

# Fire, Flora and Fauna: Understanding Species' Distributions in Fire- Prone Ecosystems to Improve Conservation Management

By

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## **Preface**

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### ***Statement on authorship***

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis accepted for the award of any other degree or diploma. No other person's work has been used without due acknowledgment in the main text of the thesis. This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

Frederick Rainsford 17<sup>th</sup> August 2020.

Chapter 2 has been published in *Austral Ecology*. This work was co-authored by Luke Kelly, Steve Leonard and Andrew Bennett. I led all stages of this work, including conception, study design, data collection, data analysis and writing. All authors contributed to the conception of the study, and Andrew Bennett and Steve Leonard made strong contributions to the design of the field study and site selection. All authors contributed to study design, interpretation of results and writing.

Chapters 3 and 4 have been prepared as manuscripts to be submitted for publication. I led all stages of these chapters: conception, study design, data collection and analysis and writing.

Andrew Bennett and Steve Leonard were involved in the conception, study design and contributed critically to drafts.

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### ***Animal welfare***

This research was approved by the La Trobe University Animal Ethics Committee (approval number: AEC 17-31).

### ***Species nomenclature***

Taxonomy of birds follows (Christidis and Boles 2008). Taxonomy of plants follows Flora of Victoria, Royal Botanic Gardens of Victoria.

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## ABSTRACT

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Ecosystems worldwide face unprecedented changes in fire regimes due to climate warming, fire management practices and land-use change. More than ever, it is crucial to understand: (a) how fire shapes ecosystem structure and function in a range of ecological settings, and (b) how fire management practices, such as prescribed burning affect ecosystems. In this thesis, I use empirical data collected from ecosystems dominated by *Eucalyptus* trees with contrasting regeneration traits (i.e. basal resprouting vs. epicormic resprouting) to test hypotheses relating to three main themes.

I show: first, the development of faunal habitat structural attributes across an 80-year post-fire chronosequence differs among ecosystems, in line with the regeneration traits of the dominant trees. I then show that, post-fire, birds respond to different habitat components in different ecosystems. Second, in structurally resilient ecosystems (i.e. trees with epicormic resprouting), bird and plant communities respond differently to fire management practices, but both taxa show resilience to prescribed fire over a 36-year chronosequence. Third, spatial attributes of fire surrounding a site (e.g. the amount of long-unburnt vegetation) influence the abundance of birds, but responses to the configuration of successional vegetation differs between ecosystems. In a final synthesis, I show that inter-continently, the influence of time since fire on birds depends on the regeneration traits of the dominant trees. In ecosystems that experience stand-replacing fires, more species respond to time since fire than in structurally resilient ecosystems.

These findings question the way in which fire-prone landscapes are categorised and managed for biodiversity, especially the level of dependence on time since fire and other temporal surrogates. Between-fire intervals guided by life-histories of plants may negatively affect birds that rely on long-unburnt vegetation. In structurally resilient ecosystems, incorporating

additional complexity (e.g. fire severity, topography) could better capture processes that shape landscape patterns of biodiversity, and improve fire management practices.

# 1 INTRODUCTION

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The sunset silhouettes smoke from a bushfire.

## **1.1 A NEW AGE OF FIRE**

Ecosystems worldwide are facing unprecedented changes in fire regimes (Moritz et al. 2012, Stephens et al. 2013, Halofsky et al. 2020). Large severe wildfires are becoming more frequent in several regions, including South America (Lizundia-Loiola et al. 2020), U.S.A (Keeley and Syphard 2019), Europe (Vitolo et al. 2019) and Australia (Boer et al. 2020, Nolan et al. 2020). From 2019 to early 2020 in Australia, wildfires burned >12 million ha of forests, destroying >2000 homes and putting populations of some plants and animals at greater risk of extinction (Boer et al. 2020, Lindenmayer and Taylor 2020, Ward et al. 2020). Altered fire regimes can change the structure of ecosystems; for example, by favouring more fire-tolerant species, (McKenzie et al. 2004, Enright et al. 2015). Furthermore, biomes in which fire has been absent for centuries/millennia (e.g. rainforests, Arctic tundra) are now experiencing more frequent fires, pushing species and communities towards extirpation (Mack et al. 2011, Alencar et al. 2015).

Uncontrolled wildfire is also a serious threat to human life and property, particularly as the interface of urban and wild lands increases worldwide (Moritz et al. 2014). As a result, there is increasing pressure on land management agencies to mitigate the consequences of wildfire for human life and property, as well as to reduce detrimental impacts on biodiversity. More than ever, it is crucial to understand: (a) how fire shapes ecosystem structure and function in a range of ecological settings, and (b) how fire management practices might affect ecosystems.

## **1.2 PERSISTENCE IN FIRE-PRONE LANDSCAPES**

Fire shapes ecosystem patterns and processes, globally (Bowman et al. 2009, Pausas and Keeley 2009, Archibald et al. 2018). Patterns of plant diversity worldwide are driven by fire generating niche spaces, reducing competition for resources and increasing landscape

heterogeneity (Pausas and Ribeiro 2017). Fire consumes vegetative material, and a pattern of recurrent fire exerts a strong selective pressure for life-history traits that allow plant populations to persist in fire-prone landscapes (Pausas et al. 2004, Keeley et al. 2011, Pausas and Keeley 2014). Knowledge of the role of species' life-history traits is crucial in understanding how fire shapes ecosystems.

For plants, the ability of individuals to regenerate and populations to re-establish following fire depends on a combination of resilience and resistance traits (Clarke et al. 2013).

Resilience traits (e.g. resprouting, fire-cued germination of seeds) enable populations to reestablish in an area when conditions are favourable following fire (Pausas and Keeley 2014). Plants resprout following fire from either below-ground or basal storage organs, or aerial stems (Clarke et al. 2013). Capacity for post-fire resprouting depends on fire intensity, the degree of protection of tissues and buds (i.e. resistance traits) and bud position (Bellingham and Sparrow 2000, Klimesřová and Klimeř 2007). Some plant species regenerate from seed stored either in soil or canopy seedbanks. Fire may trigger the release of seed from protective cones (i.e. serotiny), break seed coats to allow germination, or facilitate seed germination and seedling establishment by changing the light and hydrological environment (Keeley et al. 2011).

Resprouting and re-seeding are the two main systems of post-fire regeneration and can be used to classify species (Pausas et al. 2004). Species may have the capacity to regenerate by either: (1) resprouting only (obligate resprouters), (2) re-seeding only (obligate re-seeders), (3) resprouting *or* re-seeding (facultative resprouters), or (4) have no capacity for post-fire regeneration (fire-avoiders) (Pausas and Keeley 2014, Clarke et al. 2015). Generally, resprouting and reseeded taxa differ in juvenile growth rates, seed and fruit size, and seed-dispersal mode (Verdú 2000).

Resistance traits are adaptations that protect buds and tissues from incineration during fire and determine a species' capacity for resprouting (Burrows 2013, Clarke et al. 2013, Collins 2020). For example, bark thickness determines whether plant stems are killed by fire, or whether they can survive and resprout (Pausas 2015). The combination of resilience and resistance traits of plants determine the post-fire successional trajectories of plant communities and how susceptible they will be to changing fire regimes (Bergeron and Dansereau 1993, Keith et al. 2007, Collins 2020).

Associations between faunal species and habitat structure drive the distribution of animals (Prodon and Lebreton 1981). In fire-prone environments, animal populations fluctuate over time following fire as habitat conditions (e.g. availability of shelter, food, and foraging sites) change (Fox 1982, Jacquet and Prodon 2009, Pons and Clavero 2010, Chalmandrier et al. 2013, White et al. 2016, Doherty et al. 2017, Gosper et al. 2019). In contrast to plants, most terrestrial animals are mobile throughout their life and many species avoid the lethal effects of fire through behavioural traits (e.g. escaping), rather than specific morphological adaptations to fire (Pausas and Parr 2018). Fire changes the structure of vegetation and, therefore, the habitat components available for fauna (Haslem et al. 2011, Nappi and Drapeau 2011, Burgess et al. 2015). For example, in North America several bird species (e.g. the black-backed woodpecker *Picoides arcticus*) rely on the resources associated with standing fire-killed trees and are more abundant in recently burnt landscapes (Hutto 1995, Nappi and Drapeau 2011). In contrast, in semi-arid woodlands in Australia, the abundance of many bird species increases over decades following fire as the resources associated with mature trees develop (Watson et al. 2012b, Gosper et al. 2019). As such, successional trajectories of faunal communities may be tied to those of vegetation through associations with structural attributes.

Knowledge of species' life-history traits help explain how plants and animals persist in fire-prone landscapes (Pausas et al. 2004, Keith et al. 2007, Jacquet and Prodon 2009). However, ecological context also matters as fire-prone landscapes encompass diverse ecosystems (e.g. Keeley et al. 2005a, Alstad and Damschen 2016, Fairman et al. 2017, Kelly et al. 2017b, Beale et al. 2018). Interactions between climate and fire have driven the evolution of different biomes, characterised by differences in fire regime and persistence traits of the biota (Clarke et al. 2013). This presents a challenge for ecologists and land managers who seek generalizations about how fire shapes the distribution of species and the structure of ecosystems.

### **1.3 POST-FIRE STAND REGENERATION IN FOREST ECOSYSTEMS**

Globally, forests and woodlands are some of the most fire-prone ecosystems (Noss et al. 2006, Bradstock 2010, Moritz et al. 2014). Feedbacks between vegetation, climate and fire have driven the evolution of many forest and woodland ecosystems, which experience a range of different fire regimes (typical return intervals, intensity, extent and season of fires) (Bradstock 2010, Pausas and Keeley 2014, Archibald et al. 2018). Plant regeneration traits drive different patterns of stand-regeneration, which may have implications for post-fire ecosystem succession.

Ecosystems dominated by trees that regenerate from seed or resprout basally following fire, typically are characterized by large, high-intensity stand-replacing fires; for example, boreal forests (Greene et al. 1999, Peters et al. 2005), conifer forests of western U.S.A. (Westerling et al. 2011), semi-arid *Eucalyptus* woodlands in south-western (Gosper et al. 2013a) and south-eastern Australia (Clarke et al. 2010), and ash eucalypt forests in south-eastern Australia (Bowman et al. 2016). In these ecosystems, fire typically kills canopy tree stems and consumes the above-ground plant material, resetting the succession to 'time zero'. Tree

regeneration then happens from the ground-up, and the post-fire succession may continue for decades to centuries.

In contrast, some tree species, including many *Eucalyptus* species, several *Quercus* species, and *Pinus canariensis*, possess thick bark that allows mature stems to survive frequent fires, and resprout from epicormic buds (Keeley et al. 2011, Clarke et al. 2013, Pausas and Keeley 2017, Chergui et al. 2018). In forests dominated by epicormic resprouters, stand structure is maintained through fire, regeneration occurs rapidly, and canopy tree stems serve as post-fire biological legacies. Epicormic resprouting is common in savanna ecosystems that typically experience frequent low-intensity surface fires (Burrows et al. 2010, Charles-Dominique et al. 2015). Globally, it is rare in ecosystems that experience high-intensity crown fires, with a few exceptions: for example, *Eucalyptus* forests in Australia, *Quercus suber* woodlands in southern Europe and *Pinus canariensis* woodlands on Canary Island (Pausas and Keeley 2017, Chergui et al. 2018).

Differences in post-fire stand-regeneration can be expected to have implications for the rate of recovery of plant and animal communities in forests and woodlands following fire. The post-fire development of vegetation structure in ecosystems dominated by epicormic resprouters is likely different to that of ecosystems that experience stand-replacing fires (i.e. basal resprouters, obligate seeders). As the distribution of faunal species is driven by changes in vegetation structure, rather than fire *per se* (Sitters et al. 2014a, White et al. 2016), these different regeneration strategies are likely to also influence faunal communities. If so, this should be reflected in the management of these ecosystems.

## **1.4 HOW ARE FIRE-PRONE LANDSCAPES MANAGED?**

Essentially, fire management aims to manipulate the fire regime across a landscape to reduce perceived risk to human life and assets, and ecological values (Bowman et al. 2011, Stephens

et al. 2019). Early concepts of a fire regime described the intensity and timing (i.e. seasonality, between-fire interval) of fires typical of an ecosystem/biome (Gill 1975). Subsequently, this has been extended to include the spatial context (e.g. area, patchiness) of fires (Gill and Allan 2008). Fire regimes can be manipulated by excluding wildfire (e.g. through direct suppression), by applying prescribed fire, or by ‘managing’ wildfire (leaving low-risk fires to burn) (Stephens et al. 2016).

Approaches to fire management often differ between regions (Kelly et al. 2018). Wildfire exclusion through suppression has dominated fire management in North America (Stockdale et al. 2016), Europe (Fernandes et al. 2016) and Australia (York and Friend 2016) since the 20<sup>th</sup> Century. In North America and parts of southern Africa, there has been a recent shift towards restoring historical fire regimes to maintain or restore ecological structure and function in managed forests (van Wilgen et al. 2004, Stockdale et al. 2016). The use of prescribed fire for fuel reduction and to achieve ecological goals is increasing in parts of the U.S.A. (Stephens et al. 2012), Australia (Burrows and McCaw 2013), Africa (Van Wilgen et al. 2004) and southern Europe (Fernandes et al. 2013). Regional differences in approaches to fire management tend to reflect different historical fire regimes, or cultural legacies (e.g. fire suppression in U.S.A.) (Stephens et al. 2016, 2019).

