Burgess et al. 2015). The fire history category of each site was also included as a predictor variable for site-level responses (Appendix 3). We tested for collinearity among the predictor variables using Spearman's correlation coefficient matrix (Zurr et al. 2010). We found a high negative correlation (Spearman's rank correlation  $> 0.5$ ) between extent of unburnt habitat and extent of recently burnt habitat, and so we excluded extent of recently burnt habitat from further analysis.



**Table 8** Summary of predictor variables used in analyses.

Variable	Abbreviation	Description
<b>Landscape level</b>		
Fire-mediated heterogeneity ( <i>diversity</i> )	DivFH	Diversity of fire-mediated patch types using Simpson's diversity index. This will be influenced by both richness (no. of fire-mediated patch types) and evenness (distribution of area among different fire-mediated patch types). The higher the value the greater the diversity.
Richness of REs	RE	The number of different regional ecosystems present in a landscape <sup>†</sup> .
Range in elevation	AltRang	The difference between the highest and lowest contour in landscape (m).
Related circumscribing circle	Circ	A measure of fire-mediated patch shape complexity based on the ratio of patch area to the area of smallest circumscribing circle. CIRCLE = 0 for intact circular patches; as circle approaches 1 the patch becomes more irregular and elongated.
Extent of unburnt	ExtUB	Proportion of long unburnt habitat per landscape.
Extent of recent	ExtRec	Proportion of landscape burnt in the previous $\leq 4$ years.
<b>Site level</b>		
Fire history category	FHC	Combination of fire frequency, time since last burn and season of last burn
Mid-storey density	MS	Number of stems (averaged across sampling periods) in the 2-6 m height class per hectare (ha)

<sup>†</sup>Regional ecosystems are vegetation communities defined by their association with particular combinations of geology, landform and soil (Sattler and Williams, 1999).

### 5.3.6 Data analysis

A separate canonical analysis of principal coordinates (CAP, Anderson and Willis 2003) for response datasets at each scale was used to explore the relationship between bird community composition and the predictor variables. CAP is effective in fitting an axis through the cloud of multivariate data which has the strongest relationship with the environmental variables of interest

(Anderson and Willis 2003), despite the presence of other potentially important factors which were not measured (Anderson et al. 2008; Pryke et al. 2013). The analysis was based on Bray-Curtis similarity measures from square-root transformed abundances to reduce the weight of common species. Analyses were conducted using the PERMANOVA+ add-on package for PRIMER v6 (Anderson et al. 2008).

Preliminary graphical exploration of the relationship between the bird diversity metrics measured at each scale and the landscape predictor variables indicated some nonlinear responses. Univariate analyses using generalized linear models (GLMs) with untransformed and second-order polynomial terms were compared. Where the polynomial term was significant ( $<0.05$ ), and support for the polynomial model was higher than for the untransformed model ( $\Delta AIC > 2$ ) the polynomial term was retained (Burnham and Anderson 2002; Taylor et al. 2012).

To gain insight into the patterns affecting composition of avifaunal assemblages at the landscape scale we modelled the relationship between the landscape-level response variables as a function of the landscape-level predictors, using GLMs with a Poisson distribution in the lme4 package v.1.1-5 in R (R Core Development Team 2012). Each landscape represented a single sampling unit. All predictor variables were standardised to have a mean of zero and a standard deviation of 1 to allow direct comparisons of model parameter estimates (Quinn and Keough 2002).

Generalised linear mixed models (GLMMs) with a Poisson error distribution were used to investigate site-level bird responses to site- and landscape-level predictor variables. Mixed-effects models are a useful extension of GLMs and allow sources of correlation structure in data to be modelled as random effects (Zurr et al. 2009). Landscape was included as a random effect in each model to account for the spatial clustering of sites within landscapes.

For both of the modelling approaches, we employed an information theoretic approach to investigate the influence of the predictor variables on response variables (Burnham and Anderson 2002). For each response, alternative models from all linear combinations of predictor variables and interactions were generated from the global model (Grueber et al. 2011). The models were ranked by their Akaike weights calculated from AICc values (Akaike's Information Criterion corrected for small sample size). A 95% confidence set of models was constructed by starting with the model with the highest Akaike weight and repeatedly adding the model with the next highest weight until the cumulative sum of weights exceeded 0.95 (Burnham and Anderson 2002). For each response

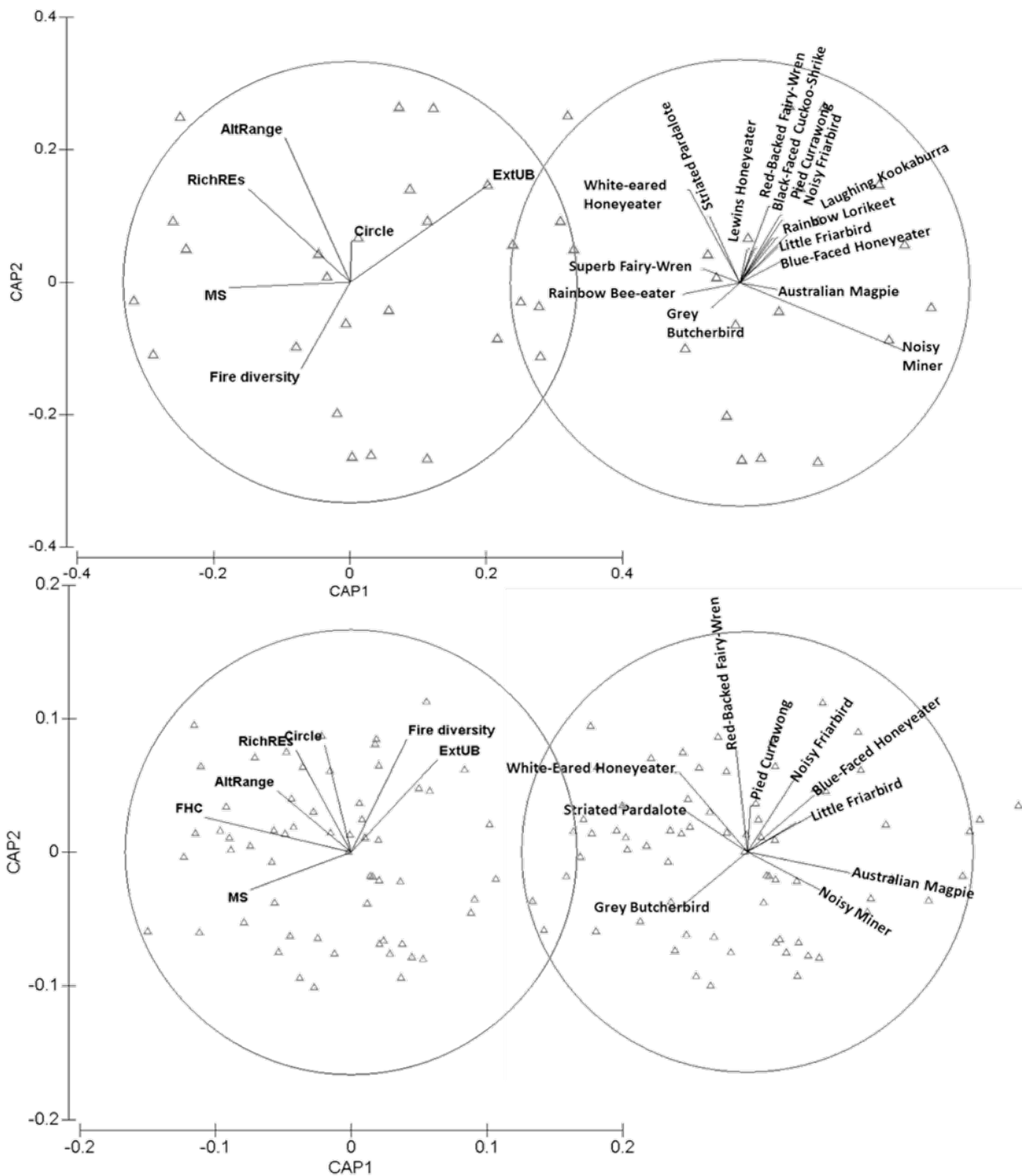
variable, the model-averaged parameter estimates and the unconditional standard errors of each estimate were calculated across all models in the confidence set (Burnham and Anderson 2002). The relative importance of each predictor variable was quantified by summing the Akaike weights for all models containing the variable (Burnham and Anderson 2002). We used the MuMIn package v1.9.5 in R (R Core Development Team 2012) to conduct these analyses. No evidence of over-dispersion was found for models of total observed species richness at either the landscape- or site-scale (following methods laid out in Zurr et al. 2009). Model fit was assessed by plotting the residuals against the predicted values. Spline correlograms of the model residuals of full models for all response variables were constructed to test for spatial autocorrelation (Zurr et al. 2009) in the NCF extension package v.1.1-4 for R (R Core Development Team 2012).

## 5.4 RESULTS

### 5.4.1 Patterns of bird community composition

There were some strong correlations between the landscape-scale bird species composition data cloud and the predictor variables. The first axis of landscape composition correlated positively with the extent of unburnt habitat (ExtUB) and negatively with the density of mid-storey stems (MS) (Fig. 16, Table 9). The second axis showed a positive correlation with topographic complexity (AltRange) (Fig. 16, Table 9). The ordination of bird species revealed an association between a suite of mainly larger-bodied birds (Blue-Faced Honeyeater (*Entomyzon cyanotis*), Laughing Kookaburra (*Dacelo novaeguineae*), Noisy Friarbird (*Philemon corniculatus*), Black-Faced Cuckoo Shrike (*Coracina novaehollandiae*) and Pied Currawong (*Strepera graculina*)) and the extent of unburnt habitat (Fig. 16). Greater topographic complexity was associated with smaller-bodied birds such as the White-Eared Honeyeater (*Lichenostomus leucotis*) and the Striated Pardalote (*Pardalotus striatus*) (Fig. 16).

Site-level species composition was driven by similar landscape-level fire properties, but site-level fire history category was also important. The first axis was negatively correlated with fire history category (FHC) (Fig. 16, Table 8) and the second axis with diversity of fire history categories in the surrounding landscape (Fig. 16, Table 8). The ordination of bird species revealed an association between Striated Pardalote and fire history category, and between the surrounding fire diversity and mainly larger-bodied birds (Noisy Friarbird and Pied Currawong) (Fig. 16).



