Fire and the conservation of the avifauna of mallee ecosystems

By

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Preface

I have written this thesis with the intention of publishing all of the data-based chapters. Consequently, each chapter includes an abstract, introduction, methods, results and discussion section. As each chapter is written to be a self contained publication there is necessarily some overlap between them, particularly regarding the description of the study site and survey design. However, I have chosen to present all chapters in full so that the reader does not need to refer back to previous sections as they read each chapter.

The work contained in this thesis was conducted as part of The Mallee Fire and Biodiversity Project; a large collaborative project between Deakin University and La Trobe University. The project began in 2006 with the objective of investigating the influence of the spatial and temporal properties of fire on a range of taxa; birds, reptiles, mammals, invertebrates and plants. The core project team included two principal researchers (Prof. Andrew Bennett and Assoc. Prof. Mike Clarke), a project leader (Dr. Kate Callister) and seven PhD students (Dale Nimmo, Lisa Spence-Bailey, Luke Kelly, Sally Kenny, Rick Taylor, Sarah Avitabile and I).

Due to the large scale of this project, a number of aspects were carried out collaboratively by the team. These included the design of the investigation, selection of the 28 study landscapes, mapping of the fire history and vegetation types of the region and field work to assess site habitat characteristics. I was involved in each of these aspects of the projects along with other members of the team. The influence of fire on avifauna within The Mallee Fire and Biodiversity Project was investigated by Rick Taylor at La Trobe University and myself. Rick and I collaboratively designed survey methods for birds, undertook bird surveys, collated bird data and conducted species detectability analyses.

The data presented in this thesis only represents a portion of that collected by Rick and I throughout this project. Data was collected using two different methods: pointcounts and 500m transects between point-counts. In this thesis the point-count data were used for all analysis because a) points were separated by relatively large distances, providing greater statistical independence and b) point-counts represented smaller areas and thus could be related directly to specific environmental attributes, whereas transects encompassed extensive environmental variation. However, transect data remains as a source of baseline data for future studies.

At the beginning of this project, Rick and I delineated separate themes for our theses to provide complementary information regarding separate questions about the bird community of this region. Rick's thesis centred on modelling habitat requirements of species and in determining changes to the diversity of avifauna and individual species in relation to the properties of landscape mosaics. In contrast, my thesis centres around the influence of fire on succession patterns at sites, the influence of spatial properties of fire on colonisation of burnt vegetation and the influence of landscape properties of fire mosaics on the composition of the avifauna.

In addition to my contribution to the collaborative aspects of the investigations (i.e. design of the study, preparatory work, field surveys, data collation and detectability

analysis), I personally reviewed all the literature, undertook all statistical analyses, prepared all figures and tables and wrote and revised all chapters in this thesis.

Due to the broadly collaborative nature of this project, several people were involved in discussions surrounding different chapters. Thus, each data chapter refers to "we" rather than "I" in recognition of the contributions of future co-authors (when this work is published). All chapters were discussed with my supervisor, Prof. Andrew Bennett, who has made comments on earlier drafts of each. Rick Taylor was involved in discussions of the research in all chapters; Dale Nimmo, Luke Kelly and Angie Haslem were involved in discussions of analysis techniques and research in Chapters 2 and 5.

During my PhD studies I also co-authored three published articles and a fourth manuscript currently in review (below). These contributions are directly relevant to the work contained herein and are appended to this thesis.

All photos within this thesis were taken by me, unless otherwise acknowledged.

Papers directly related to the work contained herein are as follows.

Published:

Clarke M.F., Avitabile S.C., Brown L., Callister K.E., Haslem A., Holland G.J., Kelly L.T., Kenny S.A., Nimmo D.G., Spence-Bailey L.M., Taylor R.S., **Watson S.J.** & Bennett A.F. (2010) Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. *Australian Journal of Botany*, **58**, 363–372

Haslem, A., Callister, K.E., Avitable, S.C., Griffioen, P. A., Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Taylor R.S., **Watson, S.J.**, Brown, L., Bennett, A,F. & Clarke, M.F. (2010) A framework for mapping vegetation over broad spatial extents: a technique to aid land management across jurisdictional boundaries. *Landscape and Urban Planning*, **97**, 296-305

Haslem, A., Kelly, L.T., Nimmo, D.G., **Watson, S.J.**, Avitable, S.C., Brown, L., Callister, K.E., Kenny, S.A., Spence-Bailey, L.M., Taylor, R.S & Bennett, A.F and Clare, M.F. (2011) Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology*, **48**, 247-256

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Acknowledgements

Completing a PhD turned out to be a mammoth undertaking. While I always knew that this would be the case, I was unaware of just how difficult the task would be. Certainly, when embarking on this journey, I was naive to the intense feelings of self-doubt that would ensue, or the anguish felt when staring at a blank computer screen. I now feel that undertaking a PhD has been a joyful experience that I would recommend to anyone... or at least anyone with a masochistic streak.

The difficulties of a PhD are vast, and I certainly feel that it would have been nigh on impossible to complete a thesis without the assistance of many people. Through the course of my studies I have been assisted by countless people that cannot all be named here. But, I am greatly appreciative of the support provided by all.

Firstly, thank you to my supervisor Andrew Bennett. Andrew's wisdom, advice and above all else patience have been critical to completion of my PhD. I feel honoured to have had the opportunity to work with Andrew, whose work-ethic and unwavering pursuit of excellence in ecology will remain an inspiration throughout my career.

To the principal members of the Mallee Fire and Biodiversity Project, I am greatly appreciative. Mike Clarke, Andrew Bennett, Kate Callister, Lauren Brown, Sarah Avitabile, Sally Kenny, Lisa Spence-Bailey, Dale Nimmo, Luke Kelly and Rick Taylor. To work in a team of 10 people, all under various amounts of stress, and not have a major falling out seems extraordinary. I am particularly thankful to Rick Taylor for being a fantastic person to work with as one half of 'Team Bird'. The members of the Landscape Ecology Research Group (Deakin University) have made coming into work a pleasure. Andrew Bennett, Michelle Bassett, Sarah Brown, Evelyn Chia, Rohan Clarke, Anna Flanagan, Heather Gibbs, Angie Haslem, Greg Holland, Luke Kelly, Lindy MacRaild, Annie Ouin, Dale Nimmo and Alistair Stewart.

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Abstract

Fire is an important disturbance process in many ecosystems around the world. Fireprone ecosystems account for greater than 40% of Earth's land surface. A key challenge for ecology and conservation is to develop an understanding of the influence of fire on biotic communities. Fire affects the biota through both temporal and spatial processes. Temporal effects of fire, particularly post-fire succession (i.e. the changes to species and communities through time), form the foundation of much of the knowledge of how fire influences ecosystems. The spatial properties of fire events (e.g. size, patchiness), and the spatial arrangement of patches of different fire history in a landscape (fire mosaics) also may influence biodiversity. However, there has been limited empirical research on the effects of the spatial properties of fires on biota. Knowledge of the influence of both spatial and temporal patterns on fauna will be critical to enact fire management strategies that will be effective for conservation of biodiversity, particularly birds. Inappropriate fire regimes are a threat to bird species around the world. In Australia alone, more than 50 bird species are threatened by fire related processes.

A large scale natural experiment was undertaken to investigate the influence of fire on birds. The study encompassed a 104,000 km² region of eucalyptus 'mallee' shrublands in the Murray Mallee region of inland south-eastern Australia. Twentyeight study landscapes, each ~1256 ha (circular areas with diameter 4 km), were carefully selected to represent different fire mosaics by stratifying by two properties: 1) heterogeneity of post-fire age-classes; and 2) a gradient in the proportional extent of mature vegetation. The avifauna were surveyed at 20 point-counts in each landscape, resulting in a total of 560 sites surveyed across the region. These sites formed a century long chronosequence.

To investigate the temporal responses of individual species of birds to fire, the influence of time-since-fire on the occurrence of 30 species was modelled, for sites spanning a 100 year post-fire chronosequence. The shape and timing of species responses were examined. Time-since-fire significantly affected the occurrence of 16 of the 30 species. The responses of these species represented a limited number of shapes: incline, decline, bell-shaped, irruptive, and plateau. One species was associated with early successional vegetation, five species peaked in occurrence between 20 and 50 years-since-fire and declined thereafter, and 10 species displayed their highest frequency of occurrence in vegetation >50 years since fire. Models of post-fire responses had only moderate predictive capacity.

Building on the knowledge of individual species responses, successional patterns through time were investigated at the level of the avifaunal community. The composition of bird communities became increasingly dissimilar between sites with increasing contrast between those sites in time-since-fire, up to at least 100 years. The rate of change in composition of the bird community slowed with increasing time-since-fire, resulting in communities occupying increasingly longer time-spans through the succession. There were three main successional stages defined by composition of avifaunal communities: <10, 20-40 and >50 years-since-fire. Older successional stages tended to support more species, but this was due to greater β diversity for sites in these seral stages, rather than an increase in α diversity in the oldest age classes. Species richness at sites is lowest directly after fire and increases up to ~10 years-since-fire, after which it plateaus.

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Time-since-fire also influenced the richness of particular species guilds. Nectarivore-insectivore and insectivore guilds each displayed low species richness in younger vegetation, increasing to a plateau at ~10 years-since-fire. The species richness of birds that forage in canopy foliage increased in older vegetation, while species richness of birds that forage on trunks and branches decreased in older vegetation.

To examine the influence of the spatial properties of fires on post-fire colonisation of sites by bird communities, the avifauna was investigated at recently burnt sites which varied in proximity to unburnt vegetation and in presence or absence of small unburnt patches of vegetation (biological legacies). Species richness, and the occurrence of some individual species, declined with increasing distance from unburnt vegetation. Sites that contained small unburnt patches displayed higher species richness and higher frequency of occurrence of one particular species (Chestnut-Quail-thrush). Patterns of decline with distance from unburnt vegetation had dissipated by 10 years post-fire. In the mallee ecosystem, most post-fire colonisation of recently burnt vegetation occurs from populations situated in vegetation outside the burnt area, rather than 'nucleated' recovery from individuals surviving within the burnt area.

The spatial patterns of individual fires (e.g. size and patchiness) and of multiple fires through time generate heterogeneous mosaics comprising patches of differing fire history (i.e. a fire mosaic). Spatial properties of fire mosaics significantly influenced the avifaunal composition in the landscape. The composition of communities changed along a gradient representing the proportional extent of recently burnt versus older vegetation in a landscape. Additionally, the composition was influenced by the position of the landscape along a geographic gradient of increasing aridity, and by the composition of vegetation types in the landscape. The spatial features of landscape mosaics also appeared to influence the incidence of primary nectarivores, which were not affected by time-since-fire at the site level. The diversity of different post-fire age-classes did not influence the avifaunal community at the landscape scale.

In general, bird communities displayed a directional succession pattern, likely to be related to changes in vegetation structure. However, there was substantial variation in successional patterns, and fire management based on temporal patterns alone may not be sufficient to conserve the avifauna. Older vegetation tended to be important for a greater number of species than younger vegetation and fire management may need to focus more on preserving this seral stage than on creating younger fire ages. The size and patchiness of fires significantly affects the time-taken for burnt areas to be colonised by birds, with smaller and patchier area being colonised more quickly than those burnt by larger and uniform fires. Because birds appear to colonise burnt areas mostly from vegetation outside the fire event or from large patches of unburnt vegetation, the context of a fire is an important feature (e.g. the amount and quality of vegetation surrounding the fire or remaining as large patches). The total extent of different seral stages, the temporal contrast of different seral stages and the scale at which landscapes are managed all need to be considered when managing fire to deliver heterogeneous mosaics. Fire management for the conservation of bird species in the Murray Mallee region may gain more predictable outcomes by primarily focusing on the required extent of particular seral stages, rather than focusing on creating diversity of fire seral stages.

Chapter 1

Introduction



Sunrise silhouettes the branches of burnt mallee eucalypts

"In the whole country I scarcely saw a place without the marks of a fire..." A comment by Charles Darwin about Australia, recorded in his diary while on the historic voyage of The Beagle, 1836.

1.1 Fire and conservation in ecological systems: a global perspective

Fire is a major agent of disturbance which significantly affects biodiversity, human society and climate patterns in ecosystems throughout the world (Bowman *et al.*, 2009). Fire has been present in ecosystems worldwide for hundreds of millennia (Bowman *et al.*, 2009), shaping historic and current distributions of biomes (Bond & Keeley, 2005; Bond *et al.*, 2005). Sixty-nine percent of the ecosystems on earth are considered fire prone (Krawchuck *et al.*, 2009). Fire has been identified as an important driver of ecosystem processes in a range of different vegetation communities including grasslands (Fuhlendorf *et al.*, 2006), savannah (Sankaran *et al.*, 2008), heathlands (Bullock & Webb, 1995), shrubland (Keeley & Fotheringham, 2001), woodlands (Hobbs, 2002), boreal forests (Angelstam, 1998), temperate forests (Burrows, 2008), tropical forests (Adeney *et al.*, 2006) and arid environments (Letnic & Dickman, 2005).

Fire influences the distribution and abundance of biota, both directly and indirectly, through a range of processes at different spatial and temporal scales. Primary (direct) effects of fire on biota are a consequence of the actual fire event. For example, direct mortality of plants and the combustion of vegetative matter alters the composition and structure of vegetation communities (Bond & Keeley, 2005; Midgley *et al.*, 2010); and the mortality and forced emigration of animals influences the composition of animal communities (Barlow & Peres, 2004b). Additionally, fires also have direct effects on abiotic components of the ecosystem, such as soil nutrients and soil water availability (Certini, 2005). The primary effects of fire can then have cascading secondary (indirect) effects on biota which may continue for many years after the fire event. Changes in resource availability (e.g. soil nutrients and soil moisture) can result in differential growth of different plant life-forms

(Keeley *et al.*, 2005), resulting in ongoing changes to the structure and composition of vegetation communities. Mortality and combustion of vegetative matter can result in competitive advantages to some plant species, affecting changes in the structure and composition of plant communities through interacting processes of inhibition/competition and facilitation (Callaway & Walker, 1997).

Secondary (indirect) effects of fire on faunal communities can come about through changes in structural resources (Jacquet & Prodon, 2009) and the availability of food resources (Barlow & Peres, 2004a), and through altered competitive interactions between species relating to these changes (Fox, 1982). At larger scales, such as landscapes, fire may affect the diversity of organisms and the distributional patterns of communities by promoting greater heterogeneity of habitats (Parr & Andersen, 2006; Klop & Prins, 2008). At even larger global scales, fire affects the biota through altered nutrient cycling (Smithwick *et al.*, 2009), by influencing the spatial extent and pattern of biomes (Bond *et al.*, 2005) and by affecting global climate patterns (Bowman *et al.*, 2009).

The processes by which fire affects biota relate to the properties of both individual fires and sequences of fires. Fire can be described by a few major properties which are outlined by the concept of the 'fire regime' (Gill, 1975), the description and history of fire events at a site or a region. The concept of the fire regime originally included three main components: the intensity of fire, the frequency of fire/inter-fire interval (Gill & Allan, 2008) and season of fire (Gill, 1975). Recently, spatial properties of fire also have been discussed as being a component of the fire regime (Bond & Keeley, 2005; Gill & Allan, 2008). Bond and Keeley (2005) conceptualised a modified fire regime which included five components: fuel

consumption and spread patterns, intensity, severity, frequency and seasonality. Components of the fire regime represent two facets: first, those which describe patterns amongst different fire events (frequency and inter-fire interval); and second, those which describe, and can differ between, individual fire events (fuel consumption and spread patterns, intensity, severity and season). The fire regime is a useful conceptual model for investigating the particular elements of fire that influence the biota.

A commonly investigated effect of fire on biota is the post-fire succession, representing the changes to the biota with time-since-fire. Understanding patterns of change in the biota over time has drawn the attention of ecologists for a long period (Cooper, 1913; Clements, 1916; Gleason, 1927; Odum, 1969). Many biotic changes in ecosystems occur with time-since-fire; for instance, changes in species richness (Keeley *et al.*, 2005), changes in the occurrence and abundance of individual species (Haney *et al.*, 2008) and changes in community composition and functional changes (Moretti *et al.*, 2009). However, detailed knowledge of processes causing these changes, and the generality (or lack thereof) amongst systems is less well understood, particularly for faunal communities (Whelan *et al.*, 2001).

Successional patterns for fauna are influenced by several ecological aspects, notably the ability of species to survive the disturbance event, the size of the post-disturbance population (Turner *et al.*, 1998; Franklin *et al.*, 2000), and the changes that occur in vegetation attributes, which affect the availability of resources for species (Fox, 1982; Jacquet & Prodon, 2009). The types of responses that species display to time-since-fire are highly varied (Woinarski & Recher, 1997); for example, some species are more abundant or occur more frequently in recently burnt vegetation (Hutto,

2008), some in temporally transient, 'mid-aged' vegetation (Brown *et al.*, 2009) and some in long-unburnt vegetation (Clarke *et al.*, 2005). The fidelity of species to particular post-fire age-classes also varies: while some species may be found almost exclusively in a particular successional stage, other species may simply occur in greater abundance in a particular stage but also be present in other stages (Hutto, 1995). Fidelity of species to particular fire-ages suggests that the presence of such age-classes through time will be important for maintaining and maximising populations of those species. However, solid understanding of changes in the abundance or occurrence of species is known only for a small number of well-studied species.

Inappropriate fire regimes, including both too-infrequent fire (Noss *et al.*, 2006) and too-frequent fire (Lindenmayer *et al.*, 2008), have been identified as threats to biota in ecosystems around the world. Consequently there has been increasing attention given to the implications of fire regimes for conservation management (Driscoll *et al.*, 2010b). Using fire as a tool for land management (e.g. prescribed burning) is widely employed in many countries, and is predicted to become increasingly prevalent in the future (Gill & Allan, 2008). Prescribed burning is used mainly to achieve two major goals: to protect human life and property (asset protection) and for ecological purposes to enhance biodiversity. These separate objectives may conflict (e.g. Driscoll *et al.*, 2010a). Management of fire is made more difficult by inadequate knowledge of the impacts of fire management scenarios on biodiversity (Driscoll *et al.*, 2010a).

Different species may respond in markedly different ways to a single fire event (Letnic, 2003), and the same species can respond differently to fires that occur in

different regions or years (Bain *et al.*, 2008; Lindenmayer *et al.*, 2009). An inability to reliably predict the impacts of different fire scenarios on biodiversity limits the ability of land managers to undertake appropriate management for conservation (Clarke, 2008). Understanding how different aspects of the fire regime affect populations and communities is critical to developing appropriate fire management for conservation (Gill *et al.*, 1999). Furthermore, anthropogenic burning can have long-lasting impacts on the biota. Indigenous Australian cultures have used fire as a tool to increase food availability throughout many areas of Australia (Bowman, 1998; Bliege Bird *et al.*, 2008), and likewise Native American cultures conducted traditional burning, such as in Californian chaparral ecosystems (Keeley, 2002). In each case, long-term changes to biota were brought about by these practices (Bowman, 1998; Keeley, 2002).

1.2 Landscapes and fire: a spatial perspective of fire

While much research in fire ecology has focussed on the impact of temporal patterns on the biota, there has been increasing interest in how spatial patterns of fire affect the biota (Bradstock *et al.*, 2005; Parr & Andersen, 2006; Gill & Allan, 2008). All components of the fire regime, their interactions and their variation in space and time generate heterogeneous landscapes, consisting of patches with different fire histories: such landscapes are often referred to as 'fire mosaics' (Bradstock *et al.*, 2005). Landscape ecology is a discipline that studies the properties of heterogeneous landscapes, with the explicit aim of ascertaining how landscape patterns influence ecological processes at broad spatial scales (Turner, 1989). Thus, investigation of the impact of the spatial aspects of fire mosaics is strongly aligned with landscape ecology principles, yet few studies have used landscape ecology as a basis for investigating the impact of fire on biota.

Fire-induced heterogeneity of landscapes can be generated through two different processes. First, individual fires generate heterogeneity through variation in the rate of fire spread and fuel consumption, creating patches of burnt and unburnt vegetation and patches of differing fire severity (Turner *et al.*, 1994) (Fig. 1.1a). Second, multiple fires through time generate heterogeneity of different vegetation ages (Fig 1.1b), and different fire histories where fires overlay each other (the 'invisible' mosaic) (Bradstock *et al.*, 2005).



Figure 1.1 Fire generated heterogeneity of landscapes, created through two processes: a) a mallee landscape in Murray-Sunset National Park, Victoria, Australia, containing burnt and unburnt vegetation elements, showing a local perspective of fine-scale heterogeneity created by an individual fire event, and b) a satellite image of a mallee landscape in Murray Sunset National Park, Victoria, Australia, showing different post-fire ages created by multiple fire events through time.

Spatial patterns of fire may affect biota at a local scale by influencing the context of sites or patches in relation to other post-fire ages. The importance of context (the

location of a patch or site in relation to its surroundings) is a core principle in landscape ecology; that is, 'context matters' (Wiens, 2009). Fire often removes species from a site, either through mortality or emigration (Barlow & Peres, 2004b). The spatial characteristics of an individual fire event, small or large, patchy or uniform, determine the proximity of recently burnt sites to refuges or source populations. In turn, this may influence the recolonisation process as isolation is a fundamental factor affecting colonisation (MacArthur & Wilson, 1967).

Further, unburnt patches represent 'biological legacies'; that is, organisms and organic material that persist through a disturbance event (Turner *et al.*, 1998; Franklin *et al.*, 2000). Biological legacies may be a critical influence on the succession of biota after the most recent disturbance event. Unburnt patches may act as refuges within the boundary of a fire, within which organisms survive and from which they recolonise burned areas (Turner *et al.*, 1998). The degree to which organisms can survive and repopulate from within a fire boundary, versus recolonising from habitats outside a fire boundary, may be an important factor in determining the time taken for faunal populations to recover from fire-induced declines (Bain *et al.*, 2008; Banks *et al.*, 2011). Even in situations where unburnt patches do not represent refuges within which species survive fire events, they may still be important habitats which provide food and structural resources (e.g. shelter, nesting locations), which may assist species to recolonise burned areas.

The spatial properties of fire mosaics may have further implications for biota when investigated at the scale of whole landscapes. Ecological studies often investigate the effect of spatial variables on biota at the scale of an individual patch or site: however, there has been increased interest in the impact of landscape processes on
the biota of 'whole landscapes' (Bennett *et al.*, 2006; Haslem & Bennett, 2008; Mortelliti *et al.*, 2010b). While site level studies can reveal important information about the impacts of different fire processes, inference about those processes must necessarily be at the scale of the unit of study, the site (Bennett *et al.*, 2006). Fire mosaics, however, comprise multiple elements representing different fire histories. To empirically investigate and understand how the properties of a fire mosaic affect the biota, both the response and predictor variables must be measured at the scale of the 'whole mosaic', or landscape (Bennett *et al.*, 2006).

Landscapes have emergent properties that are different to those of a patch or a site. Such properties include the total extent of a particular habitat type in the landscape, the composition of the landscape comprising different elements, and the spatial configuration of elements (Fahrig, 2003; Bennett *et al.*, 2006). By comparing whole landscapes as the unit of study, inferences can be made about the relative effects of different mosaic patterns and different landscape properties on the biota (e.g. Radford & Bennett, 2007; Haslem & Bennett, 2008). Undertaking studies of whole fire mosaics represents a significant challenge as there are few studies which have investigated the biota of whole mosaics, or which have investigated multiple patch types. Most such landscape-level studies have been carried out in agricultural landscapes (Radford & Bennett, 2007; Mortelliti *et al.*, 2010b), where habitats have been classified in a binary manner as 'habitat' and 'non-habitat' matrix, and have sampled the patches of habitat (Bennett *et al.*, 2006; Fahrig *et al.*, 2011). In contrast to such agricultural landscapes, few landscape studies have been undertaken in naturally heterogeneous systems such as that created by fire. Understanding fire ecology at the landscape scale is important because conservation management strategies often aim to maintain a 'mosaic' of patches with different fire histories (eg. Brockett *et al.*, 2001; Fire Ecology Working Group, 2004; Willson, 2006). However, any fire or sequence of fires will result in a mosaic; thus, the more important question is *which* mosaic is most appropriate for the target biota (Bradstock *et al.*, 2005)? In order to determine which mosaic is most appropriate (or not appropriate), the relative impacts of the different properties of fire mosaics on biota needs to be explicitly tested.

This question is particularly important in light of the increasing prevalence of 'patch mosaic burning' (PMB) for conservation management (Parr & Andersen, 2006), proposed in ecosystems around the world (Brockett *et al.*, 2001; Wilgers & Horne, 2006; Cochrane *et al.*, 2009). Patch mosaic burning is a management approach whereby fire is manipulated to maintain or increase the heterogeneity of patches with differing fire histories in a landscape (Parr & Andersen, 2006). The rationale is that a greater diversity of fire histories will provide for a greater diversity of organisms (Tews *et al.*, 2004; Parr & Andersen, 2006; Faivre *et al.*, 2011). This approach, while intuitively appealing, remains untested at the landscape scale. The rationale is largely based on inference from studies at the site scale, and does not account for the influence of spatial parameters of fire or the properties of whole landscapes (Bennett *et al.*, 2006).

A major issue with the patch mosaic burning paradigm is that it does not account for the extent (total amount) of a particular habitat element. The total extent of habitat in a landscape has commonly been identified as an important predictor of the status of the biota in human-modified landscapes (Bennett *et al.*, 2006; Radford & Bennett,

2007; Mortelliti *et al.*, 2010a) and may be an important factor influencing the persistence or localised extinctions of species (Radford *et al.*, 2005). The total extent of a particular post-fire age-class in a fire mosaic could have an equally important effect for faunal species. For a species that requires a particular post-fire seral stage, the extent of vegetation in the landscape with that history is likely to influence the size and sustainability of the population in the landscape, the total food resources available and the permeability of the landscape for dispersal.

Landscape ecology also recognises the importance of heterogeneity of patch types (composition) on diversity in ecological systems (Brennan *et al.*, 2002). In fire mosaics this can be represented by the heterogeneity of patches of differing fire history, which is the foundation of the patch mosaic burning paradigm in fire ecology and conservation management (Parr & Andersen, 2006). As discussed, heterogeneity generated by the patchiness of an individual fire may affect an organism's survival in that fire event, and also represent a 'biological legacy' which influences patterns of recovery (Franklin *et al.*, 2000). Heterogeneity generated by multiple fires through time may influence the composition of the community through other processes. For example, species may benefit from complementary resources from different fire age-classes. Some bird species are known to forage in early seral stages but require long-unburnt vegetation for nesting (Benshemesh, 1990). However, it is difficult to assess if species require diverse fire ages or simply use alternative fire ages adjacent to a population (Burbidge *et al.*, 2007).

1.3 The effect of fire on birds

Ecological studies investigating the effects of fire on birds have commonly focussed on investigating post-fire successional patterns. Following fire, burned areas are

often quickly colonised by some bird species (Reilly, 1991; Hutto, 1995; Fuhlendorf *et al.*, 2006; Lindenmayer *et al.*, 2008). Following initial colonisation, changes in species composition and turnover of species with time-since-fire are often observed, with selected species being associated with 'early' (Probst & Weinrich, 1993; Hutto, 1995), 'mid' (Brown *et al.*, 2009) or 'late' (Fontaine *et al.*, 2009; Hingston & Grove, 2010) succession vegetation, respectively. The timing of 'early', 'mid' and 'late' succession categories, however, can vary substantially between ecosystems. In grasslands, some species occurring at ~4 years post-fire are considered to be late succession species (Brawn *et al.*, 2001), whereas in forest ecosystems late succession species may be those that favour forest stands at hundreds of years since disturbance (Hobson & Bayne, 2000). Within any ecosystem, the times at which species enter or exit the succession represent critically important information for fire management for conservation, in order to maintain or provide an age-class structure of the vegetation that will provide for particular species of concern.

Detailed knowledge of the processes causing patterns of species change through time can be difficult to determine. Patterns of change are often associated with changes in resources such as food types, with change in structural features, or with interactions of both. For example, the Black-backed Woodpecker *Picoides arcticus* has been associated with early succession vegetation in forests of North America (Murphy & Lehnhausen, 1998; Hutto, 2008), where larvae of wood-boring beetles (Cerambycidae) are in high abundance (Murphy & Lehnhausen, 1998). In Australian savannas, early successional vegetation often supports higher densities of ground-foraging raptors, carrion feeders, and granivores, because fire clears dense grassy vegetation and provides access to food resources on the ground (Woinarski, 1990; Woinarski *et al.*, 1999). In North-American prairies, fire influences the

abundance of grass litter and the amount of bare-ground, which subsequently influences the presence of particular bird species, such as Henslow's Sparrow *Ammodramus henslowii*, Upland Sandpiper *Bartramia longicauda* and Killdeer *Charadrius vociferus* (Fuhlendorf *et al.*, 2006). Cavity nesting and canopy nesting species have often been associated with later succession vegetation, likely due to the time required for these structural properties to develop (Hobson & Bayne, 2000; Saunders *et al.*, 2003); larger older trees tend to have a greater abundance of cavities (Gibbons *et al.*, 2000).

There have been relatively few empirical investigations of the direct impact of fire on birds. There are conflicting reports on the level of mortality of birds caused by fire, with suggestions both of very high levels of mortality and of most birds escaping fires (Woinarski, 1999). Birds may be susceptible to mortality from fire events for two morphological reasons. First, birds have highly efficient gas transfer membranes in their respiratory systems (West *et al.*, 2006), making them potentially susceptible to death via smoke inhalation. However, several species are known to be attracted to fire fronts, taking insects flushed by the flames (Woinarski, 1999). Presumably these species at least must be able to either avoid the smoke column or have some level of tolerance. Second, many bird species are susceptible to thermal stress (Marder, 1983) and high temperatures reached in fire events could lead to direct mortality.

Contrasting views, pointing to the capacity of birds to avoid mortality from fire, also exist. Foremost is the relatively high mobility of birds and thus an ability to flee fire events. It has been noted that many species can survive the initial conflagration, but decline in abundance in the aftermath (Rowley & Brooker, 1987; Wooller & Calver, 1988; Benshemesh, 1990); the speed and intensity of the fire will play a significant role in this. Determining the impacts of fire events on mortality is inherently difficult, and it is likely that variation between fires (e.g. in intensity, patchiness) will result in different levels of mortality of birds (Whelan *et al.*, 2001), thus leading to the contrasting observed responses.

The spatial aspects of fire regimes may influence bird communities in a variety of ways. The spatial continuity of fires, represented by the level of patchiness, can vary substantially (Turner *et al.*, 1998) and the presence of unburnt patches of vegetation, representing 'biological legacies', can act as refuges which influence the survival of bird species during the fire event (Rowley & Brooker, 1987; Benshemesh, 1990) and provide shelter after fires (Benshemesh, 1990). The scale of fires may also be an important factor for bird communities; the extent of burned areas (e.g. size of a fire) can influence the species richness of birds that are prefer early succession stages because larger fire create more habitat for these species (Pons & Bas, 2005).

The context of a fire also may affect post-fire bird assemblages. Where fires occur in habitats in which species are isolated from other populations, the dispersal abilities of different species may dictate the post-fire assemblage (Brotons *et al.*, 2005). Similarly, the context of a fire relative to the different types of vegetation which surround the burnt area, may also affect the types of species available to recolonise (Moreira *et al.*, 2003). A further consideration is the context of a site *within* a fire; its position relative to unburnt vegetation can affect recolonisation of sites (Bain *et al.*, 2008; Lindenmayer *et al.*, 2009). In agricultural landscapes, habitat fragmentation (Fischer & Lindenmayer, 2007) is known to affect the richness and composition of bird assemblages which require wooded or forest vegetation. Thus it may be possible that where fire turns extensive wooded regions into fragments of

wooded vegetation in an open or shrubby matrix, bird species may be negatively affected by habitat fragmentation processes, however this hypothesis has not been supported by empirical research (Herrando & Brotons, 2002).

1.4 Mallee ecosystems

'Mallee' is a colloquial term that refers to the growth form of a tree (multiple stems arising from an underground lignotuber), and more generally to the vegetation and the region in which such trees occur. 'Mallee' vegetation occurs widely in the semiarid rainfall zone (200-500 mm) of southern Australia (Bradstock & Cohn, 2002), and encompasses an area of approximately 250,000 km² across the south of the continent (Cofinas & Creighton, 2001) (Fig. 1.2). Mallee ecosystems are characterised by a hot dry climate, with mean maximum temperatures in summer >30° C, and temperatures regularly exceeding 40° C (Australian Bureau of Meteorology, 2010).

This investigation took place in the Murray Mallee region of south-eastern Australia, encompassing an area of ~104,000 km² (Fig. 1.2). Hereafter, discussions of mallee vegetation and the mallee avifauna refer to this area. The Murray Mallee region has undergone extensive changes through land clearing since European settlement (c. 35% since 1850), although much of the *Eucalyptus* dominated mallee shrubland vegetation has remained, largely due to the poor productivity of these soils for agriculture (Bradstock & Cohn, 2002). The region is highly fire prone: small fires occur irregularly throughout the region, and large fires (10,000 - 100,000 ha) occur on an approximately decadal basis (Bradstock & Cohn, 2002; Avitabile *et al.*, 2011). However, the spatial distribution of fires is such that typically there are long intervals between fires at most sites. From 1972 to 2007, despite 40% of the area covered by mallee vegetation being burnt, only 3% was burned more than once (Avitabile *et al.*,2011). Most fires are ignited through lightning strikes (Bradstock & Cohn, 2002).



Figure 1.2 Map of the Murray Mallee study region showing fires from 1972present, mapped using satellite imagery. State and reserve boundaries are also shown. Reserves are numbered: 1) Danggali Conservation Park, 2) Gluepot Reserve, 3) Billiatt Conservation Park, 4) Murray-Sunset National Park, 5) Hattah National Park, 6) Mallee-Cliffs National Park, 7) Petro Reserve, 8) Lethero Reserve, 9) Tarawi National Park, 10) Scotia Sanctuary. Inset shows the extent of mallee vegetation across southern Australia and the location of the Murray Mallee study region.

The importance of mallee vegetation for many species of plants and animals has resulted in the creation of an extensive reserve system. This investigation was conducted across ten reserves in the region (Fig. 1.2). These extensive reserves coupled with a pattern of both historic and recent fires make mallee an excellent ecosystem in which to investigate the impacts of fire on biota.

1.4.1 Vegetation of the Mallee

'Mallee' vegetation communities generally consist of a low canopy (<10 m) formed by multi-stemmed 'mallee' *Eucalyptus* species which dominate the vegetation, and an understorey of shrubs and perennial and ephemeral grasses (Bradstock & Cohn, 2002). These communities usually exist on dry sandy soils without any natural permanent surface water and intergrade into tall woodland vegetation types near the major watercourses of the region. These woodlands of Black Box *E. largiflorens* and River Red Gum *E. camaldulensis* generally form a narrow zone between mallee vegetation and permanent water.

Three broad vegetation categories, Triodia Mallee, Chenopod Mallee and Heathy Mallee, can be recognised on the basis of the composition of plant species (Fig. 1.3) (Haslem *et al.*, 2010). Although more detailed vegetation communities have been described for parts of the region (e.g. Hill, 1989; White, 2006), such finer classification has not been done systematically across the entire region. Triodia Mallee vegetation occurs on sandy soils, has an understorey of the hummock grass *Triodia scariosa*, an overstorey dominated by *Eucalyptus dumosa* and *E. socialis*, and commonly also contains shrubs such as *Acacia rigens*, *A. wilhelmiana* and *Beyeria opaca*. In contrast, Chenopod Mallee occurs on soils with higher clay content, has a sparse understorey of shrubs such as *Olearia* spp., *Zygophyllum* spp. and chenopod species including *Maireana pentatropis*, *Enchylaena tomentosa* var. *tomentosa* and *M. pyramidata*, and an overstorey typically including *E. oleosa* subsp. *oleosa* and *E. gracilis*. Heathy Mallee is restricted mainly to southern parts of the study area, occurring primarily on deep siliceous Lowan Sands. It has a diverse shrubby understorey of 'heath-like' plants (e.g. *Callitris verrucosa, Leptospermum coriaceum, Phebalium bullatum, Babbingtonia behrii, Hakea leucoptera*) (Haslem *et al.*, 2010).



Figure 1.3 Three broad categories of mallee vegetation encountered in the Murray Mallee region: a) Triodia Mallee, b) Chenopod Mallee, c) Heathy Mallee. Note the dense understorey of *Triodia scariosa* hummock grass in Triodia Mallee, the sparse understorey of chenopod shrubs in Chenopod Mallee and the dense understorey of shrubs in Heathy Mallee. Photos: Mallee Fire and Biodiversity Project. Mallee vegetation is highly flammable and many plant species have life-history attributes related to recurrent disturbance (Pausas & Bradstock, 2007). When fire occurs it typically removes both the understorey and canopy vegetation (Noble & Vines, 1993) (Fig. 1.4), effectively returning vegetation to a structurally similar state after each fire (i.e. setting succession to year zero). Fuel continuity plays an important part in determining fire spread (Noble & Vines, 1993; O'Donnell *et al.*, 2010) and patches of vegetation may remain unburnt where fuel is discontinuous. The dominant features of fire in mallee vegetation are the death of the above ground biomass of mallee eucalypts and combustion of the grass and shrubs (Fig 1.4). Regeneration of vegetation post-fire is dominated by resprouting of the mallee *Eucalyptus sp* from underground lignotubers, and regeneration of understorey plants from both rootstock (resprouting) and recruitment from seed (Parsons, 1968; Cheal *et al.*, 1979).

In addition to differences in species composition, these broad vegetation types also vary in vegetation structure and fuel loads (Haslem *et al.*, 2011), resulting in different fire behaviours. Different patterns in the position and continuity of fuels in mallee vegetation result in different fire behaviours and fire sizes (Noble & Vines, 1993). Large fires can occur in years that are preceded by either dry or wet conditions (Cheal *et al.*, 1979; Avitabile *et al.*, 2011). In years preceded by dry or average conditions, fires tend to carry through mallee shrublands based on fuel loads of perennial *Triodia* grasses and litter, (Fig. 1.5). In years preceded by wet conditions, large fuel loads caused by hyper-abundant ephemeral grasses (eg. *Stipa* sp.) can result in very extensive wildfires (>1,500,000 ha) (Noble & Vines, 1993).



Figure 1.4 Triodia Mallee vegetation at different stages of time-since-fire: a) <1 year, b) 2 years, c) 10 years, d) 22 years, e) 52 years and f) 94 years. Note the resprouting of *Eucalyptus sp*. from underground lignotubers and regeneration of understorey grasses and shrubs, particularly *Triodia scariosa* hummock grasses. Photos: Mallee Fire and Biodiversity Project.



Figure 1.5 Fire burning in different vegetation types and carried through different fuels: a) Triodia Mallee, high flames carried through combustion of perennial *Triodia scariosa* hummock grasses with high continuity of fuel; and b) Chenopod Mallee, flames carried largely through leaf litter and small debris. Photos: Lauren Brown.

1.4.2 The avifauna of the Murray Mallee

The Murray Mallee region supports a unique avifauna that has attracted ornithologists for >100 years (Mattingley, 1909; Wilson, 1912; Chandler, 1913; Howe & Tregellas, 1914). Approximately 240 species of birds have been recorded from this region in south-eastern Australia (HANZAB, 2006); but only ~100 species are regularly encountered in mallee vegetation. Other species are vagrants or species associated with other ecosystems (e.g. waterbirds associated with the wetland and riverine ecosystems). The investigations and discussion in this thesis refer only to species which regularly use mallee vegetation. These species represent 11 orders and 30 families. Some of the avifaunal families characteristic of mallee vegetation are described below (section 1.4.3). Taxonomy for all species in this thesis follows Christidis & Boles (2008). Twenty-three species of birds which commonly use mallee vegetation are identified in threatened species legislation in at least one of the three states (Victoria, New South Wales and South Australia), or federally. Many of these threatened species have undergone severe population declines and have become locally extinct in other parts of their range, with their known distribution contracting towards mallee environments (Garnett & Crowley, 2000). Additionally, many species not listed as threatened, such as the Red-capped Robin *Petroica goodenovii* have also undergone significant declines in parts of their geographic range (Ford *et al.*, 2001; Mac Nally *et al.*, 2009). Large reserves may be important refuges for maintaining populations that cannot persist in more fragmented systems within their range.

The mallee avifauna may be strongly affected by different fire regimes. The occurrence of eleven threatened species has been positively associated with vegetation >20 years since-fire and several species with vegetation >40 years since-fire (Clarke, 2005). To date, most studies investigating the response of the mallee avifauna to fire have been of threatened species; to my knowledge this is the first study to investigate the response to fire of the overall avifaunal community across the entire region. Three species studied in greater detail are the Black-eared Miner *Manorina melanocephala* (Clarke *et al.*, 2005), Mallee Emu-wren *Stipiturus mallee* (Brown *et al.*, 2009) and the Malleefowl *Leipoa ocellata* (Benshemesh, 1990). Each of these species has a low frequency of occurrence in recently burnt vegetation. Black-eared Miners and Malleefowl display a preference for older vegetation >40 years since-fire (Benshemesh, 1990; Clarke, 2005; Clarke *et al.*, 2005), whereas the Mallee Emu-wren has its highest frequency of occurrence in vegetation 16-29 years since-fire and, although present, is less common in vegetation >29 years since-fire (Brown *et al.*, 2009).

These data support the contention that fire may locally restrict species populations (Clarke, 2005). Most investigations of birds and fire have not considered the response of species to fire over long time-frames, and consequently the length of time that species remain at their highest abundance is unknown (Clarke, 2005). Further, the few studies of the responses of species to fire in mallee ecosystems generally have not distinguished between the more southerly heathlands and malleeheath and the more northerly tree-mallee vegetation of the Murray Mallee. These ecosystems have different vegetation characteristics and changes in vegetation postfire (Cheal *et al.*, 1979; Pausas & Bradstock, 2007; Haslem *et al.*, 2011).

1.4.3 Examples of characteristic avifaunal families of the Murray Mallee region



Malleefowl mound partially filled with organic material



MEGAPODIDAE: Malleefowl Number of Species: 1

Primary Diet: Seeds and vegetative matter **Nesting:** Eggs are laid in a large mound (*c*. 5 m diameter, 1 m high) built from soil and organic matter

Threatened Species: 1 Malleefowl *Leipoa ocellata*

This species is nationally vulnerable and exceedingly rare. It requires long unburnt habitat. Fire is a key threatening process (Benshemesh, 1990; Garnett & Crowley, 2000).

Australian Ringneck Parrot Barnardius zonarius

Rohan Clarke



Major Mitchell's Cockatoo Lophochroa leadbeateri



PSITTACIDAE and CACATUIDAE: Parrots Number of Species: 8 Primary Diet: Seeds

Nesting: Tree hollows Threatened Species: 3 Major Mitchell's Cockatoo, *Lophochroa leadbeateri* Scarlet-chested Parrot *Neophema splendida* Regent Parrot *Polytelis anthopeplus*

Parrots in mallee vegetation are highly mobile and require large hollows; a habitat attribute that is influenced by fire (Haslem *et al.*, 2011).

Striated Grasswren *Amytornis striatus*

Mallee Emu-wren Stipiturus mallee



MALURIDAE: Malurid Wrens Number of Species: 4 Primary diet: Arthropods Nesting: Built nest Threatened Species: 2 Mallee Emu-wren *Stipiturus mallee* Striated Grasswren *Amytornis striatus*

Malurid wrens are small birds (adult weight = 5.5 - 21g), thus are likely to display relatively poor mobility. Mallee Emu-wren and Striated Grass-wren are strongly associated with *Triodia* hummock grasses (HANZAB, 2006), which is highly flammable and the cover of which is affected by fire (Haslem *et al.*, 2011).

Spotted Pardalote *Pardalotus punctatus*



Striated Pardalote *Pardalotus striatus*



PARDALOTIDAE: Pardalotes Number of Species: 2 Primary diet: Arthropods Nesting: Tree hollow / burrow Threatened Species: 0

Spotted Pardalotes almost solely use burrows, whereas Striated Pardalotes more commonly use tree hollows, although both species have been recorded using each nesting arrangement (HANZAB, 2006).

Shy Heathwren Calamanthus cautus







ACANTHIZIDAE: Australian Warblers Number of Species: 4 Primary diet: Arthropods Nesting: Nest / Tree hollow Threatened Species: 1 Shy Heathwren *Calamanthus cautus*

Studies have linked Shy Heathwren to both young (Woinarski, 1999) and older vegetation (Clarke, 2005). One species, Chestnut-rumped Thornbill *Acanthiza uropygialis*, uses hollows for nesting.

Brown Headed Honeyeater Melithreptus brevirostris



Grey-fronted honeyeater Lichenostomus plumulus



MELIPHAGIDAE: Honeyeaters and Wattlebirds Number of Species: 13 Primary diet: Nectar / Invertebrates Nesting: Built nest

Threatened Species: 1 Black-eared Miner *Manorina melanotis*

This family is the most diverse of mallee birds. Diets of these species are variable. Most species are somewhat nectarivorous although there are varying amounts ofinsectivory. The Black-eared Miner is critically endangered and requires vegetation >40 years since-fire (Clarke *et al.*, 2005); thus fire is a key threatening process. Chestnut-crowned Babbler Pomatostomus ruficeps White-browed Babbler Pomatostomus superciliosus



POMATOSTOMIDAE: Babblers Number of Species: 2 Primary diet: Arthropods Nesting: Built nests Threatened Species: 0

Babblers forage mostly on the ground or the lower trunk and branches of trees, are gregarious and display complex social structures. Individuals often build several nests, although only use one and the nest is often attended by helpers (HANZAB, 2006).

Chestnut Quail-thrush *Cinclosoma castanotus*



Red-lored Whistler Pachycephala rufogularis



Golden Whistler Pachycephala pectoralis



PSOPHODIDAE: Quail-thrush and Whipbird Number of Species: 2 Primary diet: Arthropods Nesting: Built nests Threatened Species: 2 Chestnut Quail-thrush *Cinclosoma castanotus* Western Whipbird *Psophodes nigrogularis*

Chestnut Quail-thrush is relatively common in mallee habitats, but has undergone severe declines in parts of their range. The mallee form of the Western Whipbird is critically endangered; fire is thought to be a primary cause of its decline (Clarke, 2005).

PACHYCEPHALIDAE: Whistlers, Shrike-thrush and Crested Bellbird Number of Species: 5 Primary diet: Arthropods Nesting: Built nests Threatened Species: 3 Gilbert's Whistler Pachycephala inornata Red-lored Whistler Pachycephala rufogularis Crested Bellbird Oreoica gutturalis

Crested Bellbirds are relatively common in mallee environments but have undergone severe declines in parts of their range. Red-lored Whistlers can be locally common, but are regionally rare (Clarke, 2005). Masked Woodswallow Artamus personatus **Grey Butcherbird** *Cracticus torquatus*





ARTAMIDAE: Butcherbirds, Cuckoo-Shrikes, Currawong and Woodswallows Number of Species: 8 Primary diet: Arthropods Nesting: Built nests & Hollows Threatened Species: 0

A diverse family, species in this group range in size and foraging strategies, with larger species being predatory on several small vertebrates. Although most Artamidae are resident in mallee, Woodswallows are summer migrants.

Red-capped Robin *Petroica goodenovi*



Southern Scrub-robin Drymodes brunneopygia

Primary diet: A Nesting: Built ne Threatened Spe Southern Scrub-1 brunneopygia Hooded Robin M Jacky Winter Mic capped Robin Pe although not three

PETROICIDAE: Robins Species: 4 Primary diet: Arthropods Nesting: Built nests Threatened Species: 2 Southern Scrub-robin Drymodes brunneopygia Hooded Robin Melanodryas cucullata

Jacky Winter *Microeca fascinans* and Redcapped Robin *Petroica goodenovii*, although not threatened species, also have declined in other parts of their range (Ford *et al.*, 2001).