## **1.5 MANIPULATING FIRE MANIPULATES ECOSYSTEMS**

Fire management practices and policies have contributed substantially to ecological change (Stephens et al. 2016). Introducing fire through prescribed burns can have different outcomes and potentially wide-ranging consequences for biodiversity, depending on the ecological context and taxonomic group in question. For example, in Western Australian *Eucalyptus* forests, Burrows et al. (2019) reported that turnover of understorey plant species over time was not related to prescribed fire regime, whereas in dry *Eucalyptus* forests in south-eastern

Australia, prescribed burning had complex effects on faunal habitat features, influenced by pre-fire forest condition (Holland et al. 2017), and in north-west U.S.A., prescribed fire was found to stimulate regeneration of plant species (e.g. Oregon white oak *Quercus garryana*) (Nemens et al. 2019). There is pressure to increase the use of prescribed fire for fuel management in forests and woodlands throughout the world, creating an urgent need to better understand how prescribed fire affects biodiversity in managed ecosystems.

Removing fire from landscapes can also have wide-ranging consequences for biodiversity. Historically, in the U.S.A., fire management has focused on excluding severe wildfires from forests through suppression (Stephens et al. 2019). This has reduced the extent of suitable habitat for early successional species, particularly those such as the black-backed woodpecker, that depend on features created by severe fire (Hutto et al. 2016, Hutto et al. 2020). In contrast, exclusion of wildfire from mountain ash *Eucalyptus regnans* forests in south-eastern Australia may be necessary to ensure between-fire intervals are long enough (>150 years) to maintain ecosystem integrity (Lindenmayer and Taylor 2020). The range of effects that fire management practices have on biodiversity highlights the need to test how fire management will alter the structure and function of ecosystems in a range of settings.

Ecologically appropriate fire management must be based on sound ecological knowledge (Driscoll et al. 2010). Below, I outline a conceptual framework that makes explicit the link between ecological knowledge and management practices. I then apply this framework to a case study in Victoria, Australia, to show how this approach can reveal knowledge gaps that, once filled, may improve fire management outcomes for biodiversity.

## **1.6 LINKING ECOLOGICAL KNOWLEDGE TO FIRE MANAGEMENT**

Understanding how fire drives temporal and spatial patterns of biodiversity across the landscape is crucial for ecologically appropriate fire management. Management agencies use

tools (e.g. maps) to guide decisions about actions to take (e.g. when to burn a patch of vegetation) (Fig. 1.1). To produce maps, landscapes are categorized into units for management that can be represented spatially (e.g. vegetation types, time since the last fire, management zone). The flow chart in Fig. 1.1 illustrates the connection between the way in which the relationship between fire and biota is analysed and understood and the management actions.

There are two main paradigms for understanding the relationships between fire and biota: (1) point/site-based analyses and (2) landscape mosaics (Fig. 1.2). In the first paradigm, measures of biodiversity (e.g. species occurrences, mortality, etc.) are associated with the environmental conditions and fire history at points/sites in the landscape. Ideally, biological data from a stratified survey design are used to associate, for example, the likelihood of occurrence of species, with specific post-fire conditions (Hutto 2008, Watson et al. 2012b), or changes in species diversity with time since fire (Gosper et al. 2013b). The outcomes of these analyses are used to identify important attributes (e.g. time since fire) that are used guide the creation of management maps. Maps may be based on simple categories (e.g. burnt/ not burnt) (e.g. Littell et al. 2009, Avitabile et al. 2013), or combined with biological responses to fire (e.g. distribution of suitable habitat, degree of canopy scorch) to create maps that represent functional processes (e.g. Collins et al. 2018, Connell et al. 2019).

In the second paradigm, landscape mosaics, site-based data or analyses are incorporated into spatial analyses. These analyses aim to relate measures of biodiversity (e.g. species' abundances, diversity indices, landscape-level responses) to the spatial context of fire regimes, such as the diversity of fire age or fire severity classes in the surrounding landscape (e.g. Tingley et al. 2016). For example, recent advances in this field include methods for determining the 'optimal' mosaic of fire age-class for biodiversity conservation (Di Stefano et al. 2013, Kelly et al. 2015, Chick et al. 2019).

The outputs of this process (e.g. maps of annual area burnt, response of species to fire) can directly influence both local management and regional policy decisions (Littell et al. 2009, Stephens et al. 2019). For example, a management agency may decide to burn a patch of vegetation to increase the proportion of early-successional vegetation in the landscape. Ultimately, the outcomes of fire management for biodiversity depend on how the relationships between fire and biota are first analysed and understood.

Introducing fire into, or removing it from, landscapes has effects on ecosystem structure. A crucial component of the management framework is ‘feedback’ (Fig. 1.1), in which the outcomes of management actions are monitored and ‘fed back’ into analyses in an adaptive management framework. In this way, management objectives, plans and actions are continually being updated as ecological knowledge develops (van Wilgen and Biggs 2011). The potential impacts of fire management on biodiversity are identified in the feedback stage (if this occurs), so a truly adaptive process of fire management for biodiversity depends on the analysis stage.

Fundamentally, understanding the outcomes of management decisions depend on the biological, fire and environmental data that are analysed at the first instance. Below, I apply this framework to a case study of fire management for biodiversity in Victoria, Australia.

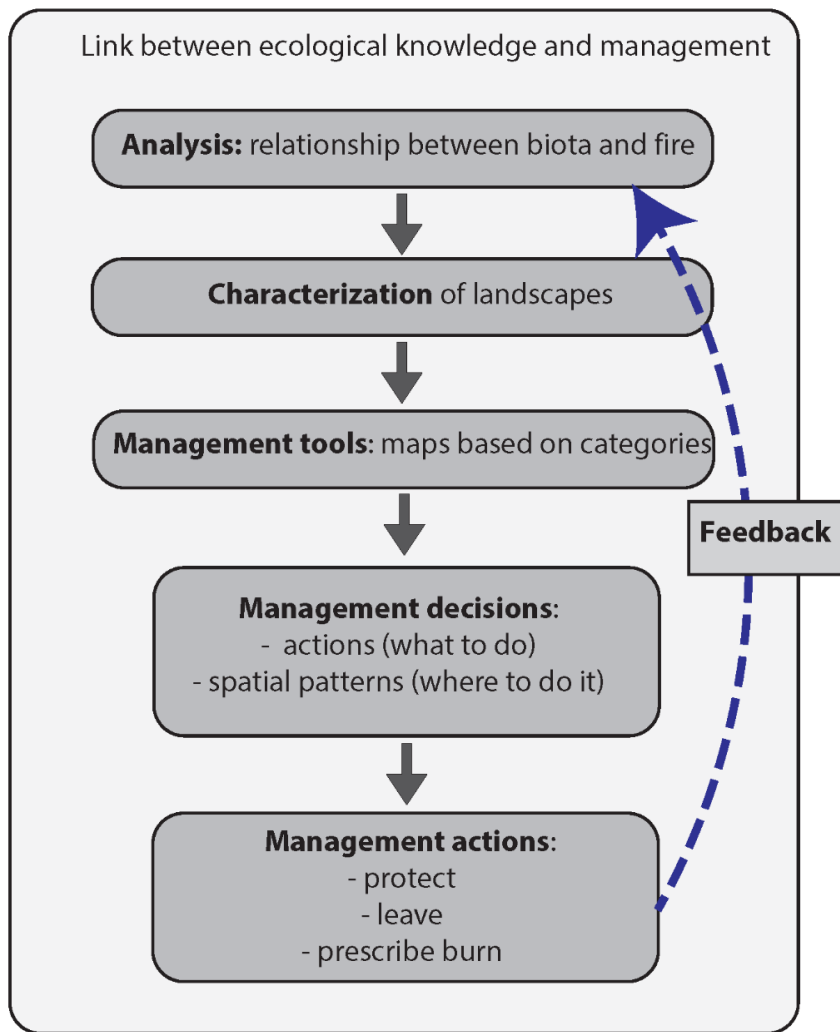


Figure 1.1. Conceptual model for understanding fire-driven patterns of biodiversity: the link between understanding the relationships between fire and biota and management.

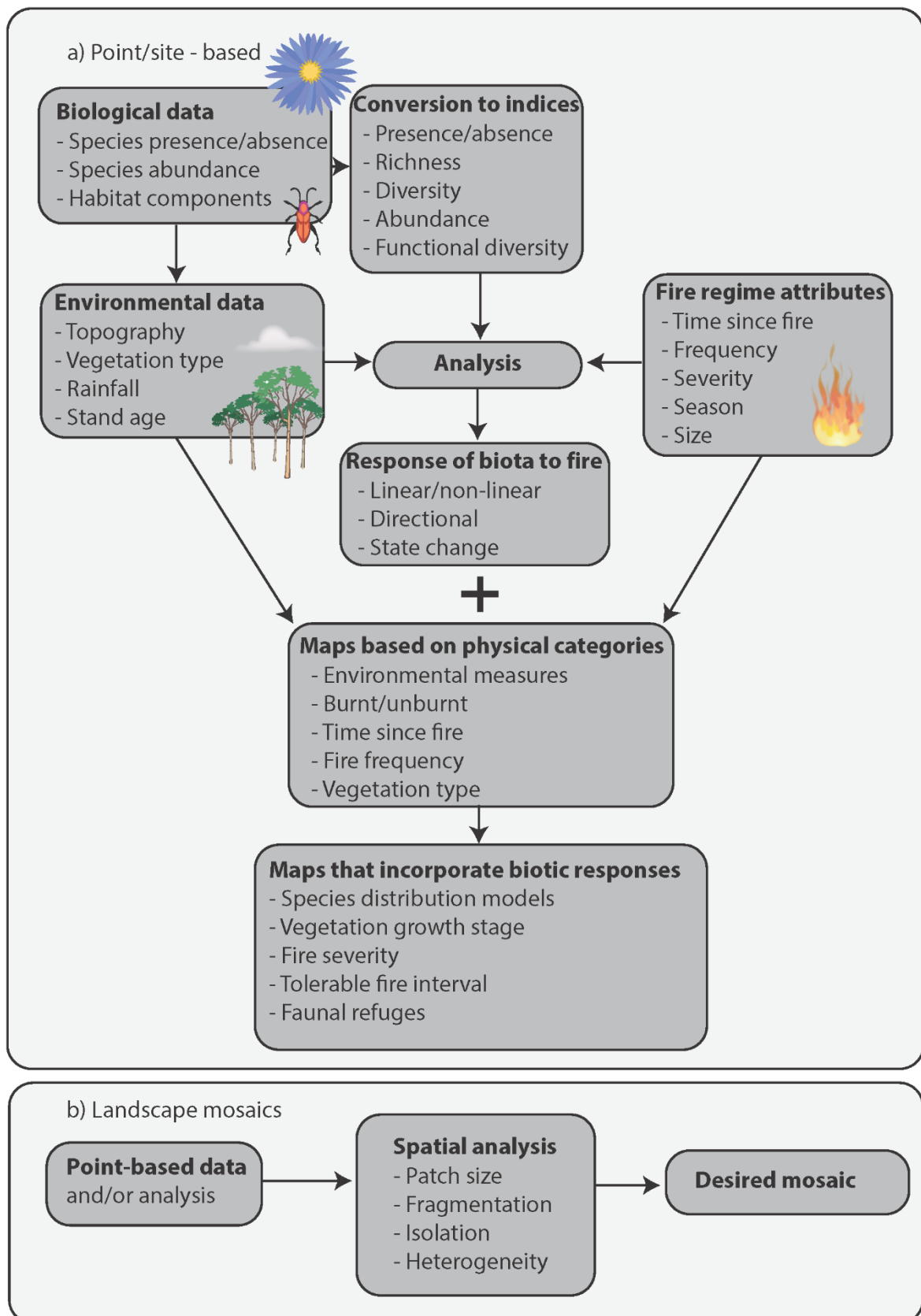


Figure 1.2. Two main paradigms through which fire-biota relationships are analysed and understood. a) point/site based, b) landscape mosaics.

## **1.7 FIRE MANAGEMENT IN VICTORIA**

Fire management for biodiversity has focused mainly on the timing of recurrent fires and the spatial arrangement of fire (Kelly and Brotons 2017). In Victoria, fire management is guided by two main paradigms: tolerable fire intervals and vegetation growth stage structure, both of which are based on the response of plants to fire (York and Friend 2016). The minimum tolerable fire interval for an ecological community is defined as the minimum time needed between fires for key plant species to reach reproductive age and successfully reproduce. The maximum tolerable fire interval refers to the maximum time before a species begins to senesce (Noble and Slatyer 1980). Vegetation growth stages are categories based on the time since last fire, that aim to represent temporal post-fire changes in plant and animal communities (Cheal 2010). The amount and distribution of vegetation in each of these categories can be manipulated (e.g. by prescribed burning or fire exclusion) through space to achieve management objectives (e.g. increase the proportion of old growth vegetation in the landscape).

To assign vegetation growth stages to ecosystems, the time since fire (fire regime attribute, Fig. 1.2) and vegetation type (environmental data) at sites are used to determine stages in the post-fire life cycle of plant species (biological data) (e.g. seedling, juvenile, reproduction age) (analysis). Growth stages are then described for an ecosystem (e.g. stages may include renewal 0-0.5 years, juvenile 0.5-3 years, adolescent 4-10 years, mature 11-35 years, stasis 36-90 years) that represent distinct stages in the post-fire succession, but depend on the ecosystem. Descriptions of growth stages are largely based on expert elicitation and observations, rather than detailed analyses. The timing of these growth stages may vary between the different broad vegetation types in a region (Cheal 2010).