**Figure 16** CAP ordination of the first two axes of the canonical correspondence analysis relating bird community composition (a) per landscape; and (b) per site to the predictor variables. For species composition per landscape these correlations were almost significant at the 0.05 level ( $P = 0.051$ ). The first two canonical correlations are both greater than 0.75 ( $\delta_1 = 0.81$ ,  $\delta_2 = 0.75$ ). For species composition per site these correlations were not significant ( $P > 0.05$ ), with the first two canonical correlations greater than 0.40 ( $\delta_1 = 0.62$ ,  $\delta_2 = 0.44$ ). The inset square shows correlations ( $> 0.2$ ) of several species with the first two CAP axes. ExtUB = proportion of long unburnt habitat

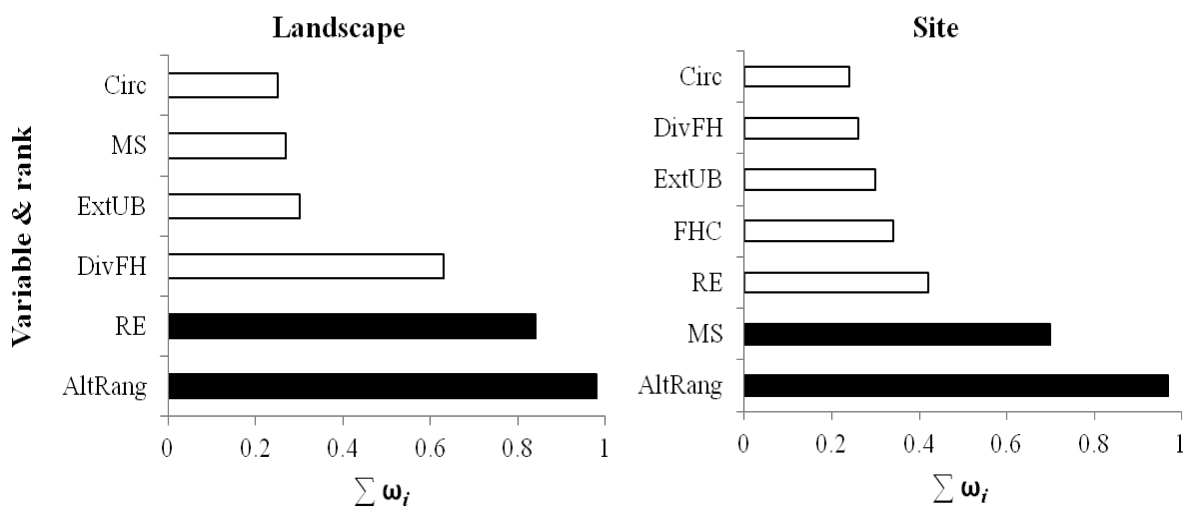
per landscape; AltRange = range in elevation; RichREs = richness of regional ecosystems; Fire diversity = richness of fire-mediated patches; Circle = mean circumscribing circle.

**Table 9** Summary of generalised canonical correlation analysis of bird species composition per landscape and per site with environmental variables (normalised)

<i>Landscape composition</i>						
Axes	1	2	3	4	Sum	
Canonical correlations	0.81	0.75	0.51	0.11	2.18	
<i>Correlations of environmental variables with axes</i>						
Circle	0.007	0.19	0.52	0.36		
Fire diversity	-0.22	-0.40	-0.36	0.23		
Richness of regional ecosystems (RichRE)	-0.45	0.42	-0.57	0.40		
Range in elevation (AltRange)	-0.29	0.65	0.08	-0.53		
Extent of unburnt habitat (ExtUB)	0.62	0.45	-0.07	0.47		
Density of mid-storey stems (MS)	-0.54	-0.03	0.51	0.40		
<i>Site composition</i>						
Axes	1	2	3	4	5	Sum
Canonical correlations	0.62	0.44	0.20	0.13	0.12	1.51
<i>Correlations of environmental variables with axes</i>						
Circle	-0.12	0.48	0.05	0.70	-0.50	
Fire diversity	0.25	0.51	0.65	-0.12	0.33	
Richness of regional ecosystems (RichRE)	-0.24	0.46	-0.51	-0.47	-0.11	
Range in elevation (AltRange)	-0.33	0.28	0.09	-0.05	0.37	
Extent of unburnt habitat (ExtUB)	0.38	0.42	-0.48	0.15	0.34	
Fire history category (FHC)	-0.65	0.16	0.21	-0.20	-0.13	
Density of mid-storey stems (MS)	-0.45	-0.17	-0.15	0.47	0.60	

### 5.4.2 Aggregate species richness

Total species richness, measured at the landscape level, was driven primarily by landscape heterogeneity, but not fire-mediated heterogeneity. Rather, range in elevation and diversity of vegetation types were most strongly related to total landscape-level species richness (Fig. 17; Appendices 7 and 8). Mean site-level species richness was also driven by range in elevation in the landscape where the site was located, but also habitat structure at the site (MS) (Fig. 17; Appendices 9 and 10).



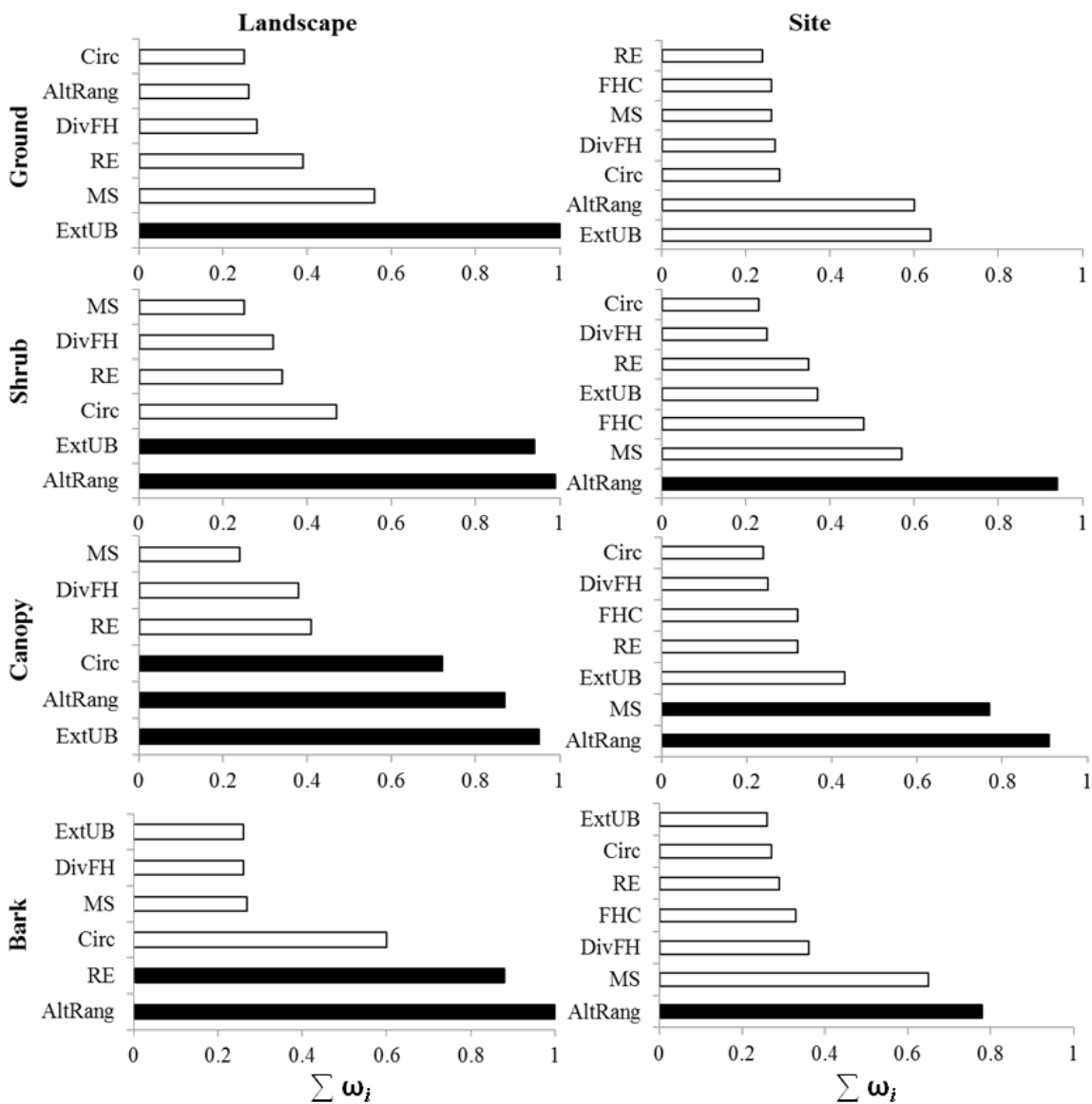
*Figure 17 Ranked summed Akaike weights ( $\sum \omega_i$ ) from model averaging of the final subset of predictor variables for total richness; and mean richness (alpha) of birds. Filled bars represent the variables for which the 95% confidence interval does not overlap zero. ExtUB = proportion of long unburnt habitat per landscape; AltRange = range in elevation; RichREs = richness of regional ecosystems; Fire diversity = richness of fire-mediated patches; Circle = mean circumscribing circle.*

The response of bird species richness to the final set of landscape variables varied among guilds more than they did across spatial scales (Fig.18-19; Appendices 7-10). Drivers of richness patterns among guilds (Fig. 18) also contrasted with those of total species richness (Fig. 17).