1.5 Overview of thesis objectives and structure

This thesis investigates the ecological influence of fire in shaping avifaunal communities of mallee vegetation in the Murray Mallee region. The avifauna of this region represents a diverse, unique and potentially fragile assemblage, with a long held fascination for many people, both scientist and enthusiast. The interest in the avifauna of this region has the potential to increase awareness of the conservation of other mallee taxa. Furthermore, birds represent a useful taxon for managers as they are conspicuous and feasible to monitor. The dataset amassed through this investigation represents the largest that has been systematically collected on the entire mallee avifaunal assemblage across this entire region. This dataset has the potential to make an important contribution to scientific knowledge and ecological management in this region.

The concept of providing useful and useable information to guide conservation and management of the avifauna with regard to fire in this region is a consistent theme throughout the chapters. My primary objective was to investigate the effects of two different, yet intricately related aspects of fire on birds: first, the relationship between temporal processes of fire and bird communities; and second the relationship between spatial properties of fire and bird communities. These two facets form complementary themes throughout the thesis.

Each data chapter focuses primarily on one or other of the major themes. Chapters 2 and 3 examine the influence of temporal parameters of fire on avifauna, whereas chapters 4 and 5 investigate the influence of different spatial properties of fire on avifauna. A brief summary of each of the chapters is given below.

Chapter 2 investigates the temporal effects of fire on the distributions of individual species. This chapter has four main objectives: 1) to investigate the influence of fire history on species occurrences; 2) to determine the different types of temporal responses displayed by species of birds to fire, and the generality of these responses amongst species; 3) to investigate the importance of different post-fire ages for the occurrence of different species; and 4) to investigate the usefulness of this type of information for predicting species distributions and thus management.

Chapter 3 aims to build on knowledge gained in Chapter 2 about individual species. This chapter investigates the temporal effects of fire at the level of the community, focussing on the patterns in the avifauna caused by succession processes. The objectives of this chapter are to investigate the effect of time-since-fire on the species richness and composition of avifaunal communities at survey sites; to examine the rate of change in species assemblages with time-since-fire and the impact this has on community distinctiveness; and to investigate potential processes influencing patterns of avifaunal succession and their impact on the richness of different guilds.

Chapter 4 navigates the importance of two spatial aspects of fire on post-fire colonisation of sites: 1) proximity to unburnt vegetation; and 2) patchiness of a fire. In this chapter, the influence of these spatial aspects on species richness and the occurrence of individuals at recently burnt sites are investigated with the objective of gaining insights into the different colonisation strategies of birds, the importance of biological legacies to site colonisation, and the time taken for colonisation to occur.

Chapter 5 uses a whole-of-landscape design to investigate the importance of the spatial properties of the fire mosaic on the composition of the avifaunal assemblage in the whole landscape. This chapter also aims to determine the processes by which landscape properties may influence species composition and affect the functional composition of the avifauna of landscapes.

Finally, in **Chapter 6** I present a summary and synthesis of the key findings of the study and discuss their implications for conservation and management of the avifauna of mallee ecosystems.



Figure 1.6 Outline of the structure of this thesis

Chapter 2

Effects of time-since-fire on bird species: how informative are generalised fire response curves for conservation management?



Yellow-plumed Honeyeater Lichenostomus ornatus



Chestnut-rumped Thornbill Acanthiza uropygialis

2.1 Abstract

Fire is a widespread disturbance process that affects the distribution of faunal species. An important issue for conservation management in fire-prone environments is to understand changes in the occurrence of species after fire, and whether such post-fire responses represent a small set of generalised species' responses to fire. We analysed the response of 30 species of birds to time-since-fire at 499 sites distributed over a 104,000 km² region of semi-arid shrubland in southeastern Australia. We used non-linear regression to model patterns in species occurrence with time-since-fire in two vegetation types and compared them with generalised response shapes from the literature. We then tested the ability of the models to predict species distributions using seven-fold cross-validation. The occurrence of 16 species was significantly affected by time-since-fire, and they displayed a limited number of response shapes. Early succession specialists appear to be uncommon in mallee ecosystems, with the frequency of occurrence of 14 of the 16 species being highest in mid or older successional vegetation (>30 years-sincefire), and only one species in early successional vegetation (<5 years-since-fire). However, the occurrence of a further five species declined between 50 - 100 yearssince-fire. Model predictive ability was reasonable for eight species, low for seven species, and little better than chance for one species. In mallee ecosystems, periodic fire is a critical influence on the habitats used by bird species. Mid and older-aged vegetation are disproportionately important, and too-frequent fire could have severe effects on species populations. Relying on time-since-fire as a surrogate for species occupancy, however, may be ineffective in light of the limited predictive ability of time-since-fire models for the distribution of species over broad spatial scales and their varied responses in different vegetation types.

2.2 Introduction

Fire is a natural disturbance process that influences the structure of ecological communities throughout the world (Bowman *et al.*, 2009). Fire can also be used as a tool for land management and conservation, being widely employed for managing fuel loads to control unplanned fires (Gill & Allan, 2008), and to provide particular fire age-classes of vegetation to promote faunal populations (Parr & Andersen, 2006). Further, it has been predicted that fire will increasingly be employed as a management tool in the future (Gill & Allan, 2008). Nevertheless, the response of many species to fire is poorly understood, and inappropriate fire regimes are a threatening process for many species and communities worldwide (e.g. Woinarski, 1999; Covert-Bratland *et al.*, 2006; Fuhlendorf *et al.*, 2006; Sara *et al.*, 2006; Slik & Balen, 2006). Birds may be particularly vulnerable to inappropriate fire regimes. In Australia alone, inappropriate fire regimes are associated with five extinct species or sub-species of birds, and are recognised as a threatening process for more than 50 species (Woinarski, 1999).

Knowledge of the pattern of occurrence or abundance of species with time since fire ('fire-response-curves') is valuable for fire management (Driscoll *et al.*, 2010). Fire-response-curves indicate the extent to which species depend on particular post-fire ages and may also identify critical thresholds in time-since-fire necessary to provide required habitat resources (Keith *et al.*, 2001; Driscoll *et al.*, 2010). If there are 'generalised' fire-response-curves, such that a limited number of patterns represent the responses of many species (see Fig. 2.1), this may offer important insights for the conservation management of species. Generalised fire-response-curves are an attractive prospect for wildlife managers, as they suggest that management to attain a limited number of fire regimes will provide for many species. However, knowledge

of temporal responses to fire is scarce for many species, even in fire-prone environments. Furthermore, there have been few empirical investigations to test whether patterns of species' responses to fire are useful in predicting their geographic occurrence at broad spatial scales.

Many studies of faunal populations and fire have focussed on the responses of just one or a few species (e.g. Breininger & Oddy, 2004; Hutto, 2008; Brown *et al.*, 2009). They have documented a diverse range of responses to time-since-fire (Whelan *et al.*, 2001): some species favour recently burnt vegetation (Hutto, 2008) while others occur in long-unburnt vegetation (Clarke *et al.*, 2005). However, comparison of responses among multiple species may provide insights into the relative importance of fire in structuring faunal assemblages and the generality of responses amongst species.

Studies that examine the responses of fauna to particular fire treatments, to single fire events, or to a few fire events are often conducted over short time-frames (eg. Smucker *et al.*, 2005; Adeney *et al.*, 2006; Covert-Bratland *et al.*, 2006; Fuhlendorf *et al.*, 2006). These provide important knowledge, but an understanding of species' responses over long time-frames, commensurate with the duration of successional processes, remains scarce in many ecosystems. While techniques such as dendrochronology have been used to assess patterns of succession in attributes such as vegetation biomass over hundreds of years (Pare & Bergeron, 1995), few investigations of faunal responses have extended over periods of a century or more. Additionally, studies that do investigate long time-frames seldom do so across broad geographic scales, which may result in localised patterns obscuring successional patterns (Johnson & Miyanishi, 2008). Investigations of long-term trends at spatial

and temporal scales commensurate with that at which ecosystems operate are an important complement to detailed short-term and manipulative studies. The former may reveal patterns not apparent at short time-scales, allowing for more informed management decisions (Clarke *et al.*, 2010).

In this study, we test the influence of fire on the occurrence of avifaunal species in a regional assemblage, and the shape of fire response curves displayed over an extended time-frame. We investigate whether fire response curves display generality amongst species in an assemblage, whether they conform to *a priori* patterns proposed in the literature (Whelan *et al.*, 2001) (Fig. 2.1), and we examine the role of different successional stages in supporting bird species. Finally, we test how informative post-fire response patterns are in determining species distributions across broad spatial extents? We use data from avifaunal surveys at 499 sites representing a 100-year chronosequence of time-since-fire in semi-arid *Eucalyptus* shrublands of south-eastern Australia.



Time since fire

Figure 2.1 Generalised post-fire response curves for species, adapted from Whelan *et al.* (2001). These curves show eight possible relationships between the frequency of occurrence of bird species and time-since-fire: a) solid line = incline (occurrence lowest in young vegetation, increases monotonically to be highest in oldest vegetation), dashed line = decline (occurrence highest in young vegetation, decreases monotonically to be lowest in oldest vegetation); b) solid line = bell (defined peak in occurrence in mid-aged vegetation), dashed line = plateau (occurrence lowest in young vegetation, peaks mid-age vegetation, maintained in older vegetation); c) irruptive responses, solid line = irruptive 1 (occurrence increases and peaks in young vegetation, rapidly declines, lowest in mid-aged and older vegetation), dashed line = irruptive 2 (occurrence peaks in youngest vegetation, rapidly declines, lowest in mid-aged and older vegetation); d) solid line = delayed incline (low occurrence until mid or old aged vegetation before increasing in occurrence), dashed line = null (occurrence not influenced by post-fire-age).

2.3 Methods

2.3.1 Study area

The study area encompassed approximately 104,000 km² in the Murray Mallee region of Australia, centred on the intersection of the states of Victoria, New South Wales and South Australia. The region has a semi-arid climate with hot dry summers and mild winters. Climatic variation across the region forms a south to north gradient of increasing aridity (Pausas & Bradstock, 2007) with mean annual rainfall declining from 350 - 200 mm per annum across this gradient. Mean maximum and minimum temperatures in the warmest month range from $32^{\circ} - 33^{\circ}$ C and $14^{\circ} - 18^{\circ}$ C, respectively; whereas in the coolest they range from $15^{\circ} - 16^{\circ}$ C and $4^{\circ} - 6^{\circ}$ C, respectively (Australian Bureau of Meteorology, 2010).

The study was conducted within the dominant 'mallee' vegetation type in the region. Mallee consists of open vegetation with a low canopy (<10 m tall) of multi-stemmed *Eucalyptus* species, and an understorey of shrubs and perennial and ephemeral grasses (Bradstock & Cohn, 2002). We categorised and mapped vegetation into three broad categories, Triodia Mallee, Chenopod Mallee and Heathy Mallee, on the basis of floristic surveys at each site (Haslem *et al.*, 2011). Triodia Mallee vegetation occurs on sandy soils, has an understorey of the hummock grass *Triodia scariosa*, an overstorey dominated by *Eucalyptus dumosa* and *E. socialis*, and commonly also contains shrubs such as *Acacia rigens*, *A. wilhelmiana* and *Beyeria opaca*. Chenopod Mallee occurs on soils with higher clay content, typically in swales between dunes, has a sparse understorey of shrubs such as *Olearia* spp., *Zygophyllum* spp. and chenopod species including *Maireana pentatropis*, *Enchylaena tomentosa* var. *tomentosa* and *M. pyramidata*, and an overstorey of *E.*

oleosa subsp. *oleosa* and *E. gracilis* (Haslem *et al.*, 2011). Sites in Heathy Mallee were excluded from this analysis (see study design).

Mallee vegetation is highly flammable and many plant species have life-history attributes related to recurrent disturbance by fire (Bradstock & Cohn, 2002). Fires occur regularly in this extensive region and they typically remove both understorey and canopy vegetation (Noble & Vines, 1993). Mallee eucalypts resprout from underground lignotubers following fire, whereas understorey plants regenerate from both roots (resprouters) and seed (Parsons, 1968; Cheal *et al.*, 1979). This post-fire regeneration produces a relatively dense vegetation layer below 2 m until ~15 years post-fire, after which there is a gradual reduction in vegetation cover within the mid stratum (0.5 m - 2 m) as shrub species become sparser and *Eucalyptus* spp. begin to develop a canopy above this height. Canopy height increases, reaching a mean height of ~5 - 8 m at approximately 60 years post-fire; from this point the growth in canopy height slows considerably (Haslem *et al.*, 2011).

2.3.2 Study design and data collection

We surveyed birds at sites representing a chronosequence from <1 year – 164 years post-fire. The post-fire age of the vegetation at each site was ascertained by using one of two methods. For sites burnt post-1972, the year of burning was determined from maps of fire history based on 15 individual years of satellite imagery combined with local knowledge of exact fire dates (Avitabile *et al.*, 2011). For sites burnt prior to 1972, fire age was estimated using regression models of the relationship between the diameter of eucalypt stems and years since fire, which were validated with independent data (Clarke *et al.*, 2010). This investigation was part of a larger study examining the influence of the properties of fire mosaics on flora and fauna, and consequently study sites were arranged in 28 clusters (landscape units), each encompassing 20 sites. We excluded from analysis 17 sites predicted to be >100 years since-fire (i.e. 101 - 164 years) as there were too few sites for adequate replication over this range. We also excluded all sites in Heathy Mallee vegetation (n=44) due to inadequate representation across age-classes: only one site was <19 years since-fire. Due to the spatial and temporal distribution of fires throughout the region and the landscape scale study design, there were few data points located in vegetation 11-20 years since-fire. The resulting dataset consisted of 499 sites representing post-fire ages between 1 and 100 years: 176 sites in Chenopod Mallee and 223 in Triodia Mallee (Table 2.1).

Time-since-fire	Triodia Mallee	dia Mallee Chenopod Mallee		
 0-10	89	21	110	
11-20	1	0	1	
21-30	56	14	70	
31-40	106	53	159	
41-50	13	21	34	
51-60	17	23	40	
61-70	16	22	38	
71-80	10	10	20	
81-90	10	6	16	
91-100	5	6	11	
Total	323	176	499	

Table 2.1 The distribution of survey sites in relation to time-since-fire in TriodiaMallee and Chenopod Mallee vegetation. Sites are categorized in 10-year intervals.

Within each landscape, sites generally were separated by 500 m to maximise independence. Surveys were conducted on four survey rounds, once each in the

Austral spring and autumn of 2006/2007 and 2007/2008. All sites were surveyed twice each by two observers (Simon Watson, Rick Taylor). At each site, all individuals were counted and recorded within a 60 m radius during a 5 min period. Surveys commenced within 15 min of sunrise, during the time of greatest vocal activity for birds and were generally completed before 12:00 PM. The distance from the centre of the point count to the location of the first detection of individual birds was recorded to permit analysis of detectability. For visual detections, distance was measured using an OPTi-LOGICTM 800LH laser range finder. For aural detections distance was estimated by the observer. Observers had initial training together to ensure comparability of procedures.

2.3.3 Statistical analysis

Variation in detectability of different species, or of the same species in different habitats, is a potential source of variation in ecological studies (Buckland *et al.*, 2001). To ascertain whether detectability was likely to be a problem in interpreting our data, we undertook multiple covariate distance sampling (MCDS) (Buckland *et al.*, 2004; Marques *et al.*, 2007) using the program Distance 5.0 release 2 (Thomas *et al.*, 2006). We modelled variation in detectability of individual species with increasing distance from the observer, also incorporating vegetation density as a covariate in the model. Species recorded too infrequently to model individually were grouped with more common species that displayed similar detection characteristics, following Aldredge *et al.* (2007). All species were successfully detected at the furthest extremities of the point-count. The lowest probability of detection for a point was for the combined taxa, Mallee Emu-wren *Stipiturus mallee* and Striated Grasswren *Amytornis striatus* (probability of detection = 0.45, 95% CI 0.31 - 0.65, N = 75). Vegetation density did not significantly reduce the detectability of any

species. Considering these results, modelling presence-absence is an appropriate approach.

We used generalised additive mixed models (GAMMs) (Wood, 2006) to model the change in species occurrence with time-since-fire. Generalised additive models (GAMs) are a non-parametric form of regression modelling that use smoothing functions to model non-linear relationships (Wood, 2006; Wood, 2008). As many of the response shapes we selected *a priori* are non-linear (Fig. 2.1), GAMs presented an appropriate method. Models were fitted using presence-absence data to model the probability of occurrence of species, where presence represents the detected occurrence of a species at a site in any of the four survey rounds.

We developed the GAMs in a mixed modelling framework (GAMMs) to account for the potential for systematic variation in the influence of the predictor variables caused by the spatial clustering of study sites in landscapes. Mixed models reduce the potentially confounding problems of spatial autocorrelation and are recommended where systematic structuring is present in the data (Zuur *et al.*, 2009). Thus, landscape unit was included as a random factor in each species' model. To ascertain whether species' response shapes varied between vegetation types (Triodia Mallee, Chenopod Mallee), we fitted models allowing a separate smoothed term for time-since-fire to be fitted for each level of this categorical variable (Wood, 2006). We also included vegetation type as a separate factor variable, and an additional variable, 'northing', was included to allow for a site's location along the gradient of aridity in the study region. The amount of smoothing used to model the response to time-since-fire was automatically selected in the model-fitting process (Wood, 2008). Species were deemed to show a response to time-since-fire if the P-value for the smoothed time-since-fire term was <0.05. Wood (2006) warns that P-values for smoothed terms are approximated, and consequently we approach P-values near 0.05 with caution following Zuur *et al.* (2009). The modelled response of the probability of occurrence of each species to time-since-fire was plotted, and species were then allocated to a response shape based on its similarity to *a priori* response shapes adapted from Whelan *et al.* (2001) (Fig. 2.1).

We evaluated the GAMMs using deviance explained (D^2) as a measure of model fit, and seven-fold cross-validation to test predictive accuracy (Pearce & Ferrier, 2000). This procedure involved splitting the data into seven groups ('folds'), fitting the GAMMs to data from six folds and predicting the occurrence of species to sites in the seventh fold, which is independent of the data used to generate the model. These predictions for sites in the seventh fold were compared with observed responses to test the predictive accuracy of the model. This process was continued iteratively until predictions had been made for all sites. Evaluation of the predictive performance of models was based on the mean discrimination (and standard error) across all folds. Model discrimination was ascertained by building a relative operating characteristic (ROC) curve, which compares the relative proportions of correctly and incorrectly classified presence and absence predictions (or true positive versus false positive responses) of the model over a continuous range of thresholds (Pearce & Ferrier, 2000). The area under the curve (AUC) gives a measure of the usefulness of the model in predicting species occurrence. Scores from 0.5 - 0.7 are considered to have some discrimination, 0.7 - 0.9 = reasonable discrimination and 0.9 - 1 = very-good discrimination (Pearce & Ferrier, 2000).

All GAMM's were built in the R statistical environment (R Development Core Team, 2009), using the "mgcv" package (Wood, 2004; Wood, 2006). Cross validation methods and source scripts were adapted from Elith *et al.* (2008).

2.4 Results

We detected 70 species of birds from 28 families during point-counts. We modelled species that occurred at >20 sites and which occurred across the entire region, resulting in models for 30 of the 69 species. One species (Grey-fronted Honeyeater *Lichenostomus plumulus*) was recorded only north of the Murray River, a biogeographic boundary, and two species (Mallee Emu-wren *Stipiturus mallee* and Purple-gaped Honeyeater *Lichenostomus cratitius*) only south of the river.

2.4.1 Response of species to time-since-fire

Sixteen of the 30 species modelled showed significant variation in probability of occurrence with time-since fire (Table 2.2). All 16 responded to time-since-fire in Triodia Mallee vegetation, but only four species displayed a significant response in Chenopod Mallee (Table 2.2).

Table 2.2 Relationship between species occurrence and time-since-fire for 30 bird species in the Murray Mallee region, derived from generalised additive mixed models. The number of sites recorded (N), the assigned response shape with time-since-fire in Triodia Mallee and Chenopod Mallee, and the statistical significance of the relationship (F, P) in each vegetation type are presented for each species.

	N.	Triodia Mallee			Chenopod Mallee		
Species		Shape	F	Р	Shape	F	Р
Australian Ringneck Barnardius zonarius		Null	0.11	0.745	nd	2.96	0.086
Mulga Parrot Psephotus varius		Null	1.25	0.264	Null	1.95	0.163
Variegated Fairy-wren Malurus lamberti		Null	1.13	0.312	Null	1.6	0.207
Striated Grasswren Amytornis striatus		Bell	6.84	< 0.001	Null	2.09	0.149
Spotted Pardalote Pardalotus punctatus	225	Bell	4.19	0.013	nd	1.71	0.183
Striated Pardalote Pardalotus striatus		Incline	9.62	< 0.001	nd	2.42	0.12
Shy Heathwren Calamanthus cautus	69	Null	0.16	0.692	Null	0.1	0.757
Weebill Smicrornis brevirostris		Plateau	5.52	< 0.001	Null	0.02	0.9
Chestnut-rumped Thornbill Acanthiza uropygialis		Irruptive	4.2	0.017	Decline	6.47	0.011
Inland Thornbill Acanthiza apicalis	61	Null	2.13	0.145	Null	0.39	0.535
White-eared Honeyeater Lichenostomus leucotis	219	Bell	3.9	0.018	Null	0.17	0.679
Yellow-plumed Honeyeater Lichenostomus ornatus	286	Plateau	21	< 0.001	Plateau	11.59	< 0.001
White-fronted Honeyeater Purnella albifrons		Null	0.9	0.343	Null	0.18	0.674
Spiny-cheeked Honeyeater Acanthagenys rufogularis		Incline	5.42	0.021	Incline	5.23	0.022
Species	N	Triodia Mallee			Chenopod Mallee		
---	------	----------------	------	---------	-----------------	------	-------
	IN .	Shape	F	Р	Shape	F	Р
Red Wattlebird Anthochaera carunculata	28	Null	1.03	0.352	Null	1.66	0.199
Brown-headed Honeyeater Melithreptus brevirostris	46	nd	2.88	0.056	Null	0	0.971
Striped Honeyeater Plectorhyncha lanceolata	20	Incline	8.04	0.005	nd	2.67	0.065
White-browed Babbler Pomatostomus superciliosus	39	Bell	3.3	0.018	Incline	5.9	0.016
Chestnut Quail-thrush Cinclosoma castanotus	148	Null	0.42	0.598	nd	3.03	0.083
Gilbert's Whistler Pachycephala inornata	23	Incline	11.7	< 0.001	Null	0.16	0.694
Golden Whistler Pachycephala pectoralis	21	Bell	4.88	< 0.001	Null	0.01	0.924
Rufous Whistler Pachycephala rufiventris	38	Incline	14.4	< 0.001	Null	0.05	0.819
Grey Shrike-thrush Colluricincla harmonica	165	Incline	6.21	0.013	Null	1.79	0.17
Crested Bellbird Oreoica gutturalis	101	Null	1.5	0.226	Null	0.18	0.674
Grey Butcherbird Cracticus torquatus	132	Null	1.11	0.292	Null	1.07	0.301
Grey Currawong Strepera versicolor	21	Null	1.41	0.236	Null	2.44	0.119
Willie Wagtail Rhipidura leucophrys	45	Incline	6.48	0.011	Null	0.19	0.667
Jacky Winter Microeca fascinans	117	Null	0.28	0.599	Null	1.06	0.304
Red-capped Robin Petroica goodenovii	21	Null	0.07	0.796	Null	1.87	0.159
Southern Scrub-robin Drymodes brunneopygia	53	Incline	15.6	< 0.001	nd	2.34	0.072

nd = A non-significant trend was present such that a null response is not appropriate.

We assigned each significant time-since-fire response to one of the *a priori* response shapes (Table 2.3 & Fig. 2.2). There was uncertainty for some species in distinguishing between an inability to detect a significant response and a null response to time-sincefire. This was particularly a problem in the less fire-prone Chenopod Mallee for which there was a lower sample size, particularly in younger vegetation (Table 2.1). Accordingly we assigned a category of "non-detection" to species that displayed nonsignificant trends, for which a null response may not be appropriate (e.g. where P-values were close to alpha, 0.05 < P < 0.1).

 Table 2.3 Summary of species response types and the number of bird species that

 displayed each response in Chenopod Mallee and Triodia Mallee.

Shana	Triodia	Chenopod	
Snape	Mallee	Mallee	
Incline	8	2	
Decline	0	1	
Bell	5	0	
Plateau	2	1	
Irruptive 1	0	0	
Irruptive 2	1	0	
Delayed	0	0	
Null	13	20	
Not Detected	1	6	



Figure 2.2 Examples of modelled post-fire response curves for bird species ± 1 SE, demonstrating the similarity of observed and hypothetical response shapes (Fig. 1); a) incline response of Grey Shrike-thrush in Triodia Mallee; b) decline response of Chestnut-rumped Thornbill in Chenopod Mallee; c) bell response of White-eared Honeyeater in Triodia Mallee; d) plateau response of Yellow-plumed Honeyeater in Triodia Mallee; e) irruptive 2 response of Chestnut-rumped Thornbill in Triodia Mallee; f) null response of Weebill in Chenopod Mallee.

There was little concordance between responses of species in the two vegetation types (Table 2.2). Of the species that displayed a significant response to time-since-fire, only two (Yellow-plumed Honeyeater, Spiny-cheeked Honeyeater) had the same response shape in both vegetation types. Two species (Chestnut-rumped Thornbill, White-browed Babbler) displayed different response shapes in each vegetation type, and eight species showed a significant response in one vegetation type and a null response in the other (Fig. 2.3) A further four species responded in one vegetation type and displayed a non-significant trend (non-detection) in the other.



Figure 2.3 Response shapes for species that had different responses to time-sincefire in different vegetation types (± 1 SE). Black line = Triodia Mallee, grey line= Chenopod Mallee; a) Chestnut-rumped Thornbill (irruptive and decline), b) Whitebrowed Babbler (bell and incline), c) White-eared Honeyeater (bell and null).

Sixteen species displayed significant responses to time-since-fire in Triodia Mallee. Of these, eight displayed an incline, five a bell-shape, two a plateau and one an irruptive response shape (Table 2.3). In Chenopod Mallee, four species displayed significant time-since-fire responses; of these two species displayed an incline, one species a decline and one species a plateau (Table 2.3). Overall, the null response was the most frequently encountered in both vegetation types (Table 2.3).

2.4.2 Evaluation of time-since-fire models

The deviance explained by models ranged from 0.04 to 0.34 (Table 2.4), suggesting a high level of variability in the explanatory power of time-since-fire, together with vegetation type and northing, on species occurrence. Note that the probability of occurrence of several species was also significantly related to the non-fire variables, northing and vegetation type (Table 2.4; Table 2.5).

The ability of time-since-fire models to predict species' responses across landscapes and regions is a key issue in determining the usefulness of such post-fire response curves for management purposes. The models of the 16 species that showed a significant response to time-since-fire had AUC values that ranged between 0.54 and 0.86 (Table 2.4). Models displayed reasonable predictive discrimination for 8 species (AUC>0.7), some predictive discrimination for 7 species (0.6<AUC<0.7), and predictive discrimination little better than chance for one species AUC = 0.54 (Table 2.4).

Table 2.4 Measures of model performance for models of the relationship between frequency of occurrence of species and time since fire. Values presented are the deviance explained (D^2) and mean area under the curve from seven-fold cross validation (AUC) (SE in parentheses), for species that display a significant response to time since fire. Models also account for variation related to geographic location and vegetation type.

Species	D^2	Mean AUC (SE		
Striated Grasswren ^{ab}	0.22	0.81	(0.046)	
Spotted Pardalote ^b	0.19	0.72	(0.044)	
Striated Pardalote ^{ab}	0.14	0.73	(0.026)	
Weebill	0.05	0.54	(0.051)	
Chestnut-rumped Thornbill ^a	0.06	0.64	(0.060)	
White-eared Honeyeater	0.07	0.67	(0.045)	
Yellow-plumed Honeyeater	0.24	0.76	(0.043)	
Spiny-cheeked Honeyeater	0.05	0.61	(0.043)	
Striped Honeyeater ^b	0.17	0.77	(0.033)	
White-browed Babbler	0.09	0.66	(0.049)	
Gilbert's Whistler ^{ab}	0.13	0.72	(0.079)	
Golden Whistler ^b	0.34	0.86	(0.060)	
Rufous Whistler	0.04	0.60	(0.080)	
Grey Shrike-thrush ^a	0.06	0.65	(0.037)	
Willie Wagtail ^a	0.07	0.69	(0.050)	
Southern Scrub-robin ^b	0.16	0.75	(0.052)	

^a Significant response to vegetation type

^b Significant response to geographic position (northing) Details of ^a and ^b (Table 2.5) Table 2.5. Relationships of the frequency of occurrence of species with the parametric variables vegetation type and northing, and tests of significance for these variables obtained from the full species models (GAMMs). Chenopod Mallee is used as the reference variable in the model, such that coefficients for vegetation refer to species responses to the Triodia Mallee vegetation in comparison with the reference variable. Significant responses (P<0.05) are shown in bold type

a :	V	egetatio	n	Northing			
Species	Coef.	SE	Р	Coef.	SE	Р	
Australian Ringneck	-0.577	0.296	0.052	1.61E-06	2.73E-06	0.557	
Mulga Parrot	-0.828	0.346	0.017	2.01E-06	2.60E-06	0.440	
Variegated Fairy-wren	-0.960	0.432	0.027	1.95E-06	3.40E-06	0.567	
Striated Grasswren	2.600	0.565	<0.001	1.76E-05	5.85E-06	0.003	
Spotted Pardalote	0.087	0.235	0.711	-1.64E-05	2.29E-06	<0.001	
Striated Pardalote	-1.200	0.232	<0.001	-6.54E-06	2.46E-06	0.008	
Shy Heathwren	-0.663	0.280	0.018	-6.40E-06	3.56E-06	0.073	
Weebill	-0.289	0.229	0.207	1.07E-06	2.16E-06	0.620	
Chestnut-rumped Thornbill	-0.835	0.247	<0.001	3.99E-06	2.37E-06	0.093	
Inland Thornbill	0.348	0.313	0.266	-3.98E-06	3.03E-06	0.190	
White-eared Honeyeater	0.422	0.250	0.093	-6.50E-06	3.92E-06	0.098	
Yellow-plumed Honeyeater	0.230	0.308	0.456	-9.97E-07	4.07E-06	0.806	
White-fronted Honeyeater	0.072	0.262	0.784	3.43E-06	3.19E-06	0.283	
Spiny-cheeked Honeyeater	-0.047	0.245	0.848	-1.78E-06	2.46E-06	0.469	
Red Wattlebird	-0.343	0.345	0.320	-2.07E-05	6.43E-06	0.001	
Brown-headed Honeyeater	-0.874	0.311	0.005	-3.10E-06	2.91E-06	0.287	
Striped Honeyeater	-0.471	0.703	0.503	-8.56E-06	3.93E-06	0.030	
White-browed Babbler	-0.366	0.382	0.338	-3.39E-07	2.58E-06	0.895	
Chestnut Quail-thrush	-1.030	0.214	<0.001	1.68E-07	1.67E-06	0.920	
Gilbert's Whistler	-1.290	0.391	0.001	1.46E-05	4.64E-06	0.002	
Golden Whistler	-0.098	0.495	0.843	-8.77E-05	2.86E-05	0.002	
Rufous Whistler	-0.654	0.358	0.068	5.36E-06	3.71E-06	0.150	

Species	V	egetatio	n	Northing			
	Coef.	SE	Р	Coef.	SE	Р	
Grey Shrike-thrush	-0.779	0.225	<0.001	7.30E-07	2.32E-06	0.753	
Crested Bellbird	-0.214	0.246	0.385	3.89E-06	1.87E-06	0.038	
Grey Butcherbird	-0.457	0.229	0.047	-4.76E-06	2.14E-06	0.027	
Grey Currawong	0.356	0.608	0.559	-4.94E-06	3.58E-06	0.168	
Willie Wagtail	-1.210	0.341	<0.001	2.43E-06	2.68E-06	0.365	
Jacky Winter	-1.250	0.232	<0.001	4.90E-06	2.00E-06	0.014	
Red-capped Robin	-0.102	0.469	0.828	-2.05E-06	3.35E-06	0.540	
Southern Scrub-robin	-0.594	0.438	0.176	9.60E-06	4.15E-06	0.021	

2.5 Discussion

Fire significantly influenced the frequency of occurrence of 16 of the 30 species investigated, highlighting the role of fire in structuring avifaunal assemblages over long time frames (up to 100 years since fire). Shapes of species response curves to timesince-fire generally corresponded with *a priori* hypothetical response curves, suggesting there is a relatively small number of 'generalised' responses within an assemblage. Species responses often differed between two major vegetation types, Triodia Mallee and Chenopod Mallee, or were significant only in one type. Despite many species having clear responses to time-since-fire, model fit was generally low and had only moderate predictive capacity across the region.

2.5.1 Influence of time-since-fire on the occurrence of birds

This research is consistent with the view that fire is an important disturbance process that influences avifaunal communities (Brawn *et al.*, 2001). Importantly, the frequency

of occurrence of species can continue to change over extended time-periods, in this system for up to at least 100 years-since-fire. This finding emphasizes the importance of interpreting time-since-fire response curves on a temporal scale corresponding with that of the disturbance process and its successional trajectory.

In this project many sites of similar time-since-fire were products of different fire events spread across a vast spatial area. Consequently, the significant responses identified here indicate that some species have responded in a similar way to similar post-fire ages generated from multiple fire events. This result is notable given the effects that the complexity of individual fire events (Whelan *et al.*, 2001; Bain *et al.*, 2008; Lindenmayer *et al.*, 2009) and other factors such as rainfall (Monamy & Fox, 2000; Letnic, 2003), can have on species succession patterns. The moderate outcomes for model fit indicate that factors additional to time-since-fire are also important.

It is important to recognise a dichotomy in the descriptions of species' responses to fire. First, there are general responses of species to fire events, represented by the overall frequency of occurrence (or abundance) of a species in particular post-fire age-class. Second, there is the response of a species to a particular fire event, which may vary depending on a range of factors. For example, the Eastern Bristlebird *Dasyornis brachypterus*, considered to prefer older vegetation and to take many years for populations to recover from fire due to a preference for dense vegetation (Baker, 2000), was found to quickly colonise recently burnt sites after a fire which burnt patchily (e.g. Bain *et al.*, 2008; Lindenmayer *et al.*, 2009). In cases such as this, we may conclude that although the species generally shows a slow response to fire events and increases

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slowly, under a specific fire scenario it may respond very differently. Thus, fire response curves, when investigated with large sample sizes and over broad spatial scales, can inform management about general responses to fire and preferred seral stages, but may not necessarily be able to predict responses to particular fire events.

2.5.2 Shapes of species' responses to time-since-fire

Modelling results for 30 species of bird revealed six generalised response shapes that resembled those identified *a priori* in the literature. Similar responses have also been described for birds in mountain rangeland systems in Europe (Pons & Clavero, 2010), suggesting that these patterns may occur in diverse ecosystems. Fire as a disturbance process has a strong filtering effect on the occupancy of sites by different types of species (Moretti & Legg, 2009): different post-fire responses result from interactions of species traits with aspects of the environment influenced by fire (Whelan *et al.*, 2001). In the case of generalised fire response curves, incline responses, plateau responses and bell responses indicate that fire events initially have a negative effect on species, and species subsequently recolonise over time. In contrast, irruptive and decline responses indicate that fire events facilitate the occurrence of a species. Null responses indicate that species are little affected by most fire events.

The shape of a species response to fire is likely to be influenced by a number of factors: these include the dependence of a species on resources which are themselves affected by time since fire, such as food (Murphy & Lehnhausen, 1998; Barlow & Peres, 2004) and the structural complexity of vegetation (Skowno & Bond, 2003); and also the ecological

traits of the species such as fecundity (Friend, 1993), dispersal capability (Brotons *et al.*, 2005) and competitive ability (Fox, 1982).

In mallee ecosystems, the shapes of species' responses to fire tend to correlate with postfire changes in attributes of vegetation on which the species are known to rely. This pattern indicates that post-fire responses are influenced by the effects of fire on vegetation structure. For instance, the Striated Pardalote, which requires hollows for nesting (HANZAB, 2006), displays an incline response. The proportion of hollowbearing stems also increases with time since fire (Haslem *et al.*, 2011). The Whitebrowed Babbler, which forages under bark on the lower branches of trees and amongst litter and debris on the ground, also displays an incline response. The amount of decorticating bark and litter also are higher in older vegetation (Haslem et al., 2011). The Striated Grasswren, which is closely associated with *Triodia* hummock grasses that it uses for refuge and nesting (HANZAB, 2006), displays a bell shaped response. Hummock grass peaks in cover at ~20-40 years post-fire (Haslem *et al.*, 2011) corresponding with the occurrence of the Striated Grasswren. The Chestnut-rumped Thornbill, which occurs more frequently in Mulga Acacia aneura shrubland (HANZAB, 2006), displays an irruptive response. Fire creates a vegetation type that is transiently more similar to Mulga shrubland, in terms of low shrubby foliage cover, but becomes less so with time since fire (Haslem *et al.*, 2011).

Interspecific competition may contribute to declines in species' occurrences (Fox, 1982). Of the five species that displayed a bell-shaped response, three (Spotted Pardalote, Golden Whistler and White-eared Honeyeater) have closely related species (i.e. Striated Pardalote, Gilbert's Whistler and Rufous Whistler, Yellow-plumed Honeyeater) of similar body-size that display incline or plateau responses and which are most prevalent in older vegetation. They may represent potential competitors which drive declines in occurrence (i.e. the downward phase of the bell-shape) in older age-classes. It is not possible to directly determine the contribution of competition to species' distributions with this data set, but it represents a potentially important factor for faunal succession processes in this system.

Thus, the shape of species responses to fire may provide insights into whether species are generally facilitated or inhibited by fire events, and comparisons with temporal changes in resources can help to interpret these response shapes. However, having the same generalised fire response shape does not necessarily imply that the same processes are affecting species in the same way, because similar response shapes may arise through multiple processes.

2.5.3 Importance of particular seral stages

Of the 16 species that had a significant response to time-since-fire, only one (Chestnutrumped Thornbill) appeared to have population growth facilitated by short-term, postfire changes in habitat structure. All other species displayed their highest frequency of occurrence in mid or later successional vegetation (>20 years since-fire). This suggests that for most species in this ecosystem, fire causes displacement from sites and they subsequently take varying times to recolonise. Consequently, in the event that large wildfires occur, there must either be refuges where species can survive fire or source populations nearby from which they can recolonise sites post-fire. While the influence of any given wildfire event on the degree of mortality or emigration from sites is not clear (Whelan *et al.*, 2001), in mallee ecosystems large wildfires dramatically alter the vegetation structure and result in severe reductions in the frequency of occurrence of a substantial proportion of the assemblage for decades. Vegetation of >30 years-since-fire supports a higher occupancy of 14 of the 16 species modelled, suggesting that older vegetation is disproportionately important for many species. However, the frequency of occurrence of six of these species declines between 50 and 100 years since fire, and it is likely that there are further reductions at >100 years since-fire. Thus, fires are an important influence on the suitability of habitats for bird species.

2.5.4 Influence of vegetation type on post-fire response patterns

Little is known about the interaction of fire with other ecological processes (Driscoll *et al.*, 2010). In this study, species' post-fire response patterns differed between vegetation associations and three times as many species showed a significant response in Triodia Mallee than Chenopod Mallee. We had less power to detect responses with Chenopod Mallee due to having fewer sites, particularly <30 years since-fire (N = 35), and consequently responses in that vegetation type must be interpreted with caution. Nevertheless the threefold difference in significant responses warrants further investigation.

Fire behaviour varies between different vegetation associations in this region. Mallee vegetation with *Triodia* grass fuels (i.e. Triodia Mallee) carries fire more readily than other vegetation associations under typical climatic conditions due to the flammable nature of *Triodia* hummocks (Noble & Vines, 1993). Furthermore, several habitat

attributes (e.g. understorey and midstorey vegetation density) differ between Triodia Mallee and Chenopod Mallee in their patterns of change with time-since-fire (Haslem *et al.*, 2011). Triodia Mallee tends to have a clearer successional pattern in vegetation structure, evidenced by the greater number of significant post-fire responses of vegetation (Haslem *et al.*, 2011). The more uniform nature and consistency of habitat changes with time-since-fire in Triodia Mallee are likely to be the main factors that contribute to the variation in time-since-fire response curves of avifauna.

Particular post-fire seral stages are often identified as important for the persistence of particular species (eg. Hutto, 1995; Clarke *et al.*, 2005). This investigation reveals that seral stage preferences of a species may differ between different vegetation associations. Thus, conservation strategies that aim to benefit species through provision of particular seral stages will be most effective where they incorporate post-fire succession differences amongst vegetation types.

2.5.5 Interpreting fire responses: the importance of the spatial and temporal scale of studies

Species responses must be interpreted within the bounds of the temporal scale of the study. Incline responses, for instance, must eventually resemble plateau or bell shaped responses: that is, the frequency of occurrence of a species (eg. Grey Shrike-thrush, Fig. 2.2a) must eventually stabilize or decline at sites >100 years since fire. As sites >100 years since fire are rare, it may be that stabilization or decline will seldom occur before another fire event. However, this is a problem of interpretation with many studies (eg. Brown *et al.*, 2009), in which older age-classes are grouped due to lack of accurate

ageing methods. For example, in an older age-class in which sites may span 50 years in age, a species may be at its maximum frequency for 30 years and at low occurrence for 20 years. Lack of detailed knowledge of age-classes may result in misleading response shapes.

A further consideration in interpreting post-fire responses of species relates to the influence of the broader context of sites. This investigation was undertaken in large expanses of continuous vegetation, which is likely to represent an environment conducive to dispersal. In contrast, in situations where habitat is fragmented, patches are small and the surrounding environment is more hostile to dispersal (e.g. agricultural land), post-fire patterns of occurrence may be influenced more by individual fire events and the local population dynamics and dispersal capabilities of species (Brotons *et al.*, 2005).

2.5.6 The predictive capacity of time since fire response curves for distribution of species across broad spatial scales: implications for conservation and management Although approximately half of the 30 species modelled showed significant responses to time-since-fire, model fit (proportion of deviance explained) varied greatly and was relatively modest, and the predictive capacity of these significant relationships was considered reasonable only for approximately half of the species. This suggests caution is required in using a time-since-fire model as a key method for understanding the geographic distributions of species in landscapes.

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Using time-since-fire as a metric to determine the amount of vegetation that requires burning or protection to improve diversity (Richards *et al.*, 1999), or alternatively to create mosaics of age-classes (Parr & Andersen, 2006), may be ineffective if other factors that also influence species' occurrence are not incorporated. Thus, generalised response curves, although useful for determining the general response to fire events and identifying important seral stages for species, may not be adequate as a surrogate to highlight species occupancy. Additional influences on the responses of species to particular fire events (e.g. post-fire rainfall, grazing pressure) may also strongly influence successional outcomes. **Chapter 3**

Changes to avifaunal community composition over a 100-year post-fire chronosequence: insights into patterns and processes of community succession



Spiny-cheeked Honeyeater Acanthagenys rufogularis

3.1 Abstract

Post-fire successional changes influence the temporal occurrence and abundance of faunal species in many ecosystems around the world. Understanding how temporal heterogeneity in community structure influences the overall faunal assemblage of a landscape or region is critical for managing fire to conserve biodiversity. We investigated the effect of fire on the structure of avifaunal communities in a 104,000 km² region of semi-arid shrubland in south-eastern Australia. Here, we focus on temporal changes in community structure following fire using data from avifaunal surveys at 462 sites representing a chronosequence from <1 - 100 years-since-fire. Species richness changed substantially between 1 - 10 years-since-fire, increasing and plateauing at sites >10 years-since-fire. However, community composition changed throughout the 100 year period. The difference in community composition between sites increased with increasing temporal difference between sites. The rate of change in communities slowed with time-since-fire, resulting in longer periods of time occupied by similar assemblages in later stages of succession. Three main successional stages were recognised (<10 years, 20-40 years and >50 years). Beta (β) diversity within post-fire age-classes (based on species accumulation curves across multiple sites) increased with time-since-fire. Species richness of two dietary guilds (insectivores, nectarivore-insectivore) and two foraging-zone guilds (foliage, 'trunk and branch') changed significantly with time-since-fire. These patterns correlated with changes in availability of food (nectar and possibly insects) and vegetation structural complexity. Management of fire needs to consider successional patterns and the level of temporal heterogeneity of fauna. Here, we show that fires can influence the structure of avifaunal assemblages for at least a century, probably related to its effects on food resources and the structural complexity of vegetation. Older vegetation is disproportionately important for the broader assemblage.

Chapter 3 – The influence of time-since-fire on the composition of avifauna Management planning for fire should explicitly consider the effects of management actions on the mechanisms which drive community responses, such as changes to vegetation structure and availability of food resources.

3.2 Introduction

Fire significantly affects the structure of faunal communities in ecosystems around the world (Gill *et al.*, 1999; Brawn *et al.*, 2001). The occurrence and abundance of many faunal species change with time-since-fire (Fox, 1982; Hobson & Schieck, 1999; Smucker *et al.*, 2005; see also Chapter 2) and some species are closely associated with particular seral stages (e.g. Hutto, 2008; Brown *et al.*, 2009). The importance of fire as an influence on faunal communities means that land managers are increasingly seeking to manage fire to benefit biodiversity (Backer *et al.*, 2004; Driscoll *et al.*, 2010a), often through prescribed burning to promote diverse seral stages (Parr & Brockett, 1999). Specifying the importance of different temporal stages to the broader diversity of assemblages (*cf.* individual species) presents a significant challenge for fire ecology and conservation management (Bradstock *et al.*, 2005; Driscoll *et al.*, 2010b). Often, there is inadequate knowledge of community change through the full post-fire succession as few studies have investigated the effects of fire over long time-frames of decades and centuries (Clarke, 2008).

Community level approaches may be particularly useful for examining the importance of seral stages to faunal assemblages. They provide a method for identifying the contribution of different sites (or seral stages) to the composition of the overall landscape assemblage (Tuomisto & Ruokolainen, 2006; Anderson *et al.*, 2011), and to assessing the distinctiveness of communities of contrasting fire ages. An important aspect of succession is the rate of change in community composition with increasing time since disturbance. That is, how do differences in faunal composition at sites of a given time contrast (e.g. 10 years difference in successional stage) change with the overall time since the disturbance event (Helle & Monkkonen, 1985)? For example how much does the composition of fauna change between 10

Chapter 3 – The influence of time-since-fire on the composition of avifauna years and 20 years since a disturbance event, compared to how much the composition changes between 50 and 60 years since the disturbance event. And additionally, what effect does variation in the rate of community change have on the temporal duration of a particular community during succession?

A further approach which may deliver insights into the contribution of different seral stages to the overall assemblage is the investigation of changes in β diversity (between-site diversity) with increasing time since fire. The β diversity within a post-fire age-class can provide information about the relative contribution of different seral stages to the diversity of the overall assemblage. Some seral stages may contribute a greater number of species to the overall assemblage than others. When viewed together with the effect of time since fire on α diversity (diversity at a site), the variation in community composition that can be attributed to temporal succession patterns, versus alternative processes that may influence avifaunal composition, can be directly investigated.