Vegetation type (static attribute) and time since fire (dynamic attribute) are assessed together to determine the spatial distribution of growth stages across a landscape at a given point in

time – which can be termed the ‘growth stage structure’ for the landscape. To guide decisions pertaining to specific management objectives (e.g. desired growth stage structure), fire managers calculate the proportion of the landscape in each growth stage (Cheal 2010). For example, if the diversity of a taxonomic group of interest is greater in younger growth stages, prescribed burns may be implemented to skew the landscape-wide distribution of growth stages towards younger vegetation (Chick et al. 2019).

For vegetation growth stages to reliably represent distinct successional communities, the distribution of plants and animals in ecosystems managed under this paradigm must be clearly related to time since fire, and these relationships be known. In ecosystems that experience stand-replacing fires (e.g. mallee woodlands), fire incinerates the above-ground component of the vegetation, it sets the successional stage of the vegetation back to time zero, and regeneration through successional stages then occurs over decades (Clarke et al. 2010). In such ecosystems, the development of habitat structural components, likewise, continues over decades (Haslem et al. 2011). In such stand-replacing ecosystems, vegetation growth stages appear to be useful in broadly representing faunal communities.

However, recent work has shown that time since fire is a relatively poor predictor of faunal species occurrences in other ecosystems, such as stringybark *Eucalyptus* forests (Sitters et al. 2014a, Kelly et al. 2017b). A key feature of stringybark *Eucalyptus* forests is the capacity for canopy trees to persist through fire and regenerate rapidly via epicormic buds (Collins 2020). In ecosystems dominated by trees that resprout epicormically, key habitat components for fauna (e.g. large old trees) are present immediately after fire. It is likely that differences in post-fire stand-regeneration system between ecosystems, correspond to differences in the influence of time since fire on ecosystem structure. If so, this has implications for the relevance and effectiveness of using vegetation growth stages as a common management approach across all ecosystems.

These observations lead to the overarching hypothesis of this thesis: that the influence of time since fire in shaping the distribution of species differs between ecosystems, depending on the regeneration traits of the dominant canopy trees. If this is true, then the approach of using growth stages in the same way across all ecosystems, as a common tool for classifying ecosystems for landscape-scale fire management needs to be reconsidered.

Below I outline the structure of this thesis in relation to three main research themes: (1) the effect of time since fire on fauna, (2) the effect of fire management practices on biodiversity and (3) the effect of spatial patterns of fire on biodiversity (Fig. 1.3).

## **1.8 THESIS STRUCTURE**

In this thesis, I use empirical data to determine how fire, habitat structure, species life-history traits and management practices shape bird and plant communities in fire-prone ecosystems. The diversity of species, life-forms and functional types, and the different evolution of birds and plants, make these taxa ideal indicator groups to explore the influence of fire on biodiversity in different settings.

Chapters 2 and 3 focus on the influence of time since fire on the distribution of faunal species (Theme 1, Fig. 1.3). In Chapter 2, I tested whether the influence of time since fire on faunal habitat structure differs between ecosystems, based on the regeneration traits of the canopy trees. I used data from sites across an 80-year post-fire chronosequence in mallee woodlands (basal resprouting, 98 sites, Fig. 1.4a-b), heathy woodlands (epicormic resprouting, 38 sites, Fig. 1.4c-d) and foothill forests (epicormic resprouting, 38 sites, Fig. 1.4e-f) to determine how attributes of the ground cover, understorey vegetation and canopy tree structure changed over time following fire.

In Chapter 3, I then modeled the associations of bird species with the habitat attributes in Chapter 2 to test whether the most limiting habitat components for bird species post-fire

differed between ecosystems. By testing: (a) which habitat components were related to time since fire; and (b) which of these limited the distribution of birds, I aimed to determine how the influence of time since fire on birds might differ between ecosystems based on the stand-regeneration pattern (epicormic resprouting vs. basal resprouting).

Chapters 4 and 5 explore the influence of fire management practices on biodiversity (Theme 2, Fig. 1.3). In Chapter 4, I determined how fire shapes the bird and plant communities in a heathy *Eucalyptus* woodland ecosystem. With this new knowledge, I then evaluated how fire management practices based on two metrics (tolerable fire intervals, vegetation growth stage structure), which were developed from the functional traits of plants, influence the bird and plant communities.

In Chapter 5, I investigated how prescribed fire shapes bird and plant communities in temperate dry forests. In Australia, temperate dry forests are likely to experience increased prescribed fire as public pressure to reduce forest fuel loads increases. This chapter addresses the key conservation question: how will more widespread prescribed burning in temperate dry forests affect the biota?

In Chapter 6, I analysed the influence of the spatial configuration of fire in the landscape (e.g. area burnt, diversity of fire ages) on the distribution of birds, and how this might differ between two broad ecosystems (mallee woodlands, foothill forests).

Finally, in Chapter 7, I synthesized the key findings from this thesis in relation to the global literature and discuss the implications for conservation management in fire-prone landscapes. To test the cross-continental applicability of the key findings, I used a systematic search of the literature and a meta-analytic approach to test the hypothesis that the influence of time since fire on bird species depends on the regeneration traits of the canopy trees.

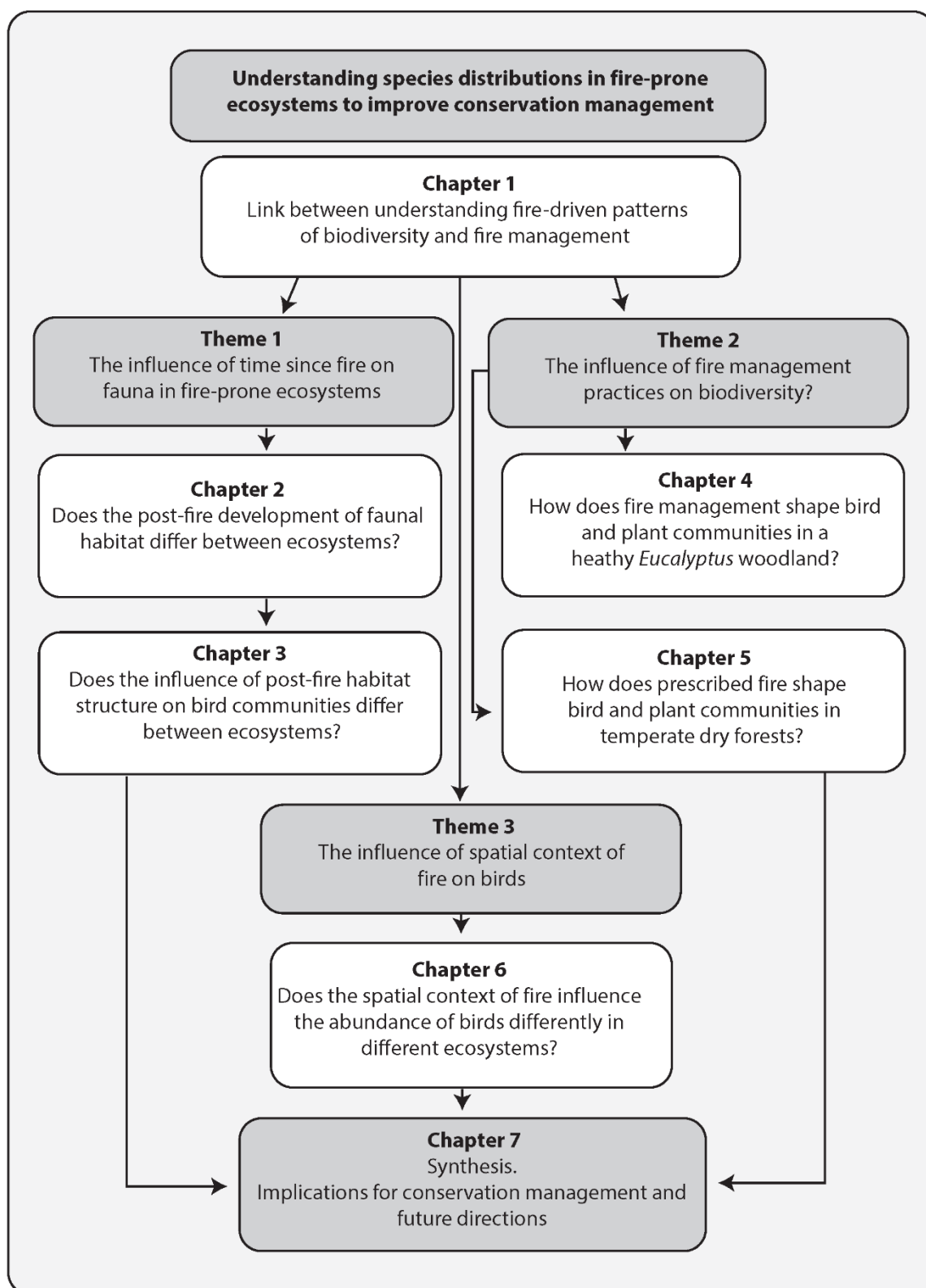


Figure 1.3. Thesis structure.



Figure 1.4. The three study ecosystems. (a – b) Mallee woodlands, (c – d) heathy woodlands, (e – f) foothill forests. Photo credits: a - b = Mallee Fire and Biodiversity Project, c - f = FR.

## **1.9 NOTE ON TERMINOLOGY**

Throughout the thesis I refer to ‘stand-replacing’ and ‘structurally resilient’ ecosystems.

These terms refer to the typical post-fire stand-regeneration patterns of ecosystems. In the literature, ‘stand-replacing’ is used to describe situations in which fire kills the canopy trees, which then regenerate from seed. Here, I have extended this to include basal-resprouting trees. Because basal-resprouting trees survive fire, technically fires do not ‘replace’ the stand of trees. However, in terms of above-ground habitat structure, these are effectively stand-replacing fires.

## 2 POST-FIRE DEVELOPMENT OF FAUNAL HABITAT DEPENDS ON PLANT REGENERATION TRAITS

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Rainsford, F. W., L. T. Kelly, S. W. J. Leonard, and A. F. Bennett. 2020. Post-fire development of faunal habitat depends on plant regeneration traits. *Austral Ecology* doi:10.1111/aec.12896.



Mallee eucalypt resprouting basally following a fire. Credit: Mallee Fire and Biodiversity Project

## 2.1 ABSTRACT

The concept that vegetation structure (and faunal habitat) develops predictably with time since fire has been central to understanding the relationship between fire and fauna. However, because plants regenerate after fire in different ways (e.g. resprouting from above-ground stems vs. underground lignotubers), use of simple categories based on time-since-fire might not adequately represent post-fire habitat development in all ecosystems. We tested the hypothesis that the post-fire development of faunal habitat structure differs between ecosystems, depending on fire regeneration traits of the dominant canopy trees. We measured 12 habitat components at sites in foothill forests ( $n = 38$ ), heathy woodlands ( $n = 38$ ) and mallee woodlands ( $n = 98$ ) in Victoria, Australia and used generalised additive models to predict changes in each variable with time since fire. A greater percentage of faunal habitat variables responded significantly to time since fire in mallee woodlands, where fires typically are stand-replacing, than in foothill forests and heathy woodlands, where canopy tree stems generally persist through fire. In the ecosystem with the highest proportion of epicormic resprouters (foothill forests), only ground cover and understorey vegetation responded significantly to time since fire, compared with all but one variable in the ecosystem dominated by basal resprouters (mallee woodlands). These differences between ecosystems in the post-fire development of key habitat components suggest there may also be fundamental differences in the role of fire in shaping the distribution of fauna. If so, this challenges the way in which many fire-prone ecosystems are currently categorised and managed, especially the level of dependence on time since fire and other temporal surrogates such as age-classes and successional states. Where time since fire is a poor surrogate for habitat structural development, additional complexity (e.g. fire severity, topography, prior land-use history) could better capture processes that determine faunal occurrence in fire-prone ecosystems.

## 2.2 INTRODUCTION

Fire-prone ecosystems have evolved under particular temporal and spatial patterns of fire occurrence (Bond and Keeley 2005, Archibald et al. 2018, Pausas and Parr 2018).

Consequently, plants have regeneration traits that help them survive and reproduce after fire, such as resprouting from dormant buds and fire-cued germination (Pausas and Keeley 2014).

However, in many regions fire regimes are changing. First, with climate change, many regions are becoming hotter and drier, increasing the likelihood of more frequent and severe wildfires in many forests and woodlands (Bradstock 2010, Stephens et al. 2013). Second, contemporary fire-management activities such as fire suppression and prescribed burning may be incongruous with natural or historic regimes (Giljohann et al. 2015, Connell et al. 2017). Third, humans have altered ignition patterns and the spread of fire through land-use changes (Bowman et al. 2011). In the face of such changes, understanding the relationships between fire, plant regeneration and faunal habitat development is essential to conserve faunal diversity while also achieving other management goals.

Fire can affect the distribution of fauna directly by removing individuals, and indirectly by changing vegetation composition and structure and, therefore, the available habitat (Fox et al. 2003, Pausas and Parr 2018). Understanding how habitat changes through time in fire-prone ecosystems can help ecologists and land managers to better predict the impact of fire on fauna and identify species that could potentially be at risk due to changing fire regimes (Haslem et al. 2011). Indeed, the time between fires is widely used as a surrogate for animal and plant distributions, an idea captured by related terms in the fire ecology literature including ‘age-classes’ and ‘successional states’ (Cohn et al. 2015, Giljohann et al. 2015).