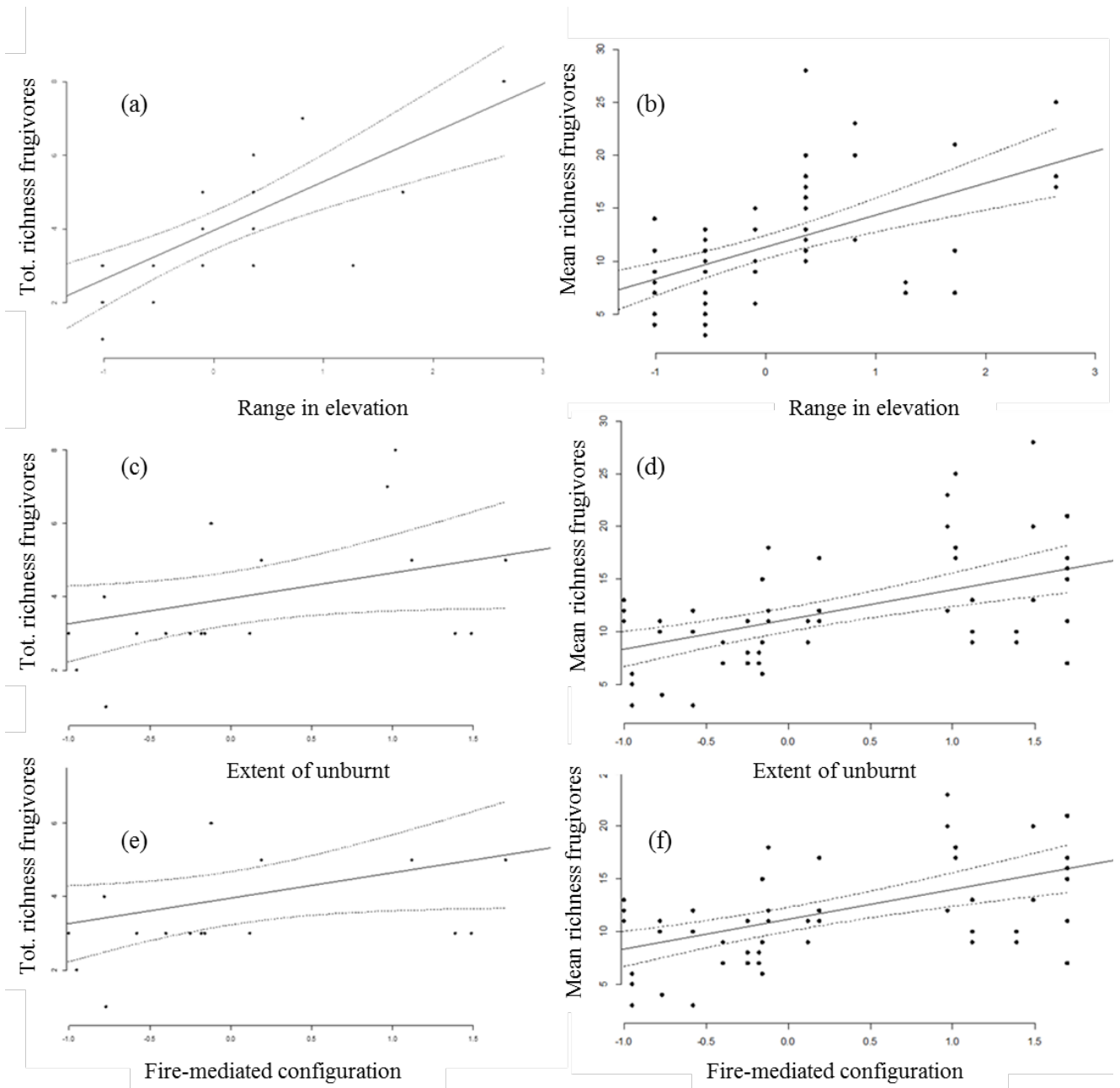
At the landscape level, the extent of unburnt habitat had a positive influence and was the most important predictor of landscape-level species richness of frugivores (Fig. 19), insectivores (Appendices 7, 8 and 11) and canopy feeders (Fig. 18; Appendices 7 and 8). At the site level, the richness of frugivores, insectivores (Appendices 9-11) and canopy feeders (Fig. 18; Appendices 7 and 8) was most strongly influenced by heterogeneity of the surrounding landscape, as measured by range in elevation; in each case, richness increased with range in elevation.

Extent of unburnt habitat was a strong predictor of the species richness of nectarivores and carnivores, measured at both the landscape- and site-levels (Appendices 7-11). Range in elevation had the greatest influence on species richness of granivores (Appendix 11), shrub and bark feeders (Fig. 18) measured at both the landscape- and site-level; the relationship with range in elevation was positive in all cases.





**Figure 18** Ranked summed Akaike weights ( $\sum \omega_i$ ) from model averaging of the final subset of predictor variables for total richness and mean richness (alpha) of birds in different feeding habitat guilds. Filled bars represent the variables for which the 95% confidence interval does not overlap zero. ExtUB = proportion of long unburnt habitat per landscape; AltRange = range in elevation; RichREs = richness of regional ecosystems; Fire diversity = richness of fire-mediated patches; Circle = mean circumscribing circle.



**Figure 19** Examples of relationship between richness of frugivores measured at both the landscape- and site-level, and key explanatory variables. Circles represent raw data. Dashed lines represent the 95% confidence interval for chosen predictor variables.

## 5.5 DISCUSSION

We hypothesised that environmental heterogeneity would be most important in promoting landscape-level species richness through its effects on turnover, while extent of high-quality habitat would be most important in driving alpha diversity. However, drivers of species richness and composition measured at both scales were similar, with landscape context variables important drivers of richness at both the site- and the landscape-level. Nevertheless, the response of foraging guilds to landscape elements did vary depending on the scale at which the response was measured, as well as the foraging guild considered. Contrary to our expectations based on our conceptual model, site-level richness was driven mainly by the heterogeneity of the landscape in which it was located, as well as the extent of unburnt habitat in the landscape.

### *5.5.1 Different responses at different scales*

The results reveal that in some cases, the scale at which the response is measured matters, with different correlates of foraging guild richness becoming evident depending on the scale under consideration (Mitchell et al. 2001). The landscape properties driving species richness of frugivores, insectivores and canopy feeders varied depending on the scale at which the response was measured. At the landscape-level, species richness of these three groups was driven most strongly by the extent of a single cover type in a landscape - unburnt habitat. However, at the site-level, the mean richness of frugivores, insectivores and canopy foragers was most strongly influenced by surrounding landscape heterogeneity – specifically, range in elevation. It is important to note that range in elevation also had a strong effect at the landscape-scale for insectivores and canopy feeders.

That landscape-level environmental heterogeneity was strongly related to richness at the site-level suggests that birds recorded at a site are moving widely through the landscape, and therefore are affected by landscape properties (Brotons et al. 2005); indeed, for mobile species such as birds, an assemblage might be best characterised at this larger scale. In other words, the scale at which many species are using the landscapes under consideration may well be closer to the 100 ha rather than the 1 ha scale. This has important implications for the spatial scale at which fire management plans should be developed and implemented, at least in relation to birds.

In the study area, topographic complexity is an important driver of landscape heterogeneity. Carnarvon Station Reserve is composed of rugged terrain, with changes in elevation occurring

frequently (400 m to >1000 m). This increased topographic complexity would be expected to support a greater diversity of microclimates, soil and vegetation types, which in turn provide a greater range of resources to be exploited (Williams et al., 2002; Pineda and Halffter 2004; Radford et al. 2005; Poulos and Camp 2010; Bishop et al. 2014). Environmental heterogeneity associated with range in elevation has been shown to support greater diversity within numerous taxa, including frogs in Mexico (Pineda and Halffter 2004), and ants in South Africa (Bishop et al. 2014).

An important consideration when interpreting the findings presented here relate to the landscape-scale approach for bird species richness. Landscape-scale richness was calculated by pooling the three 1 ha units within a single 100 ha area. Therefore, the variation among scales may be partly due to the greater sample size at the site-scale (3 times greater in this case).

Our results suggest the persistence of frugivore, insectivore and canopy forager assemblages at a landscape scale is driven by the presence of structurally complex vegetation and old-growth canopy trees, which are more likely to be present in areas that have not experienced fire for a prolonged period of time (Woinarski and Recher 1997). For example, many frugivores require large fruiting trees as their main food source; they also represent a functionally important guild for the maintenance of plant diversity (Sekercioglu 2006; Kirika et al. 2008). This agrees with past research in a tropical landscape that revealed a stronger response of specialist foraging guilds frugivores and insectivores to extent of secondary forest rather than habitat heterogeneity (De Bonilla et al. 2012).

### ***5.5.2 Components of diversity***

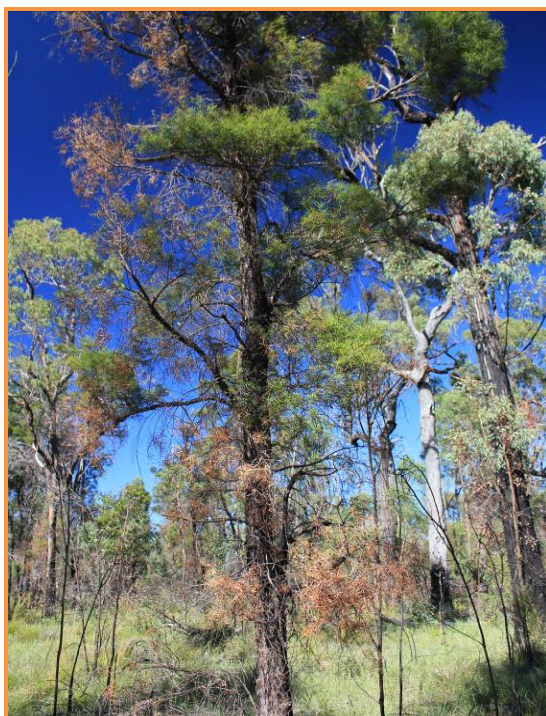
In addition to variation in responses between the two scales of measurement, the ecological factors that most influenced assemblages differed among foraging guilds. Despite landscape heterogeneity being a strong driver of aggregated richness of birds, extent of preferred habitat (in this case, proportion of long unburnt habitat) in a landscape, was a key driver across different guilds. Vegetation with a longer time since fire often has a denser, more complex structure and can be a refuge for birds in a fire-prone landscape (Watson et al. 2012; Robinson et al. 2014), including those in this region (Maron and Kennedy 2007; Howes and Maron 2009; Howes et al. 2010). Examination of the response of richness within different foraging guilds to landscape properties would provide a useful basis for development of management plans (French and Picozzi 2002) particularly for disturbance-sensitive groups such as insectivores and frugivores (Kirika et al. 2008).

### ***5.5.3 Conclusions***

The landscape elements that contribute to assemblage structure at the local and landscape spatial scales fall into two broad categories: extent of suitable habitat, and environmental heterogeneity. The importance of each of these categories varied in their explanatory power at different scales, and for different components of diversity. While site-level assemblage composition is influenced by the local fire history, site-level richness increased most strongly with the heterogeneity of the landscape in which it was located. Our study supports the idea that the variation in ecological response to landscape elements is influenced by the scale at which the response variable of interest is characterised. We suggest effective management will be influenced by the scale at which biodiversity conservation is being conceptualised.