Understanding the effects of fire on *patterns* of faunal composition provides insights for conservation management of the fauna, but it is also important to understand the *processes* by which fire drives temporal changes in faunal composition (Whelan *et al.*, 2001; Driscoll *et al.*, 2010b). Post-fire patterns of community succession vary for many reasons, for example variation in fire intensity and severity (Smucker *et al.*, 2005; Kotliar *et al.*, 2007) and effects of post-fire rainfall on food resources (Letnic & Dickman, 2005) and vegetation structure (Monamy & Fox, 2000). Consequently, it is important to supplement knowledge about patterns of fire-induced succession, with knowledge of processes that drive such changes through time, so that managers can ensure their actions target the appropriate drivers of community change. Comparison of changes within guilds during post-fire succession may provide insights into processes driving overall community change, and the effects of these changes on the functional composition of the community (Moretti & Legg, 2009). Bottom-up processes (i.e. the availability of resources) are important in determining species distributions in ecology (Gripenberg & Roslin, 2007). The effects of fire on resource availability can influence the composition and function of faunal communities (Moretti *et al.*, 2010). As such, investigating changes in species guilds may indicate the processes by which fire structures communities. Further insights may be gained by comparing changes in species guilds, with changes in relevant resources; for example nectarivores with nectar and foliage foraging birds with canopy density.

In this study, we investigate changes in the composition of avifaunal communities over a successional sequence of up to 100 years post-fire in the fire-prone Murray Mallee region of south-eastern Australia. We examine four aspects of fire-induced change in the avifaunal community. First, to investigate the influence of time-sincefire on avifaunal communities, we analyse the relationship between species richness and time-since-fire and compare the dissimilarity in community composition between sites with their dissimilarity in time-since-fire. Second, to determine how distinct assemblages are in different post-fire successional stages, we contrast community composition between sets of sites assigned to sequential post-fire ageclasses. Third, to ascertain the relative contribution of different successional stages to the regional species assemblage, we compare the β diversity amongst sites within different post-fire age-classes. Last, to determine how fire may influence bottom-up processes that structure the avifaunal community, we investigate the relationship

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Chapter 3 – The influence of time-since-fire on the composition of avifauna between time-since-fire and the richness of species guilds at sites and compare this with changes in total species richness at a site and changes in vegetation characteristics.

3.3 Methods

3.3.1 Study area

The study area encompassed 104,000 km² in the Murray Mallee region of south eastern Australia (Fig. 3.1). The climate is semi-arid, with a gradient of increasing aridity from south (mean annual rainfall 350 mm) to north (mean annual rainfall 200 mm) (Pausas & Bradstock, 2007). Temperatures in the study area range from mean daily maxima of 32°C - 33°C in the warmest month (Feb) to 15°C - 16°C in the coolest month (July), while mean daily minima range from 14°C-18°C and 4°C-6°C in the warmest and coolest months, respectively (Australian Bureau of Meteorology).

'Mallee' eucalypt shrubland is the dominant vegetation type of the region. Mallee consists of open vegetation dominated by a canopy of multi-stemmed *Eucalyptus* species and an understorey of shrubs and perennial and ephemeral grasses (Bradstock & Cohn, 2002). This vegetation is highly flammable and fires are a common feature, generally resulting in removal of both understorey and canopy (Noble & Vines, 1993). Many plant species display life-history attributes adapted to recurrent fire disturbance (Pausas & Bradstock, 2007).

Study sites were located in conservation reserves. Three reserve complexes were recognised, each encompassing several reserves in a similar geographic area within continuous tracts of mallee vegetation; 1) Hattah National Park, Murray–Sunset

Chapter 3 – The influence of time-since-fire on the composition of avifauna National Park and Billiatt Conservation Reserve (South Mallee Block); 2) Gluepot Reserve, Danggali Conservation Park, Scotia Sanctuary and Tarawi Nature Reserve (North West Mallee Block); and 3) Petro Conservation Reserve, Lethero Conservation Reserve and Mallee Cliffs National Park (East Mallee Block) (Fig. 3.1). The reserve complexes are divided by two rivers which form geographic boundaries: the southerly flowing Darling River (and associated Great Darling Anabranch) which confluences with the westerly flowing Murray River (Fig. 3.1).

3.3.2 Study design

This investigation forms part of a broader study on the relationship between spatial and temporal features of fire mosaics and avifaunal communities. Due to this, the 560 study sites were clustered in 28 landscapes, each landscape containing 20 sites. Sites generally were separated by a minimum of 500 m.

3.3.3 Post-fire age of study sites

We ascertained the post-fire age of vegetation at each site through one of two methods. First, for sites burnt after 1972, we determined the year of burning by mapping fire history. We generated maps of fire history by overlaying 15 individual years of satellite imagery between 1972 and 2007. The exact year of each fire was determined through analysis of land management agency records (Avitabile *et al.*, 2011). For sites burnt prior to 1972, we determined fire age by using validated regression models of the relationship between stem diameter of *Eucalyptus* trees and years since fire (Clarke *et al.*, 2010).



Figure 3.1 The study area and the location of study landscapes (open circles) in extant mallee vegetation (dark grey). Each study landscape included 20 survey points. Reserve complexes are denoted by rectangles; a) Gluepot, Danggali, Scotia, Tarawi (North West Mallee Block); b) Hattah, Murray-sunset, Billiatt (South Mallee Block); c) Petro, Lethero, Mallee-Cliffs (East Mallee Block). Light grey depicts vegetation other than mallee eucalypt scrubland, most of which is cleared farmland for cropping and grazing.

We recognised three broad associations of mallee vegetation based on plant species composition; Triodia Mallee, Chenopod Mallee and Heathy Mallee (Haslem *et al.*, 2010). These varied in the composition of overstorey *Eucalyptus* species and mid and understorey shrubs. Triodia Mallee occurs on sandy soils and typically has an understorey of hummock grass (*Triodia scariosa*). Chenopod Mallee occurs on soils with higher clay content and has a sparse understorey of shrubs (e.g. *Maireana* sp., *Scleroleana* sp., *Olearia* sp., *Zygophyllum* sp.). Heathy Mallee is mainly restricted to southern parts of the study area, where it occurs primarily on deep siliceous Lowan Sands and has a diverse shrubby understorey of 'heath-like' plants (e.g. *Callitris verrucosa, Leptospermum coriaceum, Phebalium bullatum, Babbingtonia behrii, Hakea leucoptera*).

Ninety-eight sites were excluded from the analysis for several reasons: 1) sites known to have burnt patchily (n = 37) were excluded to allow interpretation of avifaunal communities to single seral stages; 2) sites estimated to be >100 years since-fire were excluded due to insufficient sample sizes (only 17 sites between 101 years and 164 years); 3) sites in Heathy Mallee were excluded due to their limited geographic distribution and small sample size (only one site <19 years since-fire, and 44 in total). This resulted in 462 sites for analysis, ranging from 1 to 100 years postfire, located in Triodia Mallee and Chenopod Mallee vegetation.

3.3.5 Field survey techniques

We conducted surveys of birds on four survey rounds, once each in the Austral spring and autumn of 2006/2007 and 2007/2008. Two observers (Rick Taylor and Simon Watson) both surveyed each site twice. We counted all individuals in a 60 m

Chapter 3 – The influence of time-since-fire on the composition of avifauna radius of a central survey point over a 5 min period during each survey. Bird density generally is low in mallee vegetation (Emison & Bren, 1989; Menkhorst & Bennett, 1990). As such, we increased the number of sites surveyed as a trade-off for time spent surveying each site. This approach allowed inference about factors shaping avifaunal communities across a large spatial area. Surveys commenced within 15 mins of sunrise and continued through the morning, the time of greatest vocal activity for birds. We recorded the distance from the centre of the survey point to the location of the first detection of each individual to permit analyses of detectability. For visual detections, we measured distance using an OPTi-LOGICTM 800LH laser range finder. Aural detections were estimated by the observer. Observers initially trained together to ensure consistency.

At each survey site we measured the density of vegetation in four vertical strata (<0.5 m, 0.5 m to 1 m, 1 to 2 m and >2 m) by recording the number of contacts of vegetation (in each stratum) with a structure pole, placed vertically at 50 x 1 m intervals along a transect. We measured canopy height by using an OPTi-LOGICTM 800LH laser range finder. At each site we also recorded the presence or absence of *Eucalyptus* species that were reproductively active (i.e. presence of flowers, buds or fruits).

3.3.6 Statistical analysis

Detectability of species is a potential source of variation in ecological studies (Buckland *et al.*, 2001). We undertook multiple covariate distance sampling (MCDS) (Marques *et al.*, 2007) by using the program Distance 5.0 release 2 (Thomas *et al.*, 2006). We modelled the probability of detection of individual species with distance from the survey point and included vegetation density as a Chapter 3 – The influence of time-since-fire on the composition of avifauna covariate in the model. Species recorded too infrequently to model individually were grouped with more common species that displayed similar detection characteristics, following Alldredge *et al.* (2007). All species could be readily detected at the furthest extremity of the point-count (60 m). However, some species displayed a decline in detection probability with distance from the observer, particularly for relatively cryptic species (the lowest detection probability was for the combined Mallee Emu-wren *Stipiturus mallee* and Striated Grasswren *Amytornis striatus*, with probability of detection = 0.45 (95% CI 0.31 - 0.65, N = 75). Consequently, we estimated the density (number/ha) of each species by adjusting counts of individuals to incorporate differences in probability of detection, following Buckland *et al.* (2001). Vegetation density did not significantly reduce the detectability of any species.

To investigate how temporal fire patterns (time-since-fire) affected the general structure of avifaunal communities we used two approaches. First, we used generalized additive mixed models (GAMM's) (Wood, 2006) to model the effect of time-since-fire on species richness of the avifauna at sites. Second, we used Mantel tests (Legendre & Legendre, 1998) to examine the relationship between time-since-fire and species composition.

Generalized additive mixed models were used for three reasons. First, generalized additive models (GAM) are a non-parametric form of regression modelling which use smoothing functions to fit non-linear relationships (Wood, 2006). This allows an investigation of non-linear responses to time-since-fire. Second, a mixed model approach was used (i.e. Generalised additive mixed model, GAMMs) because they are useful when the data are structured by a factor that may systematically influence

Chapter 3 – The influence of time-since-fire on the composition of avifauna the relationship between the response and predictor variables (Zuur *et al.*, 2009). Here, we included landscape unit as a random effect to account for the clustering of sites within landscapes. Third, GAMMs allow a separate smoothing function to be fitted to each level of a categorical variable (Wood, 2006; Zuur *et al.*, 2009). We fitted a separate smoothing function to time-since-fire for each of the two vegetation types. We also included an additional variable, 'northing', in each model to represent the geographic position of each site along the south-north gradient in aridity. Models were built using the mgcv package (Wood, 2006) in the R statistical program (R Development Core Team, 2009). The proportion of the null deviance explained by the model (D^2) was used as a measure of model fit.

Mantel tests were used to examine the influence of time-since-fire on the composition of the community, by examining the correlation between matrices of dissimilarity in species composition (Bray-Curtis measure) and dissimilarity in time-since-fire (Euclidean distance), for sites in each reserve complex separately. We visually portrayed these dissimilarities using scatterplots.

To examine the distinctiveness of the community in different seral stages we used a two-way analysis of similarity (ANOSIM) (Clarke & Gorley, 2006). We grouped the data into time-since-fire categories, each spanning 10 years, and used the two-way ANOSIM to compare the similarity in community composition (Bray-Curtis measure) between sites in different time-since-fire categories grouped by reserve complex (i.e. geographic area). Thus, we were able to determine the degree to which community composition differed between time-since-fire categories, while accounting for differences in species composition between different reserves (Clarke & Gorley, 2006).

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Chapter 3 – The influence of time-since-fire on the composition of avifauna ANOSIM calculates the difference in composition between sites in different categories by calculating an R-statistic. The R-statistic compares the dissimilarity of sites *within* a category and the dissimilarity of sites *between* categories. Higher values of R represent greater distinctiveness of communities in each category. This statistic can then be tested for significance using permutation tests, although the level of significance is sensitive to sample size: when there are large sample sizes, categories may be significantly different even though compositional differences are relatively small. With small sample sizes, categories may have relatively different communities but be non-significant. Consequently, it is recommended that attention be given more to the value of the R-statistic than statistical significance (Clarke & Gorley, 2006).

We developed species accumulation curves to visualise how the rate of increase in new species detected with each additional site (β diversity) varied with increasing time-since fire. Accumulation curves were developed separately for each time-sincefire category by permutation of different combinations of sites (up to 999 permutations) to estimate the mean rate of increase in number of species with each additional site (Clarke & Gorley, 2006).

For Mantel tests and ANOSIM, we excluded sites with less than three bird species and species recorded at less than five sites, to remove 'noise' in the data because dissimilarity metrics can be sensitive to sites with very few species. This left 49 species in the dataset for analysis. For Mantel tests, where data were analysed separately for each reserve complex, we repeated this process for the subsample data. Chapter 3 – The influence of time-since-fire on the composition of avifauna Mantel tests were conducted in R (Wood, 2006; R Development Core Team, 2009) using the package 'vegan' (Oksanen *et al.*, 2009), and ANOSIM and species accumulation curves in PRIMER v6.1.10 (Clarke & Gorley, 2006).

To investigate the effects of time-since-fire on the species richness of avifaunal guilds, vegetation structure, and reproduction of eucalypts, we used GAMMs (see Table 3.1 for descriptions of response variables). Species guilds were defined by the diet and foraging zones of birds (Table 3.2) based on data presented in Schodde (1981) and the Handbook of Australian, New Zealand and Antarctic birds (HANZAB, 2006). These traits have been identified as important axes of resource partitioning among birds in mallee environments (Ford & Paton, 1976a; Schodde, 1981).

 Table 3.1 Description of response variables used in regression models and the

 distribution used in each model.

Variable	Description	Distribution
Total species	Total number of species detected at a site	Poisson
richness	combining all four visits	
Guild species	Total number of species detected within a	Poisson
richness	guild (Table 2)	
Vegetation	Total number of contacts with a structure pole	Poisson
structure	within each height stratum <0.5 m, 0.5-1 m,	
	1-2 m, >2 m	
Eucalyptus	Presence or absence of evidence of	Binomial
reproduction	reproductively active species of Eucalyptus	

Species	Dietary guild	Foraging zone guild
Common Bronzewing Phaps chalcoptera	Granivore	Ground
Galah Eolophus roseicapillus	Granivore	Ground
Australian Ringneck Barnardius zonarius	Granivore	Ground
Mulga Parrot Psephotus varius	Granivore	Ground
Rainbow Bee-eater Merops ornatus	Insectivore	Above-canopy space
Brown Treecreeper Climacteris picumnus	Insectivore	Trunk and branch
Splendid Fairy-wren Malurus splendens	Insectivore	Ground
Variegated Fairy-wren Malurus lamberti	Insectivore	Shrub
Mallee Emu-wren Stipiturus mallee	Insectivore	Shrub
Striated Grasswren Amytornis striatus	Insectivore	Ground
Spotted Pardalote Pardalotus punctatus	Insectivore	Foliage
Striated Pardalote Pardalotus striatus	Insectivore	Foliage
Shy Heathwren Calamanthus cautus	Insectivore	Ground
Weebill Smicrornis brevirostris	Insectivore	Foliage
Chestnut-rumped Thornbill Acanthiza uropygialis	Insectivore	Trunk and branch
Inland Thornbill Acanthiza apicalis	Insectivore	Foliage
White-eared Honeyeater Lichenostomus leucotis	Nectarivore-insectivore	Trunk and branch
Purple-gaped Honeyeater Lichenostomus cratitius	Nectarivore-insectivore	Foliage
Yellow-plumed Honeyeater Lichenostomus ornatus	Nectarivore-insectivore	Foliage
Grey-fronted Honeyeater Lichenostomus plumulus	Nectarivore-insectivore	Foliage
White-fronted Honeyeater Purnella albifrons	Nectarivore	Foliage
Black-eared Miner Manorina melanotis	Nectarivore-insectivore	Foliage
Spiny-cheeked Honeyeater Acanthagenys rufogularis	Nectarivore-insectivore	Foliage
Red Wattlebird Anthochaera carunculata	Nectarivore	Generalist
Brown-headed Honeyeater Melithreptus brevirostris	Nectarivore-insectivore	Trunk and branch
Striped Honeyeater Plectorhyncha lanceolata	Nectarivore-insectivore	Foliage
White-browed Babbler Pomatostomus superciliosus	Insectivore	Trunk and branch
Chestnut-crowned Babbler Pomatostomus ruficeps	Insectivore	Ground
Chestnut Quail-thrush Cinclosoma castanotus	Insectivore	Ground
Black-faced Cuckoo-shrike Coracina novaehollandiae	Insectivore	Trunk and branch
Red-lored Whistler Pachycephala rufogularis	Insectivore	Shrub
Gilbert's Whistler Pachycephala inornata	Insectivore	Shrub
Golden Whistler Pachycephala pectoralis	Insectivore	Trunk and branch
Rufous Whistler Pachycephala rufiventris	Insectivore	Foliage
Grey Shrike-thrush Colluricincla harmonica	Insectivore	Trunk and branch
Crested Bellbird Oreoica gutturalis	Insectivore	Ground
Masked Woodswallow Artamus personatus	Insectivore	Above canopy space
White-browed Woodswallow Artamus superciliosus	Insectivore	Above canopy space

Table 3.2 Dietary and foraging zone guilds for bird species.

Species	Dietary guild	Foraging zone guild
Dusky Woodswallow Artamus cyanopterus	Insectivore	Above canopy space
Grey Butcherbird Cracticus torquatus	Insectivore	Ground
Australian Magpie Cracticus tibicen	Insectivore	Ground
Grey Currawong Strepera versicolor	Insectivore	Trunk and branch
Willie Wagtail Rhipidura leucophrys	Insectivore	Sub-canopy space
Australian Raven Corvus coronoides	Insectivore	Ground
Restless Flycatcher Myiagra inquieta	Insectivore	Trunk and branch
Jacky Winter Microeca fascinans	Insectivore	Sub-canopy space
Red-capped Robin Petroica goodenovii	Insectivore	Ground
Hooded Robin Melanodryas cucullata	Insectivore	Ground
Southern Scrub-robin Drymodes brunneopygia	Insectivore	Ground

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3.4 Results

We detected a total of 6390 individual birds from 68 species, from repeated pointcount surveys at 462 sites examined in this study. Nineteen species were detected at fewer than five sites, 37 species at between five and 99 sites and 12 species at greater than 100 sites. Species richness at sites varied between 0 and 13 species. The Weebill *Smicrornis brevirostris* was the most commonly detected species (297 sites). One species (Grey-fronted Honeyeater *Lichenostomus plumulus* was recorded only to the north of the Murray River, and two species (Mallee Emu-wren *Stipiturus mallee* and Purple-gaped Honeyeater *Lichenostomus cratitius*) were restricted to south of the Murray River.

3.4.1 Influence of time-since-fire on the structure of avifaunal assemblages

Species richness displayed a strong relationship with time-since-fire in Triodia Mallee (estimated df= 7.25, F=12.51, P<0.001). We did not detect a significant response for sites in Chenopod Mallee but there was a positive trend (estimated

Chapter 3 – The influence of time-since-fire on the composition of avifauna df=2.18, F=2.66, *P*=0.066). In Triodia Mallee, species richness was lowest at sites directly after fire, but then increased sharply until 10-20 years post-fire, after which it reached an asymptote (Fig. 3.2). The position of sites along the gradient of aridity did not influence species richness (coefficient= -3.25×10^{-07} t=-0.774, *P*=0.44); however, richness differed between vegetation types and was significantly higher in Chenopod Mallee than Triodia Mallee (coefficient=-0.26, t=-5.635, *P*<0.001). The model explained a substantial proportion of the variation in species richness (D² = 0.30).



Figure 3.2 Relationship between time-since-fire and species richness of birds at sites in Triodia Mallee, points = raw data, solid line = modelled richness ± 1 SE (dashed lines).

Chapter 3 – The influence of time-since-fire on the composition of avifauna Dissimilarity in the composition of bird species between sites (Bray-Curtis dissimilarity measure) was positively correlated with dissimilarity in time-since-fire (years) between sites (Table 3.3). This was true for sites in both Chenopod Mallee and Triodia Mallee in each reserve complex, except for Chenopod Mallee sites in the East Mallee Block reserve complex (Table 3.3) where the sample size was low. The mean dissimilarity in composition between sites increased with dissimilarity in time-since-fire between sites, in a positive linear relationship (Fig. 3.3a, b). However, sites with complete dissimilarity (i.e. value of 1.0) were apparent for almost all time-contrasts (Fig. 3.3c, d). Examination of pairs of sites with the most similar avifaunal composition at each time-since-fire contrast (i.e. the lower bound points in Fig. 3.3c and d), presents a non-linear pattern; sites that differ by up to 40-50 years in post-fire age can display similar species composition, but beyond this time difference the composition of the avifauna at pairs of sites with the most similar composition become increasingly divergent.

 Table 3.3 Mantel tests of the relationship between species composition

 dissimilarity (Bray-Curtis) and time-since-fire dissimilarity (years) for sites in

 each reserve complex.
 Sample sizes (N) are based on sites with >2 species. Species

 included were those recorded at >4 sites in each reserve complex.
 P-value is based

 on 9999 permutations.

Reserve Complex	Triodia Mallee			Chenopod Mallee		
	Ν	Mantel r	Р	N	Mantel r	Р
North West Mallee Block	73	0.1627	0.0063	71	0.2352	< 0.0001
South Mallee Block	126	0.2128	< 0.0001	71	0.1305	0.0108
East Mallee Block	53	0.2243	0.0026	14	-0.0907	0.6869



Time since fire dissimilarity (years)

Figure 3.3 Changes in the dissimilarity of species composition (Bray-Curtis measure) with dissimilarity in time-since-fire (Euclidean distance) for pairs of sites. This example is for sites from the Gluepot, Danggali, Scotia, Tarawi reserve complex. The plots (upper) show the mean Bray-Curtis dissimilarity for each time-since-fire contrast in a) Triodia Mallee and b) Chenopod Mallee; and (lower) all dissimilarities between pairs of sites in c) Triodia Mallee and d) Chenopod Mallee, respectively.
Chapter 3 – The influence of time-since-fire on the composition of avifauna *3.4.2 Distinctiveness of communities in different post-fire successional stages* Mantel tests and scatterplots can identify trends in compositional dissimilarity of the avifauna attributable to differences in time-since-fire (years) between sites. They do not, however, provide information on the *timing* of changes in composition, and the relative distinctiveness of communities in different post-fire successional stages. By grouping data into 10-year time-since-fire categories and using ANOSIM, a direct comparison is possible of the difference in species composition between particular stages during succession (Fig. 3.4). Only one site fell between 11 and 20 years post-fire, and thus did not allow comparisons of this time-period with other time-periods in the temporal succession.

In Triodia Mallee, increasingly distinct avifaunal assemblages occurred between post-fire ages at opposite ends of the time-since-fire (succession) gradient (Fig. 3.4a). Also, Fig. 3.4a shows evidence of non-linearity in rates of change in composition. That is, the composition of communities changes faster with time-since-fire in early succession vegetation, such that the differences between communities separated by a given time difference become less distinct with increasing time-since-fire age. This pattern translates to increased temporal spans occupied by communities of similar species composition. Although the community composition changes continuously along the time-since-fire gradient, the patterns displayed in Fig. 3.4a suggest three major successional stages; communities of either 21-40 or >50 years since-fire. Note that although sites 91-100 years old show minimal distinction from those 21-30 years old (Fig. 3.4a), this is based on few sites (N=9) and must be interpreted with caution.

Chapter 3 – The influence of time-since-fire on the composition of avifauna Similar patterns were evidenced in Chenopod Mallee (Fig. 3.4b); however, these patterns are more difficult to interpret due to small sample sizes in the <10 years since-fire and 81-90 and 91-100 year categories (N=6 in each), giving the appearance of a lack of distinctiveness of communities between these categories. Chenopod Mallee does display evidence of subtly different successional patterns, with the transition between younger and older successional stages appearing to relate more to sites 31-40 years since fire (*cf* 41-50 years for Triodia Mallee).

3.4.3 β -diversity amongst sites within different successional stages

Species accumulation curves (Fig. 3.5) showed that in both Triodia Mallee and Chenopod Mallee vegetation, the mean rate of increase in species richness with increasing numbers of sites surveyed (β diversity) is lowest for sites <10 years since fire, and generally becomes greater for older age-classes. That is, for a given number of sites surveyed, a larger number of species is likely to be recorded in older post-fire age-classes due to greater between-site diversity. In Chenopod Mallee, the rate of accumulation of additional species differs less where sites are >60 years old.

Of the 49 species detected at >5 sites, 47 species were detected in both Triodia Mallee and Chenopod Mallee. None of the 10-year time-since-fire categories supported all species (Fig. 3.5).



Figure 3.4 The relative level of distinction (R-statistic from ANOSIM) between sites within a particular age category compared with sites in each alternative category for; a) Triodia Mallee and b) Chenopod Mallee. For example, the first part of the diagram (top left) shows the distinction in avifaunal composition between sites 0-10 years post fire and sites 21-30 years, 31-40 years, 41-50 years, 51-60 years etc. Negative R-statistics are not shown. Values of R-statistics and significance between categories are shown in the appendix (Table A3.1 and A3.2).



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Number of sites

Figure 3.5 Species accumulation curves showing the average number of species detected with increasing numbers of sites surveyed, for sites assigned to 10 year time-since-fire categories. Curves are shown for up to 25 sites, or the maximum number of sites surveyed, within the category for a) Triodia Mallee and b) Chenopod Mallee.

Chapter 3 – The influence of time-since-fire on the composition of avifauna 3.4.4 Influence of time-since-fire on the species richness of dietary and foraging zone guilds

Most bird species in mallee ecosystems are insectivorous: of 49 species found at >5 sites, 35 species were insectivores, eight species nectarivore-insectivores (i.e. their diet consists of insects and nectar depending on availability), four species were granivores and two species nectarivores (diet primarily nectar) (Table 3.2).

Species richness of insectivores and nectarivore-insectivores both displayed significant changes with time-since-fire in Triodia Mallee, whereas only nectarivore-insectivores showed a significant response in Chenopod Mallee (Table 3.4). We did not detect any significant response for species richness of granivores and nectarivore guilds, although fewer species in these guilds found at fewer sites meant that there was less power to detect responses. None of the dietary guilds showed a significant change in richness along the aridity gradient (northing), but insectivore and granivore richness was significantly higher at sites in Chenopod Mallee than Triodia Mallee (Table 3.5). Species richness of both insectivores and nectarivore-insectivores increased rapidly in the first 10 years post-fire, then reached a plateau after 10-20 years (Fig. 3.6). These two dietary groups comprised the majority of species recorded and dominate the patterns displayed for overall species richness.

There was a more even distribution of species amongst foraging zone guilds than dietary guilds (Table 3.4). The relationship between species richness of foraging zone guilds and time-since-fire revealed more subtle longer-term trends than for dietary guilds. In Triodia Mallee vegetation, all except sub-canopy foraging species displayed a significant response to time-since-fire (Table 3.4). In Chenopod Mallee, only foliage foragers showed a significant response. Each foraging zone guild with a Chapter 3 – The influence of time-since-fire on the composition of avifauna significant response to time-since-fire displayed the lowest species richness directly after fire (Fig. 3.7). Species richness of each foraging zone guild was higher in Chenopod Mallee than Triodia Mallee (Table 3.5). Species richness of foliage foraging species tended to be higher in southerly sites, whereas the richness of sub-canopy space foragers was higher in northerly sites (Table 3.5). Species richness of trunk foraging and foliage foraging species both displayed a sharp increase up to 10-20 years post-fire: in older age-classes the richness of foliage foraging species tended to continue to increase (Triodia Mallee, Fig. 3.7a) or plateau (Chenopod Mallee, Fig. 3.7 d), whereas the richness of trunk-foraging species reached a peak and then declined in the oldest vegetation (Fig. 3.7b). Richness of shrub foraging species showed a significant response in Triodia Mallee, however, the actual values only exceeded one species at a given site on three occasions. Consequently this response is not considered a robust representation of the changes in species richness of this group.

Table 3.4 Results of regression models (GAMMs) of the relationship between species richness of birds in each dietary and foraging zone guild and the time-since-fire. The statistical values (F, P values) are for the smoothed time-since-fire term for each level of vegetation type (Chenopod Mallee and Triodia Mallee). The proportion of total deviance explained (D^2) by each model is used as a measure of model fit. The estimated degrees of freedom (edf) provide a measure of the amount of smoothing in the model. Significant responses are shown in bold type.

			Triodia Mallee			Chenopod Mallee			
	Number of species	\mathbf{D}^2	edf	F	Р	edf	F	Р	
Dietary guild									
Insectivore	35	0.24	5.75	10.75	<0.001	1.79	1.56	0.196	
Nectarivore-insectivore	8	0.22	7.54	10.55	<0.001	2.6	3.64	0.017	
Granivore	4	0.05	1.68	2.03	0.140	1.00	2.58	0.109	
Nectarivore	2	0.01	1.00	2.19	0.140	1.00	0.14	0.712	
Foraging-zone guild									
Foliage	12	0.29	7.02	14.39	<0.001	2.45	3.27	0.030	
Sub-canopy space	2	0.10	1.00	2.7	0.100	1.00	0.45	0.500	
Trunk and branch	10	0.08	4.764	3.835	0.002	1.00	3.80	0.540	
Shrub	4	0.03	1.89	3.54	0.032	1.00	0.12	0.730	
Ground	16	0.07	1.96	4.24	0.016	1.00	1.33	0.250	

Table 3.5 Coefficients and significance values for linear terms (vegetation type and northing) in Generalized Additive Mixed Models of the relationship between species richness in dietary and foraging zone guilds and time since fire. Note that vegetation type is a categorical variable with two levels (Chenopod Mallee and Triodia Mallee). The statistics shown here are for Triodia Mallee with Chenopod Mallee as the reference category. Significant responses are shown in bold type.

	V	egetation typ	e		Northing			
	Coefficient	t-value	Р	Coefficient	t-value	Р		
Dietary guild								
Insectivore	-0.349	-7.01	<0.001	-7.03×10 ⁻⁰⁷	-1.41	0.159		
Nectarivore-insectivore	0.011	0.17	0.864	-8.69×10^{-07}	-1.53	0.126		
Granivore	-0.611	-3.27	0.001	6.68×10 ⁻⁰⁷	0.39	0.699		
Nectarivore	-0.034	-0.20	0.842	-4.35×10 ⁻⁰⁷	-0.24	0.814		
Foraging-zone guild								
Foliage	-0.106	-2.07	0.039	-1.35×10 ⁻⁰⁶	-2.41	0.016		
Sub-canopy space	-0.928	-6.03	<0.001	3.11×10 ⁻⁰⁶	2.45	0.015		
Trunk and branch	-0.261	-3.60	<0.001	-1.35×10 ⁻⁰⁶	-1.55	0.122		
Ground	-0.419	-5.62	<0.001	4.20×10 ⁻⁰⁷	0.68	0.495		
Shrub	-0.541	-2.11	0.035	1.02×10^{-06}	0.40	0.686		



Figure 3.6 Relationship between time-since-fire and species richness of different dietary guilds; a) insectivores and b) nectarivore-insectivores in Triodia Mallee; c) nectarivore-insectivores in Chenopod Mallee. Points = raw data, solid line = modelled richness (GAMM) ± 1 SE (dashed lines).



Figure 3.7 Relationship between time-since-fire and species richness of different foraging zone guilds; a) foliage foraging species, b) trunk and branch foraging species and c) ground foraging species in Triodia Mallee, and d) foliage foraging species in Chenopod Mallee. Points = raw data, solid line = modelled species richness (GAMM) ± 1 SE (dashed lines).

3.4.5 Influence of time-since-fire on vegetation structure

Vegetation structure (number of contacts) in all four height strata displayed a significant change with time-since-fire in Triodia Mallee, whereas only the 0.5 - 1 m and the > 2 m height strata showed a significant change with time-since-fire in Chenopod Mallee (Table 3.6). The greatest structural complexity in vegetation

across the four height strata in Triodia Mallee occurs at 10 to 30 years post-fire, when there is a relatively even density in the different strata, after which the midstory structure begins to decline and the canopy vegetation (>2 m) continues to become more dense (Fig. 3.8). In contrast to Triodia Mallee, Chenopod Mallee shows little change in understorey and mid-storey structure with time-since-fire, but there is a consistent increase in the canopy density (greater than 2 m) until ~60 years when the canopy density begins to decline (Fig. 3.8). Vegetation density <0.5 m was greater in Triodia Mallee, whereas density of vegetation >2 m was greater in Chenopod Mallee (Table 3.7). Density of vegetation 1-2 m was greater in more southerly sites (Table 3.7)

Table 3.6 Results of regression models (GAMMs) of the relationship of vegetation structure and presence of reproductive eucalypts with time since fire. Statistical values (F, P) are for the smoothed time-since-fire term for each level of vegetation type (Chenopod Mallee and Triodia Mallee). Amount of smoothing is delineated by the estimated degrees of freedom (edf). Significant responses are shown in bold type.

	Ti	ime-since-f	fire	Time-since-fire			
	(T	riodia Mall	lee)	(Chenopod Mallee)			
	edf	edf F P			edf F		
Height strata							
< 0.5 m	3.56	4.37	0.003	1.00	1.59	0.208	
0.5 – 1 m	6.67	6.92	<0.001	1.00	4.18	0.041	
1 - 2 m	5.17	11.39	<0.001	1.00	1.84	0.176	
> 2 m	4.59	30.58	<0.001	2.49	4.15	0.010	
<i>Eucalyptus</i> reproduction	1.00	65.74	<0.001	1.00	15.60	<0.001	

Table 3.7 Results for the linear terms (vegetation type, northing) in generalized additive mixed models (GAMMs) of the relationship of vegetation structure and presence of reproduction in eucalypts with time since fire. Vegetation type is a categorical variable with two levels (Chenopod Mallee and Triodia Mallee). The statistics shown are for Triodia Mallee with Chenopod Mallee as the reference category. Significant responses are shown in bold type.

	Ve	egetation t	ype	Northing			
	Coefficien	t t-value	Р	Coefficient	t-value	Р	
Height strata							
< 0.5 m	0.6	9.95	<0.001	$1.67 imes 10^{-07}$	0.306	0.760	
0.5 – 1 m	0.16	1.53	0.128	$2.78\times10^{\text{-}07}$	0.231	0.818	
1 - 2 m	0.15	2.00	0.046	-3.32×10^{-06}	-5.031	<0.001	
> 2 m	-0.38	-6.30	<0.001	-6.55×10^{-07}	-1.185	0.237	
<i>Eucalyptus</i> reproduction	2.14	2.35	0.019	-4.28×10^{-06}	-0.546	0.585	

3.4.6 Influence of time-since-fire on reproduction of Eucalyptus species

Reproduction of *Eucalyptus* sp. was strongly influenced by time since fire in both Chenopod Mallee and Triodia Mallee (Table 3.6). Little evidence of reproductive eucalypts (i.e. flowers, buds, fruit) was detected at sites <10 years since fire, whereas sites >20 years since fire almost always contained reproductive *Eucalyptus* sp (Fig. 3.9).







Figure 3.9 Relationship between the occurrence of reproductively active *Eucalyptus* species at sites and time-since-fire (± 1 SE) in Chenopod Mallee (black line) and Triodia Mallee (grey line).

3.5 Discussion

This study examined temporal changes in the structure of avifaunal communities along a 100-year, post-fire chronosequence in mallee ecosystems of south-eastern Australia. We found that the structure of communities was strongly affected by fire, a finding consistent with observations of the influence of fire on individual species of birds in this system (Benshemesh, 1990; Clarke, 2005; Clarke *et al.*, 2005; Brown *et al.*, 2009; see also Chapter 2). Both species richness and the composition of communities varied with time-since-fire. The dissimilarity in species composition between sites was correlated with the dissimilarity in post-fire age, and the distinctiveness of species assemblages was greatest at opposite ends of the succession gradient. The change in species composition slowed with increasing time-since-fire, resulting in greater temporal breadth of similar species assemblages at older post-fire ages. Communities in older post-fire ages displayed higher β diversity than those in recent post-fire ages. Patterns of change in guild structure in communities appear to be related to available food resources such as nectar and invertebrates and to changing vegetation structure over longer time-frames.

3.5.1 Influence of time-since-fire on the structure of avifaunal communities

Time-since-fire strongly affected species richness of communities in Triodia Mallee, but was not clearly detected in Chenopod Mallee, likely to be a result of small sample sizes in this vegetation (particularly in the younger age-classes) rather than there being no effect. Species richness was relatively low directly after fire and took 10 years to reach an asymptote. This suggests that fire events cause either substantial mortality or force emigration of species, and that sites are subsequently colonised by some species over a ~10 year period. Over a time-span of 100 years,

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species richness did not begin to decline at sites, in contrast with predictions of the intermediate disturbance hypothesis of highest species richness in mid-succession due to the presence of both early and late succession species (Loucks, 1970; Connell, 1978). Although species richness plateaus ~10 years, this is not necessarily an indication of assemblage 'recovery' from fire (Jacquet & Prodon, 2009); changes in species composition continued to occur for decades.

The significant relationship between time-since-fire dissimilarity and the dissimilarity of avifaunal communities shows that community composition continues to change for up to a century post-fire, supporting the notion of the importance of disturbance processes in structuring bird communities (Brawn et al., 2001). The level of dissimilarity between sites was frequently high (i.e. sites sharing no species) and this difference was detected for some sites at almost all time-since-fire contrasts. This pattern is influenced by the sampling intensity of the study (only four visits to each site), and sampling grain of sites (~1.13 ha), but suggests also that factors other than time-since-fire have important effects on species composition. For instance, post-fire successional patterns of fauna often are related to vegetation structural changes (Monamy & Fox, 2000). While many vegetation attributes in mallee systems generally change in a consistent way with time-since-fire, large confidence intervals (particularly amongst older sites) show that structural attributes vary substantially amongst sites of similar post-fire age (Haslem et al., 2011). Consequently, these sites may contain different bird communities. Additionally, site context factors, such as proximity to other fire-age classes (Chapter 4) may contribute to variation in communities at sites of similar time-since-fire.

Minimum compositional dissimilarity (i.e. sites with the most similar assemblage) changed non-linearly with time contrasts between sites. For time contrasts of up to 50 years, the most similar pairs of sites tended to have equal levels of compositional similarity; but for time contrasts of >50 years the composition of the assemblage became increasingly dissimilar. This pattern indicates that for time contrasts between sites of around 50 years or more, the differences in vegetation structure and resources will be such that assemblages will inevitably be different.

3.5.2 Distinctiveness of assemblages in different post-fire successional stages

Species composition at sites in adjacent time-since-fire categories (10-year intervals) became more similar with time-since-fire, consistent with the broader understanding that rates of change in assemblages slow with increasing time since a disturbance event (Helle & Monkkonen, 1985). This pattern results in an increased temporal breadth of similar communities as succession proceeds. In Triodia Mallee, there was a distinction between communities occupying sites <10 years, those in sites 20-40 years and those in sites >50 years, while sites 41-50 years represented a transitional stage. These seral stages in community composition correspond with the peak occurrences (or rarity) of individual species. For example, sites with vegetation < 10years-since-fire are associated with peak occurrence of Chestnut-rumped Thornbills and the rarity of otherwise ubiquitous species such as the Weebill. Mid-successional communities, 20-40 years-since-fire, correspond with the peak frequency of occurrence of the White-eared Honeyeater, Spotted Pardalote, and the Triodia dependant Striated Grasswren; and later successional vegetation, > 50 years-sincefire, is associated with the highest occurrences of the Yellow-plumed Honeyeater, Striated Pardalote and Spiny-cheeked Honeyeater.

These bird assemblages correspond generally with seral changes in vegetation structure in Triodia Mallee. Vegetation <10 years since fire represents a period of regrowth of mallee eucalypts and substantial bare ground and open areas, 20-40 years since fire represents a peak in cover of *Triodia* hummock grasses and the greatest complexity of vertical vegetation structure; and >50 years-since-fire incorporates a decline in the vertical structural complexity of vegetation and a plateau in both the height and the cover of canopy (Fig. 3.8; Haslem *et al.*, 2011).

3.5.3 Contribution of different post-fire ages to species in the regional assemblage The β diversity (between site diversity) of bird species, tended to be higher in older post-fire age categories, as demonstrated by sharper rates of increase in species accumulation curves. This pattern was displayed most clearly in Triodia Mallee. In Chenopod Mallee, β diversity peaked earlier, at 51-60 years since-fire, and declined in older fire ages; although this must be interpreted with caution due to the inequality of sampling points along the time-since-fire gradient. Sites in older vegetation tend to represent greater variation in vegetation structure (Haslem *et al.*, 2011), and thus are likely to represent a greater heterogeneity of habitats, a principle driver of β diversity in birds (Boecklen, 1986).

3.5.4 Processes influencing post-fire successional patterns of the avifauna

Although temporal patterns in post-fire succession are recognised to influence bird assemblages around the world (Brawn *et al.*, 2001), the processes by which fire causes compositional changes remain poorly understood in many systems. In this ecosystem, species richness patterns in Triodia Mallee indicate that fire initially causes either significant mortality or emigration from sites, followed by a relatively slow (~10 years) process for species richness to reach levels seen in older vegetation. The precise timing at which this level of richness is achieved is difficult to determine as we had limited sampling in sites 10-20 years-since-fire. Unlike ecosystems such as boreal forest communities, where many species rapidly colonise burnt sites in the 1-3 years following fire (Hutto, 1995; Smucker *et al.*, 2005; Haney *et al.*, 2008), the mallee bird assemblage does not appear to have a large suite of early successional specialists (Chapter 2). However, some other assemblages without recognised early succession specialists also display rapid recovery in species richness; for example 2 years in heathlands and forests of south-eastern Australia (Reilly, 1991; Lindenmayer *et al.*, 2008). We identify two factors that may affect temporal patterns in species richness and changes in species composition: 1) the amount of available energy defined by food resources, the productivity hypothesis (Wright, 1983); and 2) vegetation structural attributes (MacArthur & MacArthur, 1961; Tews *et al.*, 2004). Evidence for the importance of these processes is indicated through changes in particular species guilds with time-since-fire.

Species richness of insectivores and nectarivore-insectivores both displayed similar significant responses to time-since-fire, while nectarivores and granivores showed no relationship with time-since-fire. Species richness of insectivores and nectarivore-insectivores mirrored the overall species richness pattern, low directly after fire and plateauing at ~10 years-since-fire. Availability of food resources may be an important factor influencing temporal responses of communities post-fire. Reproduction of *Eucalyptus* species was largely absent from sites <10 years since fire, and present at almost all sites >20 years since fire. Nectar from the flowers of *Eucalyptus* species is a key energy source for birds (Ford & Paton, 1976b; Bond &

Brown, 1979) that occur in mallee environments and the lack of reproduction of regenerating mallee *Eucalyptus* species is likely to represent a massive reduction in the availability of nectar. Moreover, many species of invertebrates also use *Eucalyptus* nectar in mallee environments (Horskins & Turner, 1999) and so lack of flowering and nectar would influence their availability for insectivores or nectarivore-insectivores. There is little known about the effects of fire on invertebrates (New *et al.*, 2010). Studies of invertebrates in mallee ecosystems suggest responses may vary between taxa; ants were found to be half as abundant (although with twice as many species) in recently burnt vegetation (Andersen & Yen, 1985), while abundance of beetles showed no pattern with time-since-fire (Schlesinger *et al.*, 1997). However, most investigations have used pitfall trapping, and this information may be useful only for estimating food loads for ground-foraging birds and not for species which forage on above-ground substrates.

Given that nectar production from *Eucalyptus* species is limited in recently burnt vegetation, it initially is surprising that primary nectarivores did not respond to timesince-fire. However, there are several possible explanations for this. First, only two species occur in this category (Red Wattlebird and White-fronted Honeyeater), thus the power to detect trends is limited. Second, nectarivores in Australia are highly nomadic (Woinarski, 2006), and may transiently inhabit different fire ages (Cheal *et al.*, 1979), whereas nectarivore-insectivore species may be more reliant on consistent nectar resources. Third, the species in this category take nectar from a variety of sources other than *Eucalyptus* sp. (e.g. *Eremophila* spp., *Prostanthera* spp.), in which case they may not necessarily be limited by this reduction in nectar from *Eucalyptus* sp. (HANZAB, 2006).

Granivores also did not display a significant response to fire and species in this guild, such as Australian Ringneck and Mulga Parrot, were detected across all fire ages (Chapter 2). Granivores may not be strongly limited by fire in mallee ecosystems because these species are large, highly mobile birds which can move amongst different seral stages. Recently burnt vegetation supports a range of short-lived obligate-seeding herbs which set seed in the first 10 years-since-fire (Cohn *et al.*, 2002), thus providing food resources for granivorous species.

Many structural attributes of mallee vegetation change with time-since-fire, such as stem density, canopy height, shrub cover and cover of Triodia hummocks (Haslem et al., 2011). Structural complexity at sites, a characteristic long recognised as important in structuring bird communities (MacArthur & MacArthur, 1961), increases rapidly from very simple (few contacts) directly after fire, to peak at ~20 years after fire in Triodia Mallee (Fig. 3.8; Haslem et al., 2011). Thus, while patterns of community change are likely to be partially related to food resource availability, they also may be related to the structural complexity of vegetation, which rapidly increases in the immediate 10-20 years post-fire. Over longer timeframes, species compositional changes may be associated with vegetation structural changes. For example, models of changes in species richness of foliage foragers correspond with patterns of change in the density of canopy vegetation >2 m; increasing with time-since-fire in Triodia Mallee and more subtle changes in Chenopod Mallee. Temporal changes of species richness of trunk and branch foragers compare with those of mid-storey structure, each showing a decline in older Triodia Mallee. Thus, post-fire changes in vegetation structure appear to be a

Chapter 3 – The influence of time-since-fire on the composition of avifauna mechanism which may influence ongoing changes in bird assemblages through the fire succession, consistent with the habitat accommodation model of post-fire succession (Fox, 1982).

3.5.5 Implications for conservation and management

In this investigation we have shown that fire plays a significant role in structuring the richness and composition of avifaunal communities, and consequently it is important that the temporal patterns of succession are explicitly considered in conservation and management for birds in fire-prone environments. The long timeframe over which communities changed (e.g. up to 100 years) has important implications for conservation. Management actions such as prescribed burning, which typically set the vegetation back to year zero in the succession, may have long-lasting implications for the avifaunal assemblage.

Community-level approaches present a useful way of identifying the importance of different post-fire ages to the overall avifaunal assemblage. Using these approaches, we showed that a slowing rate of compositional change through time translates to communities occupying a greater temporal span in older vegetation age-classes. In Triodia Mallee, some major successional stages in avifaunal composition (<10 years, 21-40 years, >50 years) correspond with vegetation structural changes. Furthermore, the communities associated with older sites display greater β diversity, such that older post-fire age-classes appear to be disproportionately important for community diversity in this ecosystem.

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Both availability of food resources and vegetation structural complexity appear to be important processes influencing post-fire species richness and long-term changes in community composition. Management actions, such as prescribed burning, aimed at influencing succession should explicitly consider how these actions will affect the factors likely to determine community responses. Future research specifically investigating factors such as post-fire grazing (Cohn & Bradstock, 2000), which interact with fire to effect changes in vegetation structure and food resources, will be critical in understanding how burning operations can be used to influence faunal communities.