A common management paradigm is based on the idea that post-fire vegetation development follows a successional pathway that facilitates faunal occupancy associated with different successional states. Support for this approach has come from studies of taxa in a range of

ecosystems: for example, small mammals in shrubby heathlands in Australia (Fox 1982) and in savannas of the Brazilian Cerrado (Briani et al. 2004); reptiles in semi-arid woodlands in Australia (Nimmo et al. 2012); and birds in boreal forests in Canada (Haney et al. 2008) and in shrublands in the European Pyrenees (Pons and Clavero 2010). In each of these systems, the association of faunal species with post-fire successional states is linked to changes in vegetation structure that enhance faunal habitat.

An emphasis on post-fire succession underpins current fire management in our study region, the state of Victoria, Australia. Landscape-scale fire management is guided by two main measures: Tolerable Fire Interval (TFI) and Vegetation Growth Stage Structure (GSS) (York and Friend 2016). Tolerable fire intervals are determined for stands of vegetation based on the minimum and maximum intervals between fires that will prevent plant species loss (Cheal 2010). Vegetation Growth Stages are time-since-fire categories assumed to represent distinct assemblages of flora, fauna and habitat attributes (Cheal 2010). Fire management aims to maintain desirable combinations of Growth Stages in landscapes to conserve biodiversity. The applicability of these measures requires that biodiversity values develop predictably with time since fire.

Ecosystems may vary in the way in which vegetation structural changes correspond to time since last fire. In some ecosystems, such as those listed above, fires typically are ‘stand-replacing’: above-ground vegetation is removed, and regeneration occurs from the ground-up (Keeley and Rundel 2005, Clarke et al. 2010). In others, such as *Pinus canariensis* woodlands on Canary Island (Pausas and Keeley 2017) and stringybark eucalypt forests in Australia (Burrows 2013), canopy tree stems generally persist through fire and regeneration occurs rapidly, facilitated by epicormic buds. Thus, the role of time since fire in the long-term development of vegetation structure (and faunal habitat) may differ fundamentally between ecosystems: for example muted influence of time since fire on vertebrates in temperate

eucalypt forests (Kelly et al. 2017b) compared to a strong influence on fauna in stand-replacing ecosystems (e.g. Pons and Clavero 2010, Watson *et al.* 2012). If this is true, there may be a need to re-think the way in which some fire-prone ecosystems are currently categorised and managed. For example, if faunal habitat does not change predictably with time since fire in all ecosystems, then management strategies could be more effective by concentrating on the actual habitat features that influence fauna.

We sampled vegetation structural attributes across a chronosequence of time since fire in three eucalypt-dominated ecosystems in Victoria, south-eastern Australia: foothill forests, heathy woodlands and mallee woodlands to compare the post-fire dynamics of faunal habitat structure. These three ecosystems are dominated by *Eucalyptus* species with contrasting fire regeneration traits. The thick-barked canopy trees in foothill forests generally survive fire and regenerate rapidly from protected epicormic buds along the trunk and branches (Fig. 2.1a – c). Canopy trees in heathy woodlands may survive fire and regenerate from epicormic buds, or basally from lignotubers (Fig. 2.1d – e). Fires in mallee woodlands typically are stand-replacing: the above-ground vegetation is consumed by fire and the canopy trees resprout

basally from lignotubers, such that the system regenerates from the ground-up (

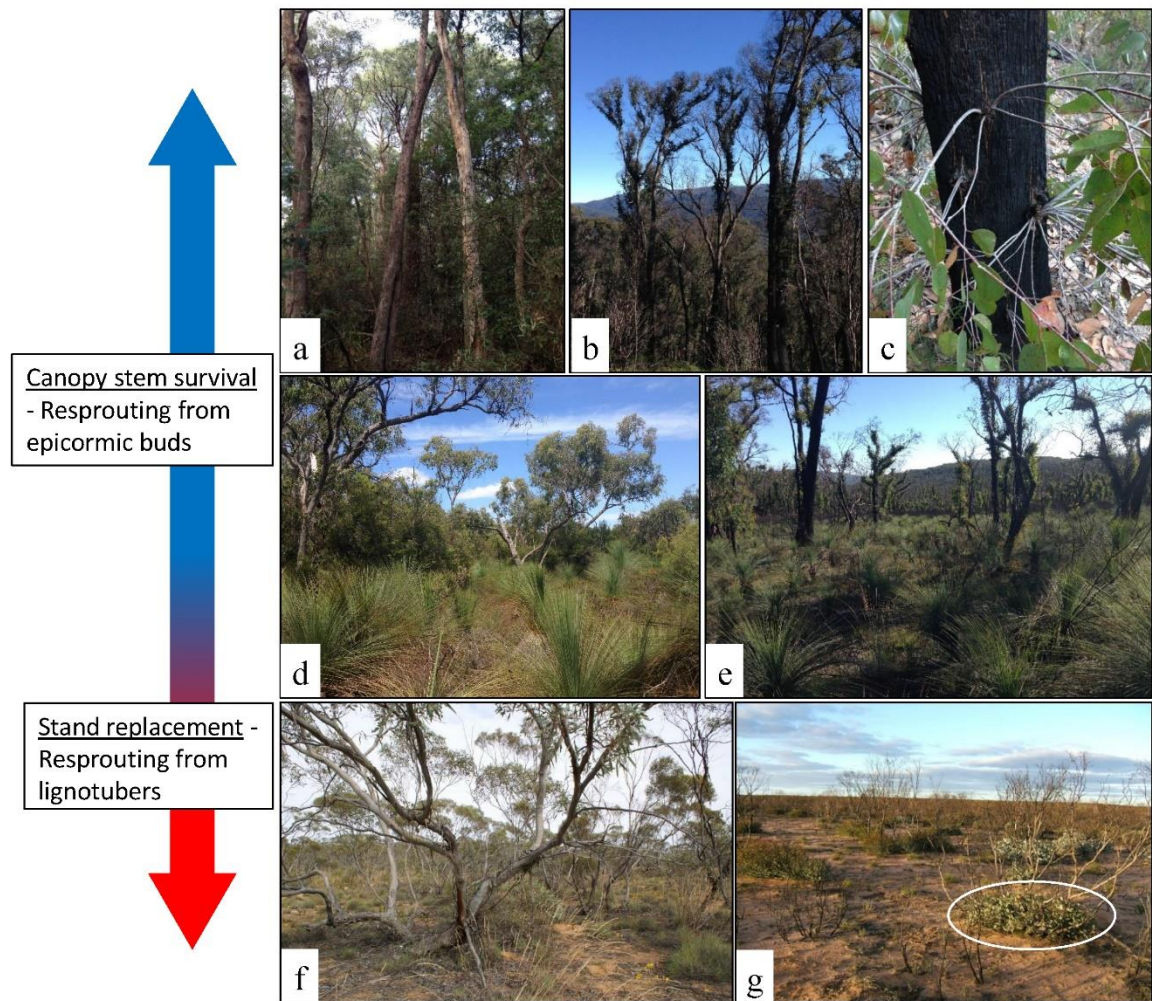


Figure 2.1 f – g).

We aimed to capture elements of the ground cover, understorey vegetation and canopy structure (Table 2.1) that represent important habitat attributes for faunal species in forests and woodlands (Table 2.2). For example, leaf litter and understorey shrubs provide foraging substrate, shelter and nesting sites for birds, invertebrates, reptiles and terrestrial mammals (Fox et al. 2003, McElhinny et al. 2006, Kelly et al. 2011, Nimmo et al. 2012); and large trees provide resources such as den sites, nest hollows and foraging substrates for arboreal mammals and hollow-nesting birds (McElhinny et al. 2006, Bennett 2016). Understanding the post-fire dynamics of these habitat attributes will provide insight into how time since fire influences the distribution of faunal species within fire-prone ecosystems.

We hypothesised that the post-fire development of faunal habitat structure differs between ecosystems, depending on the extent to which fire is stand-replacing for the dominant canopy trees, or whether canopy tree stems persist and recover rapidly. Specifically, we address the following predictions: (1) the number and breadth of habitat structural components that respond to time since fire will be greater in ecosystems in which fires typically are stand-replacing than in ecosystems where canopy tree stems persist through fire; (2) in ecosystems in which canopy tree stems persist through fire, components of the ground layer structure will be driven by time since fire, but not components of the canopy structure; and (3) in ecosystems in which fires are stand-replacing, the development of all main habitat structural components will be driven by time since fire.

## **2.3 METHODS**

### **2.3.1 Study location and ecosystems**

We studied three eucalypt-dominated ecosystems in Victoria, Australia: foothill forests, heathy woodlands and mallee woodlands (Fig. 2.2). A key difference between these distinct ecosystems is the proportion of epicormic resprouting trees vs. basal resprouting trees. Related differences, such as local climate, topography and fire regimes are described below.

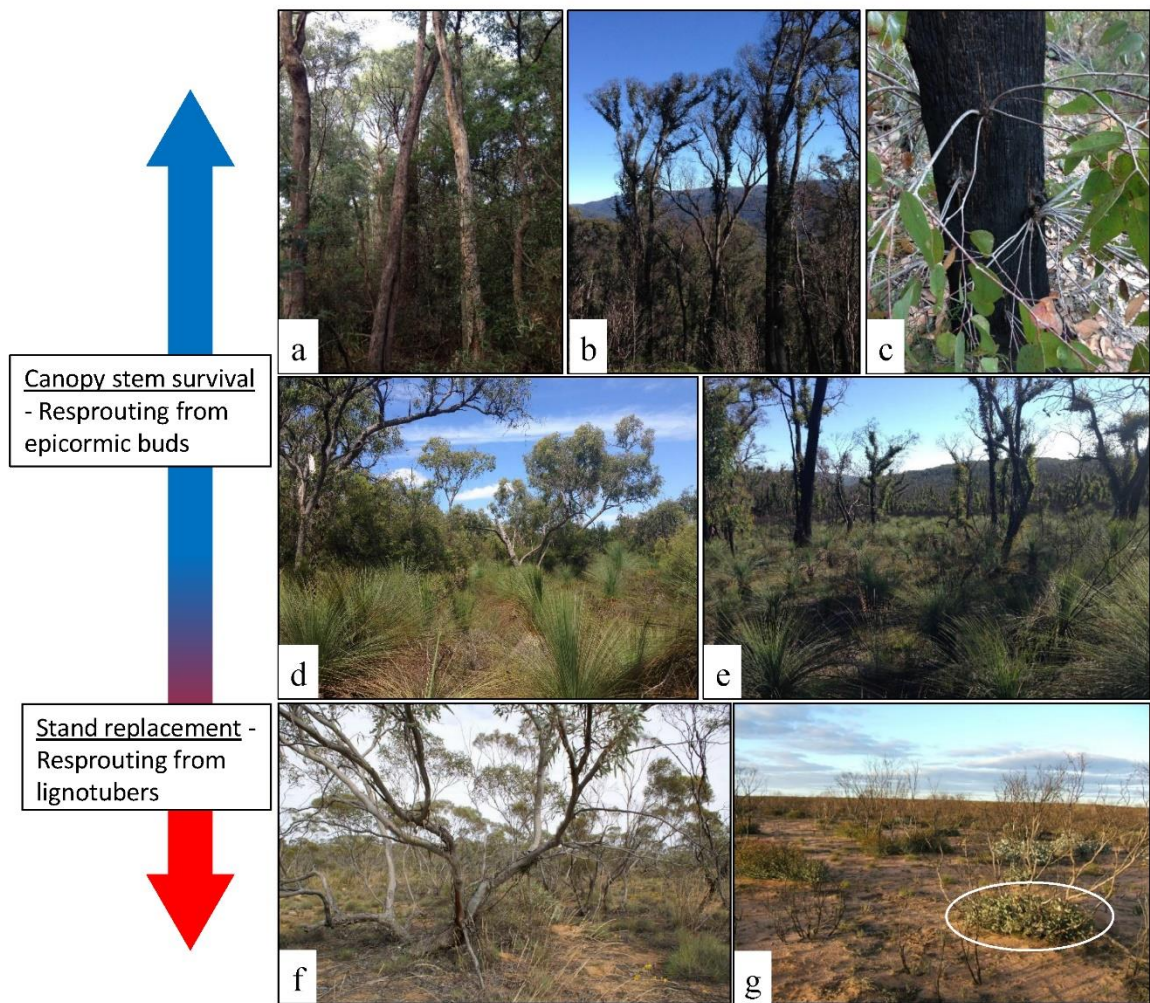


Figure 2.1 Post-fire regeneration of the vegetation in the study ecosystems. 1. Foothill forests: (a) long unburnt vegetation and (b - c) epicormic resprouting in recently burnt eucalypts. 2. Heathy woodlands: (d) long unburnt vegetation and (e) epicormic resprouting in recently burnt eucalypts. 3. Mallee woodlands: (f) long unburnt vegetation and (g) recently burnt eucalypts resprouting from lignotubers. The blue and red arrow represents a gradient of stand-replacement (bottom) to stand-survival (top). Photo credits: FR (a – e), Mallee Fire and Biota Project (f – g).