## CHAPTER 6:

### THESIS SYNTHESIS



**Plate 5:** Ground cover regenerating post-fire, Carnarvon Station Reserve.



**Plate 6:** *Angophora costata* resprouting post-fire, Carnarvon Station Reserve.

## 6.1 OVERVIEW

To achieve effective conservation of biodiversity there is a need to understand the relationship between the underlying drivers of landscape change, and the ecosystems and the taxa they support (Kutt and Martin 2010). The overarching purpose of this thesis was to provide further understanding of the relative importance of ecological processes for the persistence of floral and faunal communities in sub-tropical woodland ecosystems. This research addresses several important knowledge gaps relating to the relative influence of environmental heterogeneity and anthropogenic management regimes on biota across different spatial scales.

The open forests and woodlands of the Brigalow Belt Bioregion, Queensland, Australia have experienced extensive clearing, with 61% of native vegetation cleared since European settlement in the 1840s (Mc Alpine et al. 2002; Wilson et al. 2002). Despite this, only around 2% of the Brigalow Belt is protected in conservation reserves. The Brigalow Belt is split into two regions based upon climatic variations: the Brigalow Belt North and the Brigalow Belt South (Sattler and Williams 1999). Within the Queensland section of the Brigalow Belt South, 17% of the regional ecosystems (REs) are classified as Endangered and a further 26% are classified as Of Concern according to the Queensland legislation (Sattler and Williams 1999). Despite this it is recognised as a national biodiversity hotspot, including the greatest richness of specialist eucalypt woodland birds of any bioregion in Australia (Keto et al. 2004). However, many bird species continue to decline (ANRA 2009), with altered fire regimes recognised as one of the key threatening processes in this region, second only to land clearing and fragmentation (ANRA 2009).

My research was conducted on a private conservation reserve in the Carnarvon Ranges of the Brigalow Belt South Bioregion, central Queensland; Carnarvon Station Reserve. The reserve is currently managed by Bush Heritage Australia (BHA) with the overarching goal to restore the condition, functioning and dynamics of the assemblages of species that would have been present on Carnarvon Station prior to European settlement in this region (Bush Heritage Australia 2011). Fire is an important management tool being used to achieve this goal.

The aim of this thesis was to improve the success of biodiversity conservation and ecological fire management by increasing our understanding of the drivers of woody vegetation structure and composition, and the richness and composition of bird communities across different spatial scales. One of the initial steps involved a global review of patch mosaic burning research (Chapter 2), which highlighted important knowledge gaps, which I went on to address in subsequent chapters: (i)

how to quantify and characterise fire regimes (combined fire attributes) (Chapter 3); (ii) the response of biota to fire regimes (Chapter 3); (iii) response of birds to different measures (underlying soil / altitude derived habitat versus fire-mediated) of landscape heterogeneity, extent of habitat and landscape configuration (Chapter 4); and (iv) how the effects of heterogeneity (based on both vegetation communities and fire history) on fauna vary with the spatial scale at which the response variable is characterised (Chapter 5). This final chapter presents a summary of the main findings from this research and explains its contribution to broadening our knowledge of ecological theory and effective fire management for nature conservation.

The overall thesis aim was addressed through investigation of four key research questions:

*Research question 1: What is the global evidence-base for mosaic burning as a biodiversity management tool?*

The first question reviewed the evidence base for the widely-held view that introducing diversity in fire regimes will promote gamma diversity (i.e. the ‘pyrodiversity begets biodiversity’ or ‘patch mosaic burning’ paradigm). My global review revealed that i) all but three studies examined only alpha-diversity responses of target biota, despite the central goal of patch mosaic burning being to increase gamma diversity through generating spatial turnover; ii) the evidence base from which conclusions can be drawn about patch mosaic burning is very limited geographically and in terms of taxa considered; and iii) there is a lack of consistent terminology and generally poor definition of objectives for applying patch mosaic burning. With limited evidence available it is difficult for land managers to predict or infer the level of pyrodiversity required to maintain biodiversity.

*Research question 2: How does a variable fire regime influence stand structure and composition in subtropical woodlands?*

The post-fire response of vegetation reflects not only a single fire event but is the result of cumulative effects of previous fires in the landscape (Bradstock *et al.* 2005). For effective ecological fire management there is a need to better understand the relationship between different fire regimes and vegetation structure. This question therefore had two main components: i) the characterisation of complex fire regimes and the fire regime mosaic; and ii) the influence of the fire regime on different components of woodland structure and composition.



The way in which I characterised the spatial and temporal elements of fire history across the landscape contributes to improving classification of complex fire history data. It is therefore potentially valuable for characterising fire regimes beyond the region being studied.

I revealed that these fire history categories (unique combinations of season, frequency and time since last fire) strongly influenced both richness and abundance of plant species categorised as mid-storey trees, and those individuals currently in the mid-level strata. With regards to the attributes used to develop the fire regime categories, time since fire and fire frequency appeared to have the strongest influence on habitat structure and composition. Simplification of woodland structure could result from fires that are too frequent (> 2 fires in a 12 year period), with a short time since last fire (< 4 years since last burn). This supports past research that revealed less-frequently burnt or long-unburnt sites had a more complex structure and composition than sites burnt more frequently (Hoffman 1999; Williams et al. 1999; Woinarski et al. 2004; Radford et al. 2008; Lewis and Debus 2012).

*Research question 3: What drives bird species richness in a fire prone landscape: landscape heterogeneity or extent of preferred habitat?*

To ensure transformed landscapes can remain biodiverse, or be restored to be so, it is important to understand the relative importance of different landscape properties in shaping their faunal assemblages (Heikkinen and Birks, 1996; Niemelä 1999; Koivula 2001; Estrada 2007). I addressed this by investigating the relative importance of different processes of landscape heterogeneity generation and extent of habitat in driving landscape-scale bird richness (in this case, 100 ha units). In particular, I examined the diversity of habitat types (both natural and fire-mediated vegetation types), extent of habitat and indices of landscape configuration. I found environmental heterogeneity acts as a primary driver of bird species richness at the landscape-scale. However, despite fire-mediated heterogeneity being a notable feature of the region, it was of limited importance; rather, range in elevation and diversity of vegetation types related most strongly to bird species richness. The strongest correlates of high landscape-scale species richness were therefore factors largely not manipulable through management interventions.

Total estimated richness (Chao2) and small passerine richness, a group of conservation concern in the region, were also negatively associated with the mean abundance of Noisy Miners (*Manorina melanocephala*), a hyper-aggressive native species. Past research has shown Noisy Miners to have a

major influence on bird assemblages across eastern Australia, as their presence markedly depresses the abundance and richness of other bird species (Major et al. 2001; Maron and Kennedy 2007; Kutt et al. 2012; Maron et al. 2013). This is important because it highlights a need for management in relatively intact woodlands to not only consider heterogeneity but also complementary management targeted at controlling abundance of competitive species, in this case noisy miners.

*Research question 4: How do the spatial properties of the fire mosaic influence the composition of avifaunal assemblages at the local-level compared with the landscape-level?*

Effective management of heterogeneous landscapes relies on understanding the processes that maintain species richness across different scales the purpose of this question was to investigate the scale at which bird responses to heterogeneity are most evident (Williams et al. 2002; Farnsworth et al. 2014). For this research question I applied an information theoretic approach to investigate the relationship between properties of the fire regime mosaic, and the structure and composition of avian assemblages characterised at the site scale (1 ha) and the landscape scale (100 ha). This study demonstrated that the scale of response matters, with different correlates of bird assemblage structure and composition becoming evident depending on the scale at which the bird assemblages were characterised. Extent of unburnt habitat within the landscape was the most important driver of the landscape-scale richness of frugivores, insectivores and canopy feeders, whereas environmental heterogeneity in the surrounding landscape, as measured by range in elevation, was most important for site-scale richness of these foraging guilds. These findings emphasise that the management approaches considered appropriate are dependent on the scale at which a biodiversity conservation goal is conceptualised. For example, if the objective was to enhance richness of birds within a site or patch of woodland there is a need to maintain a diversity of habitats and woodland structure surrounding that site; but if the management objectives are focused on enhancing functional diversity across a landscape there is a need to also consider the composition of habitat types present, not just habitat heterogeneity. In the study area, the results suggest a greater extent of longer unburnt vegetation (< 10 years since last fire) will support increased richness across the landscape of important bird functional guilds such as frugivores and insectivores.

## **6.2 CONTRIBUTIONS TO ECOLOGICAL UNDERSTANDING**

This thesis makes a number of important contributions to advancing ecological theory. Several broad ecological concepts were applied in this study, including landscape ecology, biogeography and conservation biology. Although this study focused on avifaunal assemblages and woody

vegetation, there are broader ecological implications for conservation and management of other wildlife species. The main findings from this thesis are: i) environmental heterogeneity, in particular a greater range of elevation in a landscape, is an important driver of landscape- (100 ha) and site-scale (1 ha) bird species richness; (ii) that site level richness (alpha diversity) drives richness of species in a landscape slightly more than the turnover of species (beta); (iii) extent of habitat is also important, particularly influencing species composition and richness of small passerines, frugivores, insectivores and canopy feeders at the landscape scale; and (iv) different landscape properties correlate with richness and assemblage structure depending on the scale at which the response variables are measured.

Species-area relationships are near-ubiquitous features of ecological systems (McGuinness 1984; He and Legendre 1996; Olszewski 2004). One explanation for the species-area relationship is that as the area sampled increases, so does the number of different habitats (McGuinness 1984; Olszewski 2004) i.e. heterogeneity as an important driver of diversity (Pickett and Cadenasso 1995; Pino et al. 2000; Weibull et al. 2000; Bennett et al. 2006; Dufour et al. 2006; Haslem and Bennett 2008). As landscape heterogeneity increases within a given area, the amount of between-habitat (beta) diversity of species within that area is likely to increase (Tews et al. 2004; Zhang et al. 2014). Another widely accepted view is that landscapes with a greater extent of preferred or suitable habitat support more individuals, which, through passive sampling, include more species (Osman 1977; Connor and McCoy 1979; McGuinness 1984; Maron et al. 2013; Zhang et al. 2014). By definition, the mean alpha diversity (number of different species per site or habitat) in landscapes with more preferred habitat is higher. Determining whether maintaining larger areas of habitat with high alpha diversity, or inducing heterogeneity to promote beta-diversity, is most likely to result in the greatest number of species in a landscape is therefore central to conservation management.

I demonstrated that environmental heterogeneity at the landscape-scale (in this case, units of 100 ha) is the primary driver of total species richness (gamma diversity) and mean species richness (alpha) (in this case, units of 1 ha) of birds (Chapter 4 and 5). The extent of suitable habitat however, was more important for the total richness of small passerines, frugivores, insectivores and canopy feeders (Chapter 4 and 5). This finding significantly contributes to landscape and conservation ecology by encouraging researchers and managers to incorporate thinking on quality and type of habitats present in a landscape not just the number of different habitats.