3.6 Appendix

Table A3.1 Results of analysis of similarity (ANOSIM) tests on the comparisonsof the composition of avifauna at sites in different 10 year post-fire age-classesin Triodia Mallee.Values shown are the R-statistic, with significance values inparentheses.Significance value is based on 999 permutations.

time- since-fire categories (years)	0 - 10	21 - 30	31 - 40	41 - 50	51 - 60	61 - 70	71 - 80	81 - 90
0 - 10								
21 - 30	0.20 (0.001)							
31 - 40	0.33 (0.001)	0.05 (0.012)						
41 - 50	0.32 (0.002)	0.08 (0.139)	-0.02 (0.533)					
51 - 60	0.42 (0.001)	0.22 (0.001)	0.14 (0.057)	-0.04 (0.678)				
61 - 70	0.35 (0.001)	0.17 (0.010)	0.15 (0.027)	0.01 (0.412)	-0.06 (0.795)			
71 - 80	0.55 (0.001)	0.28 (0.003)	0.17 (0.046)	-0.08 (0.771)	-0.08 (0.751)	-0.03 (0.564)		
81 - 90	0.59 (0.001)	0.45 (0.001)	0.23 (0.006)	0.03 (0.252)	-0.06 (0.832)	-0.01 (0.460)	0.00 (0.441)	
91 - 100	0.47 (0.003)	0.24 (0.018)	0.05 (0.328)	-0.15 (0.896)	-0.18 (0.932)	-0.14 (0.944)	-0.08 (0.775)	-0.08 (0.730)

Table A3.2 Results of analysis of similarity (ANOSIM) tests on the comparisonsof the composition of avifauna at sites in different 10 year post-fire age-classesin Chenopod Mallee. Values shown are the R-statistic, with significance values inparentheses. Significance value is based on 999 permutations.

time- since-fire categories (years)	0 - 10	21 - 30	31 - 40	41 - 50	51 - 60	61 - 70	71 - 80	81 - 90
0 - 10								
21 - 30	0.19 (0.115)							
31 - 40	0.33 (0.011)	0.15 (0.053)						
41 - 50	0.72 (0.001)	0.24 (0.020)	-0.04 (0.718)					
51 - 60	0.74 (0.001)	0.30 (0.002)	-0.08 (0.888)	-0.04 (0.781)				
61 - 70	0.60 (0.001)	0.26 (0.010)	0.02 (0.342)	-0.02 (0.582)	0.08 (0.059)			
71 - 80	0.63 (0.004)	0.16 (0.059)	0.01 (0.423)	0.16 (0.067)	0.09 (0.193)	-0.05 (0.687)		
81 - 90	0.67 (0.080)	0.20 (0.124)	-0.01 (0.505)	0.10 (0.257)	0.09 (0.265)	0.05 (0.342)	0.06 (0.372)	
91 - 100	-0.08 (0.600)	0.02 (0.463)	0.23 (0.076)	0.42 (0.010)	0.32 (0.044)	0.28 (0.040)	0.01 (0.429)	-0.05 (0.629)

Chapter 4

The influence of fine-scale spatial patterns of fire on post-fire colonisation and species richness of birds



Patches of unburnt vegetation after a fire in Murray-Sunset National Park



Red-capped Robin Petroica goodenovii

4.1 Abstract

Predicting the response of faunal communities to fire presents a major challenge for land managers because the post-fire responses of species populations can vary between locations and fire events. Furthermore, post-fire recovery of fauna may occur in different ways; for example, as nucleated recovery from *in-situ* surviving populations, or by colonisation from *ex-situ* populations. Fine-scale spatial patterns in the patchiness of fires and the proximity of burnt sites to source populations may contribute to both the variability in post-fire responses and the processes by which populations recover. We examined the avifauna at recently burnt sites within extensive semi-arid shrublands of south-eastern Australia, including 72 sites <5 years-since-fire and 26 sites 10 years-since-fire. Study sites represented a gradient of increasing proximity from unburnt vegetation (i.e. >27 years since fire) and varied in the presence or absence of small $(25 \text{ m}^2 - 900 \text{ m}^2)$ unburnt patches of vegetation. For sites <5 years since fire, species richness was higher in closer proximity to unburnt vegetation and at sites containing unburnt patches. Patterns were no longer evident at sites of 10 years-since-fire. The occurrence of three of seven bird species modelled, decreased with increasing distance to unburnt vegetation, but the pattern was evident only at sites burnt uniformly. One species was found almost exclusively at patchily burnt sites. These results are consistent with the hypothesis that proximity to unburnt vegetation enhances post-fire occupancy, and that colonisation from ex-situ populations is an important aspect for post-fire recovery of avifauna over the first 10 years-since-fire. Additionally, small unburnt patches, acting as 'biological legacies', enhance the rapid recovery of assemblages post-fire. These patterns are important for understanding the dynamics of post-fire population recovery. Effective management of fire for ecological purposes needs to explicitly consider the spatial attributes of fires.

4.2 Introduction

Fire ecology has often focussed on the effect of components of the fire regime on biota: these include the history of fire events at a site (Gill, 1975), predominantly considered as time-since-fire (Fox, 1982); the frequency (or inter-fire interval) of fires (Bradstock *et al.*, 1997); the intensity (or severity) of a fire (Smucker *et al.*, 2005); and the season of burning (Woinarski, 1990). Consequently, much emphasis in fire management for biodiversity is based around the temporal aspects of fire (Clarke, 2008), particularly the idea of repeatable patterns of succession following fire events. However, spatial patterns of fire also may play an important role in patterns of faunal occupancy post-fire, and the processes by which populations recover after fire.

Fires often cause local loss of faunal species, either through mortality or emigration (Barlow & Peres, 2004). Commonly, there are relatively predictable patterns of colonisation after fire, and ongoing changes in species' occurrences and abundances with time since fire (eg. Fox, 1982; Hobson & Schieck, 1999; Haney *et al.*, 2008). However, ecologists have noted that recovery of faunal communities from different fire events can differ from predictions made by general succession patterns. For example, the Eastern Bristlebird *Dasyornis brachypterus*, believed to prefer older vegetation and to be sensitive to fire (Baker, 2000), quickly colonised recently burnt vegetation after a recent fire event (eg. Bain *et al.*, 2008; Lindenmayer *et al.*, 2009). Populations of the Mallee Emu-wren *Stipiturus mallee*, formerly found in several areas in Billiatt Conservation Park (Carpenter & Matthew, 1986), have not recovered from large fires in the late 1980s (Clarke, 2005), despite vegetation of an appropriate post-fire age for this species (16-29 years-since-fire) (Clarke, 2005; Brown *et al.*, 2009) becoming abundant.

The spatial pattern of a fire and the context of burned sites may affect the variability of species' responses to fire, and provide insights into patterns of species' recovery post-fire (Keith *et al.*, 2001; Whelan *et al.*, 2001). The size, shape and patchiness of a fire will affect the context of a burned site by determining the distance that animals must travel to escape fire, or to colonise sites from external source populations after fire (Brotons *et al.*, 2005; Knight & Holt, 2005). The patchiness of a fire also may affect how a species responds to that fire event. Unburnt patches of vegetation within the fire boundary are examples of 'biological legacies'; that is, organisms and organic material that persist through a disturbance event (Turner *et al.*, 1998; Franklin *et al.*, 2000). These biological legacies may act as refuges, where organisms can escape a fire event.

Little is known about the importance of biological legacies, or what constitutes a refuge for many organisms. However, the degree to which recently burnt vegetation is repopulated by species surviving *in-situ* in a refuge (i.e. nucleated recovery), as opposed to being recolonised from *ex-situ* populations may play an important role in post-fire succession patterns and in species responses to fire (Banks *et al.*, 2011). Also, biological legacies may assist post-fire colonisation by providing habitat structure and resources. The complexity of fire environments and fire events can result in a multitude of different post-fire recovery scenarios (Whelan *et al.*, 2001). Understanding how spatial patterns of fire influence post-fire recovery processes may shed light on this complexity.

To investigate post-fire colonisation and the importance of unburnt refuges for fauna, we examined four aspects of the relationship between the spatial properties of fires and post-fire bird assemblages in semi-arid shrublands in south-eastern Australia.

First, to assess whether species recolonise from populations external to the fire, we examined the effect of proximity to unburnt vegetation (>27 years since fire) on: a) bird species richness and b) the occurrence of individual species. Second, to investigate whether biological legacies, represented by small patches of unburnt vegetation $(25 - 900 \text{ m}^2)$, affect the post-fire community, we compared species richness and the occurrence of individual species at sites containing unburnt patches and those burnt uniformly. Third, to investigate the importance of small unburnt patches either as refuges (where species survive the fire and persist) or as habitats which also are colonised from *ex-situ* populations, we compared the influence of proximity to unburnt vegetation on birds at sites that contained unburnt patches and those burnt uniformly. Finally, to examine the time over which colonisation from ex-situ populations occurs, we tested whether proximity had an influence on species richness and species occurrence at different ages post-fire.

We made three predictions. First, if species recolonise burnt sites from nearby unburnt vegetation, then we expect decreasing species richness and frequency of occurrence of individual species with increasing distance from unburnt vegetation. Second, if fire patchiness assists species to recolonise sites or provides refuges for species, then species richness and occurrence of individual species will be greater at patchy sites than uniformly burned sites. Third, if patchily burnt sites represent refuges where species survive *in-situ* during fire events, then proximity to unburnt vegetation should have less influence on species richness or occurrence of species at patchy sites. On the other hand, if patchy sites are colonised from nearby unburnt vegetation, then a relationship with proximity should be equally evident for patchy sites.

4.3 Methods

4.3.1 Study area

The study was conducted in the Murray Mallee region of south-eastern Australia, situated between $33 - 35^{\circ}$ S and $140 - 142^{\circ}$ E. The climate is semi-arid, with a gradient of increasing aridity from south to north (Pausas & Bradstock, 2007). Mean annual rainfall ranges from approximately 200 - 350 mm across the region. Temperatures across the study area range from mean daily maxima of $32 - 33^{\circ}$ C in summer months and $15 - 16^{\circ}$ C in winter months; to mean daily minima from $14 - 18^{\circ}$ C and $4 - 6^{\circ}$ C, respectively (Australian Bureau of Meteorology). The region is mostly flat, with local topographic variation provided by low dune-swale systems (Wasson, 1989).

"Mallee" eucalypt shrubland is the major vegetation type, consisting of open vegetation dominated by multi-stemmed species of *Eucalyptus* and an understorey of shrubs and grasses (Bradstock & Cohn, 2002). Two major vegetation associations, Triodia Mallee and Chenopod Mallee, have been identified and mapped in the region, differing on the basis of floristic composition of the overstorey *Eucalyptus* spp. and understorey species (Haslem *et al.*, 2010). Mallee vegetation is highly flammable and large fires (>10 000 ha) occur regularly, generally resulting in removal of both understorey and canopy. Fuel continuity is important in determining the size of fires (Noble & Vines, 1993) and discontinuous fuels can result in unburnt patches (O'Donnell *et al.*, 2010). Many plant species display life-history attributes adapted to recurrent fire disturbance (Pausas & Bradstock, 2007). One conspicuous adaptation is the coppicing of mallee *Eucalptus* spp. from underground lignotubers following fire.

4.3.2 Study design and data collection

This investigation forms part of a broader study exploring the influence of the properties of fire mosaics on biota in the Murray Mallee region of south-eastern Australia. For this broader study we sampled birds at 560 sites, with 20 survey sites clustered in each of 28 landscapes. Landscapes were selected to represent mosaics of different spatial fire-history patterns. The 20 survey sites in each landscape were located such that they sampled each post-fire age-class in proportion to its extent in the landscape. The potential locations of sites were determined by using maps of fire footprints and were recorded as geographic coordinates prior to going into the field, and then checked for suitability. Generally, sites were 500 m apart.

We determined the post-fire age of vegetation by using maps of fire-footprints, developed by analysing 15 individual years of LandsatTM satellite imagery (1975-2007) and mapping the extent of each fire in the region (Avitabile *et al.*, 2011). The resolution of the satellite imagery was of individual pixels measuring 30×30 m.

For this investigation, we selected two subsets of sites. The first consisted of all sites of <5 years since fire, as at 2007 (fire years 2003-2006) (n=74), separated into two categories: those burnt <2 years prior (i.e. fire years 2005 and 2006) (n=25) and those burnt 3 - 4 years prior (i.e. fire years 2003-2004) (n=49). The second subset consisted of all sites that were 10 years since fire (i.e. burnt in 1997) and which had been burnt uniformly (n=26).

For each site we analysed the proximity to the nearest large patch of unburnt vegetation (\geq 27 years since fire) that was readily detectable with satellite imagery using ArcGIS software (ESRI, 2009). In each case these large patches were >5 ha,

although in most cases it represented the vegetation external to the fire boundary. Two outlier sites, located >700 m from unburnt vegetation (842 m and 1062 m) were excluded from the analysis. From field visits, we identified whether a site was uniformly or patchily burned at a scale smaller than could be detected by satellite imagery. A site was denoted as being burnt patchily where an area of >25 m² remained unburnt within 60 m of the survey point; it was otherwise denoted as being burnt uniformly.

We conducted four rounds of bird surveys, one in each of the Austral spring and summer of 2006 - 2007 and 2007 - 2008. Each survey consisted of a 5 min point count, for which an observer stood at a specified survey point and counted all species seen or heard within a 60 m radius, and recorded the distance of each bird detected from the observer. For visual records, the distance was measured using an OPTi-LOGICTM 800LH laser range finder: for aural detections the distance was estimated by the observer. We then combined all surveys to document the species present at each site. We analysed the distances of species' detections using multiple covariate distance sampling (Buckland *et al.*, 2004; Marques *et al.*, 2007), using the program Distance 5.0 release 2 (Thomas *et al.*, 2006) to investigate changes in detectability of species with increasing distance from the observer and with increasing vegetation density. All species were detectable at the extremities (60 m) of the point count and vegetation density did not significantly reduce the detectability of any species, thus presence or absence and species richness of sites are unlikely to be biased by false absences due to differential detectability of species.

4.3.3 Statistical analysis

We used a regression approach to investigate the relationship between species richness, and the occurrence of individual species, with the proximity to unburnt vegetation and the presence or absence of small unburnt patches at the site (patchiness). We chose to use generalised additive mixed models (GAMMs) as the regression framework (Wood, 2006; Zuur et al., 2009). These models use smoothing terms to fit non-linear responses to continuous gradients (Wood, 2006); preliminary examination of the data indicated that bird species may show non-linear responses to proximity to unburnt vegetation. Additionally, a smoothing term can be fitted to the continuous variable at multiple levels of a categorical variable (Wood, 2006). This feature allowed us to fit a separate smoothing term to each level of the categorical variable 'patchiness' (i.e patchy or uniform). Thus, we could concurrently test the influence of proximity on species richness and species occurrence at sites that were burnt either patchily or uniformly. We undertook the modelling in a mixed-model framework because the data were necessarily clustered due to the landscape design incorporated in the broader investigation. Mixed models are appropriate where there is the potential for systematic variation in the response variable caused by structuring in the data (Zuur et al., 2009).

We fitted GAMMs for species richness detected at a site (species richness) and the presence or absence of individual species at a site (species occurrence), as Poisson and binomial models, respectively. The modelling process was undertaken in two stages. First, models were fitted to the subset of sites that were <5 years since fire. These models tested the effect of proximity to unburnt vegetation (\geq 27 years since fire) and patchiness on species richness and species occurrences after fire. A

smoothing term was used for proximity to unburnt vegetation (continuous variable), fitted to each level of the patchiness variable, and patchiness was included as a categorical variable also. Additionally, time-since-fire was included as a categorical variable (i.e. 1-2 years since fire, or 3-4 years since fire) to test for patterns in occurrence of species at sites with increasing age. A variable representing the position of sites along the gradient of aridity, denoted by the geographic northing unit (World Grid System 1984), was also included to account for possible changes in occurrence of species due to broad-scale biogeographic factors. Second, to ascertain the time-frame over which colonisation from unburnt vegetation may occur, we investigated the relationship of species richness and occurrence with proximity to unburnt vegetation at sites that were 10 years since fire. This was conducted using only uniformly burnt sites. Consequently, only the proximity of vegetation and position along the gradient of aridity were included in this analysis. Model definitions are shown Table 4.1. Responses were considered significant where p<0.05 for the proximity term (which used a smoothing function) and, for linear terms, where the coefficient $\pm 2SE$ did not overlap with zero. Model fit was interpreted as the proportion of the total deviance explained (D^2) .

Table 4.1 Definitions of models of the relationship between species richness and occurrence of individual species (presence-absence) with proximity of unburnt vegetation (proximity) and patchiness of sites (patchiness). Also included are linear predictors northing and time-since-fire (1-2 or 3-4 years-since-fire). Model definitions include terms fit with a smoothing function (s) and the categorical variables at which the continuous variable is fitted to each level (by).

Dataset	Ν	Response Variable	Model Definition	Distribution
<5 years-since-fire	74	Species richness	s(proximity, by patchiness) + patchiness +time-since-fire + northing	Poisson
<5 years-since-fire	74	Individual species	s(proximity, by patchiness) + patchiness + time-since-fire + northing	Binomial
10 years-since-fire	26	Species richness	s(proximity) + northing	Poisson
10 years-since-fire	26	Individual species	s(proximity) + northing	Binomial

4.4 Results

The four surveys, at each of the 100 survey sites included in this study, detected 44 species of birds with most being recorded infrequently. Twenty-seven species were recorded at 10 or fewer sites, 12 species were detected at between 10 and 30 sites and five species between 30 and 55 sites.

4.4.1 Response of species richness to fine-scale spatial patterns of fire

Species richness of birds generally was low in recently burnt vegetation (<5 yearssince-fire) (mean = 4.12, range 0 - 14 species). Species richness was influenced by both proximity to unburnt vegetation (\geq 27 years-since-fire) and presence of unburnt patches of vegetation at the site, which together explained a large proportion of the variance in the data (Table 4.2). Species richness declined with increasing distance to unburnt vegetation (Fig. 4.1). This pattern was exhibited in both patchy and uniformly burnt sites, although patchily burnt sites showed consistently higher species richness across the entire gradient in proximity (Fig. 4.1). Species richness was higher in sites 3 - 4 years-since-fire than sites <2 years-since-fire (Fig. 4.1). At sites of 10 years-since-fire, there was no significant relationship between species richness and proximity of unburnt vegetation (Table 4.2 & Fig. 4.2). We did not detect any relationship between species richness and position along the north-south gradient of aridity, consequently values are not reported.

Table 4.2 Parameters for models of the relationship of species richness with fine-scale spatial properties of fire. Two data sets are presented; a) Sites <5 yearssince-fire, model defined by a smoothed term for proximity to unburnt vegetation fitted to both patchy and uniform sites, with patchiness and time-since-fire included as linear terms; b) 10 years-since-fire, uniformly burnt sites, smoothed term fitted to proximity to unburnt vegetation. The degree of smoothing is denoted by the estimated degrees of freedom (edf). Significant responses are shown in bold type.

Mo	odel	N	D^2	Patchiness category	edf	Proxin F	nity P	Patchiness coefficient (SE)	Time-since-fire coefficient (SE)
a)	<5 years-since-fire	72	0.60	Patchy Uniform	1 1	7.03 15.81	0.010 <0.001	0.41 (0.16)	0.48 (0.23)
b)	10 years-since-fire	26	0.06	Uniform	1	1.48	0.237		






Figure 4.2 Relationship between species richness of birds and proximity of a site to unburnt vegetation (> 27 years-since-fire) for sites 10 years-since-fire and uniformly burned.

4.4.2 Responses of individual species to fine-scale spatial patterns of fire

Models of the relationship between the occurrence of individual species and finescale spatial patterns of fire were built for species that were encountered at \geq 20% of sites in vegetation <5 years-since-fire (i.e. \geq 15 sites). This resulted in models for six species. There was substantial variation in the deviance explained by each model (Table 4.3). Probability of occurrence decreased with increasing distance from unburnt vegetation for three species, the Jacky Winter, Spotted Pardalote and the White-eared Honeyeater (Fig 4.3). This pattern was evident only at sites burnt uniformly, not at sites containing unburnt patches (Table 4.3). Species which displayed a significant response to proximity of unburnt vegetation in sites <5 yearssince-fire, were also modelled for vegetation 10 years-since-fire. In this age-class, there was no evidence for a pattern of reduced occurrence with proximity from unburnt vegetation for either the Spotted Pardalote or the White-eared Honeyeater (there were insufficient records (N=2) for the Jacky Winter to be modelled) (Table 4.3).

The ground-dwelling Chestnut Quail-thrush was strongly influenced by the presence of unburnt patches at recently burnt sites, but did not display a significant response to proximity (Table 4.3). Seventeen of the 19 records for this species were at sites that were patchily burned. This species was recorded more frequently in sites of 3-4 years-since-fire than <2 years since fire (Table 4.3).

We detected significant variation along the north-south aridity gradient for two species, the White-eared Honeyeater (coefficient = -2.69×10^{-5} , SE = 1.14×10^{-5}) and Chestnut Quail-thrush (coefficient = 1.17×10^{-5} , SE= 5.27×10^{-6}), which were recorded more commonly in southern sites and northern sites, respectively.

Table 4.3 Parameters for models of the relationship between the frequency of occurrence of species and fine-scale spatial properties of sites. Two data sets and model definitions are presented: a) sites <5 years-since-fire, with models defined by a smoothed term for proximity to unburnt vegetation fitted to both patchy and uniform sites, with patchiness and time-since-fire included as linear terms; b) 10 years-since-fire, uniformly burnt sites, with a smoothed term fitted to proximity to unburnt vegetation. Model fit is the proportion of the total deviance explained by the model. Coefficients for linear responses to patchiness and time-since-fire are measured against the reference variables of 'patchy' and '3-4 years old' respectively. Amount of smoothing is indicated by the estimated degrees of freedom (edf) for smoothing term. Significant responses are shown in bold type.

		- 2	Patchiness	Proximity			Patchiness	Time-since-fire	
Model	Ν	D²	category	edf	F	Р	coefficient (SE)	coefficient (SE)	
a) <5 years-since-fire			_						
Chestnut Quail-thrush Cinclosoma castanotus	19	0.48	Patchy Uniform	1 1	0.45 3.52	0.505 0.072	-52.36 (4.68)	-42.75 (4.31)	
Chestnut-rumped Thornbill Acanthiza uropygialis	28	0.08	Patchy Uniform	1 1	0.11 0.20	0.741 0.654	-0.32 (0.72)	0.84 (0.86)	
Grey Butcherbird Cracticus torquatus	20	0.18	Patchy Uniform	1 1	2.99 1.20	0.088 0.277	0.02 (1.07)	0.32 (0.85)	
Jacky Winter Microeca fascinans	15	0.05	Patchy Uniform	1 1	0.37 4.96	0.546 0.029	-0.63 (0.76)	1.08 (1.38)	
Spotted Pardalote Pardalotus punctatus	22	0.46	Patchy Uniform	1 1	0.58 4.17	0.451 0.045	0.09 (0.73)	-0.5 (1.84)	
Weebill Smicrornis brevirostris	31	0.32	Patchy Uniform	1 1	0.16 1.02	0.687 0.317	-2.31 (1.37)	-0.02 (0.9)	
White-eared Honeyeater Lichenostomus leucotis	27	0.57	Patchy Uniform	1 1	1.08 5.56	0.302 0.021	-0.71 (0.86)	0.93 (1.41)	
b) 10 years-since-fire									
Spotted Pardalote Pardalotus punctatus	12	0.09	Uniform	1	0.01	0.925			
White-eared Honeyeater Lichenostomus leucotis	21	0.07	Uniform	1	0.46	0.507			



Figure 4.3 The relationship between occurrence of species at sites <5 yearssince-fire with proximity of a site to unburnt vegetation (>27 years-since-fire). Plots are for three species of birds that displayed a significant response; a) Jacky Winter, b) Spotted Pardalote, and c) White-eared Honeyeater. Modelled relationship (±SE) and raw data are shown. Plots represent only uniform sites, where species displayed a significant relationship.

4.5 Discussion

We made three predictions about patterns in species richness and occurrence of individual species of birds expected under different post-fire scenarios. First, under a scenario of species colonising recently burnt sites from nearby unburnt vegetation, we predicted that species richness and occurrence would decline with distance from unburnt vegetation. This pattern was evident for species richness and for three of the seven species modelled. Second, we predicted that in a scenario where small unburnt patches act as refuges, or are preferentially colonised, species richness and occurrence would be greater at sites burnt patchily. This pattern too was evident for species richness and for one species. Third, we predicted that if small unburnt patches primarily represent refuges, rather than colonised sites, then sites that contain small unburnt patches should display lesser declines in species richness and occurrence of species with proximity from unburnt vegetation. The results for individual species and species richness varied in relation to this prediction. Species richness did decline with distance from unburnt vegetation, regardless of whether sites were burnt patchily or uniformly; however, individual species displayed a significant decline with distance from unburnt vegetation only where sites were burnt uniformly. Thus, while small unburnt patches may act as refuges for some individual species, richness patterns suggest that these sites are also colonised by species from larger patches of unburnt vegetation.

4.5.1 The effect of proximity to large patches of unburnt vegetation on post-fire occupancy of species and species richness

Our data indicate that in mallee ecosystems recently burnt vegetation is commonly colonised by birds located in unburnt vegetation *ex-situ*. These patterns are consistent with those documented for species of Orthoptera in sandhill ecosystems of

North America (Knight & Holt, 2005), and suggested for birds in Mediterranean ecosystems of Europe (Brotons *et al.*, 2005). On the other hand, the patterns seen here contrast with patterns identified in a study of small mammals, which suggested that post-fire population recovery was driven by *in-situ* survival of individuals, rather than *ex-situ* colonisation (Banks *et al.*, 2011). Different patterns across taxa indicate that multiple strategies and processes contribute to post-fire successional patterns. The relationship with proximity to unburnt vegetation disappeared by 10 years post-fire in this ecosystem, suggesting that the first 10 years are an important period of initial colonisation, a pattern consistent with increases in species richness up to 10 years post-fire, after which richness plateaus (see Chapter 2).

Patterns of colonisation from unburnt areas indicate the importance of the faunal assemblages surrounding recently burnt areas. In large conservation reserves, such as those where this investigation took place, patterns of succession may be more consistent because unburned vegetation outside the fire boundary can support large populations of many species. In fragmented systems, however, where fires can burn a substantial proportion (or the entire area) of a habitat patch in a hostile matrix (Menkhorst & Bennett, 1990), the full suite of species may not be present in remaining unburnt vegetation. In this scenario, post-fire successional patterns will be influenced by the availability of nearby source populations of species and the dispersal capacities of species that may allow them to recolonise the burnt area from outside the fragment (Brotons *et al.*, 2005). This situation is similar to that experienced by the Mallee Emu-wren in Billiatt Conservation Park (Clarke, 2005; Brown *et al.*, 2009), where almost the entire reserve was burned.

4.5.2 Influence of unburnt patches ('biological legacies') on the post-fire occupancy of species and species richness

Patchily burnt sites supported more species than uniformly burnt sites. Two mechanisms potentially play a role in determining these observed patterns. First, individual birds may survive at a site due to the patchy nature of the fire, with unburnt patches acting as refuges. In this case, the greater number of species at these sites may represent individuals which have persisted from before the fire, and are biological legacies themselves. Second, after fire, species may preferentially colonise sites burnt patchily as they represent increased vegetation structure or food resources.

Our data indicates that each of these mechanisms may be important. The clear pattern of decreasing species richness with distance from unburnt vegetation, suggests that patchy sites are being colonised from *ex-situ* populations in unburnt vegetation. On the other hand, the occurrence of individual species at patchily burnt sites did not show a decline in occurrence with increasing distance. The Chestnut Quail-thrush, a ground dwelling species, was found almost entirely at patchily burnt sites, regardless of their proximity to unburnt vegetation. These patterns lend support to the potential for unburnt patches to function as refuges, although neither of these patterns precludes the possibility of the species seeking out and travelling farther to colonise, patchily burnt sites in a landscape.

Regardless of the mechanism, these data are consistent with the hypothesis that biological legacies are an important factor to be considered when interpreting the effects of fire on biota (Turner *et al.*, 1998; Franklin *et al.*, 2000), with small patches of unburnt vegetation an important determinant of the occurrence of species postfire. Consequently, patchiness of fires should be recognised in fire management strategies. Patchy fires may result in faster recovery of avifaunal communities and potentially provide habitat for some species that may be eliminated in large uniform fires. In this investigation, the Chestnut Quail-thrush appears to be a species unable to use uniformly burnt vegetation, but it was reasonably common where vegetation was burnt patchily.

4.5.3 Conclusions and management implications

The strong influence of the proximity to unburnt habitat and the patchiness of a fire, have important management implications for species conservation. In mallee ecosystems, fires dramatically alter the vegetation structure and many bird species are lost from sites during fire events. Species primarily recolonise burnt areas from vegetation outside the fire event, and may take longer to colonise more-isolated uniformly burnt sites. Larger fires result in broader scale removal of species and consequently recolonisation is likely to take longer over greater distances. In this investigation, recovery in species richness took between 5 - 10 years over a distance of <1 km. Colonisation of recently burnt sites depends on populations surrounding the burnt area, and the dispersal ability of species.

The relative importance of small patchy fires versus large uniform fires will relate to the objectives of fire managers (Driscoll *et al.*, 2010). In ecosystems where early successional specialists are not a major part of the assemblage, such as mallee vegetation (see also Lindenmayer *et al.*, 2008), small patchy burns will likely be the quickest to be recolonised and have higher species richness. In other ecosystems, however, where early successional specialists are of key conservation concern and require severe fires (Smucker *et al.*, 2005; Hutto, 2008), small patchy burns may be

detrimental to species populations, insomuch as they may provide only a limited resource for many species. The fine-scale spatial attributes of fire are a key influence on the post-fire occurrence of avifauna, and require careful consideration in planning for conservation and fire management scenarios.

For fire sensitive species that are dependent on fire-prone habitats, such as the Mallee Emu-wren (Brown *et al.*, 2009) and Eastern Bristlebird (Baker, 2000), and here the Chestnut Quail-thrush, employing patchy fire to avoid uniform burning of key habitat for the species, but providing protection from large-scale fires that can cause severe population declines, may be a useful approach. However, this type of preventative approach may only maintain species in the short term. The importance of the spatial scale of habitat required to support viable populations of a species while burnt areas recover to a suitable seral stage is a key area requiring further research.

Chapter 5

Determining the influence of landscape properties of fire mosaics on the composition of avifaunal communities



Gilbert's Whistler Pachycephala inornata



Satellite image of mallee vegetation in Murray Sunset National Park, showing multiple fire footprints

5.1 Abstract

At landscape scales, multiple fires and the patchiness of individual fires create heterogeneous mosaics comprised of different fire-history elements (fire mosaics). Despite the well recognised influence of fire on ecosystems, there has been little investigation of the effect of the spatial properties of fire mosaics on fauna. This has created an important knowledge-gap because there is a propensity for fire management to promote mosaics comprising diverse patches of different fire histories. We examined the relationship between the landscape properties of fire mosaics and the composition of avifaunal assemblages in 26 landscapes (each ~12.6 km²) in semi-arid shrublands in south-eastern Australia. These landscapes represented fire-mosaics stratified to vary in the composition and spatial extent of fire-history elements. Using ordination and regression, we investigated the influence of five specific properties on the composition of avifaunal assemblages: 1) the proportional extent of vegetation >35 years-since-fire; 2) the proportional extent of vegetation ≤ 10 years-since-fire; 3) the diversity of post-fire age-classes; 4) the composition of vegetation types; and 5) the geographic location of the landscape. Assemblages were strongly affected by a compositional gradient, from landscapes dominated by vegetation >35 years-since-fire to those with large proportional extent of vegetation ≤ 10 years-since-fire. Assemblages were also strongly influenced by a geographic gradient in aridity from south to north and, to a lesser amount, by the proportional extent of the dominant vegetation type. These properties together explained 31% of the variation in the composition of avifaunal assemblages. The composition of the avifauna was not affected by the diversity of post-fire age patches. The relative incidences of birds in nectarivore-insectivore and nectarivore dietary guilds declined as the proportional extent of vegetation ≤ 10 years-since-fire increased, creating functionally dissimilar assemblages. These results suggest that

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the spatial properties of fire in a landscape should be explicitly considered in ecological fire management, with a focus on the proportional extent of particular seral stages rather than primarily managing for diversity of seral stages.

5.2 Introduction

Fires create complex heterogeneous mosaics of vegetation (Turner *et al.*, 2001; Lloret *et al.*, 2002; Gill *et al.*, 2003). These arise from burnt and unburnt patches created in individual fire events (Turner *et al.*, 1994) and from sequences of fire events. These processes cause spatial variation in the post-fire age and sequential fire history of different patches across a landscape (Bradstock *et al.*, 2005). The spatial aspects of fire mosaics may significantly influence biotic assemblages (Gill *et al.*, 2003; Bradstock *et al.*, 2005; Parr & Andersen, 2006), but there has been little empirical research to test this. Most research in fire ecology has focused on the temporal aspects of fire regimes. Indeed, the spatial properties of fires were not recognised in the initial concept of a fire regime (Gill, 1975), although they are now considered to be an important component (Bond & Keeley, 2005; Gill & Allan, 2008).

Different fire histories favour different species and communities (Fox, 1982; Brawn *et al.*, 2001; Keeley *et al.*, 2005; Chapter 2; Chapter 3). This has led to the paradigm that a fire mosaic which consists of multiple patches representing different fire histories will provide for the requirements of many species/communities and promote greater diversity of organisms (Weir *et al.*, 2000; Parr & Andersen, 2006; Willson, 2006). Thus, the diversity of post-fire age-classes has been given prominence as a desirable property of fire mosaics. However, there has been little empirical investigation of how fire-induced diversity may affect the *composition* of faunal assemblages, or on the potential influence of other properties of fire mosaics on fauna.

To investigate the influence of different properties of fire mosaics on the composition of faunal communities, it is necessary to take a landscape-level approach in which 'landscapes', which represent different mosaics, are compared directly as the unit of investigation. This contrasts with many studies of the role of fire for structuring faunal communities (e.g. Fox, 1982; Hutto, 1995; Barlow & Peres, 2004a; Pons & Clavero, 2010; Chapter2; Chapter 3) in which sites or patches are the unit of investigation. The properties of fire mosaics (e.g. proportional extent of a fire age-class and the diversity of fire age-classes) are landscape properties that are not apparent at sites or patches. Such an approach, comparing 'whole landscapes', is becoming more common in agricultural systems (e.g. Bennett *et al.*, 2006; Mortelliti *et al.*, 2010), but to our knowledge has not previously been applied in studies of fire ecology.

There are several properties of fire mosaics that may affect the composition of faunal assemblages: these include the spatial extent (amount) of particular elements; the spatial arrangement (or configuration) of elements; and the composition and diversity of elements (Wiens, 1995; Bennett *et al.*, 2006; Fahrig *et al.*, 2011). These different properties may influence the composition of landscape assemblages via several mechanisms. For example, the suitability of habitat for many faunal species, and communities, varies with time-since-fire (Fox, 1982; Hutto, 1995; Brawn *et al.*, 2001; Chapter 2; Chapter 3). The proportional extent of vegetation of different seral stages in a landscape may affect the abundance of habitat that supports particular species or communities, subsequently resulting in assemblages at the landscape level that are dominated by those species/communities (Pons & Bas, 2005).

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Some additional mechanisms that may influence the composition of species in landscapes include: the negative consequences of fragmentation of habitat caused by fire; the improved persistence of species afforded by refuges during fire events; and the requirement of multiple seral stages by a species. For example, in human modified landscapes, avifaunal communities can be strongly affected by habitat fragmentation and habitat loss (Fahrig, 2003). Fires can turn extensive areas of vegetation (e.g. woodland) into fragmented patches in a matrix of different vegetation (e.g. shrubland) (Herrando & Brotons, 2002). For species that require a particular seral stage, landscapes that have experienced multiple fires could be perceived as fragmented, and have communities with fewer seral stage specialists. Refuges in which organisms can survive fire events, and from which they can recolonise, may be important for many species (Bradstock et al., 2005; Firth et al., 2010; Chapter 4). Heterogeneous landscapes that have not experienced severe homogenising fires may support more refuges and thus more refuge-dependant species. Some faunal species have been associated with using multiple seral stages; for example, sheltering in one seral stage and feeding in another (Hayward *et al.*, 2005; Körtner et al., 2007). Consequently, diverse landscapes containing contrasting seral stages may support more of these species.

Fires may also affect the guild structure of communities through changes in resources. For example, loss of fruiting trees is implicated in declines of largebodied frugivorous birds in early seral stages of tropical forests in South America (Barlow & Peres, 2004b). Landscape properties, such as the extent of particular seral stages, may influence the spatial availability of resources (e.g. nectar, arthropods) and total abundance of resources in landscapes, and thus affect those guilds reliant on those resources. These changes in species guilds can provide insights into deterministic processes that affect the composition and functional relationships of communities (Simberloff & Dayan, 1991; Suding *et al.*, 2008), and help to develop a process-based understanding of the effects of spatial properties of fire on faunal assemblages (Whelan *et al.*, 2001).

In this study, we employed a whole-of-landscape design to investigate the influence of the properties of fire-induced mosaics on the composition of avifaunal assemblages in semi-arid landscapes in southern Australia. Specifically, we investigated the relative influence of the proportional extent of particular fire ageclasses, the diversity of different fire age-classes, the composition of the vegetation (represented by the proportional extent of the dominant vegetation type), and the position of the study landscape along the main climatic gradient in the region. Further, we investigated variation among landscapes in guild structure in the avifauna to gain insights into changes in guild structure of assemblages and how landscape properties may influence the processes driving these changes.

5.3 Methods

5.3.1 Study Area

The study area, of 104,000 km², is in the Murray Mallee region of inland southeastern Australia (Fig. 5.1). The region experiences regular fires, with ~ 40% of mallee vegetation in the study area being burnt since 1972 (Avitabile et al., 2011). The region has local topographic variation mainly arising from a dune-swale system (Wasson, 1989). The region has a semi-arid climate, with a strong south-north gradient of increasing aridity represented by many highly correlated climatic variables such as rainfall, temperature and evaporation (Pausas & Bradstock, 2007). Mean annual rainfall varies from $\sim 260 - 390$ mm across this gradient. Temperatures are high in summer and mild in winter. In the hottest month (February) the mean daily maxima is 33° C and in the coolest month (July) 16° C (Australian Bureau of Meteorology, 2010).

5.3.2 Vegetation

Mallee vegetation has a low canopy (<10 m high) formed by multi-stemmed 'mallee' *Eucalyptus* species and an understorey of shrubs and grasses (Lunt & Morgan, 2002). The vegetation of the region has been classified and mapped into three broad subcategories on the basis of detailed floristic analysis; Chenopod Mallee, Triodia Mallee and Heathy Mallee, (Haslem *et al.*, 2010). Here, we examine the avifaunal community of mosaics comprising the two dominant vegetation associations Triodia Mallee and Chenopod Mallee. These vegetation types vary in their soil associations and their floristic composition. Triodia Mallee occurs on sandier soils and supports an overstorey *Eucalyptus dumosa* and *E. socialis* and an understorey dominated by *Triodia scariosa* hummock grasses. Chenopod Mallee supports an overstorey of *E. oleosa* (subsp. *oleosa*) and *E. gracilis* and a sparse understorey of diverse shrubs in low abundances, such as *Olearia* spp., *Zygophyllum* spp. and chenopod species such as *Maireana* spp. and *Enchylaena* spp. (Haslem *et al.*, 2010).

5.3.3 Study Design

We employed a whole-of-landscape design, incorporating 28 landscapes, each 4 km in diameter (~12.6 km²) and selected to represent different fire mosaics (Fig 5.1). Landscapes were selected to represent a gradient in two major properties: 1) the diversity of time-since-fire age-classes (ranging from 1 - 6 post-fire age-classes) and 2) a gradient in the proportional extent of vegetation >35 years since-fire (ranging

from 0 - 100%). The spatial distribution of post-fire age-classes was examined by digitally mapping the fire history of the entire region, on the basis of 15 overlaying individual years of satellite imagery (1972 to 2007) (Avitabile *et al.*, 2011). The year of each fire was determined through consultation with land management agencies and by examining land management records (Avitabile *et al.*, 2011). Two landscapes were excluded from the analysis here, as they contained greater than 99% Heathy Mallee and were thereby not comparable with other mosaics dominated by Triodia Mallee. This resulted in a data set containing 26 landscapes.

The avifauna was surveyed by point-counts at 20 sites in each landscape. Each point-count had a 60 m radius. Point-counts were stratified in proportion to the extent of each post-fire age-class present in a landscape (Fig. 5.1), such that for every 5% of the landscape comprised of a particular post-fire age-class, one site was allocated to that age-class. Survey rounds were conducted on four separate occasions, once each in the Austral spring 2006, autumn 2007, spring 2007 and autumn 2008. All landscapes were surveyed in each survey round, one landscape per day.

In each landscape, 10 point-counts were each surveyed by Rick Taylor and Simon Watson, who alternated point-counts between each survey period. Each point-count was surveyed for 5 mins. Surveys commenced within 15 mins of sunrise, the time of highest vocal activity for birds. All detected individuals of each species were counted and recorded. The distance from the centre of the point-count to the location of the first detection of each individual was recorded. Where species were detected visually, distance to the individual was measured using an OPTi-LOGICTM 800LH laser range finder; for aural detections distance was estimated by the observer. Observers had initial training together to ensure comparability of procedures.



Figure 5.1 The location of the study region in SE Australia (inset top right corner), with the location of landscape mosaic study units shown as circles.

Dark grey represents extant mallee vegetation in the region. Two examples of different landscape mosaics showing different levels of fire heterogeneity are outset below: one consists of a single post-fire age-class and the other contains multiple post-fire ages. These landscapes also depict point-count locations (dots) stratified in relation to the proportional extent of fire ages in a landscape.

5.3.4 Detectability of species

Because variation in detectability amongst species, or of the same species in different habitats can introduce variation in ecological studies (Buckland *et al.*, 2001), we modelled the detectability of species using distance sampling (Buckland *et al.*, 2001). Species too rare to model individually were grouped with more common species that display similar detection characteristics following Aldredge *et al.* (2007). Because

distance is unlikely to be the only parameter influencing detectability, we also tested for the effects of vegetation density. Vegetation density was measured at each site using the number of contacts of vegetation with 2 m structure pole, placed at 1 m intervals along a 50 m transect. This measure was used as a covariate in multiplecovariate distance sampling (Marques *et al.*, 2007).

Density of vegetation did not significantly reduce the detectability of any species. The lowest probability of detection at a pointcount was for the combined group Mallee emu-wren *Stipiturus mallee* and Striated Grasswren *Amytornis striatus* (probability of detection = 0.45, 95% CI 0.31 - 0.65, N = 75). Distance sampling analysis was conducted in Distance 5.0 release 2 (Thomas *et al.*, 2006).

5.3.5 Properties of mosaics

Five variables, which represented four properties of fire mosaics, were investigated in this study: 1) the spatial pattern of fire history elements; 2) the composition of fire history elements; 3) the vegetation composition; and 4) the geographic location of the landscape (Table 5.1). Of many possible variables, we selected a subset for which all correlations amongst variables were <0.6 (Spearman rank correlation measure). Of the final subset of variables, two represented the spatial pattern of fire history elements; the proportional extent of vegetation \leq 10 years since-fire, and the proportional extent of vegetation >35 years since-fire. One variable represented the composition of fire history elements; the diversity of time-since-fire patches (Shannon's diversity index, see Table 5.1). Additional to variables explaining fire history elements, we investigated the extent of Triodia Mallee vegetation. Triodia Mallee and Chenopod Mallee together represented >99% cover of the 26 mosaics and consequently the extent of Triodia mallee was inversely correlated with Chenopod Mallee ($r_s = -0.99$). Thus, this variable is a measure of the composition of the native vegetation in each landscape. Lastly a geographic variable was included to represent the position of the landscape in relation to the main environmental gradient across the large study area (~220 km north-south). We chose to use a geographic variable (northing) (Table 5.1) to represent this gradient, as ecological variables (e.g. rainfall, temperature) were highly correlated, and selecting one of them could present an unsubstantiated impression of causality. Employing northing as a variable allowed examination of the influence of spatial properties of the study landscapes in the context of broad-scale biogeographic trends. Variables to represent the configuration of particular fire history elements (e.g. average patch size, connectivity of patches) were assessed but they were correlated too highly ($r_s > 0.6$) with other variables.

Table 5.1 The names and descriptions of variables selected to represent the

Variable	Description				
Spatial patterns of fire history elements					
Extent of vegetation >35	Proportion of the landscape comprised of vegetation >35				
years since-fire	years-since-fire				
Extent of vegetation ≤ 10	Proportion of the landscape comprised of vegetation ≤ 10 years-				
years since-fire	since-fire				
Composition of fire history	elements				
Diversity of	Shannon's diversity index for landscapes (McGarigal et al.,				
time-since-fire patches	2002): based on the number of age classes in the study				
	landscape and proportional extent of each age-class.				
Vegetation Composition					
Extent of Triodia Mallee	Proportion of the landscape comprised of Triodia Mallee				
Environmental Gradient					
Northing	Universal Transverse Mercator (UTM) northing unit (World				
	Grid System 84 "WGS84")				

properties of the study landscapes

5.3.6 Statistical analysis

The avifaunal data was collated to represent the incidence of each species in each landscape. Incidence was defined as the total number of sites (out of 20) at which a species was recorded in each landscape. A species was considered present at a site if it was detected at that site during any one of the four survey rounds. Only species that were detected in > 4 study landscapes and which were present in both southern and northern parts of the region were included in the analysis. This resulted in a dataset of the incidence of 46 species in each of 26 landscapes.

We used principal coordinates of neighbour matrices (PCNM) (Borcard & Legendre, 2002) to first search for spatial patterning in bird assemblages due to geographic location of study mosaics, before considering environmental (e.g. fire, vegetation) influences. In this procedure, the geographic distances between landscapes are decomposed into eigenvectors that explain the spatial relationships amongst study landscapes. These eigenvectors are then used as variables to which the response variable (i.e. the bird assemblage) is compared through canonical analysis. If patterns in bird assemblages are explained by the spatial PCNM variables, these variables can be explicitly tested in concert with environmental variables in a modelling framework. We conducted PCNM on detrended data, by which variables were computed only after significant linear trends were removed from the data, as these latter trends can be accounted for using simple linear variables (i.e. northing), rather than complex PCNM variables.

We used redundancy analysis (RDA) and variation partitioning (Legendre & Legendre, 1998) to assess the patterns, and relative influence, of the properties of fire mosaics on the composition of avifaunal assemblages among the 26 study landscapes. Redundancy analysis is a linear ordination method analogous to principal components analysis (PCA) whereby ordination is conducted on a multivariate response table (i.e. species \times sites). However, where PCA extracts all variation in the response table (explained and unexplained), redundancy analysis constrains the responses to linear combinations of a separate data set (i.e. environmental variables), as multivariate response table. In this way, the variation in the multivariate response table (all species at sites) can be attributed directly to environmental variables. This is contrasting to approaches which correlate of gradients in community composition from ordination (i.e. PCA)

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with environmental variables, which does not clearly represent the variation attributable to the environmental variable.

Redundancy analysis employs Euclidean distance as a measure of dissimilarity in the species composition data, but this measure has been criticised due to the influence zero values have on interpreting ordination data (Legendre & Legendre, 1998). To circumvent these problems, the species data matrix was transformed using the methods described in Legendre and Gallagher (2001) to visualise chord distances instead of Euclidean distances, which are robust to zero values. The measure commonly employed in redundancy analysis to explain variation (canonical R^2) can be biased by the number of predictors in a model and the sample size; consequently, we used an adjusted form (R_a^2) for all measures of variation, which is unbiased by these factors (Peres-Neto et al., 2006). We used forward selection to identify variables included in the redundancy analysis model and employed double stopping criteria to avoid inflated type I error rates (Blanchet et al., 2008). Double stopping criteria test the influence of each additional variable on the R_a^2 in addition to the usual alpha value, to determine whether additional variables should be included in the model. If an additional variable inflates the R_a^2 of the reduced model, to more than the R_a^2 of the global model (including all variables and penalised accordingly), then variable selection is stopped. This method provides good discrimination of type 1 error rates and reduces over-fitting (Blanchet et al., 2008). We used an alpha value of 0.1 as we had limited power to test significance with only 26 landscapes.

We used variation partitioning to calculate the independent and shared contribution of variables to the redundancy analysis model. In this process, variation explained by an individual component of a model (variable or group of variables) is compared to: a) variation explained by other components in the model; and b) variation explained by the full model (containing all components), and subsequently the independent and shared components of variation are then calculated (Legendre & Legendre, 1998).