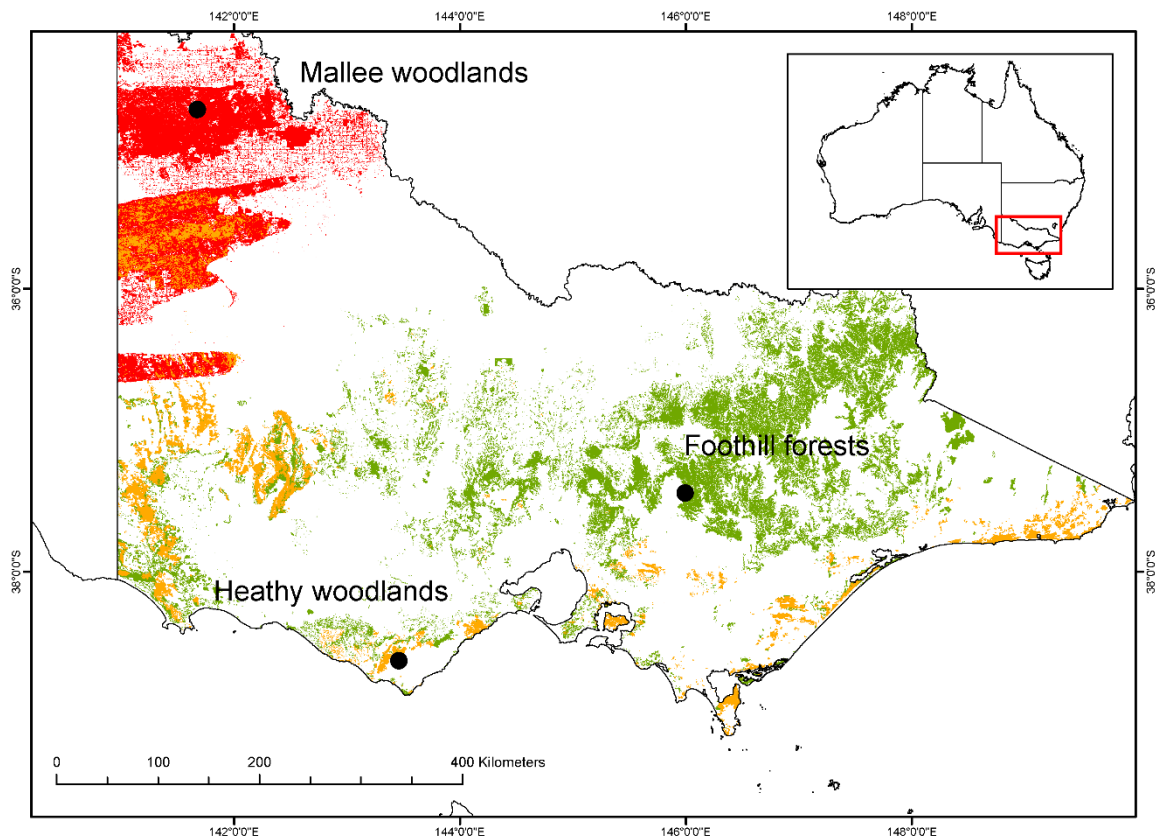


Figure 2.2. Locations of study areas in foothill forests, heathy woodlands and mallee woodlands in Victoria, Australia. The distribution of Ecological Vegetation Divisions (EVDs) that correspond to the three ecosystems studied: foothill forests (green; EVDs = foothills forest, forby forests), heathy woodlands (orange; EVD = heathland sands) and mallee woodlands (red; EVDs = chenopod mallee, hummock-grass mallee, lowan mallee) (Victorian Department of Environment, Land, Water and Planning).

### 2.3.2 Climate and topography

The generic term ‘foothill forests’ refers to temperate eucalypt forests that occur on the lower- to mid-slopes of the Great Dividing Range, covering ~75 000 km<sup>2</sup> in Victoria. The climate is temperate with a mean annual rainfall of ~850 mm. The highest rainfall occurs in winter (August) and the hottest month is February (mean daily maximum ~29°C) (Lake Eildon, station no. 083023; <http://www.bom.gov.au/>). Foothill forests occur on mountainous terrain, often with steep slopes and densely vegetated gullies. Elevation in the study area ranges between ~ 450 and 950 m above sea-level.

Heathy woodlands occur sparingly throughout coastal areas of south-eastern Australia on nutrient-poor, deep sandy soils of quartzite gravel. The climate in the heathy woodlands study area is also temperate with a mean annual rainfall ranging from 540 – 895 mm. The highest rainfall occurs in winter (August) and the hottest month is February (mean daily maximum 28°C) (Mount Gellibrand, station no. 0900351, Cape Otway lighthouse, station no. 090015; <http://www.bom.gov.au/>). The topography in the heathy woodlands study area is gently undulating with elevation ranging between ~40 and 250 m above sea-level.

Mallee woodlands cover an area of ~ 100 000 km<sup>2</sup> in the semi-arid zone of south-eastern Australia. Summers are hot and dry, and winters are mild. Mean annual rainfall is ~290 mm. The highest rainfall occurs in spring and the hottest month is January (mean daily maximum ~32°C) (Mildura Airport, station no. 076031; <http://www.bom.gov.au/>). Mallee woodlands occur on low-lying ( $\leq 100$  m above sea-level) terrain with little topographic variation. An extensive dune-swale system characterises the region with sandy dunes receding to clayey swales.

### **2.3.3 Vegetation**

Foothill forests are the tallest of the three ecosystems, with canopy trees reaching heights of 30 – 60 m, often accompanied by a secondary tree layer of *Acacia* spp. The term ‘foothill forests’ encapsulates several similar but distinct vegetation communities, ranging from wetter forest-types in gullies to drier forest-types on ridge tops and steep north-facing slopes. To avoid inherent differences in vegetation composition and structure between gullies and ridges, sites in this study were limited to a single Ecological Vegetation Class (EVC): ‘herb-rich foothills forest’ (Victorian Government Department of Sustainability and Environment 2004a). The dominant canopy species at these sites were messmate stringybark (*Eucalyptus obliqua*), broad-leaved peppermint (*E. dives*), narrow-leaved peppermint (*E. radiata*), and mountain grey-gum (*E. cypellocarpa*). Small trees and shrubs constitute the understorey,

including blackwood (*Acacia melanoxylon*), prickly currant-bush (*Coprosma quadrifida*), common cassinia (*Cassinia aculeata*), and ferns such as austral bracken (*Pteridium esculentum*). The ground layer consists of a rich cover of herbs.

In heathy woodlands, a low canopy ( $\leq 10$  m) of eucalypts occurs over a diverse array of ericoid-leaved shrubs that form a dense understorey over time, following disturbance. The dominant canopy species are brown stringybark (*E. baxteri*) and western peppermint (*E. fasciata*). The main understorey shrubs include austral grass tree (*Xanthorrhoea australis*), heath tea-tree (*Leptospermum myrsinoides*), prickly tea-tree (*L. continentale*) and silver banksia (*Banksia marginata*) (Victorian Government Department of Sustainability and Environment 2004b). Fire regeneration traits of understorey species vary: tea trees resprout from basal lignotubers, austral grasstree resprouts apically, and silver banksia regenerates from seed.

Mallee woodlands are characterised by a low ( $\leq 6$  m) canopy of multi-stemmed *Eucalyptus* species. Three broad vegetation types have been described in this system; Triodia Mallee, Chenopod Mallee and Heathy Mallee, based on their floristic and structural differences (Haslem et al. 2010). We limited this study to Triodia Mallee because responses of both flora and fauna to fire can differ between vegetation types (Haslem et al. 2011). The low canopy is generally dominated by dumosa mallee (*E. dumosa*) and grey mallee (*E. socialis*). The understorey is dominated by porcupine grass (*Triodia scariosa*) and *Acacia* spp.

#### **2.3.4 Fire regimes**

In all three ecosystems, wildfires typically occur in summer (Dec – February), whereas prescribed burns are undertaken in autumn and spring months. Large wildfires ( $> 10\,000$  ha) have occurred within the wider foothill forests region in 1939, 1962, 1983, 2003, 2005, 2006, 2009 and 2014 (Victorian Government Department of Environment, Land, Water and Planning 2015), and in the mallee woodlands region they occur approximately decadal

(Avitabile et al. 2013). Prescribed burning is undertaken in all three ecosystems to achieve management goals relating to fuel reduction and ecosystem resilience. Minimum tolerable fire intervals are used to guide the timing of prescribed burns: these are 15 years for foothill forests, 12 years for heathy woodlands and 25 years for mallee woodlands (Cheal 2010). In foothill forests, but not heathy woodlands, prescribed burns typically do not scorch the canopy (Gill 2012). In mallee woodlands, both wildfires and prescribed burns typically are stand-replacing.

### **2.3.5 Study design**

We employed a space-for-time approach in each ecosystem to compare the post-fire development of key faunal habitat components. Sites were selected to span a chronosequence from one (foothill forests and heathy woodlands) or two years (mallee woodlands) to 80 years post-fire, and to cover a range of post-fire successional states based on the vegetation growth stages described by Cheal (2010) (see Appendix 2.6.1).

We sampled foothill forests from 38 sites positioned on slopes at least 100 m from a gully and 50 m from a ridge top within an  $\sim 320 \text{ km}^2$  area of the Highlands Southern Fall ( $-37.516 \text{ S}$ ,  $146.042 \text{ E}$ ), heathy woodlands from 38 sites within an  $\sim 100 \text{ km}^2$  area of the Great Otway National Park and Forest Park ( $-38.608 \text{ S}$ ,  $143.346 \text{ E}$ ), and used data collected from 98 sites within a  $4\,200 \text{ km}^2$  area of the Murray-Sunset and Hattah-Kulkyne National Parks ( $-34.757 \text{ S}$ ,  $141.628 \text{ E}$ ) in north-west Victoria (Fig. 2.2).

There was a greater number of sites in the mallee woodlands as these were surveyed as part of a project that investigated the responses of multiple taxa to fire mosaics across the whole Murray-Mallee region, covering parts of Victoria, New South Wales and South Australia (Haslem et al. 2012, Nimmo et al. 2012, Watson et al. 2012b). To reduce the influence of rainfall and temperature gradients on vegetation structure (Kenny et al. 2018), this study was restricted to mallee sites within Victoria. There were disproportionately more sites in the 11-

35 years-since-fire category, so we took a random sample of 21 sites from this growth stage to ensure even coverage of the chronosequence (Appendix 2.6.1).

### **2.3.6 Fire history**

The fire history of foothill forests and heathy woodlands sites was determined by using spatial data maps of fire history supplied by the Victorian Department of Environment, Land, Water and Planning, and analysed using the software ArcMap (ESRI 2011). The mapped time since fire was ground-truthed at each site by looking for signs of charring on eucalypt bark and other structural features of the vegetation.

The fire history of sites in mallee woodlands was ascertained in two ways. For sites burnt post 1972, Landsat imagery and existing fire mapping were used to determine the exact year of the last fire (Avitabile *et al.* 2013). For sites burnt prior to 1972, time since fire was deduced by using regression models of the relationship between stem diameter and tree age (time since fire) (Clarke *et al.* 2010).

Fires of different severity can affect habitat structural components differently in some vegetation types (Bassett *et al.* 2017). Prescribed burns, undertaken for fire management in cooler periods, are usually of a lower intensity than wildfires and tend not to reach the canopy in foothill forests. To control for fire severity in foothill forests, fire-type of the last fire was limited to prescribed burns at all sites, except for the oldest time since fire. Prescribed burns were not used routinely in fire management until the 1970s, so sites burnt prior to this were last burnt during a 1939 wildfire. Because of recent large wildfires in the study area, limiting fire-type to wildfire while covering an adequate range of age-classes was not possible without introducing effects of climate and environmental gradients. Previous work in foothill forests found that fire-type had a relatively minor influence on the distributions of species at temporal scales similar to that used here (Kelly *et al.* 2017b).

Heathy woodlands were sampled at sites burnt either during prescribed burns or wildfires as there were insufficient sites available within a single fire-type. Based on observations of resprouting eucalypts, fire severity does not vary greatly between prescribed burns and wildfires in heathy woodlands because both fire-types typically reach the canopy. In mallee woodlands, both prescribed burns and wildfires also generally reach the canopy, consume above-ground vegetation and are stand-replacing (Haslem *et al.* 2011); as such, both fire-types were included for these two systems.

### **2.3.7 Data collection**

We sampled faunal habitat structural components in each ecosystem covering three broad categories: (i) ground cover, (ii) understorey vegetation and (iii) canopy structure (Table 2.1).

The type of ground cover and the depth of leaf litter (cm) were recorded at 1 m intervals along a 50 m transect, and these data were used to calculate percentage cover of different ground cover types and mean litter depth, respectively. At each point (1 m interval) the number of intercepts of living vegetation in different height categories was recorded using a 2 m ranging pole and these data were used to estimate the percent cover of understorey vegetation.

To assess the canopy structure in each ecosystem, we recorded the number and diameter at breast height (DBH) of living eucalypt trees at each site. In foothill forests, we used the point-centred quarter method (PCQM) (Cottam and Curtis 1956). At each site, two parallel transects were established 40 m apart that ran perpendicular to the slope. At 10 points at 20 m intervals along each transect (total of 20 points per site) we measured the DBH and distance to the nearest tree in each quarter of 360 degrees (total of 80 stems per site). A minimum of 20 points (80 stems) is required to estimate canopy tree density in forests (Ruch *et al.* 2008). In heathy woodlands a 4 m × 250 m quadrat, and in mallee woodlands a 4 m × 50 m quadrat were used to record canopy trees. To compare the post-fire development of habitat structural

components between ecosystems, we then calculated 12 variables considered to be important for fauna within each ecosystem (Table 2.1). Differences between ecosystems in the size categories for certain variables represent inherent differences in vegetation structure.

Table 2.1. Habitat structure variables calculated for foothill forests, heathy woodlands, mallee woodlands in south-eastern Australia. The range of values for each variable in each ecosystem is given, together with a description of the variable. FF = foothill forests, HW = heathy woodlands, MW = mallee woodlands.