Findings from this research also indicate that site-level richness (alpha diversity) drives richness of species in the landscape slightly more than the turnover of species (Chapter 4). However, in contrast to our expectations that extent of preferred habitat would drive alpha diversity, we found that habitat heterogeneity in the landscape surrounding a site affected landscape level richness through its influence on alpha diversity more than beta diversity. That landscape-level environmental heterogeneity was strongly related to richness at the site level suggests that birds recorded at a site are moving widely through the landscape (Elmqvist et al. 2003; Weir and Corlett 2007), and therefore are affected by landscape properties; indeed, for mobile species such as birds, an assemblage might be best characterised at a larger scale. In other words, the scale at which many species are using the landscapes under consideration may well be closer to the 100 ha rather than the 1 ha scale. This has important implications for the spatial scale at which fire management plans should be developed and implemented, at least in relation to birds.

This finding led me to further investigate the concept of spatial scale in ecology (Levin 1992). For management actions to be effective they should be implemented at scales appropriate to the processes that the manager wishes to influence (Radford and Bennett 2007). An increasing number of studies have investigated the impact of environmental heterogeneity when measured at multiple spatial scales on faunal assemblages (Saab 1999; Gabriel et al. 2010; Butler et al. 2013). Few studies, however, have considered how the effects of heterogeneity on fauna vary with the spatial scale at which the response variable is characterised. This thesis addressed this by employing a multi-scale approach to assess the influence of landscape- and local-scale environmental characteristics on avian assemblages characterised at different scales I demonstrated that in this fire-prone landscape, the landscape elements that contribute to assemblage structure at the local and landscape spatial scales fall into two broad categories: extent of suitable habitat, and environmental heterogeneity. Variables in each of these categories varied in their explanatory power for assemblages characterised at different scales, and for different functional groups (Chapter 5). Past research has advocated a multi-scale consideration of the ecological influence of different properties of landscape heterogeneity (e.g. Saab 1999; Gabriel et al. 2010; Butler et al. 2013). My findings suggest that (i) depending on the scale at which a biodiversity conservation goal is conceptualised—maximising richness at a site, or across a landscape—different landscape management approaches should be preferred; and (ii) there is also a need to consider the needs of different functional guilds to maximise effectiveness of conservation actions.

### **6.3 CONTRIBUTION TO UNDERSTANDING OF ECOLOGICAL FIRE MANAGEMENT**

Fire is recognised as an important disturbance process in many ecosystems and is increasingly used as a management tool for the conservation of biodiversity (Driscoll et al. 2010). This thesis makes a number of important contributions to our understanding of broad ecological fire management, and specifically the patch mosaic burning approach (Table 10). Until recently much research has focused on the response to specific attributes of the fire regime, with much attention on time since last burn and fire frequency (Bradstock et al. 2005). This thesis demonstrates an approach to quantifying the fire regime and mapping the fire regime mosaic based on combinations of multiple attributes: time since last fire, fire frequency and season of last burn (Chapter 3).

The diversity and abundance of fauna populations is often profoundly affected by habitat structural variables. Bird species diversity, for example, has been shown to respond to the configuration of different vegetation layers and availability of nesting sites and food resources (Mac Arthur and Mac Arthur 1961; Baker 1997; Woinarski and Recher 1997; Pons and Clavero 2010; Zhang et al. 2013). This thesis investigated the response of woodland structure and composition to a variable fire regime. Importantly, I found that variation in the fire regime (unique combinations of season, frequency and time since last fire) significantly influences woodland structure and composition. To promote a more complex habitat structure to benefit fauna, areas should be burnt less frequently and with a longer time since last burn.

Increasingly, fire management aims to promote temporal and spatial heterogeneity in elements of fire history (Bradstock et al. 2005; Parr and Andersen 2006) (Chapter 2). Yet there is limited understanding of the importance of spatial heterogeneity in fire mosaics for fauna (Chapter 2). Spatial properties of fire regimes have only recently been discussed in fire ecology (Faivre et al. 2011). In this thesis, I investigated the influence of spatial properties of the fire regime mosaic on bird assemblages characterised at two spatial scales.

From the newly-defined fire regime mosaic maps created in Chapter 3, I extracted a number of spatial fire mosaic properties for a series of study landscapes. These included measures of fire mediated diversity, fire-mediated configuration and composition of the fire regime mosaic (extent of particular fire histories) (Chapter 4 and 5). In Chapter 4 and 5, I showed that fire-mediated heterogeneity and configuration were of limited importance for bird species richness at both the site (1 ha) and landscape (100 ha) levels (Chapter 4 and 5). However, fire history category and fire-

mediated diversity did have a significant influence on bird species composition among sites (Chapter 5). For bird assemblages, the extent of unburnt habitat in the landscape was important. This supports findings from studies in south-east Australia that found the proportion of a preferred fire age class in a landscape, not pyrodiversity per se, had the greatest influence on species richness of that landscape (Kelly et al. 2012; Taylor et al. 2012) and on occurrence of individual species (Nimmo et al. 2013).

#### **6.4 FIRE MANAGEMENT ON CARNARVON STATION RESERVE**

This thesis has contributed important empirical information to support fire management of sub-tropical woodlands in the Brigalow Belt Bioregion for conservation purposes (Table 10). The overarching approach to fire management on Carnarvon Station follows the principles of patch mosaic burning (Saxon 1984; van Wilgen et al. 1998; Brockett et al. 2001), in which the past regime of few relatively large fires is replaced with one of numerous small fires. The key objectives of the fire management plan for Carnarvon Station Reserve focuses on the establishment of planned ignition strategies to shape vegetation structure of key vegetation communities. These key vegetation types include poplar box (*Eucalyptus populnea*), silver-leaved ironbark (*E. melanophloia*), and mountain coolibah (*E. orgadophila*) woodlands.

Guidelines in the fire management plan for Carnarvon Station focus on average fire return intervals specific to each broad vegetation type, and the minimum and maximum proportion of each broad vegetation type that should be burnt in any one fire season. The findings from this thesis, however, support the need for the fire management plan to consider other attributes of the fire regime (fire frequency, time since last fire and season of last burn), to fully understand the drivers of patterns in vegetation structure and composition (Chapter 3) (Gary and Morrison 1995; Gill et al. 2002; Bradstock et al. 2005; Spencer and Baxter 2006) (Table 10).

My findings suggest that variation in the fire regime over successive fire seasons is required in order to maintain woodlands with both grassy and shrubby understorey (Chapter 3). In woodlands with a predominantly grassy understorey, a fire return interval of 2-3 years is recommended in the management plan. This is to prevent a build-up of fuel that would support large, intense fires. This is supported by findings from this thesis which suggest sites burnt frequently (> 2 fires in a 12 year period), with a short time since fire (< 4 years since last burn) will maintain an open, grassy structure. However, another objective of the fire management plan is to restore woodlands with a more complex understorey in order to maintain fauna populations such as small passerines e.g.

silver-leaved ironbark woodlands with an understorey composed of vine scrub species. To achieve this, my findings suggest a fire regime of less frequent fire (< 2 fires in a 12 year period), and a longer time since fire (> 4 years since last burn) (Chapter 3).

When planning ecological burns fuel loads, past fire history and vegetation type are not the only consideration (Moritz et al. 2014). My findings revealed the importance of edaphic factors such as geology type and topography on Carnarvon Station. I found vegetation patterns are influenced by geology type and the interaction between geology and fire history (Chapter 3) (Bowman et al. 1988; Vigilante and Bowman 2004; Spencer and Baxter 2006). Geology type can influence fire pattern. For example, more productive sites such as those on basalt soils can support more frequent fires, whilst more skeletal soils or rocky substrates can be self-protecting under low to moderate intensity fires (Vigilante and Bowman 2004). I also found that greater topographic complexity in a landscape was an important driver of increased bird species richness. This is likely related to the fact that greater topographic complexity supports a greater diversity in vegetation types. In addition, the longer-unburnt patches tend to be at higher elevations and on steeper slopes. These longer-unburnt patches on steeper slopes and at higher elevations may be self-protecting against frequent fire—a result of low ground cover on skeletal soils (Vigilante and Bowman 2004). Fire management could enhance protection of these areas by strategically igniting control burns that create a fire break against large wildfires entering these areas.

In Australia, ecological fire management has tended to focus on the fire response of flora and maintaining plant diversity, assuming that this will meet the needs of fauna (Clarke 2008). This focus on the fire response of plants may correspond to a gap in knowledge on the response of fauna communities to particular fire regimes (Clarke 2008). Indeed, the fire management plans for Carnarvon Station Reserve are focused on the response of vegetation structure to planned ignition strategies. In the context of Carnarvon Station Reserve, a focus on maintaining plant diversities could have limited benefit for bird assemblages if it fails to protect an adequate extent of long-unburnt habitat (Chapter 4 and 5; Taylor et al. 2012).