In addition to redundancy analysis, we also carried out a separate analysis of avifaunal foraging guilds to gain insights into processes affecting the composition of avifaunal assemblages and the functional changes related to different landscape properties. We initially identified guilds based on primary food type, but as insectivores make up a disproportionately large portion of the avifaunal assemblage (33 of 46 species), they were further divided by their primary foraging zones. This resulted in eight guilds: nectarivores, granivores, nectarivore/insectivores (diets include varying levels of nectarivory and insectivory) and insectivores that forage primarily in the air, foliage, trunk, shrubs and ground (Table 5.2). Data on food type and foraging zones were obtained from Schodde (1981), checked and adjusted using the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB, 2006). A complete list of species in each guild is presented in Table 5.2.

We used generalized linear models (GLM) to determine the influence of landscape properties on variation in guild structure between landscapes. Response variables were the summed incidence of all species within each guild. This variable was used to provide a measure of the abundance of individuals in each guild in each landscape, and thus also indicates the amount of resources required by those guilds.

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Table 5.2 Bird species assigned to each foraging guild and the number of species

(N) in each guild

Guild	Ν	Species		
Nectarivores	2	Red Wattlebird Anthochaera carunculata	White-fronted Honeyeater Purnella albifrons	
Granivores	5	Australian Ringneck Parrot Barnardius zonarius Galah Eolophus roseicapillus	Regent Parrot Polytelis anthopeplus Common Bronzewing Phaps chalcoptera	Mulga Parrot Psephotus varius
Nectarivore- insectivores	6	Black-eared Miner Manorina melanotis Spiny-cheeked Honeyeater Acanthagenys rufogularis	White-eared Honeyeater Lichenostomus leucotis Brown-headed Honeyeater Melithreptus brevirostris	Striped Honeyeater Plectorhyncha lanceolata Yellow-plumed Honeyeater Lichenostomus ornatus
Aerial- foraging insectivore	6	Dusky Woodswallow Artamus cyanopterus Masked Woodswallow Artamus personatus	White-browed Woodswallow Artamus superciliosus Jacky Winter Microeca fascinans	Rainbow Bee-eater Merops ornatus Willie Wagtail Rhipidura leucophrys
Foliage- foraging insectivores	5	Inland Thornbill Acanthiza apicalis Spotted Pardalote Pardalotus punctatus	Weebill Smicrornis brevirostris Rufous Whistler Pachycephala rufiventris	Striated Pardalote Pardalotus striatus
Ground- foraging insectivores	12	Australian Magpie Cracticus tibicen Chestnut Quail-thrush Cinclosoma castanotus Crested Bellbird Oreoica gutturalis Hooded Robin Melanodryas cucullata	Shy Heathwren Calamanthus cautus Splendid Fairy-wren Malurus splendens Australian Raven Corvus coronoides Chestnut-crowned Babbler Pomatostomus ruficeps	Grey Butcherbird Cracticus torquatus Red-capped Robin Petroica goodenovii Southern Scrub-robin Drymodes brunneopygia Striated Grasswren Amytornis striatus
Shrub- foraging insectivores	2	Gilbert's Whistler Pachycephala inornata	Variegated Fairy-wren Malurus lamberti	
Trunk & branch- foraging insectivores	8	Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i> Chestnut-rumped Thornbill <i>Acanthiza uropygialis</i> Grey Shrike-thrush <i>Colluricincla harmonica</i>	White-browed Babbler Pomatostomus superciliosus Golden Whistler Pachycephala pectoralis	Grey Currawong Strepera versicolour Varied Sittella Daphoenositta chrysoptera

Properties of fire-mosaics were standardized to mean 0 and unit variation 1 to allow easy interpretation and comparability of regression coefficients (Schielzeth, 2010). We used an information theoretic approach and model averaging (Burnham & Anderson, 2002) for this analysis. The modelling was conducted in two steps. First, each landscape variable was tested for non-linearity of responses by fitting two univariate models, one with the variable as a linear term and one as a second order polynomial term. Variables were included as a second order polynomial term in models where they presented a better fit to the data ($\Delta AICc > 2$). Second, we conducted model averaging across models representing all combinations of variables (32 models). Model averaging was conducted using the relative weights of evidence for each variable on the basis of Akaike's information criterion (AIC) adjusted for small sample size (AICc), or QuasiAIC adjusted for small sample sizes (QAICc) if the data were overdispersed. The relative weight of evidence (w_m) for each variable was computed by summing Akaike weights across all models in which that variable occurred (Burnham & Anderson, 2002). Where coefficients $\pm 2SE$ did not overlap with 0, the variable was considered a useful predictor.

All statistical analyses were conducted in the R statistical environment (R Development Core Team, 2009). The package PCNM was used to conduct principal coordinates of neighbour matrices analysis (Legendre *et al.*, 2009). We performed redundancy analysis and variation partitioning in the "vegan" community ecology package (Oksanen *et al.*, 2009) and forward selection of variables using the "packfor" package (Dray *et al.*, 2009). Generalised linear models and model averaging for analyses of guild structure were undertaken using the R base package, and code developed by Michael Scroggie (Department of Sustainability and

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Environment) on the basis of the methodology described in Burnham and Anderson (2002).

5.4 Results

A total of 70 species of birds representing 28 families were detected from 560 sites across the entire 28 landscapes. Four species, Chestnut-rumped Thornbill *Acanthiza urophygialis*, Grey Shrike-thrush *Colluricincla harmonica*, Weebill *Smicrornis brevirostris* and White-eared Honeyeater *Lichenostomus leucotis*, were recorded in all study landscapes. In contrast, 19 uncommon species were each recorded at sites in fewer than four study landscapes (e.g. Crimson Chat *Epthianura tricolor*, White-winged Chough *Corcorax melanorhamphos*, Pied Butcherbird *Cracticus nigrogularis*). Two species, the Mallee Emu-wren *Stipiturus mallee* and Purple-gaped Honeyeater *Lichenostomus cratitius* were recorded only in study landscapes south of the Murray River and one species, the Grey-fronted Honeyeater *Lichenostomus plumulus* was recorded only in study landscapes north of the river. After excluding two landscapes that contained almost entirely Heathy Mallee vegetation, and species that were uncommon or geographically restricted (as well as raptors and night birds for which the sampling design was inappropriate), the dataset for analysis consisted of 46 species across 26 landscapes.

5.4.1 Spatial patterning in bird assemblages

The principal coordinates of neighbour matrices (PCNM) analysis did not reveal any significant spatial relationships after the data was detrended of simple linear relationships (p=0.73), and consequently no PCNM variables were included in the

analysis. The simple linear relationship in the data was best interpreted through the use of the northing variable.

5.4.2 The effect of landscapes properties on species composition

Using redundancy analysis, four variables were selected in a model relating the composition of the avifauna with properties of fire mosaics. These were northing, extent of vegetation >35 years since-fire, extent of vegetation ≤ 10 years since-fire and extent of Triodia Mallee (global model $R_a^2 = 0.31$). The remaining variable, the diversity of fire age-classes was not included on the basis of the stopping rule. The composition of species assemblages varied strongly along a gradient from south to north, and from landscapes with a proportionally large extent of recently burnt vegetation to those with a proportionally large extent of mature vegetation. To a lesser extent, the avifauna also varied along a gradient of the proportional extent of vegetation types (Fig 5.2).

The Spotted Pardalote *Pardalotus punctatus*, Golden Whistler *Pachycephala pectoralis*, and Red Wattlebird *Anthochaera carunculata* are examples of species correlated with southerly landscapes, whereas Gilbert's Whistler *Pachycephala inornata*, Southern Scrub-robin *Drymodes brunneopygi*a, and Striated Grasswren *Amytornis striatus* are examples of species correlated with northerly landscapes. The proportional extent of mature vegetation and of recently burnt vegetation (\leq 10 years since-fire) formed a single strong gradient (Fig 5.2). The Yellow-plumed Honeyeater *Lichenostomus ornatus*, Spiny-cheeked Honeyeater *Acanthagenys rufogularis*, and Striped Honeyeater *Plectoryncha lanceolata*, are examples of species associated with landscapes having a large proportional extent of vegetation >35 years since-fire. Few species were associated with landscapes having increased extent of recently burnt vegetation. The White-eared Honeyeater *Lichenostomus leucotis*, was correlated with the proportional extent of Triodia Mallee.

The landscape properties of fire mosaics explained a substantial proportion of the total variation in the composition of avifaunal assemblages ($R_a^2=0.31$). The greatest amount of independent variation (i.e. excluding components shared with other variables) was explained by the environmental gradient (northing) ($R_a^2 = 0.154$), followed by the extent of vegetation >35 years-since-fire ($R_a^2 = 0.073$), extent of Triodia Mallee vegetation ($R_a^2 = 0.049$) and extent of vegetation ≤ 10 years-since-fire $(R_a^2 = 0.023)$ (Table 5.3). The variables representing time-since-fire displayed substantial shared variation with the other variables in the model ($R_a^2 = 0.037$ and R_a^2 = 0.042 for the proportional extent of vegetation >35, and ≤ 10 years-since-fire, respectively) (Table 5.3). This suggests that these variables produced patterns in the composition of the avifauna also described by other variables in the model. In contrast, the geographic position of landscapes (northing) and the extent of Triodia Mallee, displayed negative portions of shared variation. This pattern indicates that when these variables are considered in the full model (i.e. when variables are considered with other variables) they explain a greater amount of variation than the summed variation explained by these variables when considered alone (i.e. not with the other variables) (Legendre & Legendre, 1998).



Figure 5.2 Redundancy analysis triplot displaying the relationship of the species composition of landscapes (weighted sums of species scores = solid circles) with landscape properties (constraining variables = vectors), and the relationship of species (species scores = open circles) with landscape properties. Only species with larger scores are labelled. Species and sites are scaled on the primary x and y axes, and environmental vectors are scaled on the secondary x and y axes. Length of environmental vectors indicates the strength of its relationship with the composition of the avifauna.

Considering that the proportional extent of >35 years-since-fire and of ≤ 10 yearssince-fire largely represented a single gradient in the composition of the assemblage (Fig. 5.2), we investigated the component of variation explained when these two variables are considered in combination. In this instance, the variation explained by this gradient includes a large portion of the overall variation ($R_a^2 = 0.144$) (Table 5.2).

Table 5.3 The proportion of total variation in composition of the avifaunal assemblage explained by different landscape properties obtained through variation partitioning. Results represent the variation explained independently, and shared with other variables (R_a^2), in the full RDA model. Full model $R_a^2 = 0.31$ (NB: shared variation takes on a negative value where a variable's independent contribution to the full model is greater than its variation explained in a univariate model; Legendre & Legendre, 1998).

	Independent	Shared	
Variable	component of	component of	
	variation	variation	
Individual Variables			
Northing	0.154	-0.036	
Extent of vegetation >35 years since-fire	0.073	0.037	
Extent of vegetation ≤ 10 years since-fire	0.023	0.042	
Extent of Triodia Mallee	0.049	-0.007	
Combined Variables			
Extent of vegetation >35 years since-fire	0 144	-0.025	
Extent of vegetation ≤ 10 years since-fire	0.144		

5.4.3 The effect of landscape properties on species foraging guilds

The combined incidence of bird species in five of the eight foraging guilds was significantly influenced by at least one of the landscape properties; however, the degree of influence varied amongst guilds ($D^2 = 0.11 - 0.66$) (Table 5.4). The incidence of nectarivore-insectivores declined with increasing extent of vegetation ≤ 10 years-since-fire, and there was also a trend for a similar decline in incidences of nectarivores (Table 5.4, Fig. 5.3 a & b). There was a lower incidence of granivores, and trunk and branch foraging insectivores, in landscapes with large proportional extent of Triodia Mallee vegetation, although these patterns were heavily influenced by a few points (Table 5.4, Fig 5.3 b & c). The incidence of aerial-foraging insectivores and ground-foraging insectivore were not influenced by landscape properties.

Table 5.4 Results from generalized linear models of the relationship between landscape properties and the summed incidence of species in each foraging guild. For each foraging guild, results presented include the model-averaged coefficient (SE), the relative weight of influence (summed Akaike weights of evidence = $\sum w_m$) and proportion of total deviance explained (D² calculated from the global model). Values shown in bold are those for which the coefficient ± 2SE does not overlap with zero. A 2nd coefficient is shown for second order polynomial terms where the variable was better represented by that shape than a linear response ($\Delta \text{ AICc} > 2$).

Guild		Northing	Extent of Triodia	Extent of ≤ 10	Extent of >35	Diversity of time-	D^2	
Guild		Torting	Mallee	years-since-fire	years-since-fire	since-fire patches	D	
	Coeff. (SE)	0.00 (0.05)	0.11 (0.19)	-0.29 (0.15)	0.01 (0.07)	0.15 (0.13)		
Nectarivores	2 nd Coeff. (SE)		0.08 (0.15)				0.46	
	$\sum w_m$	0.18	0.33	0.86	0.20	0.63		
	Coeff. (SE)	0.01 (0.05)	0.13 (0.16)	-0.03 (0.08)	0.01 (0.05)	0 (0.06)		
Granivores	2 nd Coeff. (SE)		0.29 (0.1)				0.51	
	$\sum w_m$	0.18	0.99	0.24	0.18	0.17		
NT / '	Coeff. (SE)	-0.1 (0.04)	0.02 (0.06)	-0.18 (0.05)	0.01 (0.03)	0.00 (0.01)		
Nectarivore-	2 nd Coeff. (SE)		0.01 (0.02)			0.00 (0.01)	0.60	
insectivores	$\sum w_m$	0.87	0.19	0.99	0.22	0.04		
Ground-foraging	Coeff. (SE)	0.01 (0.03)	-0.01 (0.03)	0.02 (0.04)	-0.02 (0.04)	0.01 (0.03)	0.11	
insectivores	$\sum W_m$	0.29	0.29	0.35	0.37	0.28		

Guild		Northing	Extent of Triodia Mallee	Extent of ≤10 years-since-fire	Extent of >35 years-since-fire	Diversity of time- since-fire patches	D^2
$ \begin{array}{c} \mbox{Shrub-foraging} \\ \mbox{insectivores} \end{array} & \begin{array}{c} \mbox{Coeff. (SE)} \\ \mbox{2^{nd} Coeff. (SE)} \\ \\ \mbox{$\sum w_m$} \end{array} \\ \end{array} $	Coeff. (SE) 2 nd Coeff. (SE)	0.84 (0.21) -0.84 (0.24)	-0.03 (0.1)	0.01 (0.08)	0.06 (0.12)	0.01 (0.09)	0.59
	>0.99	0.24	0.19	0.32	0.20		
Trunk & branch- foraging	Coeff. (SE) 2 nd Coeff. (SE)	0.00 (0.03)	-0.14 (0.06)	-0.01 (0.06) 0.01 (0.05)	0.00 (0.02) 0.01 (0.05)	-0.04 (0.07)	0.39
insectivores $\sum w$	$\sum w_m$	0.19	0.86	0.08	0.10	0.36	
Foliage-foraging insectivores Coeff. (SE) 2^{nd} Coeff. (SE) $\sum W_m$	Coeff. (SE) 2 nd Coeff. (SE)	-0.2 (0.06)	0.01 (0.04) 0.01 (0.04)	-0.02 (0.06)	-0.04 (0.04)	0.00 (0.03)	0.47
	$\sum w_m$	>0.99	0.10	0.32	0.23	0.19	
Aerial-foraging insectivores	Coeff. (SE) 2 nd Coeff. (SE)	0.03 (0.07)	0.04 (0.11)	-0.38 (0.28)	0.17 (0.12)	-0.02(0.07) 0.03(0.08)	0.66
	$\sum W_{m}$	0.29	0.26	0.63	0.73	0.21	0.00



Figure 5.3 The relationship between the summed incidences for species assigned to a foraging guild and landscape properties, for different foraging guilds; a) nectarivore-insectivores and extent of vegetation ≤ 10 years-since-fire; b) nectarivores and extent of vegetation ≤ 10 years-since-fire (trend), c) granivores and extent of Triodia Mallee d) trunk and branch foragers and extent of Triodia Mallee. Extent represents the proportion of the landscape comprising each landscape element. Points = raw data, lines = modelled response.
5.5 Discussion

Understanding the impact of the spatial properties of fire on biota is a key challenge for fire ecology and conservation management (Bradstock *et al.*, 2005; Driscoll *et al.*, 2010). To investigate the spatial properties of fire, we conducted a large-scale natural experiment, whereby we studied fire mosaics at the level of whole-landscapes (1256 ha) and related this to avifaunal composition measured at the same scale. This approach offered insights into the influence of the spatial properties of fire mosaics on biota at a scale which is commensurate with that at which land managers operate.

The spatial properties of fire mosaics were an important factor affecting the composition of the avifaunal assemblage; warranting their importance in fire management for biodiversity conservation (Driscoll *et al.*, 2010). The composition of avifaunal assemblages changed along a gradient in the proportional extent of vegetation ≤ 10 years-since-fire to vegetation >35 years-since-fire; with contrasting assemblages at each end of the gradient. Interestingly, the diversity of different time-since-fire ages did not affect avifaunal composition, questioning the degree to which heterogeneity should be a primary focus for management (Parr & Andersen, 2006). The proportional extent of Triodia Mallee and the biogeographic position of study landscapes influenced the assemblage, indicating the importance of also considering the interaction of non-fire related influences when determining the response of species to fire (Driscoll *et al.*, 2010). The relative incidence of nectarivore-insectivores was lower in landscapes with greater extent of young post-fire vegetation (≤ 10 years since-fire) and a similar response was detected for nectarivores; patterns likely to be driven by the availability of nectar. These changes

highlight that mosaic properties can affect not only species composition but also the functional composition of assemblages.

5.5.1 The effect of landscape properties of fire on the composition of avifaunal assemblages

The extent of 'habitat' is an important element affecting richness and composition of faunal assemblages in landscapes (Turner *et al.*, 2001; Bennett *et al.*, 2006; Haslem & Bennett, 2008). Post-fire seral stage is an important factor determining habitat suitability for many faunal species (Fox, 1982; Brawn *et al.*, 2001; Jacquet & Prodon, 2009; Chapter 2) and faunal communities (Hutto, 1995; Chapter 3). It follows then, that spatial parameters of seral stages (i.e. their proportional extent) will affect the spatial availability of suitable habitat for species and assemblages which depend on them.

We identified an important influence of a gradient in the proportional extent of fire age-classes, from older (>35 years-since-fire) to younger (≤ 10 years-since-fire) on the composition of avifauna in a landscape. Many bird species displayed their highest frequency of occurrences in vegetation >35 years since-fire (e.g. Yellow-plumed Honeyeater, Striated Pardalote, Spiny-cheeked Honeyeater; Chapter 2) and lowest occurrences in vegetation ≤ 10 years-since-fire, with few species showing the opposite pattern (e.g. Chestnut-rumped Thornbill; Chapter 2). Consequently, the uniform nature of this gradient means that the response of species to increasing the proportional extent of older vegetation (>35 year-since-fire) will result in a similar directional change to that of decreasing extent of younger vegetation (<10 years-since-fire). Although, several species also display bell-shaped responses, such that

the frequency of occurrence declines in older vegetation (e.g. White-eared Honeyeater and Spotted Pardalote; Chapter 2); these declines usually occurred in vegetation <35 years-since-fire.

The proportional extent of Triodia Mallee, independent of fire age, also affected the composition of the avifauna. Many species (13 out of 30 in Chapter 2) occurred more commonly in one or other of the major vegetation associations (e.g. Grey Shrike-thrush in Chenopod Mallee and Striated Grasswren in Triodia Mallee). The different vegetation types offer different resources for bird species; for example, the Striated Grasswren is associated with *Triodia* hummock grasses which it uses for refuge and nesting (HANZAB, 2006). Consequently, landscapes with a greater proportional extent of a particular vegetation type provide an increased amount of particular resources for a subset of species, thus supporting different assemblages.

A higher level of biodiversity delivered through a greater diversity of patches of different fire history is a common paradigm in fire ecology (Gill *et al.*, 2003; Fuhlendorf *et al.*, 2006; Burrows, 2008), but empirical research into its relationship with the composition of faunal assemblages is limited. A diversity of time-since-fire ages may influence the composition of assemblages in several ways, for example through reduced habitat or fragmentation of habitat for seral stage specialists, by improved persistence of species that are protected by unburnt refuges during fire events (Bradstock *et al.*, 2005; Firth *et al.*, 2010) and by provision of multiple seral stages for species that move among habitats for different resources (e.g. forage in one habitat and nest in another) (Woinarski, 1999; Hayward *et al.*, 2005; Körtner *et al.*, 2007). We did not detect an effect of fire age-class diversity on bird species

composition in these study landscapes. In large reserve systems, such as those investigated here, increased diversity of fire age-classes may be less likely to cause fragmentation or habitat reduction effects as species are likely to be able to persist in other parts of the reserve. Likewise, persistence of species in a large reserve may not be as dependant on local patchiness of fires to provide refuge or protection, as it would be in smaller and more isolated habitat patches. An important issue is that the diversity metric does not account for what types of post-fire age-classes contribute to the diversity. Landscapes with equivalent numbers of different age-classes and comprising proportionally equivalent areas can have the same 'diversity' regardless of the fire history. For example, three age-classes might be 2, 5 and 10 years; or 2, 15, and >35 years-since-fire, which would offer quite different habitats for the avifauna. Thus, while diversity *per se* may not strongly influence avifaunal composition, it is possible that particular aspects of diversity may do so: for instance, the presence of two particular time-since-fire ages (e.g. for parrot species, older vegetation that provides large hollows and younger vegetation with diverse herbage and seed production).

Studies in which 'landscapes' are the unit of investigation often are conducted over large geographic areas, and it is common that biogeographic variables are also important predictors of species assemblages (Bennett *et al.*, 2006). In this study, we detected variation in avifaunal assemblages along the south-north environmental gradient (i.e. northing). This pattern is likely to be the product of several factors, including the strong aridity gradient, which is correlated with changes in the species composition of the flora (Pausas & Bradstock, 2007). There is also a biogeographic gradient, with intergradation of species evolved in the Bassian biogeographic region to the south-east, and the Eyrean region to the north-west (Schodde, 1981). For example, there were higher incidences of the Eyrean-associated Gilbert's Whistler *Pachycephala inornata* and the Basssian associated Golden Whistler *Pachycephala pectoralis* in northerly and southerly mosaics, respectively. While in this investigation we do not aim to untangle these patterns, it highlights the importance of interpreting effects of fire-induced changes to assemblages in the light of other broad-scale processes.

Recently, Gilbert and Bennett (2010) identified some shortfalls in variation partitioning approaches, with the potential for the variation attributed to particular variables being under-represented. In light of the potential biases of variation partitioning approaches (Gilbert and Bennett, 2010), we suggest that further research will be required to untangle the relative influence of different spatial and environmental processes on faunal community composition in landscapes, ideally using manipulative experiments.

5.5.2 The influence of landscape properties on species guilds; insights into functional changes in avifaunal assemblages and processes driving changes

Understanding the processes by which changes in ecosystems are effected is a major focus of ecology (Suding *et al.*, 2008). Process-based understanding of the effects of fire on biota is critical for conservation to allow prediction of changes to species under different fire scenarios (Whelan *et al.*, 2001; Driscoll *et al.*, 2010). Fire can alter the availability of resources for different types of species. Here, the incidence of nectarivore-insectivores declined with proportional extent of younger vegetation (\leq 10 years-since-fire), and nectarivores responded similarly. Thus, landscapes with greater extent of recent post-fire vegetation resulted in functionally different avifaunal assemblages, deficient in nectar-feeding species.

Eucalyptus flowering, and hence nectar production, is much reduced in vegetation ≤ 10 years-since-fire (Chapter 3). This reduction will be magnified by the spatial extent of such younger vegetation, such that reduced nectar availability, an important food for honeyeaters (Ford & Paton, 1976a; Ford & Paton, 1976b), occurs over large parts of the landscape. In mallee vegetation, large fires occur regularly. From 1972 – 2007, 16 fires >10 000 ha occurred in the Murray Mallee region, with three fires >100 000 ha. These fire areas represent large areas which will essentially be devoid of eucalypt nectar for up to 10 years. At the site scale, the richness of nectarivore-insectivores increased from very low levels directly after fire to an asymptote reached at ~10 years-since-fire (Chapter 3). However, nectarivores did not display a relationship with time-since-fire at the site scale (Chapter 3), and thus a landscape-scale response suggests that the spatial component of nectar resource reductions is important.

At the scale of individual sites, relationships of nectarivores with time-since-fire may be masked by alternative processes, such as nomadic movements (Woinarski, 2006). However, when fires occur across large areas (e.g. >10 000 ha), as regularly occurs in the Murray Mallee, resources are restricted across broad areas. Species occurrences may be more limited by this because the total amount of the available resource within the species sphere of movement suffers greater depletion. The incidence of nectarivores typically was low in landscapes dominated by younger vegetation, but it also was low in some landscapes which had only small proportional extent of younger vegetation; thus contributing to the marginal significance of this relationship. This relationship requires further research as nectarivores are represented by two species only in this system. Nevertheless, coupled with the decline in nectarivore-insectivores, the spatial availability of nectar resources appears likely to be an important factor affecting species distributions at broader scales of landscapes and regions.

Incidences of granivores, and trunk and branch foragers, declined with the proportional extent of Triodia Mallee vegetation (and increased with proportional extent of Chenopod Mallee). The relationship for granivores should be interpreted with caution as it was heavily influenced by two landscapes. More-open Chenopod Mallee vegetation associations support a range of low shrubs (Haslem *et al.*, 2010), increased ephemeral grasses (Noble & Vines, 1993), and greater number of tree hollows (Haslem, A. unpublished data). Thus, the extent of Chenopod Mallee may affect the abundance of seed resources and nesting resources. With the exception of the Common Bronzewing, all granivores were hollow-nesting parrots. Declining incidences of trunk and branch foragers with increasing proportional extent of Triodia Mallee may be indicative of differences in mid-storey structure between the two vegetation types (Haslem *et al.*, 2011), which may influence the availability of foraging resources.

5.5.3 Conclusions and management considerations

A current propensity to focus on heterogeneity of seral stages to create complex mosaics (e.g. Burrows, 2008), has resulted in questions regarding the relative benefits of different mosaic structures for fauna (Bradstock *et al.*, 2005; Parr &

Andersen, 2006). By using a whole-of-landscape approach, we show that the spatial properties of fire mosaics have an important influence on the composition of avifaunal assemblages. In particular, the proportional extent of age-classes along a gradient from younger to older vegetation is an important property, which causes changes in the species composition and can alter resource availability and functional composition of assemblages. Diversity *per se* of different fire-ages was not found to influence the composition of avifaunal assemblages. This finding suggests that management based on manipulating the extent of specific seral stages will deliver more predictable outcomes for fauna. However, further research is required to investigate how specific types of diversity may influence biota (e.g. specific combinations or contrasts of multiple fire ages). Whole-of-landscape approaches are a novel and useful method for examining these questions. Furthermore, all fire management must take into account other factors, such as the extent of non-fire induced habitat elements, and broader environmental geographic gradients.

Chapter 6

Synthesis



Red-lored Whistler Pachycephala rufogularis

Chapter 6 – Synthesis

6.1 Overview

Fire is widely recognised as an important natural disturbance that structures ecosystems and affects biotic and abiotic processes worldwide (Bond *et al.*, 2005; Bowman *et al.*, 2009). From a theoretical ecology perspective, the ubiquity of fire in many ecosystems stimulates an inherent curiosity into its effects on ecological communities. From a conservation perspective, understanding the effects of fire on fauna is of fundamental importance, because different patterns of fire in ecosystems may preserve or threaten ecological communities (Gill *et al.*, 1999; Noss *et al.*, 2006).

Fire can have a major influence on avifaunal assemblages (Brawn *et al.*, 2001) and several bird species may be dependent on, or threatened by, particular fire regimes (Hutto, 1995; Woinarski, 1999), such that management of fire is a key conservation issue for avifaunal conservation (Brawn *et al.*, 2001; Skowno & Bond, 2003; Ukmar *et al.*, 2007). Yet, even in fire-prone ecosystems, there still remain substantial knowledge gaps concerning the effects that fire has on many avifaunal communities, or the processes by which fire brings about changes in avifaunal assemblages.

Although there has been extensive clearing of native vegetation in the Mallee region of southern Australia, large swathes of mallee vegetation and an extensive reserve system remain. Despite this, many bird species continue to decline in this ecosystem (Garnett & Crowley, 2000). Considering the importance of fire in structuring avifaunal communities in mallee ecosystems, appropriate management of fire is a critical component of the conservation of birds in mallee. Temporal changes in species' occurrence, distribution and abundance post-fire forms the foundation of much of fire ecology (Fox, 1982; Brawn *et al.*, 2001; Keeley *et al.*, 2005) and knowledge of these patterns is critical to manage fire to benefit biodiversity (Driscoll *et al.*, 2010). The temporal pattern of change in the mallee avifauna was the key theme of Chapters 2 and 3 of this thesis. In these chapters, I explored the effects of temporal patterns of fire on the occurrence of individual species and on the succession of whole communities over a century-long chronosequence. This represents important information as few studies have examined the responses of avifauna to fire at temporal scales of up to a century and across large regions greater than 100 000 km² (Clarke, 2008).

While the influence of the temporal aspects of fire on changes in bird communities is recognised (albeit not well understood) in many systems, little is known about the importance of spatial aspects of fires on fauna. This represents an important knowledge gap for fire ecology and conservation (Driscoll *et al.*, 2010), particularly as fire is becomingly increasingly used as a management tool (Gill & Allan, 2008). Moreover, there is a growing propensity to manage fire to promote heterogeneous mosaics of differing spatial arrangement of fire-history elements (Bradstock *et al.*, 2005; Parr & Andersen, 2006; Willson, 2006). In Chapters 4 and 5 of this thesis, the influence of the spatial properties of fire on the avifauna was investigated. Chapter 4 examined the effect of spatial properties of fire on the post-fire colonisation of sites and Chapter 5 examined the influence of fire mosaics on the composition of the avifauna at the landscape level.

This research has provided many insights into patterns and processes of post-fire succession in bird communities and the influence of spatial properties of fire on

avifaunal assemblages. Furthermore, detailed knowledge of the effects of fire on the avifauna of the Murray Mallee region provides important information for the conservation and management of birds in this system. In this chapter, I summarise key findings under the major themes of the effects of temporal and spatial properties of fire on avifauna (Table 6.1). I also provide a synthesis of the key results, interpret their importance for conservation and management of avifaunal communities, and identify areas that require further research.

Table 6.1 Findings of this thesis in relation to key objectives and their implications for conservation and management of birds. Objectives are

divided into two themes: the effects of temporal aspects of fire, and the effects of spatial aspects of fire.

Objectives	Key Findings
Effects of temporal aspects of fire on avifauna	
How does temporal fire history influence species occurrences?	• Time-since-fire influenced the occurrence of 16 of 30 species investigated.
What types of responses to time-since-fire do bird species display?	• Species responses to time-since-fire corresponded with six response shapes: incline, decline, bell-shaped, plateau, irruptive and null.
How important are different post-fire ages for supporting species?	 The frequency of occurrence of 10 species was highest in vegetation >50 years-since-fire. The frequency of occurrence of five species peaked 20-50 years-since-fire and declined thereafter. The frequency of occurrence of one species was highest in vegetation <5 years-since-fire.
How useful are generalised fire response curves for predicting species distributions over broad regions?	• Models of species occurrence with time-since-fire provided moderate predictive accuracy across the region.
How important is time-since-fire for structuring the richness and composition of avifaunal communities?	 Species richness was lowest directly after fire, and reached a plateau at ~10 years-since-fire. Community composition varied with time-since-fire up to at least 100 years post-fire.
In what ways did community composition change with time-since- fire?	 The rate of change in community composition slowed with increasing time-since-fire. Similar assemblages occupied longer time-frames with increasing time-since-fire. Distinct avifaunal communities occurred in vegetation <10, 21-40 and >50 years-since-fire. β diversity was higher in older vegetation.

Objectives	Key Findings
What effect did time-since-fire have on the richness of species guilds? What processes does this indicate may be important in influencing successional patterns of the avifauna?	 Species richness of nectarivore-insectivores and insectivores was influenced by time-since-fire. It was low directly after fire and increased to a plateau at ~10 years-since-fire. Species richness of foliage foragers increased with time-since-fire, and richness of trunk and branch foragers initially increased but declined in older vegetation. Responses of species guilds to time-since-fire corresponded generally with temporal changes in resources on which the guild depends (e.g. nectar, vegetation structure).
Conservation and management implications of the effects of temporal patterns of fire.	 Mallee birds and communities can be influenced by fire for up to 100 years. Fire is a critical component for regeneration of mallee habitat to support some species of birds. Older seral stages are particularly important. Provision of post-fire age-classes may not guarantee the occurrence of species. To ensure an assemblage which includes all species across a region, the distinctiveness of post-fire age-classes and influence of fire on β diversity needs to be considered.
Effects of spatial aspects of fire on the avifauna	
What influence does the proximity of a site to unburnt vegetation	• Species richness and occurrence of individual species declined with distance to unburnt vegetation.

- Species richness and occurrence of individual species was higher at sites that contained small patches of unburnt vegetation, "biological legacies".
 - Generally sites appeared to be colonised from large patches of unburnt vegetation.
- have on the assemblage of birds in recently burnt vegetation (<5 years-since-fire)?

and the presence of small patches of unburnt vegetation at a site

Are burnt areas colonised post-fire from birds located external to the burnt areas or from internal nucleated recovery?

Objectives	Key Findings
What influence do the properties of fire mosaics have on the composition of avifaunal communities at the landscape scale?	 Fire mosaic properties explained ~31% of the variation in the composition of the avifauna. Composition of the avifauna at the landscape level was influenced by: a) a gradient in the proportional extent of vegetation <10 years-since-fire vs >35 years-since-fire. b) the location of the landscape along a geographic gradient of aridity. c) a gradient in the composition of the dominant vegetation types in the landscape. Community composition did not vary with diversity of different fire age-classes.
How do the properties of fire mosaics influence the incidence of different guilds in the landscape? Does this indicate processes that may influence the composition of the avifauna at the landscape level?	• Fire mosaic properties may influence the guild structure of a community through changes in spatial availability of resources. For example, a decreased incidence of nectarivores and nectarivore-insectivores was associated with increasing proportional extent of vegetation <10 years-since-fire.
Conservation and management implications of the effects of spatial properties of fire on the avifauna.	 Large uniform fires will take longer for birds to colonise than small patchy fires. Small unburnt patches may assist the survival and post-fire recovery of fire sensitive species. The habitat remaining unburnt after fire is important for the colonisation of burnt areas. A primary focus of fire management should be on the total amount of post-fire age-classes in a landscape, not only on the diversity of post-fire ages. Management of fire needs to consider large spatial scales, and the influence of fire on the total availability of resources across a landscape and region.

Chapter 6 – Synthesis

6.2 Temporal patterns of fire and avifaunal assemblages

Patterns of succession, represented as changes in biota over time, have played a major role in ecology (Clements, 1916; Gleason, 1927; Connell, 1978). Much of the understanding of biotic changes to fire revolve around succession theory (Noble & Slatyer, 1980; Fox, 1982; Brawn *et al.*, 2001), and consequently patterns of post-fire change in biota form the backbone of fire management for conservation (Driscoll *et al.*, 2010). In this thesis, I investigated temporal variation of: a) individual species (Chapter 2) and b) the composition of the bird communities (Chapter 3), to gain insights into successional patterns of the mallee avifauna, and to examine processes that might influence these patterns.

Many species of birds displayed significant changes in occurrence with time-sincefire (Chapter 2). Responses to fire tended to represent a limited number of different response shapes: incline, decline, bell-shaped, irruptive and plateau. Only one species displayed peak occurrence in early successional vegetation (<10 years-sincefire), five species in mid-successional vegetation (20 – 50 years-since-fire), and 10 species reached their peak occurrence between 50 – 100 years-since-fire (Chapter 2). These changes formed the underpinnings of three main successional stages in the composition of bird communities: <10, 20 – 40 and >50 years-since-fire (Chapter 3).

The successional stages identified in this study increased in temporal breadth with increasing time-since-fire, such that each successive community occupied a greater time span. This pattern comes about because the rate of ecological change tends to slow with increasing time since a disturbance event (Helle & Monkkonen, 1985). Such that for any given time contrast (e.g. 10 years time difference between the post-fire age of two sites), the degree of distinction between bird communities of that

contrast decreases with increasing time since the disturbance (in this case fire). In plant communities and for sessile animals, these patterns of temporal change in community structure are often related to available energy and competitive interactions (Odum, 1969; Connell & Slatyer, 1977); however, the theory of why these patterns are seen in vagile organisms is less well understood. However, faunal succession patterns are often linked to vegetation changes (Fox, 1982; Haney *et al.*, 2008), and thus the rapidity of plant succession may influence the rate of faunal succession.

Successional patterns in the avifauna of mallee ecosystems do appear to be associated with patterns of vegetation succession, particularly vegetation structural changes (Chapter 2; Chapter 3). This suggests that mallee avifaunal succession may follow the 'habitat accommodation' model of post-fire-succession (Fox, 1982). In this model, species respond to local habitat conditions, which are altered by external factors (e.g. fire). A species enters the succession as vegetation change results in habitat becoming suitable for it and leaves, or decreases in abundance, when the habitat becomes unsuitable. Declines in occurrence may relate to an inability of species to obtain enough resources due to having reduced competitive ability in lower 'quality' habitat (Fox, 1982). Evidence for a habitat accommodation model of succession comes from a number of sources. First, the shape of the responses of species to time-since-fire often corresponds with changes in vegetation structural characteristics that those species require (e.g. abundance of hollows, Triodia cover, or density of particular vertical strata of vegetation) (Chapter 2). Second, the main successional stages in bird communities correspond with vegetation structural changes: for example, regrowth of mallee eucalypts occurs in the period <10 yearssince-fire; the cover of *Triodia* hummock grasses and the complexity of vertical

vegetation structure are at peak levels at 20 - 40 years-since-fire; and from > 50 years post-fire there is a general decline in vertical structural complexity of vegetation and a plateau in the height and the cover of the canopy (Haslem *et al.*, 2011). Finally, the species richness of some foraging zone guilds corresponded with changes in resources on which those guilds might be expected to rely; for example, species richness of foliage foragers varied in a manner consistent with canopy cover, and trunk and branch foragers with mid-storey structure (Chapter 3).

The habitat accommodation model also proposes that interspecific competition may influence successional patterns (Fox, 1981; Fox, 1982). Where species are suited to habitat of a particular seral stage, they may out-compete species that are less suited, and lead to the exclusion of those species from a location. There is some observational evidence that this may be an important factor for avifaunal succession in mallee vegetation. A decline in occurrence of several species with time-since-fire corresponded with inclines in potential competitors (Chapter 2). Competition/inhibition forms a key part of many succession theories (Connell & Slatyer, 1977) and is likely to be important in bird communities of mallee vegetation.

The successional patterns seen in bird communities in mallee are consistent with the habitat accommodation model on the basis of vegetation structural changes. However, patterns seen in dietary guilds indicate that food resources also may be an important component. Species richness of nectarivore-insectivores and insectivores was low directly after fire, increasing until ~10 years post-fire, where the species richness of these guilds reached a plateau. As patterns of change in guilds that use particular resources may indicate the importance of that resource (Simberloff & Dayan, 1991), these patterns indicate that food availability may also influence

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patterns of succession. Patterns shown by these guilds correspond with the occurrence of *Eucalyptus* reproduction, and thus the availability of nectar. The availability of nectar from *Eucalyptus* sp. is likely to be of major importance to the nectarivore-insectivore guild, as it is a primary food source for these species (Ford & Paton, 1976a; Ford & Paton, 1976b). Nectar of *Eucalyptus* sp. also is an important resource for many invertebrates (Horskins & Turner, 1999), and reduced abundance of nectar could result in significant reductions in the biomass of these species. Alternative studies have shown that the total abundance of ants (Hymenoptera) can be negatively affected by fire in mallee (Andersen & Yen, 1985).

If succession of the mallee avifauna is linked to vegetation structure and food resources, as in a habitat accommodation model, then succession patterns of the avifauna will be affected by processes that alter these attributes of habitat (Monamy & Fox, 2000). In mallee ecosystems, particular events which effect vegetation structure, for example the amount of rainfall and grazing intensity post-fire (Cohn & Bradstock, 2000) could thus result in changes to avifaunal succession, in a manner somewhat analogous to state-and-transition models proposed for rangeland and arid environments (Westoby *et al.*, 1989; Letnic & Dickman, 2010). Under state-and-transition models, vegetation communities exist in a range of 'persistent' states (e.g. shrubland or grassland) and ecological events (e.g. fire, grazing, rainfall and drought) can affect transitions between these states.

In mallee ecosystems, there are some clear directional successional patterns in both vegetation attributes (Haslem *et al.*, 2011) and bird communities (Chapter 2; Chapter 3), and thus state-and-transition models are unlikely to explain responses on their own. However, variation in the fit of models of both birds and habitat attributes

suggest that particular events may affect changes to successional patterns, although not to entirely different states. For example, in mallee ecosystems, below average monthly rainfall and intensity of grazing by mammalian herbivores (particularly introduced rabbits and goats) can reduce germination and establishment of understorey plants, including *Triodia scariosa* hummock grasses (Cohn & Bradstock, 2000), which is an important feature of vegetation communities in this ecosystem (Haslem *et al.*, 2010). Thus, rainfall and grazing processes will influence succession patterns in vegetation structure, and consequently bird communities.

The effect of post-fire grazing intensity and rainfall on differences in structure of vegetation between sites may be magnified by time-since-fire, and hence bird community differences may also be magnified. Vegetation in the younger successional stages is structurally simpler than later successional vegetation (Haslem et al., 2011; Chapter 3). Thus, bird communities that prefer younger seral stages, may be more likely to be responding to more simple structural features (e.g. foliage cover from the resprouting of the dominant Eucalyptus species) and be less affected by differences among sites related to rainfall and grazing, which affects small regenerating understorey plants. On the other hand, species that prefer older seral stages may respond to a range of mature structural attributes (e.g. midstorey shrub density, Triodia cover), which will be more contrasting as mature vegetation than as recently regenerating plants and seedlings. This premise is supported by vegetation succession data, which shows that sites in older vegetation display greater heterogeneity of vegetation structural attributes (Haslem et al., 2011). There was also higher β diversity (between-site diversity) of birds in older sites; evidenced by faster rates of increase of new species with additional sites in older seral stages (Chapter 3).

The higher β diversity at older sites is an important feature, because this pattern means that species richness at a site (α diversity) in older vegetation is lower than that expected on the basis of individual species responses (Chapter 2). Because most species peak in occurrence in older vegetation it might be expected that species richness would increase with time-since-fire. Instead, species richness increased only until ~10 years-since-fire, where it reached a plateau (Chapter 3), because species associated with older fire ages occupy different sites and hence there is greater β diversity (and not higher α diversity).

A further consideration for interpreting patterns of avifaunal succession is the influence of non-fire related variables, such as vegetation type (Triodia Mallee or Chenopod Mallee) and geographic location of sites. There were differing patterns of avifaunal succession and differences in the way some vegetation attributes changed with time-since-fire in different vegetation types (Haslem *et al.*, 2011; Chapter 2; Chapter 3). In this investigation, six bird species were more common south of the Murray River and six species north of the Murray River. Thus responses of individual species to fire need to be interpreted in light of the local abundance of the species based on broader biogeographic patterns and on their habitat requirements.

6.3 The influence of spatial patterns of fire on avifaunal assemblages

The influence of spatial properties of fire on fauna has received comparatively little attention in fire ecology; instead, most investigations have focused on temporal influences of fire. Indeed spatial properties of fire events (e.g. the size and configuration of fires) have only recently been discussed as a part of the fire regime (Gill & Allan, 2008); the history of fire events in an area or region (Gill, 1975). In this thesis, I investigated two facets of the effect of spatial patterns of fire on

avifaunal assemblages. First, I investigated the impact of the spatial pattern of fire on colonisation of recently burnt vegetation at the site level (Chapter 4). Second, I examined the broader impact of the properties of fire mosaics on the composition of the avifauna at the landscape level (Chapter 5). In both of these chapters, I discovered that spatial properties of fires can have wide-ranging impacts on the bird community at sites through its effect on the colonisation process, and on the broader assemblage of a landscape.

6.3.1 The influence of spatial properties of fire on post-fire colonisation by birds

Spatial properties of fire influence the colonisation of burnt vegetation by fauna (Bain *et al.*, 2008; Lindenmayer *et al.*, 2009; Chapter 4). Although temporal patterns of change provide important insights into the effects of fire on avifaunal species and assemblages (Brawn *et al.*, 2001), a species response to a particular fire event may be different to that expected on the basis of succession patterns (Lindenmayer *et al.*, 2009), and models of species' responses to time-since-fire had only moderate predictive accuracy over broad spatial scales (Chapter 2).

Fine-scale variation in the spatial pattern of fires represents one factor that contributes to the occurrence of species at a site. Species richness and the occurrence of individual species at sites in recently burnt vegetation were higher at sites close to unburnt vegetation (Chapter 4). Sites that contained small unburnt patches of vegetation supported more species, either through enhancing colonisation from *exsitu* populations, or through their role as refuges in which species have persisted through the fire event ('biological legacies'; Turner *et al.*, 1998; Franklin *et al.*, 2000). Consequently the configuration of fire events (level of patchiness) represents an important factor in determining patterns of post-fire colonisation by avifauna.

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Although biological legacies appeared to be an important feature influencing the post-fire bird community at a site, colonisation appeared to come mostly from larger areas of unburnt vegetation, regardless of if the site contained small biological legacies or not. This process is evidenced by sites close to large areas of unburnt vegetation having higher species richness than sites farther from fire edges of the same post-fire age. This suggests that burnt areas are colonised from reservoir populations in large patches of unburnt vegetation, which may or may not contain individuals that were evicted from the fire area during the fire event. Thus, the size and composition of unburnt vegetation that contains the reservoir of species will strongly influence the species that colonise the burnt area, and the subsequent successional patterns.

In this investigation, the patterns of succession observed (Chapters 2; Chapter 3), indicated that much post-fire colonisation occurs in a relatively predictable manner, with species' occurrences generally increasing and decreasing at predictable post-fire ages. However, this study was conducted in large areas of continuous mallee vegetation, where fires generally are surrounded by an extensive reservoir of vegetation containing a diverse assemblage of birds. In small reserves (or non-reserve habitat) that occur as patches of habitat within a hostile matrix, a single fire may burn a large percentage (or all) of the available habitat, as has occurred in isolated mallee reserves (Menkhorst & Bennett, 1990; Silveira, 2008). In this case, nearby reservoir populations may be scarce or absent, and colonisation of the burnt area will be strongly influenced the ability of species to disperse through the matrix. This can potentially result in very different communities colonising burnt areas (Brotons *et al.*, 2005).

6.3.2 Influence of the spatial properties of fire mosaics on avifauna

The way in which fire mosaics influence faunal assemblages is gaining increasing attention due to the prevalence of the patch mosaic burning paradigm (Parr & Andersen, 2006). This paradigm is based around two central themes. First, that different post-fire age-classes support different species and communities (Chapter 2 and Chapter 3), and thus increased heterogeneity will increase biodiversity. The second theme is that increased fire heterogeneity may improve the persistence of species by affording protection from large intense fires (Bradstock *et al.*, 2005). Although fire management is increasingly aimed at managing fire to create heterogeneous mosaics (Fire Ecology Working Group, 2004; Willson, 2006), there remains little empirical investigation of how the spatial properties of fire mosaics may influence biota at the landscape level.

The spatial extent of post-fire age-classes in a landscape can influence the composition of the bird community by increasing the dominance of those species for which that seral stage represents favourable habitat (Chapter 5). This mechanism is similar to that in human modified systems such as agricultural environments, where for example, the total extent of wooded vegetation in a landscape influences the richness and abundance of woodland-dependent birds (Radford *et al.*, 2005; Haslem & Bennett, 2008).