<b>Habitat category</b>	<b>Variable</b>	<b>Foothill forests</b>	<b>Heathy woodlands</b>	<b>Mallee woodlands</b>	<b>Description</b>
<b>Ground cover</b>	Bare ground cover	0-70	0-76	4-94	Percent (%) cover of bare ground
	Litter cover	28-100	20-98	0-90	Percent (%) cover of leaf litter
	Litter depth	0.4-9.4	0.13 -4.1	0-2.7	Mean depth of leaf litter (cm)
	Plant cover	0-32	0-32	0-28	Percent (%) cover of plants (includes shrubs, herbs and ferns)
<b>Understorey</b>	Lower-midstorey	21-89	42-96	0-54	Percent (%) cover of vegetation 0 – 1 m (FF, HW), 0 – 0.5 m (MW)
	Upper-midstorey	0-33	6-67	0-39	Percent (%) cover of vegetation 1 – 4 m (FF, HW), 0.5 – 2 m (MW)
<b>Canopy</b>	Basal area	23-76	0.37-2.22	0-6.9	Basal area cover of canopy trees (m <sup>2</sup> /ha)
	Density of large trees	147-324	200-1280	0-1800	Density (live stems/ha) of canopy trees with diameter greater than the median for that ecosystem (>25 cm FF; >8 cm HW; >4 cm MW).

<b>Habitat category</b>	<b>Variable</b>	<b>Foothill forests</b>	<b>Heathy woodlands</b>	<b>Mallee woodlands</b>	<b>Description</b>
	Maximum tree diameter	50-200	16-60	0-30	Diameter (cm) of the largest tree within the sample area
	Mean diameter of large trees	34-59	11.4-22.5	0-15.5	Mean diameter (cm) of trees with diameter greater than median for the ecosystem (>25 cm FF; >8 cm HW; >4 cm MW)
	Percentage of very large trees	11-45	3-76	0-100	Percent (%) of trees in the canopy stratum with diameter in the upper quartile for the ecosystem (>39 cm FF; >12 cm HW; >7 cm MW)
	Tree density	270-750	500-2900	150-2850	Density of canopy trees (live stems/ha)

Table 2.2. Key habitat attributes used by seven faunal groups, their associated resources and functions, and the habitat surrogate category used in our assessment. Adapted from a review by McElhinny *et al.* 2006 of fauna-habitat associations in Australian forests and woodlands.

Taxonomic group	Habitat attribute (McElhinny <i>et al.</i> 2006)	Associated resources/function (McElhinny <i>et al.</i> 2006)	Habitat surrogate category (present study)
Amphibians	Vegetation cover	Shelter, moist microclimate	Ground cover, understorey
	Ground debris	Shelter, refuge, foaging	Ground cover
Arboreal mammals	Foliage	Edible material	Canopy
	Flowers	Nectar, pollen	Understorey, canopy
	Bark	Exudates, invertebrates	Canopy
	Tree hollows	Den/nest sites, water	Canopy
Birds	Foliage	Exudates, invertebrates	Understorey, canopy
	Flowers	Nectar, invertebrates	Understorey, canopy
	Bark	Exudates, invertebrates	Canopy
	Ground layer	Invertebrates, small vertebrates	Ground cover
	Air spaces	Invertebrates	Understorey, canopy
	Tree hollows	Nest sites, shelter	Canopy
Bats	Foliage	Invertebrates	Understorey, canopy
(insectivorous)	Canopy space	Invertebrates	Understorey, canopy
	Hollows, decorticating bark	Roost/nest sites	Canopy
Ground mammals	Shrubs	Shelter	Understorey
	Litter	Nesting, invertebrates, fungi	Ground cover

Taxonomic group	Habitat attribute (McElhinny <i>et al.</i> 2006)	Associated resources/function (McElhinny <i>et al.</i> 2006)	Habitat surrogate category (present study)
Invertebrates	Foliage	Edible material, sap, shelter	Understorey, canopy
	Flowers	Nectar, pollen	Understorey, canopy
	Bark	Shelter, exudates, prey	Understorey, canopy
	Shrubs	Foliage, flowers, shelter	Understorey
	Litter, woody debris	Food, prey, shelter	Ground cover
Reptiles	Basking sites	Temperature regulation	Ground cover
	Litter	Invertebrates, cover	Ground cover
	Shrubs	Cover, invertebrates	Understorey

### 2.3.8 Data analysis

We used generalised additive models (GAMs) to determine the relationship between faunal habitat structure variables (Table 1) and time since fire (years). From visualisation of the observed data and consultation with the literature, GAMs were deemed appropriate as they model both linear and non-linear relationships and are useful when responses are unknown *a priori*. Generalised additive modelling is a regression modelling technique that uses a smoothing term to fit response curves to predictor variables (Wood 2019). We used a mixed-model approach (GAMM) for mallee woodlands as these data were collected from points clustered in landscapes (Haslem *et al.* 2011). Mixed models were fitted with landscape unit (1 – 12) as a random effect to account for spatial autocorrelation among sampled sites. Residual plots were examined to assess adherence to assumptions of normality of variance prior to analysis. Degrees of freedom ( $K$ ) for the smoothing term was initially set at four for all variables. However, model exploration indicated better models were fitted when  $K$  was set to three for the following variables: bare ground cover, mean diameter of large trees, and maximum tree diameter.

All analyses were conducted using the R statistical environment (R Development Core Team 2013) and the mgcv package (Wood 2019) and source scripts adapted from Elith *et al.* (2008) to calculate model deviance.

## 2.4 RESULTS

There were differences between ecosystems in the percentage of faunal habitat structure variables that responded to time since fire. In foothill forests, 33% (4/12) of variables had a significant response (i.e. p-values of regression models  $< 0.05$ ) to time since fire, compared with 58% (7/12) in heathy woodlands and 92% (11/12) in mallee woodlands (Fig. 2.3).

### **2.4.1 Foothill forests**

In foothill forests, two of the four ground cover variables, litter cover ( $P < 0.001$ ) and litter depth ( $P < 0.001$ ), increased significantly with time since fire (Fig. 2.3). Litter cover increased rapidly, reaching a peak at  $< 20$  years since fire, whereas litter depth increased linearly across the chronosequence. Both lower- ( $P < 0.001$ ) and upper-midstorey ( $P < 0.01$ ) vegetation cover increased with time since fire. However, none of the canopy structure variables showed a significant response to time since fire.

### **2.4.2 Heathy woodlands**

In heathy woodlands, three of the four ground cover variables, bare ground cover ( $P < 0.001$ ) litter cover ( $P < 0.001$ ) and litter depth ( $P < 0.001$ ), responded to time since fire (Fig. 2.3). Bare ground cover decreased rapidly to almost zero in late-successional states. Litter cover increased rapidly until  $\sim 20$  years since fire, after which it plateaued. Litter depth increased until  $\sim 25$  years since fire and then decreased before plateauing. Both lower- ( $P < 0.01$ ) and upper-midstorey ( $P < 0.001$ ) vegetation cover responded to time since fire. Lower-midstorey vegetation increased until  $\sim 25$  years since fire, then decreased to plateau at  $\sim 60$  years since fire. Upper-midstorey vegetation cover plateaued at  $\sim 50$  years since fire. Two of the five canopy structure variables, basal area ( $P < 0.05$ ) and maximum tree diameter ( $P < 0.01$ ) increased moderately with time since fire.

### **2.4.3 Mallee woodlands**

All but one of the faunal habitat structure variables that were modelled in mallee woodlands responded significantly to time since fire (Fig. 2.3). Bare ground cover ( $P < 0.001$ ) decreased with time since fire until  $\sim 40$  years post-fire. Litter cover ( $P < 0.001$ ) and litter depth ( $P < 0.01$ ) both increased linearly with time since fire. Plant cover increased with time since fire, but this was not significant ( $P = 0.283$ ). Lower-midstorey vegetation cover decreased with time since fire ( $P < 0.01$ ). Upper-midstorey vegetation cover showed a bell-shaped response,

peaking at ~ 30 years since fire ( $P < 0.01$ ). The size, density and distribution of large trees all increased, whereas tree density ( $P < 0.01$ ) decreased linearly with increasing time since fire.

Model outputs can be found in Appendix 2.6.2.

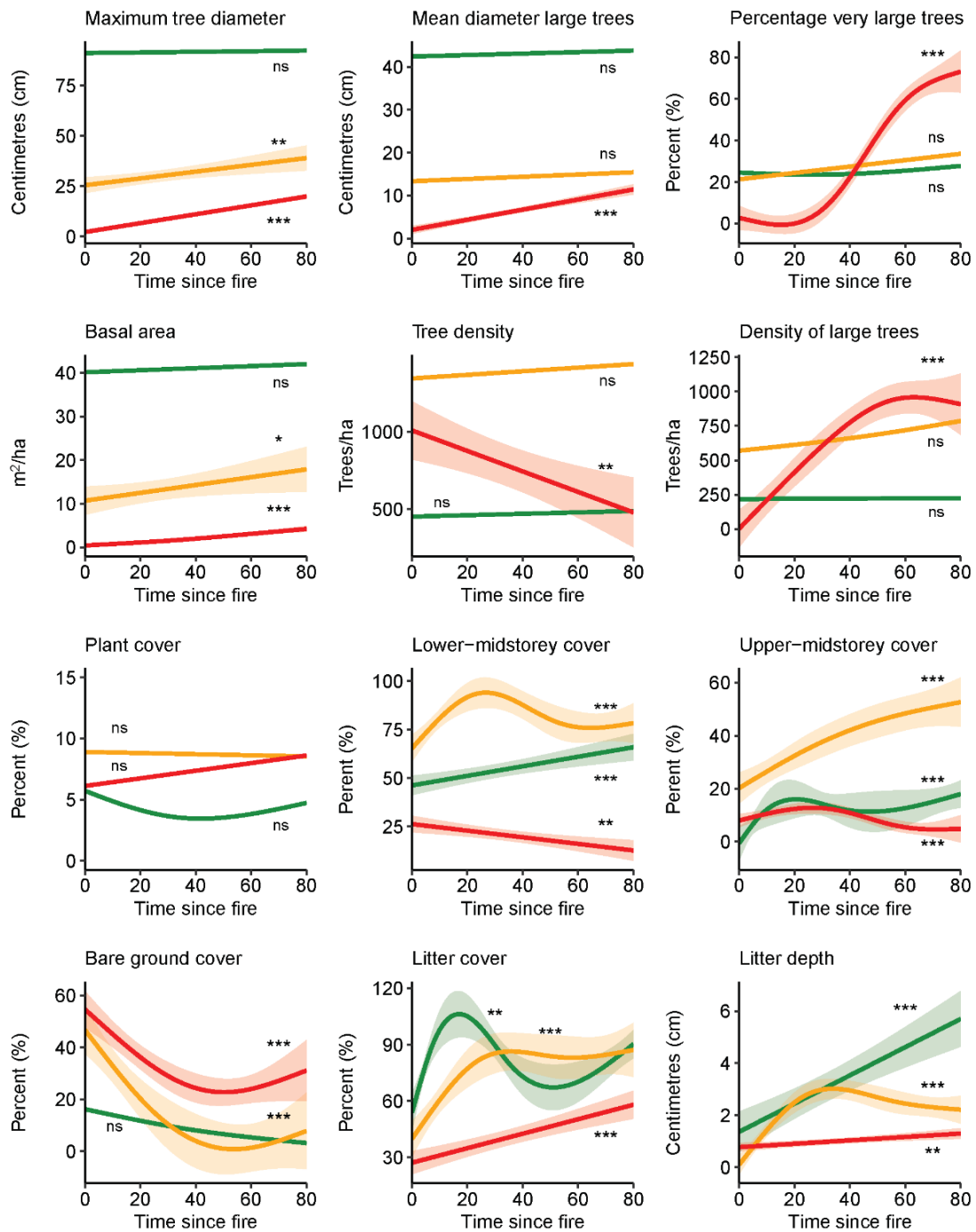


Figure 2.3. Predicted patterns of post-fire temporal dynamics of faunal habitat components in foothills forests, heathy woodlands and mallee woodlands. Green lines (foothill forests), orange lines (heathy woodlands), and red lines (mallee woodlands) are fitted smoothed terms from generalised additive models and shaded areas are 95% confidence intervals. Asterisks represent significance level of the smoothed term: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , ns = not significant. Lines with no shaded ribbon represent non-significant relationships. ‘Large’ and ‘very large’ trees refer to trees with trunk diameter above the median, and within the upper quartile for that ecosystem, respectively.

## **2.5 DISCUSSION**

This study shows that the post-fire development of habitat structural variables differs between ecosystems, and that these patterns are consistent with the fire regeneration traits of the dominant tree species. In mallee woodlands, where fires typically are stand-replacing, more structural components were driven by time since fire than in foothill forests and heathy woodlands, where stands of canopy trees generally persist through fire. The shape of the fire-response curve for most structural components also differed between ecosystems. For faunal species that respond to these habitat structural components, there may be fundamental differences between ecosystems in the role of fire in shaping distributional patterns. These findings have implications for the way in which ecosystems are categorised and managed for biodiversity conservation, which we discuss in the sections below.

### **2.5.1 Temporal development of faunal habitat structure**

Most notably, the three ecosystems differed in the post-fire development of canopy structure. In mallee woodlands, all variables measuring canopy structure responded to time since fire. Overall, the observed pattern was for large trees to increase in mean diameter, occur at a higher density and constitute a greater proportion of all canopy trees, in later successional states. In mallee woodlands, the above ground component of canopy trees typically is killed by fire and resprouts basally from lignotubers, and so stands of canopy trees take decades following fire to grow to maturity (Clarke et al. 2010). Resprouting from basal buds is the most common form of post-fire resprouting, globally (Pausas and Keeley 2017). This trait is especially prevalent in drier biomes of lower productivity where crown fires are experienced (Clarke et al. 2013), like semi-arid woodlands.