**Table 10** Summary of findings of this thesis in relation to ecological fire management in sub-tropical woodlands

Knowledge gaps	Key findings
<p>How to characterise and map the fire regime mosaic (<i>Chapter 3</i>)</p>	<p>This study showed:</p> <ol style="list-style-type: none"> <li>1) the importance of mapping fire scars digitally (Landsat and ArcGIS)</li> <li>2) Fire regimes can be mapped in ArcGIS software by combining information contained in attribute tables from different fire scar layers e.g. date of burn, type of fire. This is an important step towards revealing the ‘invisible’ attributes of the fire regime mosaic e.g. frequency of burn (Bradstock et al. 2005)</li> <li>3) Empirical evidence that season of burn did not have a strong influence on woody vegetation. Vegetation responded more strongly to combinations of time since last fire (recent = <math>\leq 4</math> years since last fire; old = <math>&gt; 4</math> years since last fire) and fire frequency (frequent = <math>\geq 3</math> burns in 11 years; infrequent = <math>\leq 2</math> burns in 11 years)</li> <li>4) Support for patches not burnt for <math>&gt;10</math> years to be classified as long unburnt in sub-tropical woodlands</li> </ol>
<p>What components of vegetation structure and composition in open eucalyptus woodlands respond to a variable fire regime? (<i>Chapter 3</i>)</p>	<p>This study found that:</p> <ol style="list-style-type: none"> <li>1) Fire history category of a site significantly influenced abundance of stems and total species richness of woody vegetation.</li> <li>2) Woodland structure: individuals currently in the mid-level strata (1-2 m and 2-6 m) responded most strongly to fire history category</li> <li>3) Woodland composition: sites with the same fire history and a similar fire history had comparable species composition of live, native woody vegetation. Species categorised as mid-storey trees responded most strongly</li> </ol>



Knowledge gaps	Key findings
	<p>to fire history category.</p> <p>4) <i>Eucalyptus</i> and <i>Corymbia</i> species had a higher abundance in sites with a fire history of frequent fires and a short time since last fire.</p> <p>5) Species associated with semi-evergreen vine thicket, a threatened ecosystem type, tended to be found in areas that had experienced long inter-fire intervals.</p>
<p>Does fire history category influence avifaunal communities? (Chapter 5)</p>	<p>This study showed:</p> <ol style="list-style-type: none"> <li>1) Empirical evidence that local scale bird species composition responded strongly to site-level fire history category</li> <li>2) Empirical evidence that particular fire history categories are more important than others for determining species richness and composition. For bird species richness and assemblage structure in sub-tropical woodlands unburnt fire history category has the strongest influence</li> </ol>
<p>What influence do spatial properties of the fire regime mosaic have on structure and composition of avifaunal communities? (Chapter 4 and 5)</p>	<p>This study found that:</p> <ol style="list-style-type: none"> <li>1) Aggregate measures of bird species richness did not reveal a strong response to spatial properties of the fire regime mosaic at the site or landscape level</li> <li>2) Landscape-level community composition (beta diversity) varied with diversity in fire history categories</li> <li>3) Extent of unburnt habitat had a strong positive influence on the species richness of nectarivores and carnivores, measured at both the landscape- and site-level; and a positive influence on total estimated species richness, and on observed species richness of small passerines, frugivores, insectivores and canopy feeders at the landscape-level</li> <li>4) Properties of the fire regime mosaic may influence the guild structure of bird communities through its influence</li> </ol>

Knowledge gaps	Key findings
	<p>on the availability and spatial configuration of resources, and on habitat structure. For example, a decreased incidence of frugivores was associated with a decrease in proportional extent of woodlands &gt; 10 years since last fire</p>

## 6.5 LIMITATIONS OF THE STUDY AND FUTURE RESEARCH

Although this thesis has contributed to understanding of the landscape drivers of biodiversity pattern in a fire-prone landscape, it has some limitations, and here I outline these in order to assist with planning future research. The first limitation relates to the characterisation of spatial properties of the fire regime mosaic. We calculated the diversity of fire histories by applying Simpson's diversity index. The Simpsons index calculates a diversity measure based on the number and evenness of different fire history categories within a pre-defined landscape. By focusing on the number and evenness of different fire history categories this study fails to consider the composition of fire histories within each landscape. The strong influence of extent of unburnt habitat within a landscape (Chapters 4 and 5) suggests further research into bird response to composition of fire histories in a landscape is warranted.

The second limitation relates to the spatial scale selected for characterising both the environmental variables and the response variables in this study. This thesis investigated the implications of spatial patterns of fire for bird assemblages characterised at both the site (alpha diversity) and landscape-level (gamma diversity). This revealed interesting results in relation to the scale of response to landscape properties. However, the size of the site and landscape was set (1 ha and 100 ha respectively) – inferring processes at these scale. Avenues for future research would be the investigation of response at broader scales, and the fire response of the different components of beta diversity—nestedness and turnover (Baselga 2010).

At the site (1 ha) and landscape scale (100 ha) fire-mediated heterogeneity was of limited importance for bird assemblages. Instead, extent of longer unburnt vegetation was important at a scale of 100 ha. It is possible that at larger scales (> 100 ha), fire-mediated heterogeneity is of greater importance. This is because a larger area could contain a greater extent of preferred habitat

(longer unburnt vegetation) and the species associated with it (Osman 1977; Connor and McCoy 1979; McGuinness 1984; Brotons et al. 2005; Maron et al. 2013; Zhang et al. 2014). Thus a diversity of fire age classes could become important for driving broad scale diversity patterns.

In addition to the spatial scale at which the fire-regime mosaic is characterised, it is important to consider the response of the different levels of diversity. This study considered the response of the three levels of diversity: gamma (species richness pooled across all sites within a landscape), alpha (number of different species within a site), and beta (species composition among sites and landscapes). Beyond the scope of this study was examination of the different components of beta diversity: nestedness of assemblages and spatial species turnover (Baselga 2010). Nestedness occurs when the species composition of a site is a subset of the total species at a richer site i.e. a process of species loss (Ulrich and Gotelli 2007). Spatial turnover is a measure of the number of unique species between sites i.e. the replacement of some species by others (Baselga 2010). To fully understand how landscape properties and in particular, properties of the fire regime mosaic influence beta diversity patterns there is a need to disentangle the response of turnover and nestedness.

## **6.6 CONCLUSIONS**

Fire is an important ecological disturbance, and increasingly represents an important tool in conservation management. However, managing species in fire-prone landscapes will become increasingly challenging under the predicted changes in future climate and the impact of this on fire regimes. Therefore, enhancing ecological knowledge on response to landscape properties and disturbance is important to more accurately predict future impacts. This thesis has demonstrated that fire is a key component of sub-tropical woodlands, with the fire regime significantly influencing woodland structure and composition. Whilst environmental heterogeneity is an important driver of bird species richness at the site (1 ha) and landscape level (100 ha), fire-mediated heterogeneity is of limited importance for birds. Instead, the extent of a preferred fire age class (longer unburnt vegetation) is an important driver of bird species richness and particular foraging guilds. The importance of environmental heterogeneity, in particular range in elevation, and the extent of habitat vary depending on the scale and foraging guild under consideration. These findings are important contributions to our understanding of drivers of patterns of diversity in fire-prone landscapes, and provide useful information to improve management of biodiversity in these landscapes.

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## APPENDICES

### APPENDIX 1

#### Chapter 3

Results of PERMANOVA pairwise comparison tests of woody vegetation community composition among fire history categories, geology type and vegetation type. Only significant pairwise comparisons are given.

Groups		
<i>FHC</i>	<i>t-value</i>	<i>P(perm)</i>
LFR - UB	1.7	0.05
LFR - EIO	2.4	0.02
UB - LIO	1.5	0.003
UB - EIR	1.4	0.03
LIO - EIR	1.5	0.01
EIO - LIR	1.6	0.03
<i>Geology</i>		
Alluvium – Basaltic Flows	2.2	0.002
Basaltic Flows – Pebbly Quartz Sandstone	1.4	0.01
<i>Vegetation type</i>		
Mixed eucalypts – Poplar box	2.1	0.003
Poplar box - Ironbark	1.5	0.005

## APPENDIX 2

### Chapter 3

SIMPER analysis of dissimilarity of species composition among fire history categories for which significant differences were detected from pairwise PERMANOVA analysis. The top 5 contributing species are included. These are based on fourth-root transformed abundance data.

Species	Mean abundance		Contribution to dissimilarity %
	LFR	UB	
<i>Eucalyptus melanophloia</i>	0.43	1.73	4.7
<i>Angophera floribunda</i>	1.39	0.14	4.2
<i>Acacia muelleriana</i>	0	1.17	3.5
<i>Jasminum simplicifolium</i>	0.7	1.1	3.3
<i>Eucalyptus chloroclada</i>	0.9	0	3.1

Species	Mean abundance		Contribution to dissimilarity %
	LFR	EIO	
<i>Jasminum simplicifolium</i>	0.7	1.6	5
<i>Angophera floribunda</i>	1.4	0	4.9
<i>Eucalyptus melanophloia</i>	0.4	1.4	4.3
<i>Macrozamia moorei</i>	0.4	1.2	3.5
<i>Eucalyptus chloroclada</i>	0.9	0.5	3.1

Species	Mean abundance		Contribution to dissimilarity %
	UB	LIO	
<i>Acacia leiocalyx</i>	0.2	1.4	3.2
<i>Acacia muelleriana</i>	1.2	1.1	2.8
<i>Dodonaea triangularis</i>	0	1	2.5
<i>Eucalyptus decorticans</i>	0.1	1	2.4
<i>Alphitonia excelsa</i>	0.5	1.1	2.4

Species	Mean abundance		Contribution to dissimilarity %
	UB	EIR	
<i>Corymbia erythrophloia</i>	0.4	1.3	3.3
<i>Acacia muelleriana</i>	1.2	0.1	3
<i>Grewia latifolia</i>	0.3	1.3	3
<i>Macrozamia moorei</i>	0.9	1.6	2.8
<i>Senna coronilloides</i>	0.7	0.7	2.6

Species	Mean abundance		Contribution to dissimilarity %
	LIO	EIR	
<i>Acacia leiocalyx</i>	1.4	0.2	3.6
<i>Corymbia erythrophloia</i>	0.2	1.3	3.5
<i>Grewia latifolia</i>	0.1	1.3	3.4
<i>Alphitonia excelsa</i>	1.1	0.1	3
<i>Acacia muelleriana</i>	1.1	0.1	2.8

Species	Mean abundance		Contribution to dissimilarity %
	EIO	LIR	
<i>Eucalyptus melanophloia</i>	1.4	0.6	4.2
<i>Jasminum simplicifolium</i>	1.6	0.6	3.9
<i>Pimelea strigosa</i>	0.5	0.8	3.3
<i>Corymbia erythrophloia</i>	0.5	0.8	3.1
<i>Lespedeza juncea</i>	1	0.4	3

## APPENDIX 3

### Chapter 4

#### Fire history categories

The spatial fire history of the reserve was mapped using images from Landsat MSS satellite imagery and the north Australian fire information (NAFI) website, in addition to ground truthing by managers. Ground truthing was based on a combination of the GPS ignition points and GPS points recorded along the edge of the fire boundary. The spatial and temporal fire history was classified into fire history categories (Table S1) based on frequency, season of burn and time since last fire. These fire regime attributes were deemed most important based on review of literature (e.g. Mentis and Bailey 1990; Bradstock et al. 1997; Vigilante and Bowman 2004; Bradstock et al. 2005).