Variation in the proportional extent of different seral stages can also influence the spatial availability of resources (e.g. nectar), which in turn can influence the assemblage of species at the landscape level in ways not predictable from individual sites. For example, the incidence of nectarivores in the study landscapes appeared to

be limited by the proportional extent of recently burnt vegetation, which represents reduced nectar availability, especially from mallee eucalypts (Chapter 5). However, at the site scale the occurrence of nectarivores was not clearly influenced by younger age-class, associated with reduction of nectar. Local reduction of nectar may be offset by strategies such as nomadism (Woinarski, 2006), or the local availability of nectar resources from plants other than mallee eucalypts that reach reproductive status more quickly (Ford & Paton, 1976a; Ford & Paton, 1976b). However, when nectar availability decreases at the landscape scale, due to extensive areas recently burnt, nectarivores are negatively affected.

Thus, the spatial extent of the landscape over which fire occurs may cause population changes (booms or crashes) for species or guilds that rely on resources affected by fire. In mallee ecosystems, fires regularly burn large areas: for example, 16 fires of >10 000 ha have occurred over the 35 year period 1972-2007 across the 104 000 km² Murray Mallee study area (Avitabile *et al.*, 2011). Fires of this magnitude represent substantial reductions in temporally varying resources over broad spatial scales. While such resources are absent, species must maintain and grow populations in the remaining areas of suitable habitat, while these resources re-establish in the burnt areas. In systems where early successional specialists rely on resources produced by fires (Murphy & Lehnhausen, 1998; Hutto, 2008), a lack of large fires could likewise represent a dearth of resources. The magnifying influence of the spatial extent of fires is particularly important considering the potential for the extent of burnt areas to vary under climate change scenarios (Cary, 2002).

The spatial extent of particular post-fire age-classes in a landscape can also influence the diversity of organisms in the landscape. Here, β diversity (as species

accumulation curves) was greater in older vegetation (Chapter 3). Consequently, an increasing proportional extent of older vegetation can be expected to result in greater richness of bird species, which was the observed pattern (Rick Taylor, unpublished data). Increased heterogeneity in structural attributes in older vegetation is proposed as a reason for the increased β diversity with time-since-fire (Chapter 3). Landscapes with a greater proportional extent of older vegetation may represent greater diversity of habitats, or increased landscape texture (Fischer *et al.*, 2008), reported as predictors of faunal diversity in agricultural environments (Bennett *et al.*, 2006; Fischer *et al.*, 2008; Haslem & Bennett, 2008; Fahrig *et al.*, 2011).

At the scale of the landscapes in this study in mallee ecosystems (2 km radius), species richness of birds did not increase with the diversity of fire age-classes in the landscape (Rick Taylor, unpublished data). This lack of a relationship is difficult to reconcile with knowledge of changes to species communities with time-since-fire. However, the results from species accumulation curves with time-since-fire may provide an explanation for this pattern. The rate of increase in the species accumulation curve in older vegetation is greater than that in younger vegetation, and so the addition of younger vegetation (and hence age-class heterogeneity) will not increase diversity as rapidly as having further older vegetation. Where the species accumulation relationship of older vegetation begins to plateau, the addition of different post-fire ages may increase the diversity of species, particularly if species are strongly differentiated between the different fire age-classes. However, in this ecosystem, many species occur in multiple age-classes, albeit in different abundances.

If species accumulation curves are taken to represent species area curves, then the scale of the study landscapes may also influence the observed pattern. At a scale of 2 km radius, the species-area curve for older vegetation may be increasing at a rate faster than is achieved through the addition of new fire ages. However, for larger landscapes, which can contain a greater area of older age-class and thus a more complete suite of species which respond to older vegetation, then diversity of post-fire age-classes may become more important. Thus the scale at which the influence of diversity of fire age classes is measured may result in different interpretations of its importance.

In this study, there was no evidence that species composition was strongly influenced by processes related to diversity of post-fire ages (Chapter 5). The importance of having multiple habitat elements for fauna has been suggested for a number of ecosystems (Law & Dickman, 1998), for instance for species that require different vegetation for nesting and feeding. Additionally a diverse history of fires has been suggested as an important factor to improve persistence of species by affording protection from large intense fires that cause large-scale mortality and homogenise the landscape (Bradstock *et al.*, 2005).

The relationship between attributes of bird communities and the diversity of post-fire age-classes may also be influenced by the measure of diversity employed in this study (Chapter 5). This measure (Shannon-Wiener diversity index) represented the diversity of post-fire age-classes regardless of the age of those patches. For example, a hypothetical landscape containing three post-fire age-classes of 5 years, 7 years and 10 years-since-fire would have a similar diversity index to one that contains post-fire age-classes of similar area of 5 years, 20 years and 40 years-since-fire.

Consequently, the response of species or communities to the presence of particular contrasting fire ages may not be detected by this measure.

6.4 The implications for conservation and land management of birds in fireprone environments.

Fire is increasingly recognised as an important ecological disturbance, the management of which is critical to conservation of biota. Consequently, fire is becoming increasingly prevalent as a management tool (Gill & Allan, 2008; Driscoll *et al.*, 2010b). Findings in this thesis support the contention that fire is a critical component of mallee ecosystem, with far reaching implications for the conservation and management of many bird species (Clarke, 2005; Clarke *et al.*, 2005; Brown *et al.*, 2009).

In many ecosystems around the world, the occurrence of species and the composition of communities vary in relation to post-fire seral stages (Fox, 1982; Schieck & Song, 2006; Pons & Clavero, 2010; Chapter 2; Chapter 3), and species may decline in late succession vegetation and in the absence of fire (Fuhlendorf *et al.*, 2006; Hutto, 2008; Brown *et al.*, 2009; Chapter 2). Thus, in fire-prone ecosystems, fire is an important process that can develop and regenerate habitats, and management aimed at protection of biodiversity needs to allow for, or promote fire (Noss *et al.*, 2006). The dilemma for management of birds in mallee ecosystems is that many species are negatively affected by fire, at least in the short term, and older vegetation is disproportionately important for the avifaunal assemblage as a whole (Chapters 2 and 3). Thus, on the one hand fire management needs to protect vegetation from burning, while on the other hand allowing fire to burn habitats. In each case, too much young vegetation or too much old vegetation may potentially threaten biodiversity. The

challenge is to define an appropriate age-class structure, at a regional scale, that will ensure the ongoing provision through time of suitable amounts of required habitat for all bird species.

As young, mid and old vegetation are unable to exist in the same space at the same time, a mosaic of different fire age-classes is an intuitive management option. However, defining the spatial and temporal scale of such a mosaic is difficult. Through this thesis I have shown that avifaunal assemblages can be influenced by fire in a variety of ways. Fire management for biodiversity will need to consider all of these factors if it is to achieve successful outcomes. It seems unlikely that a onesize-fits-all approach across ecosystems will be appropriate, particularly considering the inherently unpredictable nature of complexities of wildfire (Whelan *et al.*, 2001).

An important factor for fire management aimed at biodiversity conservation is the degree to which (unplanned) wildfire will occur in the system, and its consequences for the distribution of fire age-classes in the region. This will dictate the degree to which anthropogenic introduction of fire, or prevention of fire may be required to achieve a desired age-class structure. In some ecosystems, a focus on prevention of fire has negatively affected biota (Noss *et al.*, 2006), and anthropogenic management of fire may be required to introduce heterogeneity and restore habitats (Davis *et al.*, 2000; Gill & Allan, 2008; Beghin *et al.*, 2010). In the Murray Mallee region, over the past 35 years (1972-2007), there have been 16 fires of >10 000 ha (Avitabile *et al.*, 2011), which have burnt >40% of all mallee vegetation. Considering that successional patterns continue for at least 100 years, and >40% of vegetation is <35 years-since-fire, protection of older fire age-classes may be more important in

achieving a balanced age-class structure than the introduction of fire across much of this region.

When planned burning is considered, the influence of the properties of fires on recovery of populations, mortality or removal of species, and the colonisation strategies those species employ must be considered. Patchy fires can enhance recovery of populations through acting as refuges, or assisting colonisation of burnt areas (Rowley & Brooker, 1987; Smith, 1989; Chapter 4). Thus, in ecosystems where prescribed burning is employed (Willson, 2006), increasing the patchiness of fires may assist recovery of fire sensitive species (i.e. those species removed by fire or require vegetation attributes that take a long time to regenerate) (Bain *et al.*, 2008; Lindenmayer *et al.*, 2009). However patchy burns may not promote extensive enough resources that they require (Smucker *et al.*, 2005; Hutto, 2008; Brown *et al.*, 2009).

Because most bird species in mallee colonise burnt areas from large areas of unburnt vegetation (Chapter 4), management strategies that promote fires need to carefully consider not only the area being burnt but the context of the fire (i.e. the amount and type of vegetation that remains unburnt adjoining unburnt areas). Large areas of unburnt vegetation appear to be where most species recolonise from (Chapter 4). Such 'reservoirs' may need to support populations for many years before burnt habitat is suitable to recolonise. For example, the Striated Grasswren, which prefers *Triodia* hummock grasses of 15-40 years-since-fire, will need to survive in *ex-situ* vegetation while Triodia regenerates in the burnt area to a suitable size (i.e. 15

years). In the event that suitable habitat is not present in nearby surrounding areas, this species may suffer long-term exclusion from an area.

In small reserves (or non-reserve habitat) that occur as patches of mallee within a highly modified environment (e.g. croplands) (Menkhorst & Bennett, 1990; Silveira, 2008), management may need to be scaled to ensure reservoir populations are maintained within the reserve. Large fires that homogenise areas and leave little 'reservoir' vegetation need to be avoided. As the ratio of burnt to unburnt vegetation (or vice versa) increases in a landscape, there is a greater influence on the overall community composition in the landscape (Chapter 5). Furthermore, large fires can potentially result in severe temporal reduction of some resources such as eucalypt nectar (Chapter 5) or *Triodia* hummocks (Haslem *et al.*, 2011). In events where large fires have occurred and largely homogenised suitable habitat for species, populations of those species have been severely depleted, for example Mallee Emu-wren in Billiatt Conservation Park, South Australia (Clarke, 2005).

If the goal is to promote heterogeneity, it is important to define the components of heterogeneity, because diversity of post-fire age-classes *per se* did not influence the composition of the avifaunal community in a predictable way (Chapter 5). In this system, avifaunal communities appear to respond to three main seral stages, <10, 20-40 and >50 years-since-fire (Chapter 3). Thus long-term management may aim to ensure that representative areas of each of these seral stages always exist (Chapter 3). However, each seral stage does not contribute equally to the overall assemblage. Older seral stages supported more species spread across a greater number of sites (Chapter 3) and consequently may need to have greater representation in the age class structure of the landscape.

Chapter 6 – Synthesis

In managing the age-class structure and geographic distribution of seral stages, the total amount of a particular seral stage is important as it tends to have the strongest influence on the composition of avifauna. Rather than simply managing for a diversity of post-fire age-classes, management may be more effective if it focuses primarily on the requisite amount of particular seral stages required to support species of concern or communities. In this ecosystem, vegetation >30 years-since-fire needs to be well represented due to the increased number of species that are supported by vegetation of this age (Chapters 2 and 3). Managing for a greater proportional amount of older vegetation may be an appropriate precautionary management strategy because many species use long unburnt vegetation. This will allow for unplanned fires (i.e. wildfires), which will inevitably occur, and may reduce risk of creating an overabundance of younger vegetation.

Fire management needs to be conceptualised at broad scales that encompass the whole assemblage being managed. In the Murray Mallee region, fire management is conducted by three separate states, Victoria, New South Wales and South Australia. However, avifaunal assemblages overlap amongst reserves in different states and management should likewise occur across state boundaries (Saunders & Briggs, 2002). It is also important to recognise that there are strong natural gradients in the occurrence of species with geographic position in the region. Thus, managing fire to promote the Golden Whistler in far northern parts of this study area may not be effective as this species is naturally rare in this part of the region. Likewise, it is important to manage fire in the context of other habitat requirements of species. For example, provision of the suitable fire age-classes for Striated Grasswren in Chenopod Mallee vegetation will be ineffective because this species depends on

Triodia hummock grass, which is all but absent in this vegetation type (Haslem *et al.*, 2010).

6.5 Future directions for research into the influence of fire on avifauna

In this investigation a number of variables were associated with successional patterns of the bird community (e.g. vegetation structure, food resource availability). Further research is required into the deterministic processes that influence the patterns of avifaunal succession. For instance, manipulative experiments to alter the vegetation structure and food resources in different seral stages could be used to test the relative importance of different processes in influencing long-term succession patterns. Moreover, understanding the way that fire patterns (e.g. patchiness) and species ecological attributes (e.g. mobility) interact will assist managers to predict the influence of fire on the mortality of individuals.

I investigated the implications of spatial patterns of fire for bird assemblages at both the site level and the whole-of-landscape level. The whole-of-landscape design has many advantages, particularly to study the composition of fire age classes (e.g. diversity in this thesis) because composition is a property of whole landscapes: investigations at a patch or site level can infer processes only at the level of the investigation (Bennett *et al.*, 2006). However, whole of landscape designs require the size of the landscape to be set, and inference is restricted to that scale. A critical area for future research is to investigate the responses of biota to mosaics of fire patches at different spatial scales, to provide improved knowledge about the scales at which management needs to operate. There is a need for a greater understanding of the importance of the configuration and connectivity of vegetation of different seral stages through time. These are attributes of the 'invisible mosaic'; the spatial distribution of fires historically (Bradstock *et al.*, 2005). In this study, the spatial parameters of fires generally represented only the most recent fires, because over the period of available satellite imagery (1972-2007) less than 4% of mallee vegetation burnt more than once (Avitabile *et al.*, 2011). However, the avifaunal assemblages may also be related to the historic availability of seral stages (Lindenmayer *et al.*, 2008). Past events, such as the recurrences of large fires that homogenise fire-age across large areas, or the exclusion of fire from large areas, may influence the availability of source populations to recolonise after a fire event. Ecosystems such as grasslands, where successional patterns are much shorter (Fuhlendorf *et al.*, 2006) may provide model systems to investigate the influence of the 'invisible mosaic'.

Throughout this thesis, I have reiterated that fire is an important process influencing bird communities and that the birds of mallee ecosystems display general succession patterns. Some level of ongoing fire will be needed in mallee vegetation. In the event that wildfires do not occur, prescribed burning may be used to regenerate particular succession stages (Davis *et al.*, 2000). Other factors such as post-fire grazing by herbivores and rainfall may influence establishment of plant species (Cohn & Bradstock, 2000), including key species such as *Triodia scariosa*. Simply burning mallee vegetation may not result in the vegetation structure on which target species rely, and further management such as control of grazing animals may be required. Furthermore, management burns are often small and may consequently be susceptible to higher rates of herbivory on regenerating plants (Knight & Holt, 2005). Given the increasing prevalence of the use of planned fire for management of

biodiversity (Gill, 1975; Parr & Andersen, 2006; Driscoll *et al.*, 2010), knowledge of the capacity of this burning to deliver the intended outcomes is of paramount importance (Miller & Hobbs, 2007).

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Appendix 1

Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems

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Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems

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Abstract. A critical requirement in the ecological management of fire is knowledge of the age-class distribution of the vegetation. Such knowledge is important because it underpins the distribution of ecological features important to plants and animals including retreat sites, food sources and foraging microhabitats. However, in many regions, knowledge of the ageclass distribution of vegetation is severely constrained by the limited data available on fire history. Much fire-history mapping is restricted to post-1972 fires, following satellite imagery becoming widely available. To investigate fire history in the semi-arid Murray Mallee region in southem Australia, we developed regression models for six species of mallee eucalypt (Eucalyptus oleosa F. Muell. ex. Miq. subsp. oleosa, E. leptophylla F. Muell. ex. Miq., E. dumosa J. Oxley, E. costata subsp. murrayana L. A. S. Johnson & K. D. Hill, E. gracilis F. Muell. and E. socialis F. Muell. ex. Miq.) to quantify the relationship between mean stem diameter and stem age (indicated by fire-year) at sites of known time since fire. We then used these models to predict mean stem age, and thus infer fire-year, for sites where the time since fire was not known. Validation of the models with independent data revealed a highly significant correlation between the actual and predicted time since fire (r=0.71, P < 0.001, n = 88), confirming the utility of this method for ageing stands of mallee eucalypt vegetation. Validation data suggest the models provide a conservative estimate of the age of a site (i.e. they may under-estimate the minimum age of sites >35 years since fire). Nevertheless, this approach enables examination of post-fire chronosequences in semi-arid mallee ecosystems to be extended from 35 years post-fire to over 100 years. The predicted ages identified for mallee stands imply a need for redefining what is meant by 'old-growth' mallee, and challenges current perceptions of an over-abundance of long-unburnt' mallee vegetation. Given the strong influence of fire on semi-arid mallee vegetation, this approach offers the potential for a better understanding of long-term successional dynamics and the status of biota in an ecosystem that encompasses more than $250\,000\,\text{km}^2$ of southern Australia.

Introduction

Fire is an ecological process that shapes ecosystems throughout the world (Bond et al. 2005; Bowman et al. 2009). It has profound effects on ecosystem function in arid and semi-arid shrublands (Keeley 1995; Pausas and Bradstock 2007) where the prevailing fire regime strongly influences vegetation composition and structure (Noble et al. 1980; Bradstock 1989; Noble and Vines 1993). In turn, the vegetation provides resources for fauna, such as food, cover and nest sites (Bos and Carthew 2003; Brown et al. 2009). In semi-arid 'mallee' shrublands of southern Australia, the status of many species of animal is influenced by the fire regime (Cheal et al. 1979; Gill 1994). For example, the globally endangered mallee emu-wren (*Stipiturus mallee*) primarily occurs in *Triodia*-dominated mallee vegetation that has not been burnt for at least 15 years (Brown et al. 2009). The malleefowl (*Leipoa ocellata*) requires vegetation from which fire has been excluded for at least 10 years, and reaches its

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maximum breeding capacity at sites at least 40 years post-fire (Benshemesh 1989). Clarke *et al.* (2005) suggested that the endangered black-eared miner (*Manorina melanotis*) is most abundant in mallee vegetation not burnt for between 45 and 60 years.

Because different taxa respond to fire in different ways, many fire managers aim to maintain a mosaic of vegetation representing different post-fire age classes (Brockett *et al.* 2001; Bradstock *et al.* 2005; Parr and Andersen 2006; Burrows 2008). However, this requires knowledge of the proportion of vegetation in different age classes within a land-management unit. Such information forms the necessary basis for determining how much of the unit will be subjected to planned burning, or protected by fire suppression (e.g. Fire Ecology Working Group 2002). A major limitation to fire planning throughout most of Australia is that systematic mapping of fires at a regional scale is possible only from 1972 onwards, when satellite imagery

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first became widely available. However, many eucalypt forests and woodlands clearly commenced life well before 1972. In the absence of spatially explicit knowledge of when vegetation was last burnt, areas of unknown fire history are often grouped into a single older cohort (e.g. Letnic *et al.* 2004; Driscoll and Henderson 2008; Lindenmayer *et al.* 2008).

Ecologically important components of habitat for faunal species may take decades, or even centuries, to develop (e.g. 144-194 years to develop hollows in blackbutt, *Eucalyptus pilularis*; Mackowski (1984)). Consequently, grouping all areas of unknown 'older' fire history into a single category may fail to distinguish between ecologically significant age classes. In the case of mallee eucalypt species, which resprout multiple stems from a lignotuber following fire, it is not clear whether stems that have not been burnt for some 38 years (i.e. since 1972) should be regarded, ecologically, as 'old'. Holland (1967 cited in Ogden 1978) reported trees of oil mallee (Eucalyptus oleosa) to be 150 years of age. This suggests that at least some mallee eucalypts have the potential to persist close to 4-fold longer than the age at which they may be grouped as 'old', on the basis of the current limits of mapping fire history. It clearly would be advantageous to be able to age different cohorts of eucalypts across a land-management unit. Unfortunately, standard dendrochronological techniques are time consuming, expensive and have met with mixed success (Ogden 1978).

Mallee vegetation has a low canopy (generally <5 m), and so almost all fires (prescribed or wildfire) result in the canopy burning and the death of above-ground stems and branches. New stems then arise post-fire from synchronous resprouting from the lignotubers. Consequently, most mallee stems in a particular location are the consequence of a single fire event, unless the fire was patchy or resprouting was in response to insect attack, drought or frost. This offers the possibility that stem diameter may be correlated with time since fire and that this relationship might be used in a predictive fashion to estimate the age of stands of mallee vegetation. This approach has been applied fruitfully to ageing the stems of snow gum (*E. pauciflora* subsp. *niphophila*), a eucalypt that also exhibits a multi-stemmed, 'mallee' growth form, although in a highly seasonal subalpine environment (Barker 1988; Rumpff *et al.* 2009).

The aim of the present study was to examine the relationship between stem diameter and time since fire as a basis for estimating the potential age of stands of mallee for which the time of last fire is not known.

Materials and methods

Study area

Data were collected between July and August 2007 at 835 sites, spread across 28 study mosaics (4-km-diameter circles) located in large reserves (>5000 ha) in tree mallee vegetation of New South Wales, Victoria and South Australia (Fig. 1). The locations of mosaics were selected to capture a broad mixture of time since fire age classes within the mosaic (some mostly recently bumt, some with up to four different age classes, others predominantly unburnt for at least 35 years). Mosaics were a minimum of 2 km apart. The locations of sites within each mosaic (up to 30 sites) were chosen to ensure they were representative of the known time-since-fire age classes and the range of landscape positions (e.g. swale, dune crest, slope of dune) present within the mosaic. Sites were generally at least 200 m apart, and included vegetation ranging from mallee eucalypts over a heathy understorey, to mallee with a predominantly *Triodia* understorey, to more-open stands of mallee with chenopod understorey.

Collection of initial field data

Data were collected from a total of 835 survey sites. The year of the last fire (and hence time since fire) was determined from firehistory maps for 485 sites, whereas the remaining 350 sites were known not to have been burnt since 1972 (i.e. the earliest available Landsat imagery used in creating the fire-history maps), but otherwise were of unknown age. At each site, data on stem diameters were collected systematically from trees located within 2 m either side of a 50-m transect (as part of a broader collection of vegetation data at each site). The diameter of all stems (dead or alive) of each mallee eucalypt was measured to the nearest cm at ~30 cm above ground. Stems that were <1 cm in diameter were not measured. At each site, stems of the first 10 trees encountered along the transect were measured. Where there appeared to be more than one age cohort of trees at a site (trees whose stems consistently differed by more than ~2 cm in diameter), the first 10 trees of each cohort encountered were measured. The species of each tree was identified. We obtained estimates of the mean annual rainfall for each site from the Australian Bureau of Meteorology.

Modelling growth in stem diameters for sites of known fire-age

The mean stem diameter was calculated for each individual tree at each site, using only data for live stems. Analyses of changes in stem diameter with time since fire were restricted to data from sites of known fire age (1–35 years post-fire), and for which preliminary inspection of the size distribution of stems suggested a uniform age class at the site (n = 282 sites) (i.e. excluding many sites that may have burned patchily). Note that we refer in the present paper to the age of stems rather than trees, because mallee trees generally are not killed by fire; the lignotuber of the tree survives and generates a new cohort of stems.

The relationship between the mean stem diameter of trees and time since fire was modelled separately for each of six species of mallee eucalypts by using generalised linear models (GLMs). The mean annual rainfall at each site was included as a second predictor variable (in addition to time since fire) to allow for a gradient in aridity across the region, which influences productivity of vegetation (Pausas and Bradstock 2007). For all species, data on stem diameter were slightly right-skewed and transformations were ineffective in improving normality. Inspection of residuals revealed that models using raw data for stem diameter and a Gaussian error distribution were not appropriate. Therefore, models were developed using a Gamma error distribution (with an identity link function). The Gamma distribution is appropriate for continuous, positive, right-skewed data with a large coefficient of variation (Bolker 2008), as was the case here. Fitting the models with a Gamma distribution resulted in normally distributed, homogeneous residuals. Exploratory analysis was undertaken to test whether growth in

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Fig. 1. Location of study mosaics and validation sites across the Murray Mallee region, south-eastern Australia.

stem diameter may plateau over time. The following three forms of the variable 'time since fire' were modelled: (1) untransformed, (2) \log_{10} transformed and (3) square-root transformed. Models with the transformed variables did not provide a better fit (i.e. deviance explained) and so the linear models were used. This indicates that growth in mallee eucalypt stems did not begin to plateau over the time period modelled (i.e. up to 35 years). We averaged predictions arising from these species-specific models so as to estimate the time ince a site last experienced fire. GLMs were generated with the R statistical program (R Development Core Team 2009).

Validation of models for predicting post-fire age

To test the ability of this approach to reliably predict the age of mallee eucalypt vegetation beyond the limits of the current fire mapping, we collected additional data in February 2009 at 'validation' sites of known age >35 years since fire. From records of land-management agencies, we identified five areas (across a geographic range of 209 km) where fires had occurred in 1917, 1932, 1951, 1957 and 1964, respectively (i.e. 45-92 years since fire). In each area, multiple sites were located at least 200 m apart to sample spatial variation, including that owing to topographic position. In total, we measured 1894 stems from 636 trees across 88 validation sites, using the field methods outlined above.

We compared the known age of these validation sites with the predictions generated from the GLMs of the mean stem diameter by using correlation coefficients.

Results

The initial data set comprised measurements of 41 410 stems on 7840 mallee eucalypt trees across 835 sites. Models were developed for six eucalypt species for which samples were adequate (Table 1). A strong linear relationship between stem diameter and time since fire was detected for all six species over the first 35 years of post-fire growth (Table 2, Fig. 2). Even though mean annual rainfall varied by ~100 mm across the study region, it was found to have a significant influence on the stem size of only one species (coefficient $\pm 2 \times$ s.e. did not overlap with zero) where it had a relatively minor influence on stem growth rate (Table 2).

Modelling indicated that individual eucalypt species exhibited different growth rates, with *E. oleosa* subsp. *oleosa* stems growing much faster than those of the other five species, whereas *E. leptophylla*, *E. dumosa* and *E. gracilis* exhibited the slowest growth rates (Fig. 2).

Stem diameter data collected at the additional 88 validation sites of known age of \geq 45 years (but not used in the model generation process) were used to test the ability of the models to

Table 1. Summary of the numbers of sites of known fire-age, trees and stems used in modelling the relationship between stem diameter and time since fire for six species of mallee eucalvpts

The number of stems does not include stems <1-cm diameter or dead stems						
Species	No. of sites	No. of trees	No. of stems			
E. socialis	137	266	1625			
E. dumosa	150	386	2307			
E. costata subsp. murrayana	67	210	912			
E. leptophylla	83	204	1086			
E. oleosa subsp. oleosa	39	93	527			
E. gracilis	47	99	550			
Total	282	1258	7007			

predict the time since fire. For all six species, the age of stems predicted by using the species-specific models was significantly correlated with the known time since fire for validation sites (Pearson correlation, r=0.57-0.79) (Table 3). To account for differences in species-specific growth rates, while maximising the information used to generate an estimate of the time since fire for each site, we calculated a mean of the predictions from species-specific models for all species at the site. There was a highly significant correlation (r=0.71, P < 0.001) between the predicted and actual time since fire at the validation sites, by using this method.

Comparison of the predicted and actual time since fire indicated that the models typically underestimated the time since fire for a site by an average of $23\% \pm 2.1$ (s.e.) (Fig. 3). This suggests that beyond 35 years, the growth rates of stem diameters of mallee trees in the region may slow as the stem ages. The initial models we built to test for non-linear growth of stem diameter with time (i.e. by using square root or log-transformations of diameter – see Materials and methods) did not perform better in predictions from the linear models were more strongly correlated with the actual age of validation sites, than were predictions from models with transformed variables.

Nevertheless, to further examine the possibility that growth rate slows in later years, we generated six new species-specific models on the basis of the combined data from known-age sites (<35 years of age) plus the validation sites (Appendix 1, Table 1). For four of six species, models that used a squareroot transformation of time since fire provided the strongest fit, whereas for two species, the linear model was the strongest. We

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re-estimated the age of sites of unknown age by using an average of the predictions arising from the best new model for each species. The predicted ages of sites when generated by the original models (using data only from sites <35 years of age) and the new models (sites 0–94 years of age) were highly correlated (Appendix 1, Fig. 1); within the bounds of the data from which the models were built (~100 years), the Pearson correlation coefficient r=0.94 (P<0.001). However, predictions of the ages of sites with larger stems (e.g. >12-cm diameter) arising from the new models are likely to have considerable uncertainty; minor changes in stem diameter equate to large changes in the predicted age because of the flattening of the (years).

We based our predictions of the age of sites of unknown age (n=346) on the more conservative original linear models, because (1) these models have been validated and (2) their predictions are highly correlated with those of the alternative models (which have not been validated). The predicted ages were determined by calculating the average of the predictions of time since fire for each tree species at each site (by using the species-specific models in Table 2). Estimates could not be generated for four sites where there was uncertainty over the species of eucalypt present.

The 346 sites of unknown fire history were spread across the majority of the 28 sampling mosaics and were chosen with no knowledge of their likely age other than that they had not been burnt since 1972. If one assumes they are a representative sample of the distribution of pre-1972 age classes in the region, a comparison can be made of the distributions of age classes generated with, and without, the age estimates arising from our models. The age-class structure generated using fire mapping based on Landsat imagery is profoundly truncated (Fig. 4*a*) and suggests a predominance of a single age class across the region (i.e. >35 years since fire).

By contrast, our estimate of the likely age structure of 346 sites falling within the single >35 years age class shows there is not a predominance of a single age class, rather a range of different age classes. This range includes some rare age classes incorporating sites that have remained unburnt for more than 160 years (Fig. 4b).

Discussion

These analyses have demonstrated a strong relationship between the mean stem diameter at a site and time since fire

 Table 2. Coefficient estimates and standard errors (s.e.) for models of the change in mean stem diameter (cm) in relation to time since fire (years) for six species of mallee eucalypts in the Murray Mallee region

 D² values represent the percentage of deviance explained by the overall model

Species	Coefficients for predictor variables						
	(Intercept)		Time since f	Time since fire (years)		Mean annual rainfall (mm)	
	Estimate	s.e.	Estimate	s.e.	Estimate	s.e.	
E. socialis	1.558	0.468	0.138	0.006	-0.0010	0.0019	79.5
E. dumosa	1.682	0.583	0.111	0.007	-0.0016	0.0022	69.5
E. costata subsp. murrayana	1.426	0.847	0.142	0.010	-0.0009	0.0031	69.4
E. leptophylla	1.207	0.717	0.106	0.008	0.0006	0.0028	64.6
E. oleosa subsp. oleosa	4.495	1.482	0.194	0.018	-0.0141	0.0064	79.3
E. gracilis	3.748	1.332	0.115	0.013	-0.0099	0.0052	52.2

Appendices

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Fig. 2. Species-specific models of changes in the mean stem diameter for mallee eucalypts in relation to known time (years) since fire during the first 35 years post-fire (dotted lines indicate 95% confidence intervals).

Table 3. Correlations between the predicted and actual time since fire for 88 validation sites in mallee vegetation

Correlation coefficients are presented for each of the individual species models, and for the average of the predicted ages for each species that occurred at the site. The number of stems does not include stems <1-cm diameter

Species	No. of sites	No. of trees	No. of stems	Pearson correlation (r)	Р	
E. socialis	42	104	329	0.65	< 0.001	
E. dumosa	63	232	687	0.72	< 0.001	
E. costata	21	95	261	0.79	< 0.001	
E. leptophylla	28	72	208	0.60	< 0.001	
E. oleosa	20	86	259	0.55	0.011	
E. gracilis	14	47	150	0.57	0.033	
Average for all species present at a site	88	636	1894	0.71	< 0.001	

(i.e. the age of the stem) for six species of mallee eucalypts in the Murray Mallee region. Application of the present technique offers a cheaper and more efficient method of estimating the age of mallee vegetation, particularly in areas of unknown fire history, than standard dendrochronological techniques (e.g. Holland 1969). The relationship between the mean stem diameter and time since fire is strong, particularly given potential sources of variation that could arise. First, the potentially localised nature of rainfall events in the semi-arid region could add 'noise' to the growth rates of stems among sites across the region, possibly obscuring clear patterns. However, we found that the mean annual minfall was of minor importance in predicting growth rates. Second, we assumed that all stems on a site arose after a common fire event. It is unlikely that this is always the case, as an occasional stem may survive a fire and others may arise many years post-fire in response to some other stimulus such as damage by wind or herbivores. Third, we had no way of

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Fig. 3. The relationship between the predicted and actual time (years) since fire for validation sites (n=88). The predicted time was based on averages from species-specific models for eucalypt species at each site. The solid line depicts where a 1:1 correspondence between the predicted and actual ages of sites would fall.

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controlling for variation in the size of the lignotuber from which different trees were sprouting stems. If larger lignotubers have access to more moisture or nutrients, then one might expect this to introduce further variance into growth rates among trees at the same site. Our approach of averaging the age predictions derived from species-specific models, for each species present at a site, and each of these species models being based on the averaged stem diameter for multiple trees at a site, probably reduced the influence of some of this variability.

Examination of interspecific differences in growth rates was not a primary goal of the present study. However, the faster growth rates of *E. oleosa* than, for example, *E. costata*, may well reflect differences in growth form and position in the landscape. *E. oleosa* more commonly occurs in the heavier soils in the swales and *E. costata* more commonly on sandy dune slopes and crests (Sparrow 1989, 1990; Parkes and Cheal 1990). We incorporated this interspecific variation when making predictions of time since fire for sites of unknown age, by calculating the average of the predicted ages for each species at a site. An alternative, potentially simpler, approach could be to model and make predictions on the basis of all stems at a site regardless of tree species. We tested this latter approach (see Appendix – Table 2) and found that although



Fig. 4. (a) Percentage of tree mallee vegetation in the Murray Mallee region of Victoria, NSW and South Australia known to fall into particular age classes for time since fire. Percentages were calculated from GIS maps of the region's fire history, derived from all available Landsat imagery for the region (S. C. Avitabile, K. E. Callister, A. Haslem, L. T. Kelly, D. G. Nimmo, S. J. Watson, S. A. Kenny, R. S. Taylor, L. M. Spence-Bailey, A. F. Bennett and M. F. Clarke, unpubl. data.). (b) Percentage of tree mallee vegetation in the tri-state region *estimated* to fall into particular age-classes for time since fire. Darker bars depict percentages calculated from GIS maps of the region's fire history (as above). Lighter bars depict the distribution of the >35 years age class, on the basis of the assumption that it is proportional to the age-classe distribution of 346 sites whose age was predicted using the stem diameter models.

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it was less effective than the species-specific models, it still performed moderately well. For example, for sites of known age of <35 years, a linear model based on mean diameter of all stems at a site (regardless of species) accounted for 52% of variation in the data (Appendix 1), compared with a mean of 69% (range 52–79%) for the species-specific models of the same dataset (Table 2).

Our validated models assumed a linear increase in mean stem diameter with age. This contrasts with much work in dendrochronology that has revealed that the rings on a tree often decrease in width as the tree ages; that is, the rate of growth slows over time (Ogden 1978). However, Barker's (1988) study of E. pauciflora showed no sign of the rate of growth of stems slowing before 100 years of age, and possibly before 300 years (although the data are sparse). By assuming a linear increase in the mean stem diameter with age, our models generate conservative estimates of stem age and underestimate the likely age of sites as a consequence. Nevertheless, the models we created by using all available data (Appendix 1) suggest nonlinear (slowing) growth rates at older ages for some species. However, these models require validation with independent data, particularly from sites in the older age ranges (e.g. >100 years post-fire).

Although it is clear that mallee vegetation can attain post-fire ages well in excess of 100 years, we believe caution is required in making and using predictions in these older age classes. Linear models of age v. mean stem diameter may underestimate such ages, whereas models in which age is transformed (square-root transformation) will have large confidence limits because estimates of the age of sites with larger stems vary greatly, with minor changes in mean stem diameter. At the two sites of greatest predicted age in the present study (tentatively ~160 years), the diameter of the five largest stems ranged from 25 to 40 cm and 30 to 50 cm, respectively. Although this estimate of site age cannot be interpreted as a maximum age of mallee stems in the region, it is consistent with the maximum estimated ages reported by Holland (1967, cited in Ogden 1978) of 150 years for E. oleosa, and by Ogden (1978) of 300 years for an E. pauciflora, as indicated by a ring count. Even larger stems were encountered in the study region, particularly along roadsides in otherwise cleared landscapes (M. Clarke, pers. obs.). After allowing for the likely superior soils in the cultivated regions (Land Conservation Council 1987) and the possibility of slightly faster growth rates, these roadside trees are likely to be very old and contain resources (e.g. hollows) less common in the younger vegetation in conservation reserves. Note that the models presented here are not appropriate for estimating the age of individual stems of mallee eucalypts. Rather, they are most appropriately used to predict the age of mallee vegetation at a site because they are based on the mean stem diameter of all trees of a particular species at a site.

A primary goal in fire ecology is to understand how the distribution and abundances of organisms change with time following a fire (Friend 1993; Fox *et al.* 2003; Torre and Diaz 2004), and then to understand the processes that drive those changes. Many such analyses have been constrained by the limited fire history available for most sites (rarely >40 years before present) (e.g. Fire Ecology Working Group 2002), thus restricting the focus to shorter-term changes in ecosystems

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following fire (Clarke 2008). Our approach makes it possible to determine the time since fire efficiently for sites in mallee shrubland up to at least 100 years post-fire, and therefore to identify ecological changes that may occur more slowly, or much later, in successional pathways. Only when we have a more complete picture of a successional pattern will we be able to understand the key ecological processes that drive changes during succession (Lunt 2002). This approach will allow a more precise quantification of the age-class preferences of many species of the mallee fauna, for example, the malleefowl (Benshemesh 1989) and black-eared miner (Clarke et al. 2005), that previously have simply been classified as favouring vegetation greater than 40 years of age. It will also enable a more comprehensive examination of the time periods over which key ecological resources used by faunal species (e.g. litter layers, Triodia hummocks, tree hollows) develop following a fire (A. Haslem, L. T. Kelly, D. G. Nimmo, S. J. Watson, S. A. Kenny, R. S. Taylor, S. C. Avitabile, K. E. Callister, L. M. Spence-Bailey, A. F. Bennett and M.F. Clarke, unpubl. data).

These analyses also challenge current understanding of the age-class distribution of mallee vegetation across the study region (e.g. Fire Ecology Working Group 2002). In contrast to a perception that conservation reserves in the region currently contain a disproportionate abundance of 'older' mallee vegetation (>35 years post-fire, Fig. 4a), the present results suggest a more diverse distribution of sites in this age category, and that mallee vegetation older than 100 years of age is quite rare. Given that several threatened species in mallee ecosystems are reported to prefer long-unburnt habitats (e.g. Emison and Bren 1989; Bradstock and Cohn 2002; Clarke 2005), spatially explicit maps showing the location and sizes of stands of mallee vegetation of different age classes, including those up to an estimated 100 years post-fire, would be a valuable resource for management. We are currently developing such a map for the Murray Mallee region in south-eastern Australia by using our study sites and their predicted ages as 'training sites' for a modelling analysis using remote-sensing imagery (P. Griffioen, unpubl. data).

This simple approach to estimating the age of mallee vegetation at sites offers great potential for studying long-term successional changes in mallee ecosystems. This approach could also be applied in other states and in other contexts, with appropriate calibration for local species and climatic variation. Given that mallee shrublands and woodlands occupy some 250 420 km² in southern Australia (National Land and Water Resources Audit 2001), there is scope for greatly enhancing our current understanding of ecosystem function across a significant portion of the continent.

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Appendix 1. Coefficient estimates and standard errors (s.e.) for models of the change in mean stem diameter (cm) per site in relation to time since fire for six species of mallee eucalypts in the Murray Mallee region Models are based on data from sites of known time since fireranging from 0 to 94 years. Alternative models are presented for which time (years) is modelled in linear

form and square-root transformed (sqr). D^2 = the percentage of deviance explained by the model							
Species	Coefficients for predictor variables						D^2
	(Intercept)		Years since	Years since last burnt		Mean annual rainfall (mm)	
	Estimate	s.e.	Estimate	s.e.	Estimate	s.e.	
E. socialis (linear)	1.212	0.506	0.121	0.005	0.001	0.002	80.2
E. socialis (sqr) ^A	1.960	0.460	0.961	0.035	-0.007	0.002	82.0
E. dumosa (linear) ^A	1.690	0.546	0.102	0.005	-0.001	0.002	78.7
E. dumosa (sqr)	1.962	0.542	0.841	0.037	-0.007	0.002	76.4
E. costata subsp. murrayana (linear)	1.140	0.908	0.118	0.008	0.001	0.003	68.8
E. costata subsp. murrayana (sqr) ^A	1.088	0.780	0.961	0.051	-0.004	0.003	73.7
E. leptophylla (linear)	1.092	0.742	0.096	0.007	0.001	0.003	66.1
E. leptophylla (sqr) ^A	1.861	0.719	0.796	0.050	-0.006	0.003	66.8
E. oleosa (linear)	2.373	1.838	0.134	0.014	-0.004	0.008	67.0
E. $oleosa (sqr)^A$	5.792	1.385	1.278	0.090	-0.025	0.006	80.0
E. gracilis (linear) ^A	3.530	1.219	0.109	0.009	-0.009	0.005	71.2
E. gracilis (sqr)	4.693	1.189	0.917	0.071	-0.018	0.005	69.1

^AModel that provides best fit to data for each species.

Appendix 2. Coefficient estimates and standard errors (s.e.) for models of the change in mean stem diameter (cm) per site in relation to time since fire for mallee eucalypts in the Murray Mallee region Models are based on data recorded from all mallee eucalypts at a site, regardless of species. Models are presented for datasets based on sites of <35 years since

Models are based on data recorded from all mallee eucalypts at a site, regardless of species. Models are presented for datasets based on sites of <35 years since fire and 0–94 years since fire, respectively. In each case, alternative models are presented for which time (years) is modelled in linear form and square-root transformed (sqr). D^2 values represent the percentage of deviance explained by the overall model

Dataset		Coefficients for predictor variables					
	(Intercept)		Years since last burnt		Mean annual rainfall (mm)		
	Estimate	s.e.	Estimate	s.e.	Estimate	s.e.	
Sites <35 years since fire (linear) ^A	2.292	0.805	0.122	0.007	-0.003	0.003	0.520
Sites <35 years since fire (sqr)	1.183	0.879	0.884	0.053	-0.004	0.003	0.486
Sites 0-94 years since fire (linear) ^A	3.272	0.754	0.099	0.004	-0.005	0.003	0.661
Sites 0-94 years since fire (sqr)	1.326	0.754	0.915	0.036	-0.005	0.002	0.660

^AModel that provides best fit to data for each dataset.



Appendix 3. Relationship between the predictions of two methods of generating time-since-fire predictions by using (1) the average across species of the best linear or square-not species-specific models from the combined dataset of 0-94 years (x-axis) and (2) the average across-species time-since-fire predictions from the linear species-specific models built only on 0-35-year data (y-axis) (Pearson's correlation (r)=0.94, P < 0.001). The solid line depicts where a 1 : 1 correspondence between predicted ages of sites determined by each model would fall.

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Appendix 2

A framework for mapping vegetation over broad spatial extents: a technique to aid land management across jurisdictional boundaries

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A framework for mapping vegetation over broad spatial extents: A technique to aid land management across jurisdictional boundaries

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ABSTRACT

Mismatches in boundaries between natural ecosystems and land governance units often complicate an ecosystem approach to management and conservation. For example, information used to guide management, such as vegetation maps, may not be available or consistent across entire ecosystems. This study was undertaken within a single biogeographic region (the Murray Mallee) spanning three Australian states. Existing vegetation maps could not be used as vegetation classifications differed between states. Our aim was to describe and map 'tree mallee' vegetation consistently across a 104,000 km² area of this region. Hierarchical cluster analyses, incorporating floristic data from 713 sites, were employed to identify distinct vegetation types. Neural network classification models were used to map these vegetation types across the region, with additional data from 634 validation sites providing a measure of map accuracy. Four distinct vegetation types were recognised: Triodia Mallee, Heathy Mallee, Chenopod Mallee and Shrubby Mallee. Neural network models predicted the occurrence of three of them with 79% accuracy. Validation results identified that map accuracy was 67% (kappa = 0.42) when using independent data. The framework employed provides a simple approach to describing and mapping vegetation classification suitable for use across this biogeographic region; (2) a consistent vegetation map to inform land-use planning and biodiversity management at local and regional scales; and (3) a quantification of map accuracy using independent data. This approach is applicable to other regions facing similar challenges associated with integrating vegetation data across jurisdictional boundaries.

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1. Introduction

There is widespread recognition of the importance of considering entire ecological systems, or biogeographic regions, when planning for conservation management (Caldwell, 1970). However, the boundaries of natural ecosystems do not always match those of the administrative or political regions within which land management is undertaken (Christensen et al., 1996). Further, natural ecosystems can be transected by human-defined boundaries at many levels of jurisdiction: local, regional and national (Van Eetvelde and Antrop, 2009). Consequently, tools used to inform land management may not be consistent across, or even available for, the entire area in question (Brody et al., 2003).

Patterns of vegetation distribution reflect abiotic characteristics, and have a fundamental influence on ecological processes and the occurrence of biota (Hooper and Vitousek, 1997). Therefore, vegetation maps play a crucial role in asset inventory, land-use planning, conservation management and research development (Cihlar, 2000; Keith and Simpson, 2008). For example, vegetation maps indicate the relative extent of different vegetation types in a region, thus guiding conservation priorities (Crumpacker et al., 1988). They also assist the management of disturbance events, such as fire, that differ in prevalence between vegetation types (Bradstock et al., 2002). For maps to be useful in these applications, it is essential the information they provide is consistent for the entire area of interest (Pressey et al., 2000). Individual vege-tation maps can differ considerably in relation to the vegetation types recognised, as well as the method, resolution and currency of both vegetation description and mapping (Hansen and Reed, 2000; Thogmartin et al., 2004). Such variation makes it difficult to integrate the information contained in different maps, even in the

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absence of issues associated with multiple governance boundaries (Keith and Simpson, 2008).

Previous approaches to integrating mapped information include frameworks for evaluating and ranking alternative maps based on attributes such as accuracy, coverage and resolution (Keith and Simpson, 2008), and protocols for translating and harmonising land-cover legends (Herold et al., 2008). For example, an information hierarchy framework was used to combine 67 regional-scale datasets from across Australia into the single National Vegetation Information System (Thackway et al., 2007). Using this approach, detailed vegetation classifications were compiled into broad categories of native, non-native and non-vegetated cover. However, as Van Eetvelde and Antrop (2009) identified when developing a land-cover map for Belgium, differences in the scale and classification of existing data sources may make their integration into a single dataset impossible.

Another consideration in the use of existing mapped information is that of map accuracy. Validation of vegetation maps is uncommon (Özesmi et al., 2006; but see Kozak et al., 2008; Cunningham et al., 2009) despite being a critical step in the process of mapping spatial data (Congalton, 2001). This means that users have no measure of map accuracy, an important consideration when assessing the suitability of contained information for the specified application (Congalton, 2001; Bach et al., 2006).

The use of remotely sensed data to produce maps covering large areas provides another solution to the challenge of describing vegetation across multiple jurisdictions (Fuller et al., 1998). However, the classification detail contained in such maps may be broad (Smith and Wyatt, 2007), and floristic data are less often incorporated (Hobbs et al., 1989). For example, some simply describe the occurrence of a single vegetation class (Pressey et al., 2000; Kozak et al., 2008), while others map the distribution of a few, broad land-cover types (Eva et al., 2004; Huang and Siegert, 2006). Validation of maps produced using remotely sensed data, when undertaken, is often based on satellite imagery or existing maps (Mayaux et al., 2002; Eva et al., 2004). Therefore, such maps may not include field data at any stage in their production or validation.