In recently burnt mallee woodlands, the density of live stems was high because of vigorous resprouting but decreased over time as canopy trees grow. Some resources that large trees provide for faunal species, such as tree hollows, take many decades to develop and are not

present until later successional states (~ 60 years since fire) (Haslem et al. 2012). As a result of the slow development of these and other resources (e.g. hummock grass), many faunal species in mallee woodlands are associated with mid-later successional vegetation (Kelly et al. 2012, Connell et al. 2017).

By contrast, in foothill forests, where stands of canopy trees survive fire and resprout epicormically, none of the canopy variables we modelled responded to time since fire. These structural variables are proxies for important resources for animals provided by the forest canopy. For example, the availability of tree hollows that provide essential nesting and shelter sites for arboreal mammals and hollow-nesting birds is directly related to the distribution of large trees (Lindenmayer et al. 1993, Remm and Löhmus 2011). In foothill forests, large canopy trees were still present immediately after fire and throughout the chronosequence, thus serving as biological legacies (Pulsford et al. 2016) that do not depend on time since fire. Further, the percentage of trees in the canopy stratum that were ‘very large’ was generally modest (~ 25%) across the range of successional states. This suggests that canopy tree regeneration in foothill forests happens continually and does not follow a clear post-fire successional pathway.

Globally, epicormic resprouting is rare in ecosystems that experience high-intensity crown-fire regimes, such as Mediterranean-type and warm-temperate forests and woodlands (Pausas and Keeley 2017). Taxa that resprout epicormically, additional to *Eucalyptus* species, include *Pinus canariensis* on Canary Island, *Protea nitida* in South Africa, *Quercus agrifolia*, *Q. kelloggii* in California and *Q. suber* in the Mediterranean Basin (Pausas and Keeley 2017). This adaptation enables rapid canopy regeneration and makes these species and their associated habitat features resilient to most fire regimes. Epicormic resprouting is also widespread in tree species in grassy-savanna ecosystems (e.g. in northern Australia) that experience frequent grass-fuelled fires. In such savanna ecosystems, fire frequency, fire

season and fire severity are more influential fire parameters for biota than simply the time since last fire (Murphy et al. 2010, Andersen et al. 2012). These ecosystems represent examples of situations where simple classifications based on time since fire may not be sufficient to capture fire-driven dynamics for faunal species.

In south-eastern Australia, recent large wildfires in foothill forests have reduced the temporal range of post-fire successional states associated with wildfire. Consequently, to cover the breadth of age-classes without introducing effects of vegetation type, climate and environmental gradients, it was necessary to sample prescribed burns for age-classes <80 years since fire. A limitation is that we may have underestimated the potential effects of severe fires on habitat structure. However, Haslem et al. (2016) showed that the main effect of fire severity in foothill forests is on canopy cover, and this effect diminishes rapidly (after ~ 10 years since fire). The interacting effects of fire severity and time since fire on habitat structure would be a fruitful area for further research.

In general, the cover of understorey vegetation responded positively to time since fire in all three ecosystems, except for lower-midstorey vegetation in mallee woodlands which responded negatively. However, the shapes of the responses differed: in foothills forests upper-midstorey cover increased rapidly and peaked earlier than in both heathy woodlands and mallee woodlands. Similar patterns to those shown here have been observed previously in temperate eucalypt forests (Swan et al. 2015, Haslem et al. 2016) and mallee woodlands (Haslem et al. 2011). Understorey vegetation provides nesting, foraging and shelter sites for many bird and mammal species typical of these and similar ecosystems (Ford et al. 1986, Fox et al. 2003, Simonetti et al. 2013, Swan et al. 2015, Verdon et al. 2019). Consequently, the temporal responses of such faunal species to fire are likely to be positively influenced by these post-fire trajectories in habitat suitability (e.g. Fox 1982, Watson et al. 2012). However, early post-fire succession can also create short-term opportunities for species that favour

more-open habitats and which decline in occurrence as understorey vegetation recovers (e.g. Watson et al. 2012).

Biomass allocation in plants (i.e. habitat structure for animals) depends on environmental factors as well as disturbance regimes (Clarke et al. 2013). Factors, such as climate, soils and productivity influence development of habitat structural components: plant growth rate is higher in mesic than semi-arid biomes. Environmental influences will be most evident when comparing structural components that are removed by fire and regenerate from the ground-up (e.g. rate of increase in understorey vegetation). However, plant regeneration traits are fundamental in explaining the differences we observed between ecosystems, as they provide the mechanism that determines whether or not key structures are present within certain successional states.

### **2.5.2 Fire regeneration traits and ecosystem succession**

Support for the idea that, following fire, vegetation development follows a successional pathway that facilitates faunal occupancy has mainly come from studies of stand-replacing ecosystems (Briani et al. 2004, Haney et al. 2008, Pons and Clavero 2010, Watson et al. 2012b). In such stand-replacing ecosystems, categories based on time since fire have proved useful for predicting landscape-scale impacts of fire on faunal species (Connell et al. 2017, Regos et al. 2018). In contrast, in epicormic-resprouting systems, in which canopy tree stems generally persist though fire, the successional pathway is not reset to ‘time-zero’ by burning. Rather, the occurrence and distribution of some key structures, such as large trees tend to be a legacy from past disturbances rather than a product of the time since the last fire. If key components of habitat structure, such as large trees and their associated resources, do not show strong temporal patterns of post-fire development, the fauna that rely on those components are less likely to be associated with distinct successional stages. In epicormic resprouting ecosystems such as the foothill forests, the resources provided by canopy trees in

forests and woodlands (e.g. foliage, hollows, bark, large limbs, flowers: Table 2), are important for a wide range of faunal species (McElhinny et al. 2006). Consequently, in such ecosystems, categorising landscapes into successional states is likely to be less useful for predicting the landscape-scale impacts of fire.

### **2.5.3 Implications for fire management**

The primary finding of this study, that post-fire development of faunal habitat components differs between ecosystems, has implications for the way in which fire-prone ecosystems are understood and subsequently managed. The habitat components studied here are surrogates for important resources for fauna, so differences in their pattern of post-fire development are likely to influence the fire-responses of species that rely on them. Clearly, an important next step is to directly test the relative influence of time-since-fire on faunal species in these disparate ecosystems.

If differences between ecosystems in the fire-response of habitat components reflect real differences in the role of time since fire in shaping faunal distributions, then it will be necessary to rethink how some landscapes are understood and categorised for fire management. For example, fire managers often aim to maintain mosaics of post-fire vegetation age-classes (surrogates of time since fire) across the landscape (Bradstock et al. 2005). This approach is likely to be more effective in maintaining biodiversity values in ecosystems in which vegetation age-classes are structurally and functionally distinct, and support distinct faunal assemblages (Kelly et al. 2012, Watson et al. 2012). Where there is less difference between age-classes, and factors such as pre-fire structure and environmental gradients are influential (e.g. in foothill forests), a more nuanced approach that recognises both time since fire and the biological legacy of historical disturbance regimes, is required.

We recommend that when using a patch mosaic approach in landscape-scale fire management, the ‘patches’ incorporate the most ecologically meaningful fire regime and

environmental parameters. For example, in grassy savanna ecosystems of northern Australia (Davies et al. 2018) and conifer forests of western U.S.A. (Tingley et al. 2016), management strategies that aim to maintain patch mosaics based on fire frequency and fire severity, rather than simply time since fire, are understood to benefit biodiversity across landscapes. In foothill forests, an approach that similarly incorporates additional complexity (beyond time since fire) could improve conservation management outcomes for fauna. A key question to address is ‘how do other aspects of the fire regime (e.g. fire severity) and environmental conditions (e.g. topography) interact with time since fire to influence faunal species at the landscape scale’?

#### **2.5.4 Conclusions and future directions**

Incorporating the needs of fauna into fire management remains a challenge in fire-prone regions worldwide. Our finding that the regeneration traits of the dominant canopy species in wooded ecosystems influences the development of key habitat components, suggests there are fundamental differences in the mechanisms underpinning fire-habitat-fauna dynamics between disparate ecosystems. In systems where fire is not stand-replacing, the persistence of pre-fire structural attributes (e.g. tree size, tree density) as post-fire legacies can mediate the influence of temporal post-fire succession. The next step is to directly examine how the coupling of time since fire and habitat structural development influences the distribution of faunal species in disparate ecosystems, to test whether observed differences in habitat dynamics equate to real influence on the occurrence and status of faunal species.

## 2.6 APPENDICES

### 2.6.1 Distribution of study sites in relation to post-fire vegetation growth stages

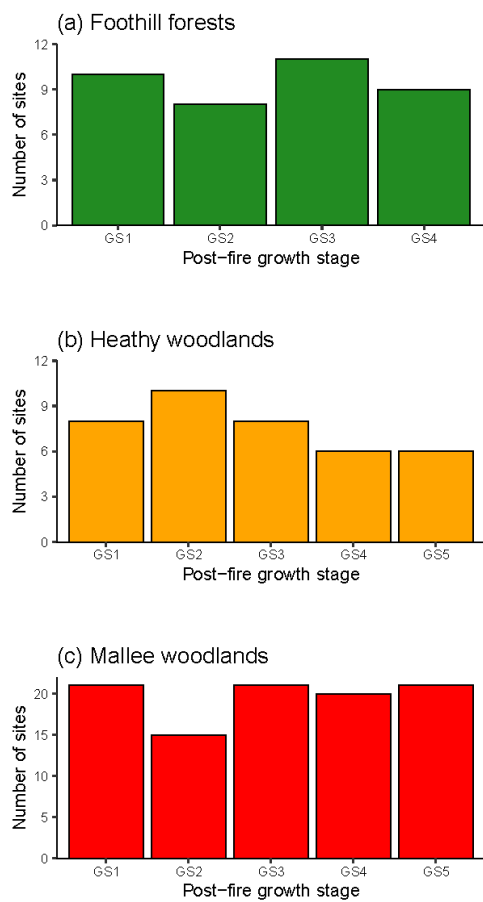


Figure S1. Distribution of study sites in relation to post-fire vegetation growth stages (GS) described by Cheal (2010). Growth stages represent time-since-fire classes and differ between ecosystems. In (a) foothill forests (n=38 sites), GS1 = 0-3, GS2 = 4-10, GS3 = 11-40, GS4 = >40 years since fire. In (b) heathy woodlands (n = 38), GS1 = 0-3, GS2 = 4-10, GS3 = 11-35, GS4 = 36-55, GS5 = >55 years since fire. In (c) mallee woodlands (n=98), GS1 = 0-3, GS2 = 4-10, GS3 = 11-35, GS4 = 36-55, GS5 = >55 years since fire.

## 2.6.2 Model outputs

Table S1. Outputs from GAM(M)s of the relationship between faunal habitat structural attributes and time since fire in foothill forests, heathy woodlands and mallee woodlands. Model significance (*P* - value) and deviance explained (%) were calculated from univariate models built for each of the faunal habitat attributes.

Habitat attribute	Foothill forests		Heathy woodlands		Mallee woodlands	
	<i>P</i> -value	Deviance explained (%)	<i>P</i> -value	Deviance explained (%)	<i>P</i> -value	Deviance explained (%)
Bare ground cover	0.062	13	<0.001	53	<0.001	34
Litter cover	<0.001	50	<0.001	58	<0.001	26
Litter depth	<0.001	48	<0.001	75	0.001	13
Plant cover	0.663	4	0.914	<1	0.283	2
Lower-midstorey cover	<0.001	32	0.001	39	0.001	15
Upper-midstorey cover	0.001	39	<0.001	53	0.001	20
Basal area	0.706	<1	0.047	10	<0.001	53
Tree density	0.536	1	0.715	<1	0.001	19
Density of large trees	0.744	<1	0.126	8	<0.001	64
Maximum tree diameter	0.939	<1	0.003	22	<0.001	80
Mean diameter of large trees	0.568	1	0.080	8	<0.001	54
Percentage of very large trees	0.412	6	0.165	5	<0.001	87

### 3 DOES THE INFLUENCE OF POST-FIRE HABITAT STRUCTURE ON BIRDS DIFFER AMONG ECOSYSTEMS?

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Grey fantail *Rhipidura albiscapa* nest in foothill forests.

### 3.1 ABSTRACT

The distribution and abundance of faunal species is driven by the availability of resources, which vary through space and time following fire. Time since fire (or a similar surrogates) is often used in fire management to understand changes in faunal communities following fire. For conservation in fire-prone landscapes, it is crucial to know which habitat attributes influence the post-fire distribution of faunal species in a range of ecosystems. I modelled the response of bird species to habitat attributes that were sampled along an 80-year post-fire chronosequence in three eucalypt-dominated ecosystems with contrasting regeneration traits to determine whether post-fire, birds responded to different attributes in different ecosystems. The most limiting attributes for birds were those known to be related to time since fire, but these differed among ecosystems. In foothill forests and heathy woodlands (which have epicormic resprouting trees) birds responded strongly to upper-midstorey vegetation (1 – 4 m). In mallee woodlands (in which trees resprout basally), birds responded strongly to canopy tree size (stem diameter). Most (~60%) species that occurred in multiple ecosystems responded to different habitat attributes in each ecosystem. In foothill forests, fewer bird species were associated with habitat attributes known to be related to time since fire, so it is unlikely that temporal surrogates will accurately represent successional changes in bird communities. To better represent bird communities in such ecosystems, fire management strategies should incorporate the processes driving the distribution of habitat attributes and bird species (e.g. fire severity, topography). Fire management strategies that aim to conserve the habitat of species in one setting may not be applicable to the same species or taxonomic group in other settings.