Season is assumed to provide a measure of intensity, with more intense fires expected later in the dry season as compared with early dry season fires (Parr et al. 2004; Andersen et al. 2005; Radford et al. 2012). Early dry season relates to fires ignited during February to June. Late dry season relates to fires ignited during July to October. As few fires occurred outside of these dates it was decided to combine any outliers into one of the two categories: fires occurring during November to December were classed as late dry season, and fires occurring in January were classed as early dry season. Fire frequency was based on the number of times burnt since 2001, using the classification: infrequent = 1-2; frequent =  $\geq 3$  (Whelan 1995). Time since last burn was classified as recent if it occurred  $\leq 4$  years; not recent if  $> 4$  years; unburnt if  $> 10$  years i.e. last burn was pre-2001 (Table S1). The polygons resulting from the intersection of these three spatial datasets represented the fire regime mosaic for the study area. The fire history categories correspond to different vegetation structures from very open, eucalypt woodlands with few saplings in the mid storey and a grassy ground layer, to a more complex vegetation structure composed of a dense mid-storey including vine-thicket associates (for further information see Burgess et al. 2015).



Attributes selected to categorise the fire regime mosaic of Carnarvon Station Reserve for study landscape selection. The first letter in the abbreviation refers to the season (early or late). The second letter refers to the fire frequency (frequent or infrequent). The last letter refers to the time since last fire (recent or old). UB = unburnt since at least 2001.

Fire History Category	Category description		
(no. sites)	Season	Fire frequency	Time Since Last Burn (y)
UB (10)	-	0	> 10
EIR (8)	Early Dry Season	Infrequent	≤ 4
LIR (7)	Late Dry Season	Infrequent	≤ 4
EIO (8)	Early Dry Season	Infrequent	> 4
LIO (7)	Late Dry Season	Infrequent	> 4
EFR (6)	Early Dry Season	Frequent	≤ 4
LFR (4)	Late Dry Season	Frequent	≤ 4
†EFO (0)	Early Dry Season	Frequent	> 4
†LFO (0)	Late Dry Season	Frequent	> 4

† Fires in June 2012 and Jan-Feb 2013 burnt a large portion of these fire history categories and so sites were not located in them.

## APPENDIX 4

### Chapter 4

AICc, Akaike weight ( $\omega_i$ ),  $\Delta$  value and model fit (deviance) for models of total observed species richness, and observed richness of small passerines for models within 2  $\Delta$  of the best model.

Deviance relates to the magnitude of unexplained variance and the smaller the deviance, the better the model fit.

<b>Response</b>	<b>Variables</b>	<b>AICc</b>	<b><math>\omega_i</math></b>	<b><math>\Delta</math></b>	<b>deviance</b>
Total	Veg+ElvRange+RichFMP	461.5	0.18	0.00	0.24
	Veg+ElvRange+avgNM+RichFMP	462.5	0.11	1.07	0.26
	Veg+ElvRange	463.2	0.08	1.72	0.22
Small passerines	avgNM+ElvRange+ExtUB+Veg	404.4	0.32	0.00	0.45
	avgNM+ElvRange+ExtUB+Veg+RichFMP	405.7	0.17	1.27	0.45
	avgNM+ElvRange+Veg+RichFMP	406.1	0.14	1.69	0.44
	avgNM+ElvRange+ExtUB+Veg+Circle	406.2	0.13	1.83	0.45

## APPENDIX 5

### Chapter 4

Averaged coefficients from models and their unconditional standard error (SE) for each response variable.

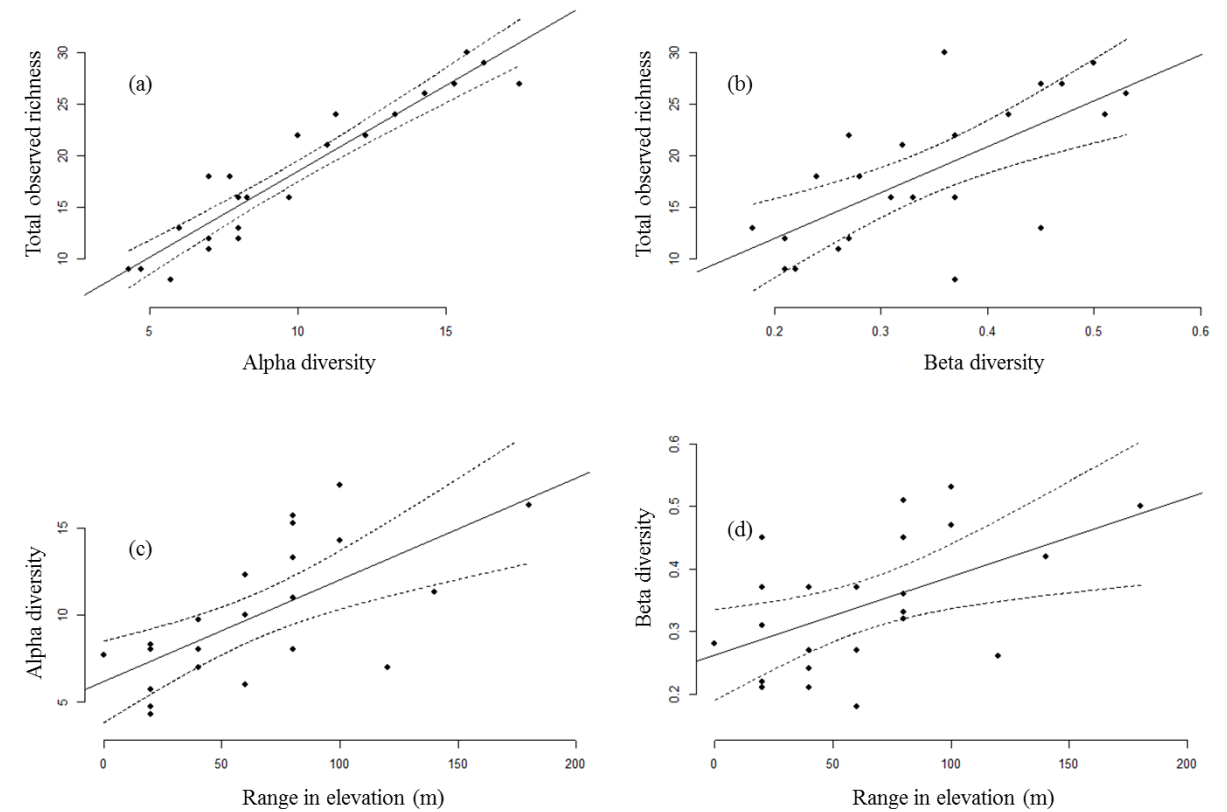
Richness	Intercept	ElvRange	Veg	AvgNM	RichFMP	Ext	Circ
						UB	
Total	2.02 (0.1)	<b>0.13 (0.04)</b>	<b>0.31 (0.15)</b>	-0.02 (0.02)	-0.08 (0.04)	0.02 (0.05)	-0.01 (0.04)
Small passerines	1.6 (0.2)	<b>0.21 (0.06)</b>	<b>0.93 (0.28)</b>	<b>-0.17 (0.03)</b>	-0.09 (0.07)	<b>0.14 (0.07)</b>	0.05 (0.05)
Chao2	3.6 (0.12)	0.02 (0.04)	0.23 (0.13)	<b>-0.08 (0.02)</b>	-0.07 (0.04)	<b>0.11 (0.04)</b>	<b>0.07 (0.03)</b>

Bold type indicates predictor variables for which the 95% CI did not overlap zero.

## APPENDIX 6

### Chapter 4

Scatterplots of landscape-level richness against a) alpha diversity; and b) beta diversity per study landscape; and c) alpha diversity; and d) beta diversity against range in elevation (m).



## APPENDIX 7

### Chapter 5

Model averaged coefficient estimates ( $\pm$ SE) for predictor variables for each response group at the landscape (gamma diversity) scale. Values in bold indicate a significant coefficient estimate ( $P < 0.05$ ).

Response	Predictor							
	AltRang	AltRang <sup>2</sup>	RE	MS	MS <sup>2</sup>	ExtUB	Circ	DivFH
<i>Gamma – richness</i>								
Tot. obs.	<b>0.13</b>	-	<b>0.35</b>	0.02	-	0.03	-0.01	-0.08
richness	<b>(0.04)</b>		<b>(0.15)</b>	(0.04)		(0.05)	(0.04)	(0.04)
Nectarivore	0.03	-	0.1	-0.04	-	<b>0.2</b>		-0.02
	(0.05)		(0.2)	(0.05)		<b>(0.05)</b>	0.07 (0.04)	(0.06)
Frugivores	0.08	-	-0.02	-0.02	-	<b>0.2</b>	<b>0.08</b>	-0.03
	(0.04)		(0.2)	(0.04)		<b>(0.05)</b>	<b>(0.04)</b>	(0.05)
Insectivores	<b>0.08</b>	-	0.17	-0.02	-	<b>0.1</b>	0.04	-0.04
	<b>(0.04)</b>		(0.13)	(0.04)		<b>(0.04)</b>	(0.03)	(0.04)
Carnivores	0.01	-	-0.46	-0.09	-	<b>0.22</b>	-0.04	-0.03
	(0.08)		(0.23)	(0.08)		<b>(0.15)</b>	(0.06)	(0.1)
Granivores	<b>0.2</b>	-	0.02	-0.02	-	0.05	0.03	-0.1
	<b>(0.06)</b>		(0.2)	(0.07)		(0.07)	(0.06)	(0.06)
Ground	0.01	-	-0.17	-0.07	-	<b>0.16</b>	0.01	-0.03
	(0.04)		(0.15)	(0.05)		<b>(0.07)</b>	(0.04)	(0.06)
Shrub	<b>0.12</b>	-	0.13	0.01	-	<b>0.12</b>	0.05	-0.04
	<b>(0.04)</b>		(0.14)	(0.04)		<b>(0.04)</b>	(0.03)	(0.05)
Canopy	<b>0.1</b>	-	0.17	-0.002	-	<b>0.14</b>	<b>0.07</b>	-0.06
	<b>(0.04)</b>		(0.14)	(0.04)		<b>(0.05)</b>	<b>(0.04)</b>	(0.05)
Bark	<b>0.34</b>	-	<b>1.14</b>	-0.06	-	0.03	0.17	0.05
	<b>(0.1)</b>		<b>(0.5)</b>	(0.12)		(0.13)	(0.1)	(0.12)

## APPENDIX 8

### Chapter 5

AICc, Akaike weight ( $\omega_i$ ),  $\Delta$  value and model fit (deviance) for models of all landscape-level species groups within  $2 \Delta$  of the best model. Deviance relates to the magnitude of unexplained variance and the smaller the deviance, the better the model fit.