This study was prompted by difficulties encountered when collating existing vegetation data for our study region: a 104 000 km² area of the Murray Mallee in south-eastern Australia. The Murray Mallee lies within a single biogeographic region that comprises three state-level jurisdictions and 16 local government districts (NSW Government, 2008; Government of South Australia, 2009; State Government of Victoria, 2009). While numerous vegetation maps exist for the region (e.g. Fox, 1990; Westbrooke et al., 1998; Val, 2001; White et al., 2003; Department for Environment and Heritage, 2005), none cover all of it. These existing maps were of limited value for region-wide use as they differed in scale, and the number and characteristics of vegetation types recognised. Further, those with the largest coverage (state-level maps) were spatially disjunct, making their integration difficult. In addition, no measure of map accuracy was available for any of them.

Here, we present a framework for classifying vegetation types and producing a validated map of their distribution across a broad spatial extent. We set three objectives: (1) to identify and provide a consistent description of vegetation types common to the whole Murray Mallee region; (2) to map the distribution of these vegetation types across all jurisdictional units comprising the study area; and (3) to validate the map using independent data, thus providing users with an indication of map accuracy. In meeting these objectives, we have employed relatively simple methods to ensure this approach can be applied in other regions facing similar challenges.

2. Methods

2.1. Study area

The study area encompasses 104 000 km² of the Murray Mallee and incorporates parts of three Australian states; Victoria, New South Wales and South Australia (Fig. 1). The Murray Mallee is an area of low relief (\leq 100 m above sea level) and little topographic variation (White et al., 2003). Extensive dune systems characterise the region: linear calcareous dunes follow an east–west orientation while siliceous parabolic/irregular dunes are more variable in form



Fig. 1. The Murray Mallee study area in south-eastern Australia, showing the location of 28 study landscapes in Victoria, South Australia and New South Wales. Floristic data were collected at between 29 and 31 sites in each 1256 ha landscape.

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(Land Conservation Council, 1987). The climate is semi-arid, with annual rainfall between 220 and 330 mm (raw data supplied by the Australian Bureau of Meteorology). High temperatures are common in summer, with mean daily maxima often exceeding $32 \,^{\circ}$ C, while winter months are mild (mean daily maxima of around $16 \,^{\circ}$ C) (LCC, 1987).

Native vegetation in the region comprises a number of broad types, from semi-arid shrublands and woodlands to treeless plains (LCC, 1987). Since settlement by Europeans in the 1840s, native vegetation has been extensively cleared for agricultural production, primarily cropping and grazing (Harris, 1990). We focus on the most common type of native vegetation in the study area: 'tree mallee'. Tree mallee vegetation is characterised by the occurrence of multi-stemmed ('mallee') eucalypt trees above lower strata of shrubs and perennial and ephemeral grasses (Parkes and Cheal, 1990; Bradstock and Cohn, 2002).

2.2. Study design

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This study forms part of a project investigating the response of flora and fauna to different fire mosaics. Site selection was guided by methodological considerations imposed by the wholeof-landscape approach employed in the broader study. Data were collected from 835 sites, grouped in circular study landscapes of 1256 ha spread across the study region. In each study landscape, between 29 and 31 sites were sampled in tree mallee vegetation. Sites were distributed among all fire-age classes, in proportion to their extent in the landscape, and were selected to encompass topographic variation (dune/swale). The latter consideration ensured that sites were representative of tree mallee vegetation types (see LCC, 1987). Study landscapes were separated by a mean distance of 130 km (range: 6.3-217.7 km) and, within individual landscapes. sites were positioned an average of 1.5 km apart. All study landscapes were located in conservation reserves, 8155-631 942 ha in size, composed of stands of relatively continuous native vegetation.

At each site a quadrat of $10 \text{ m} \times 50 \text{ m}$ was used for sampling the flora: perennial plant species were identified and their coverabundance assessed using a modified Braun-Blanquet scale (1 or 2 plants, $\leq 5\%$ cover, 6-25%, 26-50%, 51-75%, 76-100%). Annual and semi-perennial species were not recorded as their occurrence and abundance varies greatly in response to rainfall events. To avoid potential misclassification, plants were identified to genus level when species-level identification was uncertain. Nomenclature follows relevant state flora texts and census lists (Ross and Walsh, 2003; Barker et al., 2005). Vegetation sampling was undertaken between June and August 2007.

Additional environmental characteristics were compiled for each site. Soil texture was assessed following McDonald et al. (1990). The topographic position of sites was classified using the following categories: dune crest (uppermost dune point), dune slope (any point between dune crest and base), swale (clay/sandy) and flat-plain (terrain with little relief). The fire-age of sites was determined from fire history mapping of the region (Avitabile et al., unpublished data). Fire mapping was based on Landsat imagery recorded on 15 occasions between 1972 and 2007, at intervals of 2–4 years. Time-since-last fire was estimated as the number of years between 2007 (when floristic data were collected) and the midpoint of this 2–4 year interval.

2.3. Identification of mallee vegetation types

Hierarchical cluster analyses were used to identify vegetation types. These analyses were based on Bray Curtis similarity matrices derived from cover-abundance data for perennial species. Species recorded at <10 sites were excluded due to their potential, as 'rare' species, to exert a disproportionate influence on cluster groupings. Sites burnt within the last 10 years were also excluded as their vegetation and appearance on satellite imagery may differ markedly from mature vegetation of the same type. Thus, data for 106 species from 713 sites were included in these analyses (Appendix A).

Floristic differences between distinct clusters of sites were compared by using similarity percentage (SIMPER) analysis. SIM-PER results also identified species making a strong contribution to the within-cluster similarity of different groups of sites. A non-metric multidimensional scaling (NMDS) ordination of the similarity matrix was used to further examine variation between different site groupings. Comparison of the soil type and topographic position of sites in different clusters provided additional insights. Cluster, SIMPER and NMDS analyses were undertaken in PRIMER v.G.1.9 (PRIMER-E, 2007).

Results identified a clear split of eight groups of sites that separated at a similarity level of 22%. Three of these groups were retained (n = 65, 231 and 399 sites) and five were discarded due their very small size (all <10 sites). A second cluster analysis examining floristic variation within the two largest groups split the group with 231 sites into two further groups (similarity 27%: n = 52 and 179 sites). Thus, four distinct types of mallee vegetation were identified: Triodia Mallee (TM), Heathy Mallee (HM), Chenopod Mallee (CM), and Shrubby Mallee (SM).

For some sites, vegetation type was assigned independently of the cluster analyses. This was necessary for sites: (a) excluded from analyses (i.e. burnt <10 years ago: n = 122); (b) belonging to small, discarded clusters (n = 18); and (c) identified as outliers, based on the NMDS ordination and soil type/topographic position (n = 21). These sites were allocated to the most appropriate vegetation type based on species cover-abundance data and assessment of site photographs.

The most frequently sampled, and widely distributed vegetation type was Triodia Mallee. Overall, 61% of sites (n = 508) were classified as Triodia Mallee. Chenopod Mallee, the second most common vegetation type (n = 200), was also widely distributed across all three states. Heathy Mallee and Shrubby Mallee were both sampled much less frequently, 66 and 61 sites, respectively, with the former being the most geographically restricted vegetation type.

Vegetation types differed on the basis of canopy dominants, understorey composition, soil characteristics and topographic position. In all cases, canopy species made a strong contribution to within-vegetation type similarity (Table 1). Triodia Mallee was dominated by *Eucalyptus dumosa* and *Eucalyptus socialis*, the latter species also being characteristic of Shrubby Mallee. In contrast, *Eucalyptus oleosa* subsp. *oleosa* and *Eucalyptus gracilis* characterised canopy vegetation in Chenopod Mallee. Heathy Mallee was the only vegetation type in which species other than eucalypts contributed to canopy composition: *Eucalyptus costata* subsp. *murrayana* and *Callitris verrucosa* were both recorded at over 90% of sites in Heathy Mallee.

Triodia scariosa was recorded relatively commonly in all vegetation types (Table 1) but was particularly characteristic of Triodia Mallee, where it was recorded at highest cover abundance. Shrubs such as Acacia rigens, Acacia wilhelmiana and Beyeria opaca were also common at sites in Triodia Mallee, which often supported a high cover of medium to tall shrubs. In Heathy Mallee, ground strata were commonly dominated by a diverse range of small woody shrubs, including heathy species such as Phebalium bullatum, Cryptandra tomentosa and Spyridium subochreatum var. subochreatum. Below-canopy vegetation in Chenopod Mallee was characterised by a range of low shrubs occurring at low abundances, including Olearia spp., Zygophyllum spp. and chenopod species such as Maireana pentatropis, Enchylaena tomentosa var. tomentosa and Maireana pyramidata. The understorey of Shrubby Mallee was characterised by relatively low abundances of a range of tall shrubs

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Perennial species characteristic of four tree mallee vegetation types: Triodia Mallee (TM), Heathy Mallee (HM), Chenopod Mallee (CM) and Shrubby Mallee (SM). The average similarity (%) of sites within each type is shown, as is each species' contribution (%) to within-type similarity² (parentheses contain the percentage of sites in each vegetation type at which species were recorded).

Species	Contribution to within-vegetation type similarity (%)				
	TM	HM	CM	SM	
Average similarity (%)	35.0	46.6	35.1	35.5	
Acacia burkittii				1.7 (34)	
Acacia colletioides				7.8 (69)	
Acacia rigens	1.6 (25)	2.6 (56)			
Acacia sclerophylla var. sclerophylla			1.5 (30)		
Acacia wilhelmiana	2.6 (31)				
Aotus subspinescens		2.6 (61)			
Babingtonia behrii		5.0 (62)			
Baeckea crassifolia		2.0 (55)			
Beyeria opaca	1.6 (26)			4.2 (41)	
Callitris verrucosa		14.3 (94)			
Calytrix tetragona		1.5 (45)			
Chenopodium desertorum				2.6 (46)	
Cryptandra tomentosa complex		3.4 (68)			
Dodonaea viscosa subsp. angustissima				3.5 (46)	
Eucalyptus costata subsp. murrayana	5.7 (37)	12.7 (91)			
Eucalyptus dumosa	16.9 (72)		7.0 (53)	2.1 (30)	
Eucalyptus gracilis			10.9 (59)	5.2 (49)	
Eucalyptus leptophylla	6.5 (46)	5.6 (59)	1.1 (21)		
Eucalyptus oleosa subsp. oleosa			29.3 (79)		
Eucalyptus socialis	12.8 (68)		2.2 (35)	13.1 (75)	
Eucalyptus sp.	7.0 (66)	9.7 (88)	3.2 (53)		
Enchylaena tomentosa var. tomentosa				7.5 (72)	
Eremophila crassifolia			2.2 (5)		
Eremophila glabra			1.1 (33)	6.4 (69)	
Eremophila scoparia				2.2 (36)	
Eremophila sturtii				1.5 (33)	
Grevillea pterosperma		1.8 (47)			
Hakea leucoptera subsp. leucoptera		3.8 (64)			
Hibbertia riparia		3.3 (70)			
Leptospermum coriaceum	1.3(17)	11.4 (91)	()		
Maireana pentatropis			2.7 (40)	1.4 (31)	
Maireana pyramidata			1.8 (31)		
Maireana sp.			1.1 (30)	4.5 (20)	
Olearia muelleri			2.1 (40)	1.5 (39)	
Olearia pimeleoides subsp. pimeleoides		17 (71)	1.1 (31)		
Phebalium bullatum		4.7 (71)			
Scierolaena diacantha			10.7 (85)	10.5 (75)	
Senna artemisioides subsp. coriacea				3.3 (46)	
Senna artemisioides subsp. filifolia			1.5 (30)	3.9 (51)	
Senna artemisioides subsp. petiolaris				6.9 (61)	
Senna artemisioides subsp. zygophylla		0.0 (50)		1.9 (33)	
Spyriaium subochreatum var. subochreatum	25.0 (02)	3.0 (59)	21(20)	2.2 (22)	
I FIOAIA SCAFIOSA	35.0 (93)	3.9 (59)	2.1 (28)	2.3 (38)	
westringia rigida			1.2 (29)	10(24)	
zygopnynum apiculatum Zwanskillium apiculatum			4.4 (49)	1.6 (34)	
zygopnynum aurantiacum subsp. aurantiacum			3.9 (50)		

^a Species contributing to >90% of the similarity of vegetation types are shown.

including Acacia colletioides, Senna spp., Dodonaea viscosa subsp. angustissima, B. opaca and Eremophila sturtii.

Triodia Mallee occurred predominantly on lighter, sandier soils and on dunes and flat-plains while Heathy Mallee occurred on sandy soils in all topographic positions. Chenopod Mallee was more common on heavier soils with some clay content, and occurred most often on flat-plains and swales. Shrubby Mallee showed a closer association with soils with some loam content than Chenopod Mallee, and occurred most frequently on flat-plains.

2.4. Mapping of mallee vegetation types

Table 1

Vegetation types identified by the cluster analyses were then mapped across the region. To do this, information on vegetation type, together with a range of additional environmental variables (see below) for the 835 study sites were used to model vegetation type. Neural network classification models (Duda et al., 2001) were used in this process. Neural network models are ideal for modelling complex ecological systems as they incorporate heterogeneous data in a single framework, without needing to explicitly define underlying relationships (Scardi, 1996). Further, this technique is highly effective at modelling non-linear and interacting relationships (Özesmi et al., 2006). Numerous studies have demonstrated the successful use of this approach for modelling a range of vegetation characteristics over broad spatial extents (Foody and Arora, 1997; Linderman et al., 2004; Cunningham et al., 2009).

Ninety-three environmental variables were included in the modelling process, as follows: geographic position (n = 2 variables); Normalized Difference Vegetation Index, representing vegetation 'greenness' (n = 1: Tucker, 1979); Landsat imagery, including between four and seven spectral bands for 15 different years (1972–2007: n = 81); mallee vegetation distribution (n = 3); radiometric data, representing soil characteristics (n = 2: Cook et al., 1996); Topographic Wetness Index, representing topographic and hydrologic processes (n = 3); and altitude (n = 1). Satellite imagery was acquired from Landsat Multi Spectral Scanner (1972, 1977,

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1980, 1985 and 1988), Landsat Thematic Mapper (1989, 1991, 1992, 1995, 1998, 2004, 2005 and 2007) and Landsat Enhanced Thematic Mapper Plus (2000 and 2002). Pre-processing of these images included ortho-correction, radiometric correction, mosaicing of images, and calibration to a common geographic and spectral base (Australian Greenhouse Office year 2000 base: see Furby, 2002).

Environmental variables were extracted from digital maps at the geographic coordinates of all 835 study sites. To counter the possibility of these locations coinciding with sparse vegetation or bare ground, due to the natural openness of tree mallee vegetation, eight additional neighbouring locations were sampled (centre-points of surrounding 150 m pixels). These additional data points were assumed to be of the same vegetation type as the central study site. The benefits of this approach, by ensuring that environmental data for each site were accurate and representative of local conditions, outweighed potential issues associated with spatial autocorrelation in these neighbouring data points. This process resulted in a sample size of 7515 data points.

Exploratory radial bias function (RBF) neural network models (Duda et al., 2001) were used to identify environmental variables that showed a strong relationship with vegetation type, and to remove those showing high intercorrelation. Following this process, the performance of RBF and multi-layer preceptron (MLP) networks (Duda et al., 2001), both with varying numbers of neurons in the hidden layer, were compared. Examination of the error statistics and mapped output for the two best models, as identified by their confusion matrices, indicated both performed very well given the training data. The best model was then used to map vegetation type at a spatial resolution of 25 m (dictated by the resolution of the Landsat imagery).

The resultant vegetation map covered the entire region, including areas not comprising tree mallee vegetation (i.e. cleared land, other vegetation types). Consequently, a second map, describing the distribution of mallee vegetation relative to non-mallee vegetation, was created to restrict this vegetation map to only areas with tree mallee vegetation. Mallee/non-mallee vegetation was modelled using MLP neural network models, with the final model being an average of 15 alternate models. These models included information on vegetation type (mallee, non-mallee), together with a subset of the environmental variables used previously, for 27 627 data points spread across the study region. These data points were remotely identified as locations known to occur in mallee or nonmallee vegetation. All neural network classification models were created in Statistica 6.0 (StatSoft Inc., 2004).

The accuracy of the mallee/non-mallee map was assessed by workers familiar with vegetation in the study area. Based on this assessment, the threshold probability for mapping mallee vegetation relative to non-mallee vegetation was reduced from 50% to 40%. A median filter with a kernel size of five pixels was then applied to reduce speckling and smooth the output image (Gonzalez and Woods, 2002).

The original vegetation map was then clipped by the mallee/non-mallee map, producing a final vegetation map covering only areas of tree mallee vegetation.

2.5. Map validation

Independent data from two sources were used to validate the vegetation map. Vegetation type was assessed in the field, by people involved in the original floristic surveys, at a number of new sites located across all three states. In addition, geographically referenced flora records drawn from a range of sources, and held within the Victorian Flora Information System (FIS), were available for part of the mapped region (Department of Sustainability and Environment, 2004).

Field-assessed validation data were systematically collected in all vegetation types in Victoria and South Australia. Sites were sampled at 500 m intervals along tracks in two originally surveyed reserves located in the southern part of the study region. Site selection was guided by the following protocols: (a) the first and final site on each track was located at least 1 km from the external boundary of tree mallee vegetation; (b) sites were surrounded by ≥ 100 m of the same vegetation type; and (c) sites were not placed in non-mallee vegetation. Sampling continued until 50 sites had been surveyed in each mapped vegetation type. In addition, a second set of field-assessed sites distributed across New South Wales and Victoria was also available for map validation. Sites located outside the extent of mapping were discarded, resulting in 226 independent field-assessed sites for map validation.

FIS records used to validate the map were limited to those within the geographic extent of the mapping, and those considered likely to be located in tree mallee vegetation (as assessed by species' records). For the 441 sites meeting these criteria, records of all species included in the cluster analyses were extracted from the FIS database. A series of hierarchical rules, based on the SIMPER results and comparisons with floristic characteristics of sites included in the cluster analyses, were used to assign FIS sites to the mapped vegetation types. Firstly, for example, FIS sites were classified as a particular vegetation type when only those species identified by the SIMPER analysis as being particularly characteristic of that vegetation type were recorded. Rules became progressively less restrictive, in terms of the required number of characteristic species from the given vegetation type, relative to those more strongly associated with other vegetation types, until FIS sites could no longer be allocated into particular vegetation types with confidence. Using these rules, 408 FIS sites were assigned a vegetation

The use of FIS data for map validation was subject to some limitations, potentially causing map accuracy to be underestimated. First, information to assess the suitability of FIS records was rarely available (e.g. plot size, survey protocols and completeness). Second, information on site characteristics known to influence vegetation composition was lacking (e.g. soil type, topographic position, fire history). Third, vegetation types were identified by complex multivariate analyses, and defined by floristic characteristics specific to the original dataset. Assigning new records, on a case-by-case basis, to these vegetation types was prone to uncertainty. To assess the potential influence of this final limitation on validation results, the performance of rules used to assign FIS sites to vegetation types was investigated. This was done by determining how well the rule set performed when assigning vegetation type to sites of known vegetation type (i.e. those for which vegetation type was identified by the original cluster analyses). The rules were correct in 90% of cases: therefore, assigning FIS sites to vegetation types was considered reasonably accurate, but not without error.

Validation of the vegetation map involved determining the accuracy with which the neural network model predicted vegetation type for all 634 validation sites. Map accuracy was compared between validation datasets and across vegetation types. Kappa coefficients, which range in value between 0 and 1 and provide an estimate of map accuracy accounting for chance agreement between the map and validation data (Congalton, 1991), were also calculated for each dataset.

3. Results

3.1. Mallee vegetation map

The neural network classification models used to create the mallee/non-mallee map showed an average accuracy of 91% when

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Fig. 2. Distribution of three tree mallee vegetation types across the study region, mapped at a 25 m resolution. Unshaded (white) areas are non-mallee vegetation.

identifying data points known to be located within tree mallee (range of 15 models: 84–97%), and 78% when identifying nonmallee data points (71–82%). Neural network models were also successful in mapping the distribution of three vegetation types, at a resolution of 25 m, across the entire study region (Fig. 2). This approach was unable to consistently distinguish between the two vegetation types showing greatest similarity (as identified by their grouping together in the first cluster analysis): Chenopod Mallee and Shrubby Mallee.

The model used to map vegetation type was an RBF network with 88 neurons in the hidden layer. This model, which included 20 explanatory variables, correctly classified vegetation type for 79% of the 7515 data points. Prediction accuracy varied between vegetation types: 87% of data points in Triodia Mallee, 59% of those in Chenopod/Shrubby Mallee, and 90% of data points in Heathy Mallee were predicted correctly by the model.

Following clipping by the mallee/non-mallee map, the vegetation map covered 3233735 ha. Most tree mallee vegetation occurred in New South Wales (1 407 197 ha) and least in Victoria (676 371 ha). Overall, 58% of the mapped area comprised Triodia Mallee, 35% Chenopod/Shrubby Mallee, and 7% Heathy Mallee. Within the same area covered by the vegetation map, 31 different Ecological Vegetation Classes were recognised in Victoria (White et al., 2003), 19 vegetation types were mapped in New South Wales (Val, 2001), and 16 in South Australia (Department for Environment and Heritage, 2005). Comparison of state-level maps with current results identified that the association between individual vegetation types in these different maps was not strong. This indicates that simply combining state-level classifications would not produce equivalent groupings across the entire region.

3.2. Map validation

A priori predictions of expected validation results were made by combining the level of inaccuracy associated with: (a) assigning vegetation type to independent data (FIS sites only: 10%); and

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Results of validating the vegetation map with independent data from two sources. The number of validation sites assigned to Triodia Mallee (TM), Heathy Mallee (HM) and Chenopod/Shrubby Mallee (CM/SM) by the map (rows) and by expert opinion or rules (columns) are shown for field-assessed and FIS sites, respectively. Measures of user's accuracy (% mapped sites that were correct) and producer's accuracy (% known sites mapped correctly) are included for both datasets.

		'True' vegetation type				User's accuracy
		тм	HM	CM/SM	Total	
Field-assessed sites (kappa coefficient = 0.54)						
Mapped vegetation type	TM	103	13	26	142	73%
	HM	0	29	2	31	94%
	CM/SM	18	0	35	53	66%
	Total	121	42	63	226	74%
Producer's accuracy		85%	69%	56%	74%	
FIS sites (kappa coefficient = 0.31)						
Mapped vegetation type	TM	134	10	96	240	56%
	HM	4	1	4	9	11%
	CM/SM	36	0	123	159	77%
	Total	174	11	223	408	63%
Producer's accuracy		77%	9%	55%	63%	

(b) the model used to produce the vegetation map (21%). The maximum accuracy expected, therefore, for field-assessed validation sites was approximately 80%, while for FIS validation sites it was considered unlikely that results would show >70% accuracy.

The map correctly predicted vegetation type for 425 (67%) of the 634 validation sites. As expected, accuracy differed between validation datasets: 74% of field-assessed sites were mapped correctly, resulting in a kapa coefficient of 0.54, while a lower level of accuracy was identified for FIS sites (63%, kappa coefficient 0.31: Table 2). Of the 59 field-assessed sites that were mapped incorrectly, almost three-quarters (n =43) were within two pixels (<50 m) of the correct vegetation type, with the greatest mappingerror distance being 634 m.

Further examination of FIS results identified that producer's accuracy (% known sites mapped correctly) differed in relation to the rules used to assign new records to vegetation type (range: 50–85%), thus confirming that validation results were influenced by this process. Nevertheless, comparison of validation results with a priori expectations which accounted for inaccuracies associated with the map itself and the classification of FIS sites, confirmed that the vegetation map performed well when validated with independent data.

Validation results also differed between vegetation types (Table 2). Triodia Mallee had higher producer's/user's accuracy than Chenopod/Shrubby Mallee for both validation datasets. The only exception was the user's accuracy (% mapped sites that were correct) of FIS sites: Chenopod/Shrubby Mallee was mapped more accurately than Triodia Mallee for these sites. Validation results from the FIS dataset identified a poor performance for Heathy Mallee. This is likely related to the limited distribution, and therefore limited sampling, of this vegetation type in the study area (see Fuller et al., 1998) and the fact that validation sites were located in only part of the overall distribution of Heathy Mallee (Victoria). Field-assessed validation data revealed a higher mapping accuracy for Heathy Mallee (Table 2).

4. Discussion

Floristic data collected at over 800 sites distributed across three Australian states have enabled the identification and description of four distinct types of tree mallee vegetation common to the study region. Three were mapped across 104 000 km² of the broader Murray Mallee bioregion. These vegetation types were characterised by differences in the dominant canopy species, understorey assemblages and soil and topographic associations. Previous work has recognised vegetation types differentiated by similar factors. For example, vegetation types identified by Cheal et al. (1979), Fox (1990) and White et al. (2003) were all distinguished on the basis of similar understorey dominants to those described here: namely *T. scariosa*, tall non-chenopod shrubs, chenopods, and heathy shrub species.

The similarity between vegetation types identified here, and existing vegetation descriptions, verifies current results. Critically, however, while existing vegetation descriptions are broadly similar across the region, the specific communities identified and mapped in each state differ. Variation in mapping classifications can be caused by differing objectives for map production, as perceptions of land-cover types will vary between maps produced for different reasons (Fuller et al., 1998; Van Eetvelde and Antrop, 2009). This study consistently describes and maps vegetation types across all jurisdictions in the Murray Mallee, providing a more complete overview across this biogeographic region than previously available. Vegetation maps for different parts of the region, based on different classification systems, preclude such an understanding but effective conservation management at the scale of entire ecological systems depends on it (Pressey et al., 2000).

Conversely, a disadvantage associated with mapping vegetation over broad geographic extents is the loss of fine-scale differentiation (Smith and Wyatt, 2007). The mapping of fewer vegetation types here than in existing state-level maps exemplifies this unavoidable loss of detail. However, the current map forms a uniform vegetation description that can be supplemented by existing maps if finer classification details are required.

4.1. Map accuracy

When using independent data not subject to internal error (i.e. field-assessed validation sites), a kappa accuracy statistic of 0.54 was achieved for the vegetation map. Other validations of broad-scale maps with independent field data have identified higher levels of map accuracy (between 69% and 88%: Bach et al., 2006; Cunningham et al., 2009), and Bach et al. (2006) similarly found that accuracy differed between mapped classes. To our knowl-edge, existing vegetation maps for the study region have not been objectively validated with independent data. Assessment of the accuracy of the current map, in comparison to alternative information sources, is therefore difficult.

Large-scale, empirical datasets have been used in both the production and validation of vegetation maps (Fuller et al., 1998; Marvin et al., 2009). Such datasets, like the FIS database used here, provide a valuable and cost-efficient source of independent data for map validation. However, as noted by Fuller et al. (1998),

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there is potential for subjectivity to affect the classification of these data into mapped classes. In addition, details important for assessing the appropriateness of such data for map validation, such as information on survey techniques, may be lacking. These issues highlight a consideration applicable to map validation more broadly: the validation process necessarily, but not always correctly, assumes that independent or reference data are accurate (Congalton, 1991). If this assumption is invalid, map accuracy may be underestimated. Furthermore, care must be taken when interpreting potential validation datasets, as no single dataset provides a universally appropriate standard against which to assess the accuracy of all maps (Fuller et al., 1998).

4.2. Applications to land-use planning and management

The framework employed here for producing consistent broadscale vegetation maps has many potential uses for land-use planning and conservation management. The vegetation map provides baseline information against which to assess temporal change to the amount and distribution of tree mallee vegetation. Understanding the rate and pattern of change in vegetation cover is important for future land management and policy development (Başkent and Kadioğullari, 2007). To accurately provide such understanding, maps must be based on data collected at the same time across their full spatial extent (e.g. Bach et al., 2006).

The map describes the extent and type of mallee vegetation outside the reserve system. Such information can be used to guide reservation priorities and ongoing conservation actions (Margules and Pressey, 2000) by identifying key patches of vegetation that connect existing reserves, or areas where connectivity could be enhanced (see Taylor et al., 1993). Establishing monitoring programs to assess vegetation condition, an important characteristic that is infrequently incorporated into mapping, also requires comprehensive baseline information on vegetation cover (Thackway et al., 2007).

In conjunction with an understanding of fire behaviour and flammability in mallee vegetation communities (Bradstock and Cohn, 2002), this map can aid fire management planning. Management of disturbance events, such as fire, that threaten human safety across jurisdictional boundaries is compromised if information used in planning is not consistent across the potential extent of the disturbance.

Lastly, the map provides a basis for investigating patterns in the distribution of fauna. A number of critically endangered, threatened, and vulnerable species, such as the Black-eared Miner *Manorina melanotis*, Malleefowl *Leipoa ocellata*, Common Dunnart *Sminthopsis murina* and Millewa Skink *Hemiergis millewae* (Clarke, 2005; Bennett et al., 2007; Nimmo et al., 2008) occur in the Murray Mallee. Vegetation maps help identify important habitat for these species, and thus guide management for their conservation.

5. Conclusion

The framework developed in this study provides a relatively simple approach to describing and mapping vegetation consistently, and at high resolution, across broad spatial extents. The use of independent validation data has allowed for a measure of map accuracy, and our use of two datasets in this process has provided insight into the relative value of pre-existing data for this purpose. This approach has a range of potential uses in land-use planning and conservation management at both local and regional scales. It is also applicable to other regions facing similar challenges associated with the integration of vegetation data across jurisdictional boundaries.

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Appendix A. Perennial flora species included in the cluster analyses, and the number of sites at which they were recorded

Asteraceae

Boraginaceae Halgania cyanea Brassicaceae Lepidium leptopetalum Caesalpiniaceae Senna artemisioides subsp. coriacea Senna artemisioides subsp. filifolia Senna artemisioides subsp. petiolaris	19 12 143 26 125
Brassicaceae Lepidium leptopetalum Caesalpiniaceae Senna artemisioides subsp. coriacea Senna artemisioides subsp. filifolia Senna artemisioides subsp. petiolaris	125
Caesalpiniaceae Senna artemisioides subsp. corlacea Senna artemisioides subsp. filifolia Senna artemisioides subsp. petiolaris	40
Senna artemisioides subsp. zygophylla	76 108 108 59
Casuarinaceae Allocasuarina pusilla	12
Chenopodiaceae Atriplex stipitata Chenopodium curvispicatum Chenopodium desertorum subsp. desertorum Enchylaena tomentosa var. tomentosa Maireana appressa Maireana georgei Maireana georgei Maireana pentatropis Maireana pentatropis Maireana sp. Maireana sdifolla Maireana sdifolla Maireana sp. Rhagodia spinescens Sclerolaena dicantha Sclerolaena obliquicuspis Sclerolaena parviflora	56 19 38 177 15 171 34 33 129 97 38 19 42 116 18 330 25 133
Cupressaceae Callitris verrucosa Callitris sp.	108 13

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Dilleniaceae Hibbertia riparia Hibbertia virgata	50 73
Epacridaceae Astroloma conostephioides Brachyloma ericoides Leucopogon cordifolius	12 13 18
Euphorbiaceae Bertya tasmanica subsp. vestita Beyeria opaca	33 207
Fabaceae Aotus subspinescens Bossiaea walkeri Daviesia benthamii subsp. acanthoclona Eutaxia microphylla Pultenaea densifolia Templetonia sulcata	61 21 41 33 14 19
Goodeniaceae Scaevola spinescens	38
Gyrostemonaceae Codonocarpus cotinifolius	27
Lamiaceae Prostanthera aspalathoides Prostanthera serpyllifolia subsp. microphylla Westringia rigida	13 44 148
Leguminosae Dillwynia uncinata	18
Mimosaceae Acacia acanthoclada subsp. acanthoclada Acacia barchybotrya Acacia burkittii Acacia colletioides Acacia ligulata Acacia rigens Acacia sclerophylla var. sclerophylla Acacia wihelmiana	13 26 63 150 68 172 98 177
Myoporaceae Eremophila crassifolia Eremophila glabra Eremophila glabra subsp. glabra Eremophila scoparia Eremophila scoparia Eremophila scoparia Eremophila sturtii Myoporum platycarpum	69 241 19 25 56 28 170
Myrtaceae Babingtonia behrii Backea crassifolia Calytrix tetragona Eucalyptus costata subsp. murrayana Eucalyptus costata subsp. murrayana Eucalyptus dumosa Eucalyptus dumosa Eucalyptus dumosa Eucalyptus gracilis Eucalyptus gracilis Eucalyptus oleosa subsp. oleosa Eucalyptus socialis Eucalyptus socialis Eucalyptus so. Leptospermum coriaceum Melaleuca acuminata subsp. lanceolata Melaleuca uncinata	47 73 38 49 252 18 505 240 316 231 463 514 145 27 103 33
Pittosporaceae Pittosporum angustifolium	21
Poaceae Triodia scariosa	591
Proteaceae Grevillea huegelii Grevillea ilicifolia subsp. ilicifolia Grevillea pterosperma Hakea leucoptera subsp. leucoptera	136 15 46 44
Ranunculaceae Clematis microphylla	11

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Rhamnaceae Cryptandra tomentosa Cryptandra tomentosa complex Spyridium subochreatum var. subochreatum Stenanthemum leucophractum	24 45 40 13
Rutaceae Boronia coerulescens subsp. coerulescens Phebalium bullatum	15 66
Santalaceae Exocarpos aphyllus Exocarpos sparteus	15 28
Sapindaceae Alectryon oleifolius subsp. canescens Dodonaea bursariifolia Dodonaea viscosa subsp. angustissima	17 127 127
Violaceae Hybanthus floribundus subsp. floribundus	14
Xanthorrhoeaceae Lomandra leucocephala subsp. robusta Lomandra sp.	78 66
Zygophyllaceae Nitraria billardierei Zygophyllum apiculatum Zygophyllum aurantiacum subsp. aurantiacum	15 137 120

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Appendix 3

Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire

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Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire

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Summary

1. Managing fire to achieve hazard reduction while providing for biodiversity conservation is complex in fire-prone regions. This challenge is exacerbated by limited understanding of post-fire changes in habitat and fuel attributes over time-scales commensurate with their development, and a paucity of empirical research integrating the effects of fire on these attributes.

2. We used a 110-year post-fire chronosequence to investigate temporal development in habitat resources used by fauna, and fuels for fire in semi-arid Mallee vegetation, south-eastern Australia. Fire-history mapping previously limited investigation to 35 years post-fire. The patterns of temporal change over 110 years for 13 variables, representing key attributes of habitat and fuel, were explored using nonlinear mixed models and data from 549 sites.

3. Most habitat and fuel attributes exhibited changes in abundance and rate of development over extended periods, emphasizing the importance of documenting post-fire dynamics over long time-frames. Further, developmental patterns were mostly nonlinear, indicating that a shorter temporal perspective (e.g. 20–30 years post-fire) may obscure, or provide an inaccurate understanding of, long-term changes.

4. There were striking differences in the post-fire dynamics of some habitat and fuel attributes. Leaf litter and spinifex grass *Triodia scariosa*, which function as both habitat and fuel, increased rapidly after fire followed by a plateau or slow decline after 20–30 years. In contrast, live tree stems were not predicted to develop hollows until 40 years, after which time the density of live hollow-bearing stems, an important habitat feature, increased steadily.

5. Synthesis and applications. Fire affects the development and abundance of resources over substantially longer periods than can be examined using fire-mapping based on satellite imagery. Our results demonstrate that post-fire changes in mallee vegetation influence fire hazard and faunal habitat in different ways. Critically, the cover/abundance of most primary fuel sources did not increase substantially beyond around 30 years post-fire; whereas important habitat attributes changed in ways that affect faunal occurrence for over a century. Fire management must explicitly acknowledge the potential for fire to affect fauna and fuel differently, and for these effects to operate over time-frames that may extend well beyond current understanding.

Key-words: Australia, fire chronosequence, generalized additive mixed model, mallee vegetation, prescribed fire, succession, wildfire

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Introduction

Fire is a natural process that shapes the structure and function of ecosystems across the globe (Bowman et al. 2009). Wildfire can also threaten human life and assets in fire-prone regions (Bradstock 2008). For both reasons, considerable attention and resources are invested in fire management, with prescribed fire commonly being used to reduce the risk of uncontrollable wildfires (Fernandes & Botelho 2003). Fire management for hazard reduction, however, may not be compatible with conservation objectives (Morrison et al. 1996). The potential for prescribed fire to negatively affect biodiversity is increased by inadequate understanding of biotic responses to fire (Clarke 2008; Driscoll et al. 2010) and strong public pressure to minimize fire hazard (Stephens & Ruth 2005). Successfully balancing fuel reduction and biodiversity considerations is a challenge faced by managers in fire-prone systems throughout the world (James & M'Closkey 2003; Ucitel, Christian & Graham 2003).

A key issue in addressing the potentially competing demands of fuel reduction and biodiversity conservation is the length of time over which successional processes operate, compared with the short time-period over which changes in fuels or biota have often been documented. Techniques such as dendrochronology and radiocarbon dating have allowed examination of post-fire dynamics across extended time-frames (e.g. 230 years: Pare & Bergeron 1995; 2355 years: Lecomte *et al.* 2006), but more commonly research is constrained to periods of known fire-history (e.g. <40 years: Sah *et al.* 2006; Driscoll & Henderson 2008). Temporal mismatches between decades or centuries of successional change (Lecomte *et al.* 2006; Mack *et al.* 2008), and the much shorter period over which changes in biota frequently have been studied, hamper effective fire management.

A second issue concerns understanding of post-fire dynamics in fuel sources and habitat attributes used by fauna for foraging, refuge or breeding. Empirical research into fire-fauna relationships has largely been undertaken in isolation from studies investigating the association between fire and fuel (Ucitel, Christian & Graham 2003). Thus, there are few explicit guidelines for managers attempting to address both considerations.

Post-fire responses of fauna are often interpreted using a framework of secondary succession (Friend 1993; Fox, Taylor & Thompson 2003; Torre & Diaz 2004). This approach is based on the understanding that vegetation succession following fire drives faunal occurrence via the differential availability of resources along post-fire temporal gradients (Fox 1982). Other factors may also influence faunal responses to fire, such as altered biotic interactions (Higgs & Fox 1993), abiotic conditions (Letnic *et al.* 2004), and fire frequency/scale (Bradstock *et al.* 2005). However, associations between faunal occurrence and habitat attributes, and the strength of post-fire succession in many vegetation types (Hanes 1971; Vandvik *et al.* 2005), means that understanding fire–fauna relationships will benefit from knowledge of changes in habitat resources over time-frames commensurate with successional processes.

Management of fuel-fire relationships has been informed by the positive associations between fuel availability, wildfire severity, and time-since-fire (Hanes 1971; Sah *et al.* 2006). Thus, the use of prescribed fire is often guided by fuel characteristics, and understanding temporal patterns in fuel accumulation (Fernandes & Botelho 2003). For example, estimates of fuel loads are widely used to measure fire hazard in parts of southern Australia (McCarthy, Tolhurst & Chatto 1999). Such estimates can identify maximum tolerable fuel loads (Burrows 2008) and, when combined with predictions of fuel accumulation, suggest optimum inter-fire intervals for hazard reduction (Department of Sustainability and Environment 2008). Documenting temporal patterns in fuel development is critical if such management approaches are to effectively reduce wildfire hazard (Sah *et al.* 2006).

Our study system, the Murray Mallee region in south-eastern Australia, is strongly influenced by fire. Large wildfires (c. 100 000 ha) typically occur somewhere in the region on a bi-decadal basis (Noble & Vines 1993), and prescribed fire is used to minimize the risk of wildfires burning extensive areas (Sandell et al. 2006). Fire also affects the status of native fauna (Brown, Clarke & Clarke 2009; Kelly et al. 2010). Current fire-history mapping based on satellite imagery restricts investigation of post-fire responses in habitat and fuel to a 35-year period. We use empirical data and age predictions for sites of previously unknown fire-age (Clarke et al. 2010) to investigate post-fire dynamics over a chronosequence extending to 110 years. We address two objectives: (i) to document post-fire resource dynamics across a 110-year chronosequence, and establish whether extending the time-scale under examination alters the resultant understanding of post-fire change; and (ii) to explicitly compare post-fire trajectories of habitat attributes and fuel sources.

Materials and methods

STUDY AREA

The study area encompasses ~100 000 km² of the Murray Mallee, a low-lying region covering parts of Victoria, South Australia and New South Wales, Australia (see Fig. S1, Supporting Information). The climate is semi-arid (220–330 mm rainfall/year) with high summer temperatures (mean daily maxima \geq 32 °C) and mild winters (mean daily maxima 16 °C) (data supplied by the Australian Bureau of Meteorology). The region is characterized by extensive dune/swale systems that reflect underlying variation in soil characteristics and moisture availability (Land Conservation Council 1987).

The current distribution of native vegetation has been strongly influenced by agriculture, primarily cereal cropping and stock grazing: remnant native vegetation occurs predominantly on less fertile soils of the dunefields (Land Conservation Council 1987). The most common vegetation, tree mallee, comprises short (typically <5 m), multi-stemmed ('mallee') *Eucalyptus* trees above an understorey of shrubs and perennial and ephemeral grasses. An important feature of this vegetation is the ability of mallee eucalypts to regenerate from underground lignotubers after fire by coppicing multiple new stems (Gill 1981).

Fire is a dominant process in the study area. Tree mallee vegetation is highly flammable and the reproductive strategies of many plant

species are strongly tied to fire events (Bradstock & Cohn 2002). Key components of perennial fuels include the hummock-forming grass *Triodia scariosa* N.T. Burbidge, leaf litter accumulated beneath trees, and decorticating ribbons of bark (Bradstock & Cohn 2002). After large rainfall events, ephemeral grasses also provide a critical fuel source that connects the otherwise patchily-distributed perennial fuels (Noble & Vines 1993). Wildfires are actively suppressed in much of the region and prescribed fire is used predominantly to reduce fire hazard (Sandell *et al.* 2006).

STUDY DESIGN

This study is part of a project examining landscape-level responses of multiple taxa to the properties of fire mosaics. Consequently, the 549 sites included here were grouped in 26 clusters, each representing an individual landscape unit of 12-6 km² (Fig. S1). The mean distance between study landscapes was 130 km (range: 6–218 km) and all were located within conservation reserves.

Previous work identified and mapped three broad types of tree mallee vegetation across the region (Haslem et al. 2010). Here, we focus on the two most extensive types: Triodia Mallee (TM) and Chenopod/Shrubby Mallee (hereafter Chenopod Mallee, CM). These communities differ on the basis of canopy dominants, understorey composition, soil and topography. Triodia Mallee is characterized by an increased abundance of *T. scariosa*, an important habitat component for fauna (Bennett, Lumsden & Menkhorst 2006) and a key source of fuel (Noble, Smith & Leslie 1980). The understorey of Chenopod Mallee comprises a diversity of low chenopod shrubs, many of which have low flammability (Pausas & Bradstock 2007).

We employed a space-for-time approach to investigate post-fire temporal dynamics, with sites of differing fire-ages representing a post-fire chronosequence. Fire in tree mallee vegetation removes both the canopy and understorey (Caughley 1985), resetting the system to 'year zero'. Importantly, for this reason both wildfires and prescribed fires in this system are commonly 'stand-replacing' and have similar effects on post-fire succession. To ensure results were not influenced by fire intensity, sites considered to have been burnt only partially/patchily in the most recent fire, based on the occurrence of multiple cohorts of eucalypt stems, were excluded from analyses.

DATA COLLECTION

A range of vegetation characteristics was assessed at each site. The percentage cover of different types of ground cover (bare ground, cryptogamic crust, leaf litter, plant matter, logs), and the depth of leaf litter, were recorded at 1-m intervals along a 50-m transect (n = 50 sample points). Vegetation structure was assessed at each sample point by recording the number of vegetation contacts with a vertical ranging pole in four height strata (<0.5 m, 0.5-1 m, 1-2 m, >2 m). Quadrats were established to record: (i) the characteristics of *Eucalyptus* trees and stems (50 × 4-m quadrat) including canopy height, number of trees, number stems/tree, stems with hollows, amount of decorticating bark/tree; and (ii) the number of logs (50 × 10-m quadrat). Vegetation data were collected between June and August 2007.

We selected 13 variables to represent habitat attributes for fauna, and fuel sources for fire (Table 1). These variables include measures of the availability of specific habitat or fuel resources (e.g. *T. scariosa*, leaf litter, tree hollows), and characteristics of habitat structure and fuel distribution (e.g. vegetation cover in different height strata). They are referred to as 'habitat' when viewed from the perspective of fauna, and 'fuel' when considered in relation to fire; many constitute both. For example, *Triodia* hummocks and leaf litter are used for foraging

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and refuge by many of the 55 reptile species occurring in the region; but also are a primary source of surface fuels that sustain fires. Ephemeral grasses, associated with large fires (Noble, Smith & Leslie 1980), were not investigated as their occurrence is more strongly influenced by rainfall than time-since-fire.

The fire-age of study sites was determined using two methods. Landsat satellite imagery from 15 individual years (1972-2007), combined with local knowledge, was used to identify the exact year of the most recent fire for sites burnt since 1972. For sites burnt before 1972, the lack of historical records and satellite imagery necessitated an alternative approach. We used linear regression models to quantify the relationship between tree age (indicated by fire-year) and mean stem diameter for each eucalypt species at sites of known fire-year (Clarke et al. 2010). These models were then used to predict tree age (thus infer fire-year) for sites where fire-year was unknown but stem diameter data were available. Validation of these models with independent data from new sites revealed a highly significant correlation between known and predicted tree ages (r = 0.71, P < 0.001, n = 88) (Clarke *et al.* 2010) confirming the reliability of this approach. The fire-age of sites was calculated as the difference between actual/predicted fire-year and 2007 (when vegetation data were collected). Sites with a predicted fire-age >110 years were excluded from analyses due to low sample sizes.

Table 2 shows the distribution of sites across the 110-year fire chronosequence, and two vegetation types, investigated. The lack of sites aged between 11 and 20 years reflects reduced fire activity between 1987 and 1996.

STATISTICAL ANALYSES

We used generalized additive mixed models (GAMMs: Wood 2006; Zuur et al. 2009) to investigate patterns in the development of each habitat/fuel attribute across the post-fire chronosequence. Three factors contributed to the selection of this approach. First, inspection of raw data showed that nonlinear models were appropriate. Generalized additive models (GAMs) are nonparametric regression models that use smoothing functions to fit nonlinear response curves (Wood 2006). Secondly, the clustered distribution of sites (grouped in landscape units) suggested a mixed model approach. Mixed models are recommended when data are structured by some factor (here, landscape unit) that introduces systematic variation of potential influence over the relationship between predictor and response variables (Zuur et al. 2009). Lastly, differences in the structure, floristic composition and abiotic associations of Triodia Mallee and Chenopod Mallee indicated that time-since-fire responses might differ between vegetation types. To account for this, we used 'variable coefficient' GAMMs which produce different smoothed terms for each level of a categorical variable (Wood 2006; Zuur et al. 2009).

Models were fitted with 'landscape' as a random effect and a separate smoothed term for time-since-fire in each vegetation type. The amount of smoothing used to model time-since-fire was selected internally during the model-fitting process (Wood 2004). Outliers, as identified by residual plots, were removed from final models (see Table 3). Models were evaluated using a measure of model fit (deviance explained) and cross-validation.

Sevenfold cross-validations were used to assess the stability and predictive accuracy of models (Pearce & Ferrier 2000). This involved randomly dividing study landscapes into seven groups ('folds'), fitting a model to data from six folds, then using it to predict to data from the seventh fold. This process continued until all sites had predictions derived from independent data. The mean correlation (and associated

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Table 1. Variables used to represent habitat and fuel attributes	n tree mallee vegetation, and their	roles in providing these resources
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		Role of resource		
Variable	Description	Habitat ^b	Fuel ^c	Abbreviation
Specific resource types Triodia scariosa	Percent cover of <i>Triodia scariosa</i> (<0.5 m high)	F/R/B	S,f	Triodia
Leaf litter	Mean depth (cm) of leaf litter ≥1 cm deep	F/R/B	S,f	Litter
Overall ground fuel	Combined percent cover of leaf litter (\geq 1 cm deep), plant matter and logs	F/R	S,v	GroundFuel
Logs	Density of logs >3 cm diameter and >50 cm length (no./ha)	F/R/B	S,c	Logs
Decorticating bark	Mean ordinal measure across trees, where: (i) no hanging bark (> 30 cm in length); (ii) hanging bark present < 50% stem surface area; (iii) hanging bark present > 50% stem surface area	F/R	L,c	Bark
Tree hollows – live stems	Estimated density of live hollow-bearing tree stems (no./ha)	R/B	n/a	Hollows(Live)
Tree hollows – dead stems	Estimated density of dead hollow-bearing tree stems (no./ha)	R/B	n/a	Hollows(Dead)
Tree hollows – proportion stems	Overall proportion of tree stems containing a tree hollow	R/B	n/a	HollowProportion
Habitat structure/fuel dis	tribution			
Tree stems	Estimated density of tree stems (no./ha)	Collectively represent habitat structure rather than specific habitat resources	Represents coarse standing fuel density	StemDensity
Low vegetation cover	Percent cover of plant matter (dead or alive) < 0.5 m high		S,v	LowCover
Mid vegetation cover	Percent cover of plant matter (dead or alive) 0.5–2 m high		U,v	MidCover
Canopy vegetation cover	Percent cover of plant matter (dead or alive) > 2 m high		C,v	CanopyCover
Canopy height ^d	Canopy height (m) determined using a range finder		Represents canopy fuel height	CanopyHeight

v.2.8.0 (R Development Core Team 2008).

^a Information collated from cited references. ^b F = foraging habitat, R = refuge/shelter habitat, B = breeding habitat. ^c S = surface fuel, U = understorey fuel, L = ladder fuel, C = canopy fuel, f = fine fuel (<3 cm), c = coarse fuel (>3 cm), v = variable fuel size.

 $^{\rm d}$ Data available for a reduced number of sites (see Table 3).

standard error) between observed and predicted values, averaged across folds, was used to evaluate models. The median of three crossvalidation trials is reported. Regression modelling and cross-validation were undertaken using

the mgcv package v.1.4-1 (Wood 2004) and source scripts (also used

to calculate model deviance: Elith, Leathwick & Hastie 2008) in R

Results

All habitat/fuel attributes except the density of dead hollowbearing stems, Hollows(Dead), showed a significant relationship with time-since-fire (Table 3). Two attributes, Triodia and MidCover, exhibited significant post-fire responses in only one

Table 2. Distribution of 549 study sites across the 110-year post-fire chronosequence. Years-since-fire has been split into 10-year intervals for Triodia Mallee (TM) and Chenopod Mallee (CM) vegetation

	Number of sit	es
Years-since-fire	TM	СМ
1-10	89	12
11-20	0	0
21-30	50	6
31-40	124	51
41-50	15	22
51-60	28	30
61-70	22	25
71-80	13	12
81-90	15	10
91-100	8	7
101-110	5	5
Total	369	180

Table 3. Results of models describing the relationship between habitat/fuel attributes and time-since-fire. Details of the smoothed terms for time-since-fire in Triodia Mallee (TM) and Chenopod Mallee (CM) are shown for each attribute, together with the number of sites sampled in each

H-biase (Grad	Variation	C:+	Smoothed term for time-since-fire		
attribute	type	(no.)	edf ^a	F	Р
Triodia	TM	369	5.33	15.55	< 0.001
	CM	180	1.00	0.12	0.824
Litter	TM^{b}	367	5.26	17.11	< 0.001
	CM ^b	178	3.27	4 ·85	0.001
GroundFuel	TM	369	6.06	26.07	< 0.001
	CM	180	3.63	6.00	< 0.001
Logs	TM ^b	368	6.71	3.72	0.001
	CM	180	1.00	4.94	0.014
Bark	TM	368	1.83	54.04	< 0.001
	CM	180	1.00	29.06	< 0.001
Hollows(Live)	TM	369	3.78	12.53	< 0.001
	CM	180	2.70	11.22	< 0.001
Hollows(Dead)	TM	369	1.00	0.27	0.696
	CM	180	1.00	2.22	0.124
HollowProportion	TM	369	3.03	16.85	< 0.001
	CM	180	1.00	24.62	< 0.001
StemDensity	TM	369	4.39	21.26	< 0.001
	CM ^b	179	4.74	19.37	< 0.001
LowCover	TM	369	5.66	4.54	< 0.001
	CM	180	1.00	4·18	0.026
MidCover	TM	369	6.68	7.07	< 0.001
	CM	180	1.00	0.10	0.853
CanopyCover	TM	369	5.59	32.19	< 0.001
	CM	180	3.08	5.87	< 0.001
CanopyHeight	TM	241	4.48	98·91	< 0.001
	СМ	130	3.84	33.61	< 0.001

^aEstimated degrees of freedom.

^bOne outlier removed (large residual value).

vegetation type: Triodia Mallee. Post-fire dynamics did not differ markedly between vegetation types for most attributes, as shown by overlapping confidence intervals of predictions (Fig. 1).

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Most attributes exhibited nonlinear patterns of change following fire (Fig. 1); the trend and rate of their development were not consistent across the 110-year post-fire chronosequence. For example, tree stem density increased relatively rapidly for the first 20 years following fire and then declined; rapidly at first and then at a slower rate after around 50 years post-fire (Fig. 1). Linear responses to time-since-fire were observed only in Chenopod Mallee: the variables HollowProportion and Bark increased, while Logs and LowCover decreased, as time-since-fire increased (Fig. 1).

No attribute had reached a stable state by 35 years-sincefire, the current extent of fire-history records (Fig. 1). The rate of development in some attributes did decrease after 35 years (e.g. GroundFuel [CM], CanopyCover [TM]) but few showed no further change after this time. In contrast, many attributes still exhibited change at 110-years post-fire (e.g. HollowProportion, Bark, Triodia [TM], Litter [TM]).

All attributes, except Bark, showed a marked change in the rate of development at around 20–30 years post-fire (Fig. 1). Developmental shifts took one of three forms: (i) rapid increase followed by slower increase or plateau (Litter, GroundFuel, LowCover, CanopyCover, CanopyHeight); (ii) rapid increase followed by decline (Triodia, Logs, StemDensity, MidCover), or (iii) minimal change followed by increase (Hollows(Live), HollowProportion).

Both methods used to evaluate models, cross-validation and model fit, returned similar results (Fig. 2). CanopyHeight, Triodia and CanopyCover showed the strongest relationship with time-since-fire, and these models had relatively high predictive accuracy and stability. Time-since-fire explained comparatively less variation (<15%) in MidCover and Logs, and the mean cross-validation correlation for these attributes was low (<0.3). Between 24% and 37% of variation in the remaining eight attributes was related to time-since-fire, with cross-validation indicating a moderate performance of models explaining these relationships (Fig. 2).

To further examine temporal development in tree hollows, the mean proportion of hollow-bearing stems that were alive and dead was compared for each 10-year post-fire interval (Fig. 3). On average, over 80% of all hollow-bearing stems were dead in fire-age periods \leq 40 years-since-fire. Parity in the proportion of live and dead stems containing hollows was not reached until 60 years since last burn.

Discussion

Most habitat and fuel attributes investigated here showed a significant response to time-since-fire, emphasizing the influence of fire on the temporal availability of resources used by fauna, and fuel accumulation patterns. Time-since-fire had a stronger effect on some attributes than others: over half the variation in the cover of the hummock grass *Triodia scariosa* was attributed to the influence of time-since-fire; whereas it explained only 10% of variation in log density. Many factors other than timesince-fire affect the abundance and development of these resources. For example, other potential influences on log

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Fig. 1. Predicted post-fire dynamics in habitat/fuel attributes across a 110-year time-frame. Predicted trends and their 95% confidence intervals are shown for Triodia Mallee (black) and Chenopod Mallee (grey). Vertical lines indicate the extent of temporal understanding based on fire-history records. See Table 1 for Y-axis measurement unit.



Fig. 2. Measures used in model evaluation: (a) percentage deviance explained (crosses); (b) mean cross-validation correlation (squares, including standard error bars).

density include inter-fire interval and termite activity (Whit-ford, Ludwig & Noble 1992).

LONG-TERM RESOURCE DYNAMICS FOLLOWING FIRE

Fire-age predictions for sites of previously unknown age (Clarke *et al.* 2010) allowed us to investigate post-fire resource dynamics over a chronosequence three times that provided by fire-history mapping. Extending the chronosequence provided a greater understanding of post-fire changes. First, it highlighted that different resources develop and change in abundance over different time-scales. For example, leaf litter depth and the cover of *Triodia* hummocks increased rapidly post-fire, reaching a maximum within 20–30 years (Fig. 1). Other

attributes displayed a much longer process of development: canopy height reached an asymptote at around 60 years, while the proportion of tree stems with hollows, and the abundance of decorticating bark, continued to increase for over a century (Fig. 1). Such variation in the temporal scale of resource development makes identifying inter-fire intervals that are appropriate for all management objectives difficult.

Secondly, it revealed how attributes change in abundance over long time-frames. The density of fallen timber, for example, varies through time. In Triodia Mallee vegetation, it peaks in the first 20 years post-fire as dead stems collapse, declines over the subsequent 20 years as these stems decay, and gradually increases from 50 to 100 years post-fire as the next cohort of maturing trees shed limbs. The nonlinearity of long-term trends identified here, and in other systems (e.g. Pare & Bergeron 1995; Hall, Burke & Hobbs 2006), has important implications. It suggests that reduced temporal understanding may lead to an inaccurate interpretation of post-fire dynamics. Trends observed over the first 35 years of the chronosequence (the limit of known fire-history) were not indicative of patterns observed in following decades for most attributes. This may have repercussions if feedback mechanisms govern the relationship between vegetation characteristics and fire (e.g. Bradstock 1989a), as management based on shorter-term understanding may favour some species and communities at the expense of others.

TEMPORAL DEVELOPMENT OF HABITAT AND FUEL ATTRIBUTES

The relatively rapid increase in the cover of *Triodia* hummocks and the depth of litter layers following fire (Fig. 1) has implications for fauna, as well as fuel accumulation. Mallee vegetation



aged across sites in time-since-fire intervals of 10 years. Data for Triodia Mallee and Chenopod Mallee have been pooled; mean numbers of hollow-bearing stems/tree are shown for sites in each interval.

Fig. 3. Proportion of hollow-bearing stems

that were dead (black) and alive (grey), aver-

may be suitable for Triodia-associated reptiles, such as southern mallee ctenotus Ctenotus atlas, within six years post-fire (Caughley 1985), while at least 15 years is required before vegetation is suitable for the Triodia-dependent mallee emu-wren Stipiturus mallee (Brown, Clarke & Clarke 2009). In terms of its development as a fuel source, it takes around 15 years before Triodia hummocks carry fire (Noble & Vines 1993). In contrast, leaf litter often accumulates rapidly to flammable levels, sometimes within five years (Raison, Woods & Khanna 1983). It takes longer for litter layers to provide adequate habitat for the litter-nesting malleefowl Leiopoa ocellata, which exhibits highest breeding-density 60 years post-fire (Benshemesh 1989); and litter-dependent reptiles, including Boulenger's skink Morethia boulengeri Ogilby, which are most likely to occur 100 years post-fire (D. Nimmo unpublished data). However, strong fauna-habitat associations do not always translate into predictable fauna-fire relationships (Driscoll & Henderson 2008). Nonetheless, variation in faunal responses to time-since-fire (see also Briani et al. 2004) highlights the complexity of managing fire for biodiversity conservation, even before hazard reduction imperatives are considered.

The slow development of some resources over long periods also has implications for the occurrence of fauna, and the provision of fuel sources. Recently burnt areas are unlikely to provide sufficient decorticating bark for species that use this resource, such as the endangered black-eared miner Manorina melanotis which forages amongst bark ribbons (Woinarski 1999). As a fuel resource, hanging bark will likewise have greater influence on fire behaviour in older tree mallee vegetation. Dead trees present similar challenges in the USA, where park management often involves the removal of this fuel type, yet dead trees provide important microhabitats used by many lizard species for shelter, foraging and courting (James & M'Closkey 2003). Species that depend on tree hollows, such as the hollow-nesting striated pardalote Pardalotus striatus (Woinarski 1999), are unlikely to find tree mallee suitable for all their requirements until it is at least 40 years old (Fig. 1). It will take many more decades (>100 years) before live eucalypt stems are of a diameter suitable for large hollow-nesting species

like Major Mitchell's cockatoo *Cacatua leadbeateri* (Clarke 2005). Recurrent fires within 40 years will result in hollows being provided predominately by dead stems (Fig. 3) which are more susceptible to fire. While fire may create hollows or increase their rate of development (Inions, Tanton & Davey 1989), our results suggest it will not markedly increase hollow availability in mallee vegetation, especially in the long-term. The occurrence of hollow-bearing stems was proportionally lowest in early post-fire years, and the density of dead hollow-bearing stems was not related to time-since-fire.

The identification of habitat resources that develop over many decades, and the documentation of associated developmental patterns, can inform fire management by identifying minimum and maximum fire intervals for fauna, as undertaken using plant species attributes (e.g. age at first seed set, longevity: Noble & Slatyer 1980). Management based primarily on fire intervals derived from plant attributes will not be adequate for the provision of all faunal requirements, due to the extended time-frames over which some habitat resources develop (Clarke 2008).

Fuel continuity plays an important role in influencing wildfire behaviour (Van Wilgen, Lemaitre & Kruger 1985). The continuity of most primary fuels in tree mallee vegetation does not increase substantially beyond around 30 years since fire. After this time, there is a greater distance between surface and canopy fuels, fewer eucalypt stems (coarse standing fuels), and a reduced cover of understorey fuel. The 'opening-up' of vegetation as time-since-fire increases has been observed in this and other systems (Hanes 1971; Clarke, Boulton & Clarke 2005). Nonetheless, there is strong potential for bark to contribute to spotting behaviour in fires (Bradstock & Cohn 2002). Bark continues to accumulate on trees after 30 years post-fire, and may increase fuel continuity and fire-spread in older mallee vegetation.

Post-fire changes in vegetation structure and complexity also have implications for faunal habitats and assemblages (Catling, Coops & Burt 2001; Fox, Taylor & Thompson 2003). For example, the composition of bird communities in tree mallee vegetation aged between 10–30 years differs from

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communities occupying older vegetation with a sparser understorey and taller canopy (Woinarski 1999; S. Watson, unpublished data). Patterns of vegetation succession represent a sequence of habitats which benefit different species; hence, descriptions of post-fire change in habitat structure do not provide clear guidance for ecological fire management unless fire plans target particular species (e.g. MacHunter, Menkhorst & Loyn 2009).

FURTHER IMPLICATIONS FOR FIRE MANAGEMENT

Our results demonstrate that the temporal scale of investigation influences the perception of post-fire resource dynamics. Critically, extension of the chronosequence alters understanding of fire-fauna and fuel-fire relationships in different ways, such that management recommendations derived from shorter (<30 years) and longer (110 years) temporal scales may differ. Results from the longer, 110-year chronosequence indicate greater scope for integrating management for conservation and hazard reduction objectives. Fuel quantity and continuity increased rapidly in early post-fire years, as previously documented in this (Bradstock 1989b; Noble & Vines 1993) and other systems (Raison, Woods & Khanna 1983; Sah et al. 2006). However, the longer perspective revealed that most primary sources of fuel did not increase substantially after around 30 years-since-last burn, suggesting a potential plateau in fuel-related fire hazard. In contrast, a short-term perspective precludes appreciation of the importance of the long-term development of some habitat resources (e.g. mature canopy layer, tree hollows) and ongoing changes in vegetation structure and complexity. In combination, these insights suggest a reduced urgency to burn 'long-unburnt' mallee vegetation for the purpose of hazard reduction, and a corresponding opportunity for fire planners to focus greater attention on conservation objectives

Attributes such as Triodia hummocks, leaf litter and decorticating bark provide both important resources for fauna and fuel for fire (Bradstock & Cohn 2002). At local scales, management to reduce these fuels is incompatible with the requirements of animals using these resources for foraging or shelter (e.g. James & M'Closkey 2003; Ucitel, Christian & Graham 2003). Strategic use of prescribed fire to reduce the risk of wildfire involves a trade-off. Maintaining vegetation in early postfire conditions as a 'fire-break' may prevent extensive wildfire (e.g. >100 000 ha) and facilitate the persistence of a greater proportion of the landscape at more advanced stages along the post-fire chronosequence (Sandell et al. 2006). However, the use of prescribed fire over large areas (e.g. landscape burning) demands careful consideration of the overall amount and spatial distribution of vegetation of all fire-ages (Clarke 2008), and recognition that some habitat components continue to develop for at least a century after fire.

In contrast with tree mallee vegetation, where prescribed fires and wildfires result in similar post-fire changes, in many other ecosystems (such as forests) differing fire severity combined with taller canopy vegetation mean that prescribed fire and wildfire may initiate different post-fire trajectories (e.g. Sah *et al.* 2006). Consequently, the resources available in prescribed fire and wildfire scars of identical fire-ages will also differ. Further research is needed before explicit recommendations can be made about the spatial properties of fire plans, and the effect of differential post-fire trajectories (e.g. prescribed fire cf. wildfire) on resource availability at broad spatial extents. Nevertheless, the impacts of fire on the dynamics of fuel *and* habitat attributes must be considered in fire planning if management is to successfully contribute to both hazard reduction and conservation objectives. Furthermore, the potential for post-fire resource dynamics to operate over temporal scales that exceed current understanding must be factored into management plans.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Location of 26 study landscapes in Victoria, South Australia and New South Wales, Australia. All study sites (n = 549) were situated within these landscapes. As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Fig. S1. Location of 26 study landscapes in Victoria, South Australia and New South Wales, Australia. All

study sites (n=549) were situated within these landscapes.



Appendix 4

Spatially and temporally consistent fire mapping provides insights into fire regimes of the semi-arid Murray Mallee, south-eastern Australia

In review: Avitable, S.C., Callister, K.E., Kelly, L.T., Fraser, L., Haslem, A., Clare, Nimmo, D.G., **Watson, S.J.**, M. Kenny, S.A., Taylor R.S., Spence-Bailey, L.M., & Bennett, A.F. (in review) Spatially and temporally consistent fire mapping provides insights into fire regimes of the semi-arid Murray Mallee, south-eastern Australia. *International Journal of Wildland Fire*

Abstract

Fire is a natural disturbance process that shapes ecosystems world-wide and which operates at a scale that crosses jurisdictional boundaries. However, in many fire-prone areas accurate fire records and systematic fire maps are lacking. We used Landsat imagery to map the fire history of the Murray Mallee region of south-eastern Australia from 1972 to 2007. This semi-arid, fire-prone ecosystem encompasses a region of 104,000 km². An area equivalent to 40% of the tree-mallee vegetation was burnt during the 35-year period, but less than 5% of this vegetation experienced more than one fire in this time. Large fires (>10,000 ha) accounted for 89% of the area burnt and were the main influence on the distribution of fire age-classes in conservation reserves. Different vegetation types burned disproportionately, illustrating the value of combining region-wide vegetation mapping with fire history mapping. Although the perception is that large fires occur on a roughly decadal cycle following years of above-average rainfall, spatially-explicit analyses revealed that large fires are not tightly associated with years of above-average rainfall. The distribution of fire age-classes differed profoundly between reserves and across states, highlighting the need to manage fire-prone landscapes at ecologically-meaningful regional-scales that cross jurisdictional boundaries.

Introduction

Fire is a fundamental process in ecosystems throughout the world (Bowman *et al.* 2009), shaping vegetation structure and composition (Cleary and Gennert 2004; Bond and Keeley 2005). Fire is a landscape-scale, natural disturbance with spatial and temporal characteristics to which biota in fire-prone ecosystems demonstrate many adaptations (van Wilgen *et al.* 2007; Kelly *et al.* 2010). Anthropogenic changes to fire regimes affect biodiversity (Keeley and Fotheringham 2001) and inappropriate fire regimes have been identified as a threatening process for species in fire-affected systems (Woinarski and Fisher 2003; Letnic and Dickman 2006; Hutto 2008). However, there is limited information on the requirements of many animal and plant species with regards to both the temporal and spatial characteristics of fire regimes (Parr and Andersen 2006; Clarke 2008; Driscoll *et al.* 2010) and, despite recognition of the importance of fire, the fire history of many ecosystems is poorly known (Whelan 2009; Wittkuhn *et al.* 2009).

Accurate fire histories are required for both ecological research and land management (Whelan 2009). Although land managers may lack detailed information, they are required to make decisions about issues such as fire suppression and prescribed burning, and resulting fire management strategies have the potential to alter fire regimes in ways that advantage, or disadvantage, the biota (Stephens and Ruth 2005). Production of accurate fire history maps has been aided by the use of satellite imagery to remotely sense fire scars (e.g. Russell-Smith *et al.* 1997; Hudak and Brockett 2004; Roder *et al.* 2008; Gill *et al.* 2000; Greenville *et al.* 2009). The utility of fire maps depends on the scale of the imagery used to map the fires and the scale at which these data are subsequently mapped and analysed (Morgan *et al.* 2001). Spatial resolution of maps is important to detect patchiness of fires (Gill *et al.* 2000; Hudak and Brockett 2004; Yates *et al.* 2008).

Accurate mapping of the fire history of a region has many benefits. The resulting maps provide data on important spatial characteristics of fire, such as their size and spatial configuration (Minnich 1983; Keeley *et al.* 1999; Haydon *et al.* 2000; Díaz-Delgado *et al.* 2004). They can also be used to determine fire frequency, to link fire to environmental variables, and to determine the susceptibility of different vegetation types to fire and therefore, identify fire-prone areas (Lloret *et al.* 2002; Morgan *et al.* 2001; Díaz-Delgado *et al.* 2004).

Such knowledge can then guide fuel management (Morgan *et al.* 2001; Bowman *et al.* 2003) and the planning of appropriate burning regimes (Haydon *et al.* 2000; Morgan *et al.* 2001). Accurate fire maps can also be used to evaluate the success of fire suppression and fuel management activities and their impact on the overall fire regime of an area (Minnich 1983; Keeley *et al.* 1999; Díaz-Delgado *et al.* 2004), as well as identifying gaps in knowledge of fire regimes for further study (Morgan *et al.* 2001).

Our focus was on the fire history of the semi-arid Murray Mallee region of south-eastern Australia, a highly fire-prone region (Bradstock and Cohn 2002). The region is typical of many regions where knowledge of fire history is essential for sound land management and conservation of biodiversity. In this region, inappropriate fire regimes have been identified as a key threatening process for several taxa (e.g. Black-eared Miner *Manorina melanotis*, Mallee Emu-wren *Stipiturus mallee*). Because this

region spans several states (Victoria, New South Wales, South Australia), there is a need for coordinated fire planning across jurisdictional boundaries. Mapping of fire history had been undertaken in each state but not in a consistent manner, or at a consistent scale, leading to limitations in the capacity to interpret fire history across the region. For example, such inconsistencies have prevented region-wide evaluation of the extent and location of unburnt islands, which may be important sources for recolonisation by fauna.

The aim of this study was to produce a consistent fire-history map for the Murray Mallee region, spanning jurisdictional boundaries, as a basis for an analysis of the fire history of the area. The aims of our analysis were to: 1) determine changes in fire characteristics such as size, frequency and vegetation types burnt over the last three decades, 1972-2007; 2) examine the relationship between the occurrence of large fires and rainfall patterns; 3) calculate fire intervals typical of mallee vegetation in this ecosystem; and 4) determine the age-class distribution of mallee vegetation across jurisdictional boundaries.

Methods

Study area

The Murray Mallee region of Victoria, New South Wales and South Australia, is an area of some 104,000 km². The word 'mallee' describes the multiple aerial stems that emerge from a lignotuberous rootstock of eucalypts, as well as being a general term for areas that are dominated by eucalypts of this form (Noble 1984). The climate is semi-arid with mean annual rainfall between 220-330 mm (raw data supplied by the Australian Bureau of Meteorology), high summer temperatures (mean daily maxima \geq 32°C) and mild winters (mean daily maxima 16°C) (Land Conservation Council 1987). The broad characterisation of the mallee landforms is one of dune-swale geomorphology with variable soil types underlying different areas (Noble 1984; Bradstock and Cohn 2002).

Vegetation communities in the Murray Mallee vary with both climate and soil type (Noble 1984). On sandy soils, the vegetation typically comprises an overstorey of mallee eucalypts and an understorey of hummock grasses (Triodia and Austrostipa species) or sclerophyllous shrubs (Melaleuca spp., Leptospermum spp. and Acacia spp.) (Parsons 1994). On heavier clay or loamy soils, mallee eucalypts occur over an understorey of chenopod or succulent shrubs (Parsons 1994). Mallee vegetation had not previously been described or mapped consistently across all three states in the study region. We used cluster analysis of floristic data from 713 sites to identify four broad vegetation types that occur in tree mallee, three of which were able to be mapped reliably across the region; Triodia Mallee, Chenopod Mallee and Heathy Mallee (Haslem et al. 2010). Triodia Mallee is dominated by Eucalyptus dumosa and E. socialis with an understorey of the hummock grass Triodia scariosa. Chenopod Mallee is characterised by an overstorey of E. oleosa subsp. oleosa and E. gracilis and a range of low shrubs in the lower strata, including Olearia spp., Zygophyllum spp. and chenopod species such as Maireana pentatropis, Enchylaena tomentosa var. tomentosa and M. pyramidata. Heathy Mallee is characterised by E. costata subsp. murrayana and Callitris vertucosa with ground strata commonly dominated by a diverse range of small woody shrubs, including heathy species such as *Phebalium* bullatum, Cryptandra tomentosa and Spyridium subochreatum var. subochreatum. Other (non-mallee)

vegetation types that occur in the region include heathlands, *Melaleuca uncinata* dominated shrubland, and woodlands dominated by *Callitris columellaris*, *Allocasuarina luehmanni* and *Allocasuarina cristata* (Land Conservation Council 1987).

Fire mapping

Satellite imagery was acquired from Landsat Multispectral Scanner (MSS) (prior to 1989) and Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) (1989-2005) images. These data were available for the entire study area for 14 epochs (1972, 1977, 1980, 1985, 1988, 1989, 1991, 1992, 1995, 1998, 2000, 2002, 2004, 2005 and 2007). Therefore, the total dataset of 15 images from 1972-2007 allowed the fire history of the 35 year period from 1972-2007 to be investigated. The time interval between consecutive images ranged from 1-5 years. Pre-processing of the satellite data was completed by the Department of Climate Change (see Furby 2002 for detailed methods). Pixel size was re-sampled at 50 x 50 m for Landsat MSS and 25 x 25 m for Landsat TM and ETM+.

We used ENVI 4.2 geographic information system (GIS) software (ITT VIS 2005) to create false colour composite images from three consecutive Landsat images. We used band 4 (far infrared) of Landsat MSS images and band 7 (middle infrared) of Landsat TM and ETM+ images (Haydon *et al.* 2000). The resulting chronosequence depicted major disturbances to vegetation (fire or extensive clearing) in a consistent and unique colour for each of the two time periods in the chronosequence. Generally, fire scars were easily distinguished from vegetation clearance by the distinctive pattern of a fire, compared with clearing which is commonly performed in a geometric pattern. Additionally, vegetation clearance was usually a permanent change, as opposed to fire scars which showed signs of recovery in subsequent images.

Fire boundaries were digitised on-screen, and by linking the chronosequence to images of pre-and post fire it was possible to confirm the fire scar and time-period in which it occurred. The minimum patch size recorded was four pixels, for both fires and unburnt islands within fires. The image interpretation process aimed to smooth edges around pixel boundaries and fire boundaries are estimated to be accurate to within 1 pixel. Due to the size of the study area, images were mapped by multiple experts. All data layers were checked by one data manager.

The resulting polygons of fire scars were exported to ArcView 9.2 (ESRI 2007) for checking and to add attribute data. Fire patches initially were dated to the satellite images between which the fire occurred (e.g. 1972-1977, 1992-1995). To obtain a more precise date and other details of the fire, all fires were compared with existing spatial data from state agencies in Victoria (DSE) and South Australia (DEH), and fire history information was sourced from relevant government reports (Cheal *et al.* 1979) and people with local knowledge. A precise fire year was able to be assigned to 270 (25%) of the total 1060 fires mapped across the study area. This represents 95% of the total area burnt in the region between 1972 and 2007, as large fires were more likely than small fires to be recorded by state agencies or mentioned in published literature.

Often a single fire event was represented by multiple polygons, due to minor discontinuities in fuels or fire spotting close to the fire front. State agency data assisted in grouping many fire polygons into single fire events. Where a fire was not mapped by the state agency, all polygons mapped between the same image start and end date, and within 500 m of each other, were considered to belong to the same fire event. For fires over 1,000 ha, polygons within 3 km were considered part of the same fire event, as spotting from larger fires can occur within such distances (Sandell *et al.* 2006).

Area calculations

Using the region-wide vegetation map (Haslem *et al.* 2010), the areas burnt in Triodia Mallee, Heathy Mallee and Chenopod Mallee were calculated for each epoch interval. From this, we determined the overall area burnt in each vegetation type, the area of each vegetation type burnt in large fires and the area of each vegetation type burnt more than once.

Fire intervals

The area of tree-mallee vegetation that experienced more than one fire during the 35 year period of the study was calculated by investigating the area of overlap of fire polygons between epoch intervals. Fire intervals were calculated using the midpoint of the epoch between consecutive satellite images, as many fires were not able to be attributed an exact date of occurrence. Many areas of overlapping fire scars were very small (<5 ha) and may have been due to slight inconsistencies between image layers, so for the analysis of fire intervals, only areas of overlap (or patches) greater than 5 ha were included.

Large fires

Large fires (>10,000 ha) were analysed in more detail as these accounted for 89% of the area of treemallee vegetation burnt during the study period. Exact dates and the source of ignition were attributed to each large fire using existing agency fire maps, published literature and information from land managers and local residents. To investigate the relationship between these large fires and rainfall patterns, long-term rainfall data were sourced from the Mildura Airport weather station (Lat 34.24°S, Long 142.09°E; Bureau of Meteorology data). For each large fire, associated rainfall was quantified in a number of ways: yearly rainfall total, cumulative monthly rainfall (12 month moving total of monthly rainfall), residual yearly rainfall (actual yearly rainfall taken from the mean) and cumulative residual monthly rainfall. The data were explored with scatterplots using three response variables: presence/absence of large fires per year, number of large fires per year, and total area burnt by large fires each year. Exploratory analysis of the data indicated that statistical models of the relationship between large fires and rainfall would be strongly influenced by one or two data points, and so a descriptive approach was used.

Results

A total of 1,060 separate fires were mapped in the study region for the period 1972-2007 (Fig 1). Sixteen fires were greater than 10,000 ha and three burnt over 100,000 ha. However, fires were generally relatively small, with the vast majority less than 100 ha (Fig. 2). The result of these fires was that during this period, 14% of the total study area experienced at least one fire (Fig. 1). Most fires occurred in tree-mallee vegetation (89%) (*cf* non-mallee vegetation) and they burned an area

equivalent to 40% of the total amount of such vegetation in the region, i.e. an average of 1.14% of the area per annum.

The largest fires occurred during the decade of the 1970s (Fig. 1). The overall area burned has been less in later decades, but the number of fires per year has increased (Figs. 3a, b).

Fig. 1. here

Fig. 2 here

Fig. 3 here

Large fires

Sixteen large fires of >10,000 ha occurred between 1972-2007 (Table 1) and accounted for 89% of the total area of tree-mallee burnt during the study period. Eight occurred in the 1970s, with the largest fire (>650,000 ha) occurring in New South Wales. Six of the large fires occurred in Murray-Sunset National Park, Victoria. With one exception, all the large fires were during late spring or summer and were ignited by lightning strikes. The exception began as a prescribed fire during September in 2006, but escaped control and burnt approximately 25,000 ha.

While large fires often occurred during extreme weather, there is some evidence to suggest that they did not necessarily result in a homogenous landscape and may leave unburnt areas as the result of changing weather conditions and spotting ahead of the fire front. In an on-ground assessment of 835 sites across the study area, 30% of sites had been patchily burnt at a scale that was not possible to detect using satellite imagery (with 25 x 25 m pixels) but was evident on the ground.

There was no obvious relationship between large fires and rainfall (Fig. 4). Large fires have occurred in years following increased rainfall. However, not all years of high rainfall were followed by fire (e.g. 1993, Fig. 4). Furthermore, large fires also occurred during drought years (e.g. Nov 2006) and so were not restricted only to years immediately following wet periods. Thus, the relationship between large fires and increased rainfall was variable, precluding identification of strong trends.

Table 1 here

Fig. 4 here

Fire intervals

Very little tree-mallee vegetation (2.3% of the total area of tree-mallee vegetation) had been burnt more than once since 1972 (Fig. 5), although this is equivalent to a total area of 74,598 ha.

Fig. 5 here

Of the small area that experienced more than one fire, the average inter-fire interval (\pm sd) for patches burnt twice was 21 ± 8 years in Triodia Mallee and 18 ± 8 years in both Heathy and Chenopod Mallee, although there was less re-burnt area in the latter two vegetation types than Triodia Mallee. Most areas of Triodia and Chenopod Mallee that experienced two fires had intervals of 20-32 years (Fig. 6). Heathy Mallee areas had a more even spread of interfire intervals across a greater range of years postfire (10-32 years).

Fig. 6 here

Comparison between vegetation types

Triodia Mallee had the greatest proportion of area burnt during 1972-1980 (Fig. 7). The largest area of Triodia Mallee was burnt in 1972-1977, with relatively small areas burnt since then. The largest area of Heathy Mallee was burnt in 1985-1988 and this also represented the vegetation type with the greatest proportion burnt during 1980-1989 (Fig. 7), although Heathy Mallee covers considerably less area than the other two vegetation types. Chenopod Mallee was the least burnt vegetation type in any decade. Over the entire period 1972-2007, only 21% of the total area of Chenopod Mallee burnt, whereas 50% of Triodia Mallee and 51% of Heathy Mallee vegetation were burnt.

Fig. 7 here

Fire age-class distribution

The distribution of fire age-classes in tree-mallee was examined at the scale of individual conservation reserves, jurisdictional areas (states) and areas of continuous mallee vegetation, which may occur across reserve and state boundaries. At the reserve scale, there were marked differences in fire age-class structures (Fig. 8). While many reserves are dominated by the 35+ years fire age-class (e.g. Hattah-Kulkyne National Park, Calperum Station and Tarawi Nature Reserve), some reserves experienced large fires that resulted in markedly different age-class distributions (e.g. greatest area in 18-27 year fire age-class, Billiat Conservation Park; 0-7 year fire age-class, Taylorville Station). Murray-Sunset National Park (Victoria) had the most even age-class distribution.

A comparison between states revealed differences in the distribution of fire age-classes, with Victoria having a broader spread across all mappable fire age-classes than the other states (Fig. 9). South Australia had the largest percentage area of long unburnt (>35 years) mallee. Not only did South Australia have more than twice the area of long unburnt mallee than Victoria (894,342 ha v. 346,312 ha), the spatial aggregation of this fire age-class was quite different (Fig. 1). The long unburnt mallee in Victoria was distributed as small patches between the multiple fire scars across Murray-Sunset NP, whereas in South Australia there were very large patches of long unburnt mallee. The distribution of mallee vegetation in New South Wales is more dissected by other vegetation types and cleared land than in South Australia and Victoria. Consequently, patches of mallee in NSW were more likely to be of a single age-class than in the other states (Fig 1).

If one adopts a landscape-scale approach, ignoring reserve and state boundaries, and examines the age-class distribution of tree-mallee in areas that form continuous blocks (e.g. Fig. 9), a quite different picture of the available age-classes emerges from that gained by viewing reserves or states in isolation. There are two large continuous blocks of tree-mallee vegetation protected within reserves, one north and one south of the Murray River. These blocks account for 22% and 17%, respectively, of the entire area of tree-mallee in the region and have different fire age-class distributions (Fig. 9). The northern block has experienced less fire (23% of tree-mallee burnt) than the southern block (57% of tree-mallee burnt) in the last 35 years.

Fig. 8 here

Fig. 9 here

Discussion

Fire patterns in the mallee

The pattern of fire in the Murray Mallee region over the past 35 years has been dominated by infrequent large fires ignited by lightning in late spring or summer. Despite our study encompassing an area equivalent to the entire nation of Iceland, there were insufficient data to directly determine an unbiased estimate of the average fire interval in mallee, since such a small percentage of the study area (<3%) experienced two or more fires during the study period. This suggests the average inter-fire interval is well beyond 35 years and that a site being burned more than once within such a period is the exception, rather than the rule. This finding contrasts with a perception of more frequent burning arising from observations that large fires occur every 10-20 years in this landscape (Noble and Vines 1993; Morelli and Forward 1996; Bradstock and Cohn 2002; Willson 1999). However, although there may well be a large fire *somewhere* in the region on a roughly decadal basis, our data indicate it is extremely rare for any particular site to be burnt more than once in a 35 year period. Indeed, examination of the post-fire ages of specific sites showed that some remained unburnt for well over 100 years (Clarke *et al.* 2010). This finding highlights the value of spatially explicit examination of the occurrence of fire, rather than just focussing on simple temporal patterns of conspicuous events.

Fires in the Murray Mallee region became more frequent, but burnt less area, between 1972 and 2007, reflecting an increase in the number of small fires and a decrease in the number, and area, burnt by large fires. This result contrasts with findings in many Mediterranean systems worldwide where *large* fires have increased in frequency (e.g. California: Keeley *et al.* 1999, Minnich 1983, Spain: Díaz-Degaldo *et al.* 2004, Pausas 2004). Nevertheless, infrequent large fires still accounted for the majority of area burnt in the mallee, as well as elsewhere in Australia (Haydon *et al.* 2000, Yates *et al.* 2008), California (Keeley *et al.* 1999, Moritz 1997), South Africa (Van Wilgen 1987) and Spain (Díaz-Delgado *et al.* 2004, Röder *et al.* 2008).

The decline in the area burnt by large fires in the Murray Mallee in recent years could be explained in several ways. The apparent trend might be an illusory consequence of a sample period of an inadequate length (only 35 years). It may reflect low fuel production due to a combination of few

years of above average rainfall and many years of drought during the latter half of the study period. Increased rainfall during the preceding seasons has been positively correlated with increased area burnt in arid areas of Israel (Levin and Saaroni 1999), Spain (Littell *et al.* 2009) and Australia (Greenville *et al.* 2009). In Mediterranean systems, fire activity and area burnt have been positively associated with periods of drought (Keeley and Zedler 2009, Röder *et al.* 2008). The extensive fires in the Murray Mallee in 1974/75 were associated with above average rainfall during 1973 and 1974 which led to widespread growth of speargrass (*Austrostipa* spp.) (Noble *et al.*1980). The resulting continuity of fuel was considered a key factor in the large fires that subsequently occurred across New South Wales (Noble *et al.* 1980). However, these 1970s fires are the only clear occurrence of a link between increased rainfall and large fires. The large fire in South Australia in 2006 was during a period of severe drought. That mallee occurs in the *semi*-arid climatic zone (250-400 mm pa) may account for it exhibiting a fire history pattern intermediate between arid and Mediterranean systems, at least during the 35 year history used in this study.

It is possible that the decline in the area burnt by large fires in the Murray Mallee in recent years is a consequence of successful preventative measures (prescribed burning) and active suppression during this period. However, there appears to have been no published quantitative examination of the degree to which different prevention or suppression methods have worked under particular fire conditions. Such analyses are inhibited by limited records of the location, extent and nature of past prevention and suppression methods during much of the study period. It was not possible to determine whether there was correlation between the extent and incidence of large fires and extent of prescribed burning in the region, as the latter was not consistently documented in any state. This inability to examine the effectiveness of prevention and suppression methods due to a lack of baseline data undermines the capacity of agencies to engage in truly adaptive management of fire for either asset protection or ecological management (Holling 1978, Gill 2008).

Vegetation communities

This study highlights the value of combining fire history mapping with regional vegetation mapping to identify the different propensities of different vegetation types to ignite and carry fire. For example, the fact that Chenopod Mallee is less flammable and less likely to re-burn in a given period than Triodia Mallee can be used when considering the strategic placement of prescribed burns whose aim is to halt the run of large fires. This approach would capitalise on the inhibitory effect of some vegetation types on fire spread. Prior to this study, a lack of consistent region-wide vegetation and fire history mapping impeded the application of such basic information in fire planning and management.

Fire age class distribution

This study highlights the need to consider the management of fire-prone landscapes at ecologicallymeaningful regional scales that cross jurisdictional boundaries, rather than at the reserve or state scale; which is currently the common practice world-wide (e.g. Willson 1999; USDI-NPS 2004, 2009; Biggs *et al.* 2006; Department of Sustainability and Environment 2008). The temporal and spatial distribution of fire age-classes differed between reserves, states and major blocks of mallee. This is likely to be a consequence both of differences in fire management between jurisdictions, and variation in the fire regime along a north-south latitudinal gradient in this region. Pausas and Bradstock (2007) showed that there was a pattern of decreasing fire frequency associated with increasing aridity from south to north. They proposed that with increasing aridity there is a decrease in productivity, such that the amount and connectivity of fire fuels are reduced and fires become less frequent.

If the distribution of the fire age-classes in each reserve in a region is managed in isolation, then undesirable ecological outcomes could inadvertently arise. For example, the nationally endangered Black-eared Miner (*Manorina melanotis*) requires large continuous areas of long-unburnt mallee (Clarke *et al.* 2005; Taylor *et al.* unpublished data). Perhaps not surprisingly, given the fire history of the region, it maintains a stronghold in the large blocks of long unburnt mallee in South Australia (Clarke *et al.* 2005), and is now rarely recorded in Murray-Sunset National Park, where patches of long unburnt mallee are more fragmented. If managers of the South Australian reserves did not appreciate the regional scarcity of large blocks of long unburnt mallee, local planning decisions could be made to the detriment of regionally endemic endangered fauna, like the Black-eared Miner. It is important that the management of ecological assets, like stands of long-unburned vegetation, are considered across ecologically-meaningful landscape management units; not just according to jurisdictional boundaries.

The presence and connectivity of potential source populations able to re-colonise habitats and conservation reserves following fire is a critical issue. It is likely to result in quite different perceptions of what constitutes a desirable age-class distribution for a particular reserve, depending on the size of the reserve (relative to the size of fires) and its spatial context: that is, whether it is surrounded by extensive vegetation or whether it is isolated from similar vegetation. While many plants and animals may have adaptations to cope with the 'typical' past pattern of infrequent large fires, they now face a different situation where habitats have become fragmented and isolated. The isolated nature of some conservation reserves make it undesirable for large proportions of the reserve to burn in a single event, because sources of re-colonists following fire may be lacking.

A precautionary approach to fire management in isolated reserves would be to reduce the risk of a large fire burning the majority of the reserve in a single fire event. To evaluate alternative means of achieving this aim will require detailed information on: i) the effectiveness of various prevention and suppression methods when faced with typical fire conditions; ii) the inherent risk of prevention or suppression methods escaping control lines and burning the very asset one is trying to conserve; and iii) anticipated changes in the likelihood of large wildfires with global warming (e.g. Bradstock 2008, Driscoll *et al.* 2010).

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Figure captions

Fig. 1. Fire history map of the entire Murray Mallee region, south-eastern Australia, from 1972-2007. Fire scars are grouped into decades. Unburnt mallee vegetation is shown in light green, and white areas are non-mallee vegetation, cleared or agricultural land. Reserves outlined are 1 Danggali Conservation Park, 2 Calperum Station (Bookmark Biosphere), 3 Gluepot Reserve, 4 Taylorville Station (Bookmark Biosphere), 5 Billiat Conservation Park, 6 Murray-Sunset National Park, 7 Hattah-Kulkyne National Park, 8 Mallee Cliffs National Park, 9 Petro Reserve, 10 Lethro Reserve, 11 Tarawi Nature Reserve, and 12 Scotia Sanctuary.

Fig. 2. The relative occurrence of fire size-classes mapped for the entire Murray Mallee region, 1972-2007.

Fig. 3. a) Area (ha) burnt in each decade since 1972, b) number of fires in the region in each decade from 1972 to 2007. As decadal intervals are not even, annual averages in each decade are also shown.

Fig. 4. Relationship between large fires in the study region between 1972-2007, the area of treemallee vegetation burnt (ha; bars), cumulative total of previous 12-month rainfall (mm. solid line) and long-term average annual rainfall (mm; dotted line).

Fig. 5. Percentage area of tree-mallee vegetation that has not been burnt during 1972-2007, and the area burnt from 1-4 times. Note that areas burnt three and four times, each constitute less than 1% of all tree-mallee vegetation.

Fig. 6. Distribution of the inter-fire intervals of fire patches (areas of overlapping fire scars >5 ha) in each mallee vegetation type burnt twice during 1972-1977; TM Triodia Mallee, HM Heathy Mallee, CM Chenopod Mallee.

Fig 7. Amount of the three mallee vegetation types burnt in each decade from 1972-2007, as a proportion of the total area of each vegetation type in the study region.

Fig. 8. Fire age-class structure in conservation reserves and parks of the Murray Mallee region; fire age-classes (years since last fire) are broadly in decades, constrained by available satellite image layers (> 35 years = unburnt since the earliest image in 1972).

Fig. 9. Comparison of fire age-class structure of tree-mallee vegetation within a) each state (Victoria, New South Wales and South Australia), b) within continuous blocks of tree-mallee {Southern block includes Murray-Sunset NP and Hattah-Kulkyne NP; Northern block includes Scotia Sanctuary, Tarawi Nature Reserve, Danggali Conservation Park, Calperum Station (Bookmark Biosphere), Gluepot Reserve and Taylorville Station (Bookmark Biosphere)} and over the entire Murray Mallee region.

Year	State	Month	Fire type	Overall area	Vegetation types (% of burn)			
				burnt (ha)	СМ	HM	TM	NM
1974	NSW	Nov	W	657987	12	0	69	19
1975	NSW	Jan	W	19355	<1	0	80	19
1975	NSW	Jan	W	20271	<1	0	81	18
1975	NSW	Jan	W	38069	14	0	81	5
1975	Vic	Feb	W	45788	38	0	58	3
1975	Vic	Nov	W	21272	64	0	35	1
1975	SA	Dec	W	10402	26	0	48	26
1976	Vic	Nov	W	13371	11	<1	87	1
1976	Vic	Nov	W	13493	4	<1	92	3
1976	Vic	Nov	W	12664	67	<1	31	2
1980	Vic	Dec	W	124366	8	26	65	<1
1984	SA	Dec	W	44109	75	0	19	6
1985	Vic	Jan	W	10773	11	1	61	26
1988	SA	Jan	W	52972	<1	97	<1	3
2006	Vic	Sept	PB/W	24763	6	83	10	<1
2006	SA	Nov	W	118783	14	0	82	4

Table 1. Details of sixteen large fires (>10,000 ha) that occurred in the Murray Mallee region during 1972-2007.

For each fire, the year and month of occurrence, type of fire, area burnt (ha) and the proportion of each vegetation type burnt within the fire is shown.

W = WILDFIRE, PB = PRESCRIBED BURN, CM= CHENOPOD MALLEE, HM = HEATHY MALLEE, TM = TRIODIA MALLEE, NM = NON-MALLEE VEGETATION



Appendices

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Fig. 5.













Appendices



Appendices





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Murray Mallee region

7-18

18-27

Years since last fire

27-35

>35

0-7