Response	Variables	AICc	$\omega_i$	$\Delta$	Deviance
<i>Richness</i>					
Tot. Obs.	AltRang+RE+DivFH	436.3	0.22	0	48.51
<i>Richness</i>					
	AltRang+RE	438.09	0.09	1.78	43.33
Nectarivore	Circ+ExtUB	471.65	0.14	0	2.24
	ExtUB	471.94	0.12	0.28	1.24
	Circ+ExtUB+MS	473.23	0.06	1.57	4.14
	AltRang+ExtUB	473.4	0.06	1.75	10.66
	AltRang+Circ+ExtUB	473.44	0.06	1.78	11.19
	Circ+ExtUB+RE	473.51	0.05	1.85	4.14
	ExtUB+MS	473.62	0.05	1.97	3.14
Frugivore	AltRang+Circ+ExtUB	484.93	0.20	0	57.19
	Circ+ExtUB	486.23	0.10	1.29	22.41
	AltRang+Circ+ExtUB+DivFH	486.75	0.08	1.82	59.02
Insectivore	AltRang+ ExtUB	496.58	0.14	0	24.31
	AltRang+Circ+ExtUB	497.17	0.1	0.59	27.24
	AltRang+ ExtUB+RE	497.47	0.09	0.89	33.62
	AltRang+Circ+ExtUB+RE	497.92	0.07	1.34	37.24
	AltRang+ ExtUB+DivFH	498.22	0.06	1.64	24.14
Carnivore	ExtUB+RE	322.93	0.16	0	2.1
	ExtUB+RE+MS	323.93	0.1	1	2.28
	ExtUB	324.52	0.07	1.58	0.4
	Circ+ExtUB+RE	324.66	0.07	1.73	8.58
Granivore	AltRang+DivFH	372.79	0.16	0	26.09
	AltRang	373.75	0.1	0.96	25.91
	AltRang+ExtUB	374.35	0.07	1.57	26.09

<b>Response</b>	<b>Variables</b>	<b>AICc</b>	<b><math>\omega_i</math></b>	<b><math>\Delta</math></b>	<b>Deviance</b>
Ground	AltRang+DivFH+MS	374.59	0.07	1.81	30.74
	AltRang+Circ+DivFH	374.71	0.06	1.93	26.09
	ExtUB+MS	420.06	0.13	0.00	22.52
	ExtUB	420.52	0.11	0.46	21.25
	ExtUB+RE+MS	421.03	0.08	0.97	31.27
	ExtUB+RE	421.2	0.08	1.14	29.55
Shrub	ExtUB+DivFH+RE	421.6	0.06	1.54	29.94
	AltRang+ExtUB	483.86	0.18	0	29.43
	AltRang+Circ+ExtUB	484.17	0.15	0.31	36.06
	AltRang+ExtUB+RE	485.25	0.09	1.39	30.05
	AltRang+Circ+ExtUB+RE	485.45	0.08	1.59	36.83
Canopy	AltRang+ExtUB+DivFH	485.66	0.07	1.80	29.58
	AltRang+Circ+ExtUB	507.55	0.17	0	33
	AltRang+Circ+ExtUB+RE	508.49	0.11	0.94	33
	AltRang+Circ+ExtUB+DivFH	508.71	0.09	1.16	37.38
Bark	AltRang+ ExtUB	509.09	0.08	1.54	15.51
	AltRang+Circ+RE	244.86	0.21	0	23.49
	AltRang+RE	245.71	0.14	0.85	22.94
	AltRang+Circ+RE+MS	246.68	0.08	1.82	23.49
	AltRang+Circ+RE+DivFH	246.85	0.08	1.99	23.64

## APPENDIX 9

### Chapter 5

Model averaged coefficient estimates ( $\pm$ SE) for predictor variables for each response group at the site (alpha diversity) scale. Values in bold indicate a significant coefficient estimate ( $P < 0.05$ ).

<b>Response</b>		AltRang	RE	MS	FHC	ExtUB	Circ	DivFH
<i>Alpha richness</i>								
Tot. obs.	<b>0.23</b>	0.3	<b>0.1</b>	0.03	0.06	-0.02	-0.03	
richness	<b>(0.07)</b>	(0.22)	<b>(0.05)</b>	(0.03)	(0.08)	(0.06)	(0.07)	
Nectarivore	0.16	0.18	0.07	-0.006	<b>0.19</b>		0.04	
	(0.09)	(0.27)	(0.06)	(0.03)	<b>(0.09)</b>	0.03	(0.1)	
						(0.08)		
Frugivores	<b>0.2</b>	0.03	0.08	-0.001	<b>0.17</b>	0.03	0.02	
	<b>(0.07)</b>	(0.23)	(0.05)	(0.03)	<b>(0.08)</b>	(0.07)	(0.07)	
Insectivores	<b>0.19</b>	0.27	<b>0.1</b>	0.04	0.08	-0.01	0.01	
	<b>(0.07)</b>	(0.24)	<b>(0.05)</b>	(0.02)	(0.08)	(0.07)	(0.08)	
Carnivores	0.14	-0.32	0.06	0.01	<b>0.2</b>	-0.08	0.01	
	(0.1)	(0.31)	(0.08)	(0.04)	<b>(0.1)</b>	(0.09)	(0.12)	
Granivores	<b>0.28</b>	0.16	0.09	0.02	0.01	-0.04	-0.03	
	<b>(0.07)</b>	(0.27)	(0.06)	(0.03)	(0.09)	(0.07)	(0.08)	
Ground	0.12	-0.02	0.03	0.01	0.13	-0.04	0.02	
	(0.07)	(0.08)	(0.05)	(0.03)	(0.07)	(0.06)	(0.08)	
Shrub	<b>0.22</b>	0.26	0.08	0.04	0.09	-0.01	-0.002	
	<b>(0.07)</b>	(0.23)	(0.05)	(0.02)	(0.08)	(0.07)	(0.08)	
Canopy	<b>0.22</b>	0.24	<b>0.11</b>	0.02	0.11	0.02	-0.002	
	<b>(0.07)</b>	(0.25)	<b>(0.05)</b>	(0.03)	(0.09)	(0.07)	(0.09)	
Bark	<b>0.69</b>	0.8	0.39	0.11	-0.09	0.19	0.37	
	<b>(0.32)</b>	(1.1)	(0.2)	(0.13)	(0.4)	(0.32)	(0.35)	



## APPENDIX 10

### Chapter 5

AICc, Akaike weight ( $\omega_i$ ),  $\Delta$  value and model fit (deviance) for models of all site-level species groups within 2  $\Delta$  of the best model. Deviance relates to the magnitude of unexplained variance and the smaller the deviance, the better the model fit.

Response	Variables	AICc	$\omega_i$	$\Delta$	Deviance
<i>Richness</i>					
Mean Obs.	AltRang+MS	352.28	0.12	0	23.64
<i>Richness</i>					
	AltRang+RE+MS	353.06	0.08	0.77	25.42
	FHC+AltRang+MS	353.96	0.05	1.68	24.4
	AltRang+ExtUB+MS	354.17	0.05	1.88	24.17
Nectarivores	AltRang+ExtUB	339.45	0.08	0	15.12
	ExtUB	340	0.06	0.56	11.66
	AltRang+ExtUB+MS	340.71	0.04	1.26	16.5
	AltRang	340.99	0.04	1.55	10.09
	ExtUB+MS	341.14	0.04	1.69	12.93
Frugivore	AltRang+ExtUB	373.08	0.11	0	21.69
	AltRang+ExtUB+MS	373.33	0.10	0.25	24.12
	AltRang+MS	374.77	0.05	1.69	19.68
Insectivore	AltRang+MS	414.83	0.10	0	21.55
	FHC+AltRang+MS	415.37	0.08	0.53	23.69
	AltRang+RE+MS	416.13	0.05	1.30	22.78
	AltRang+ExtUB+MS	416.62	0.04	1.78	22.21
	FHC+AltRang+RE+MS	416.65	0.04	1.82	24.99
Carnivore	ExtUB	275.59	0.08	0	7.21
	ExtUB+RE	276.91	0.04	1.32	8.52
	Circ+ExtUB	276.99	0.04	1.40	7.21
	AltRang+ExtUB	277.12	0.04	1.53	8.25
	AltRang	277.33	0.03	1.75	4.73
Granivore	AltRang+MS	324.33	0.11	0	32.5
	AltRang	324.35	0.11	0.02	30.13

<b>Response</b>	<b>Variables</b>	<b>AICc</b>	<b><math>\omega_i</math></b>	<b><math>\Delta</math></b>	<b>Deviance</b>
Ground	FHC+AltRang	325.96	0.05	1.63	30.82
	AltRang+RE	326.22	0.04	1.89	30.55
	AltRang+DivFH	326.29	0.04	1.96	30.46
	AltRang+Circ	326.32	0.04	1.98	30.44
	AltRang+Circ+MS	326.32	0.04	1.99	32.87
	ExtUB	359.33	0.07	0	8.3
	AltRang+ExtUB	359.40	0.07	0.06	11.31
	AltRang	359.58	0.06	0.25	8.61
	AltRang+Circ+ExtUB	360.95	0.03	1.61	8.3
	FHC+ExtUB	361.12	0.03	1.79	8.97
Shrub	Circ+ExtUB	361.19	0.03	1.86	8.86
	ExtUB+DivFH	361.29	0.03	1.94	8.75
	AltRang+MS	395.73	0.08	0	21.46
	FHC+ AltRang+MS	396.49	0.06	0.76	23.34
	FHC+ AltRang	396.63	0.05	0.90	20.38
	AltRang+RE+MS	397.12	0.04	1.39	22.59
	AltRang+ExtUB+MS	397.19	0.04	1.45	22.52
	AltRang	397.29	0.04	1.56	16.78
	FHC+ AltRang+ExtUB	397.72	0.04	1.99	21.88
	Canopy	AltRang+MS	397.56	0.13	0
AltRang+ExtUB+MS		398.56	0.08	1	23.99
AltRang+RE+MS		399.18	0.06	1.62	23.27
FHC+AltRang+MS		399.42	0.05	1.86	22.99
Bark	AltRang+MS	144.35	0.09	0	16.88
	AltRang+DivFH+MS	144.8	0.07	0.45	17.75
	AltRang	145.81	0.04	1.46	15.02
	AltRang+ExtUB+MS	146.27	0.03	1.92	19.55
	AltRang+RE+MS	146.29	0.03	1.94	20.64

## APPENDIX 11

### Chapter 5

Ranked summed Akaike weights ( $\sum \omega_i$ ) from model averaging of the final subset of predictor variables for total richness and mean richness ( $\alpha$ ) of birds in different foraging guilds. Filled bars represent the variables for which the 95% confidence interval does not overlap zero.