## 3.2 INTRODUCTION

Disturbances such as fire alter the distribution of resources (e.g. food, shelter, nest sites) through space and time, thereby affecting the distribution of faunal species (Haslem et al. 2011, Nappi and Drapeau 2011, Barton et al. 2014, Sitters et al. 2014a, White et al. 2016). Surrogates are often used by fire ecologists and managers to represent the habitat conditions created by fire. For example, fire severity classes are used to represent ecological communities associated with the conditions created by high, medium or low severity fires (Hutto et al. 2016). Similarly, temporal surrogates (e.g. vegetation growth stages) are used to represent ecological communities associated with key stages in post-fire succession (Di Stefano et al. 2013, Kelly et al. 2015, York and Friend 2016). The capacity of such surrogates to represent fire-driven changes in faunal communities across landscapes depends on: (a) how fire influences the distribution of important habitat attributes; and (b) how these habitat attributes influence the distribution of faunal species. In fire-prone regions that encompass diverse vegetation types, understanding how the dynamics of fire, habitat and fauna differ between ecosystems is crucial for biodiversity conservation.

When fire incinerates stands of vegetation, populations of faunal species fluctuate over time as habitat conditions become more or less favourable (Fox 1982, Jacquet and Prodon 2009, Davis et al. 2016, Gosper et al. 2019). However, a growing body of research is showing that post-fire distribution of habitat features is not always simply a product of the time since disturbance (Burgess et al. 2015, Pulsford et al. 2016), but also is influenced by plant regeneration traits, which may differ between ecosystems (Pausas et al. 2004, Rainsford et al. 2020). Interacting pressures of fire regimes and climate have driven the evolution of a range of plant traits in fire-prone landscapes (e.g. serotiny, fire-cued germination, resprouting from protected buds) (Archibald et al. 2018). Of particular relevance to the post-fire development of habitat attributes are regeneration traits that relate to stand-persistence, such as method of

resprouting (e.g. epicormic vs basal), that can influence the rate of vegetation recovery and ecosystem function (Clarke et al. 2013, Rainsford et al. 2020).

In some ecosystems, fires are stand-replacing. For example, in boreal forests of Canada (Hannon and Drapeau 2005), broom shrublands in the European Pyrenees (Pons and Clavero 2010) and semi-arid mallee woodlands of southern Australia (Haslem et al. 2011), the above-ground component of canopy trees typically is consumed by hot fires, and regenerates from the ground-up. In ecosystems with stand-replacing fires, the abundance and rate of development of key habitat features often follow predictable post-fire trajectories (Haslem et al. 2011, Gosper et al. 2013a). Consequently, for faunal species that have close associations with specific post-fire habitat features, time since fire (and similar temporal surrogates) can be useful for predicting post-fire occurrences (Pons and Clavero 2010, Nappi and Drapeau 2011, Watson et al. 2012b, Davis et al. 2016, Gosper et al. 2019, Hutto et al. 2020).

In other ecosystems, tree stems survive fire and regeneration happens rapidly. In cork oak *Quercus suber* forests in the Mediterranean Basin and stringybark *Eucalyptus* forests in Australia, the protective bark of canopy trees enables post-fire resprouting from epicormic buds along the trunk and branches (Pausas and Keeley 2017). In epicormic-resprouting ecosystems, even high-severity fires generally are not stand-replacing and canopy trees are present immediately after fire (Collins 2020). These contrasting regeneration patterns have implications for post-fire habitat development (Chergui et al. 2018, Rainsford et al. 2020). Similarly, I expect there will be implications for post-fire faunal distributions and for fire management for biodiversity.

Further, understanding how post-fire changes in habitat conditions limits the distribution of faunal species in different ecosystems may benefit management of fire-dependant species. For example, the post-fire time ‘window of occurrence’ can guide the timing and placement of prescribed burning to help conserve species (Pons et al. 2012). The time window of

occurrence of faunal species is based on associations between species' occurrences and post-fire habitat development, and can vary within and between species, depending on environmental conditions or habitat preferences (Puig-Gironès et al. 2017, Verdon et al. 2019). Determining the associations between faunal species, habitat attributes and time since fire in different ecological settings will provide important insights for fire management across broad regions, including how wide-ranging species will be impacted by altered fire regimes throughout their range.

Here, I tested how bird species respond to post-fire habitat structural attributes in three ecosystems dominated by *Eucalyptus* trees with contrasting regeneration traits. Specifically, I aimed to determine whether, across an 80-year post-fire chronosequence: (1) birds respond to different habitat attributes in mallee woodlands (trees resprout basally), heathy woodlands and foothill forests (trees resprout epicormically); and (2) bird species that occur in multiple ecosystems respond to the same habitat attributes in each ecosystem.

### **3.3 METHODS**

#### **3.3.1 Study location and ecosystems**

I modelled the relationship between the relative abundance of bird species and habitat attributes across an 80-year post-fire chronosequence in each of three ecosystems: foothill forests, heathy woodlands and mallee woodlands. Details of study locations (Fig. 2.2) and ecosystems can be found in sections 2.3.1 – 2.3.3.

#### **3.3.2 Study design**

I used bird species occurrence (reporting rate) and habitat structural data from sites in each ecosystem: foothill forests (n = 38 sites), heathy woodlands (n = 38), and mallee woodlands (n = 98). The study design and fire history are described in detail in sections 2.3.5 and 2.3.6.

### **3.3.3 Data collection**

#### *3.3.3.1 Habitat structure*

Twelve structural variables were selected to represent the same attributes in each ecosystem (Table 3.1). See section 2.3.7 for details of how habitat attribute data were collected and how the variables were calculated.

#### *3.3.3.2 Birds*

At each site in foothill forests and heathy woodlands, a 2-ha plot (250 m transect  $\times$  80 m) was established and birds were surveyed over a 20-minute period by a single experienced observer (FR) a total of six times: three times during the austral autumn/winter and three times during spring/summer between 2017 and 2018. Bird surveys were conducted within four hours of dawn, except for two winter survey rounds during which sites were each surveyed once in the morning and once in the afternoon.

Mallee woodland sites were surveyed over the austral autumn and spring of 2006 and 2007. At these sites, five-minute point-counts were conducted by two experienced observers a total of four times; twice in autumn/winter and twice in spring/summer. Each site (from point to 60 m radius) was surveyed by each observer twice, once in each season, in the morning within four hours of dawn (for details see Watson et al. 2012).

All species either seen or heard were recorded. The distances (m) to all detections, either from the transect line in foothill forests and heathy woodlands, or from the survey point in mallee woodlands, were estimated to test for differences in detectability between sites.

### **3.3.4 Data analysis**

To account for potential issues of detectability in foothill forests and heathy woodlands, I used simple linear regression to test for a relationship between the distance to detection of species (or groups of similar species) and midstorey vegetation cover (see Appendices 4.6.2,

5.6.1). For several species/groups, there was a weak negative relationship between midstorey vegetation cover and distance to detection, suggesting that some individuals of these species may have been un-detected at sites with high midstorey vegetation cover. To control for potential errors due to detectability, I used a presence/absence-based index (reporting rate) to compare the relative abundance of species between sites. Because it does not rely on counts of individuals, reporting rate is less prone to biases caused by differences in detectability or flocking behaviour. This approach is a robust alternative to model-based approaches (i.e. distance analysis) for which modelling assumptions cannot be met (Hutto 2016). See Watson et al. (2012) for detectability analysis of mallee woodlands data.

To determine the relationship between the reporting rate of bird species and habitat structural attributes, I used non-linear regression models (Wood 2017). Generalized additive models (GAMs) were used for foothill forests and heathy woodlands, while generalized additive mixed-models (GAMMs) were used for mallee woodlands as these were collected from points clustered in landscapes (Watson et al. 2012b). Mixed models were fitted with the landscape unit (from 1 - 12) as a random intercept.

The response variable was the reporting rate of a species (represented by a Poisson error distribution), the number of survey rounds during which a species was detected. Variation in reporting rate between sites is often a result of variation in the abundance of individuals and so is a reliable proxy for relative abundance (and this term is used throughout the chapter) (Royle and Nichols 2003). Models were built for species that occurred at >20% of sites in each ecosystem. Initially, degrees of freedom of the smoothing term ( $K$ ) were set automatically in the GAM(M) model-fitting process, but model-exploration found that better models were fit when this was set at three. If overdispersion of data was detected, an observation-level random factor was used in a mixed-model framework following Harrison (2014). GAMs were built by using the *mgcv* package in R (Wood 2017).

To determine whether the reporting rate of bird species post-fire was influenced by the same habitat attributes in each ecosystem, first, I built models for each individual species and each habitat variable (total = 12 univariate models per species). I then calculated the percentage of species that were significantly related to each habitat attribute. To determine which attributes were the most influential in each ecosystem, I selected the three strongest models for each species, based on the lowest Akaike Information Criterion (AIC) values, and calculated the percentage of species that were significantly related to each habitat attribute, based on this smaller set of models.

Lastly, I calculated the percentage for species detected in more than one ecosystem: (a) that was significantly related to the same habitat attributes; (b) whose strongest model was with the same attribute; (c) that was related to at least one of the same attributes; (d) that was related to none of the same attributes; and (e) that was significantly related to no attributes in each ecosystem. Percentages were compared between ecosystems using a bar plot.

Table 3.1. Habitat structural attributes included in generalized additive models for bird species in foothill forests, heathy woodlands and mallee woodlands. Whether the attribute was significantly related to time since fire (from Rainsford et al. 2020) is indicated by asterisks (\*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$ ). FF = foothill forests, HW = heathy woodlands, MW = mallee woodlands.

Habitat category	Variable	Foothill forests	Heathy woodlands	Mallee woodlands	Description
<b>Ground cover</b>	Bare ground cover	ns	***	***	Percent (%) cover of bare ground
	Litter cover	**	***	***	Percent (%) cover of leaf litter
	Litter depth	***	***	**	Mean depth of leaf litter (cm)
	Plant cover	ns	ns	ns	Percent (%) cover of plants (includes shrubs, herbs and ferns)
<b>Understorey</b>	Lower-midstorey	***	***	**	Percent (%) cover of vegetation 0 – 1 m (FF, HW), 0 – 0.5 m (MW)
	Upper-midstorey	***	***	***	Percent (%) cover of vegetation 1 – 4 m (FF, HW), 0.5 – 2 m (MW)
<b>Canopy trees</b>	Basal area	ns	*	***	Basal area cover of canopy trees (m <sup>2</sup> /ha)
	Density of large trees	ns	ns	***	Density (live stems/ha) of canopy trees with diameter greater than the median for that ecosystem (>25 cm FF; >8 cm HW; >4 cm MW).
	Maximum tree diameter	ns	**	***	Diameter (cm) of the largest tree within the sample area
	Mean diameter of large trees	ns	ns	***	Mean diameter (cm) of trees with diameter greater than median for the ecosystem (>25 cm FF; >8 cm HW; >4 cm MW)
	Percentage of very large trees	ns	ns	***	Percent (%) of trees in the canopy stratum with diameter in the upper quartile for the ecosystem (>39 cm FF; >12 cm HW; >7 cm MW)

Habitat category	Variable	Foothill forests	Heathy woodlands	Mallee woodlands	Description
	Tree density	ns	ns	**	Density of canopy trees (live stems/ha)

### 3.4 RESULTS

A total of 96 bird species was recorded at sites in the three ecosystems (43 species in foothill forest, 44 in heathy woodlands and 50 in mallee woodlands). The most species-rich families across all ecosystems were Acanthizidae (thornbills), Artamidae (magpies and butcherbirds), Meliphagidae (honeyeaters) and Pachycephalidae (whistlers). The mean number of species per site was highest in foothill forests (18, range: 13 – 29), with 16 in heathy woodlands (range: 9 – 22) and six in mallee woodlands (range: 2 – 14).

#### 3.4.1 The influence of habitat structure on bird communities

Models were built for 43 species across the three ecosystems (28 species in foothill forests, 21 in heathy woodlands and 12 in mallee woodlands). The most important habitat attributes for bird species (i.e. based on the three strongest habitat relationships) across the 80-year chronosequence varied among ecosystems (Fig. 3.1). In foothill forests (Fig. 3.1a), the most influential habitat attributes for the bird community were upper-midstorey cover (21% of species responded, e.g. white-browed scrubwren *Sericornis frontalis* Fig. 3.2b) and plant cover (14% of species responded, e.g. sacred kingfisher *Todiramphus sanctus* Fig. 3.2a). Few species in foothill forests responded to variables representing the tree structure, although the relative abundance of the grey fantail *Rhipidura albiscapa* was significantly positively related to the size of large trees at sites (Fig. 3.2c).

In heathy woodlands (Fig. 3.1b), the most influential habitat variables were upper-midstorey cover (38% of species responded, e.g. silvereve *Zosterops lateralis* Fig. 3.2e) and bare ground cover (33% of species responded, e.g. common bronzewing *Phaps chalcoptera* Fig.

3.2d). The size of canopy trees was influential for several species: for example, 19% of species were significantly related to maximum tree diameter (e.g. white-throated treecreeper *Cormobates leucophaea* Fig. 3.2f).

In mallee woodlands (Fig. 3.1c), variables relating to canopy structure were the most influential. Fifty percent of bird species were significantly related to maximum tree diameter (e.g. yellow-plumed honeyeater *Lichenostomus ornatus* Fig. 3.2i), 25% were significantly related to the density of large trees (e.g. striated pardalote *Pardalotus punctatus* Fig. 3.2g) and 25% were significantly related to basal area (e.g. shy heathwren *Hylacola cauta* Fig. 3.2h).

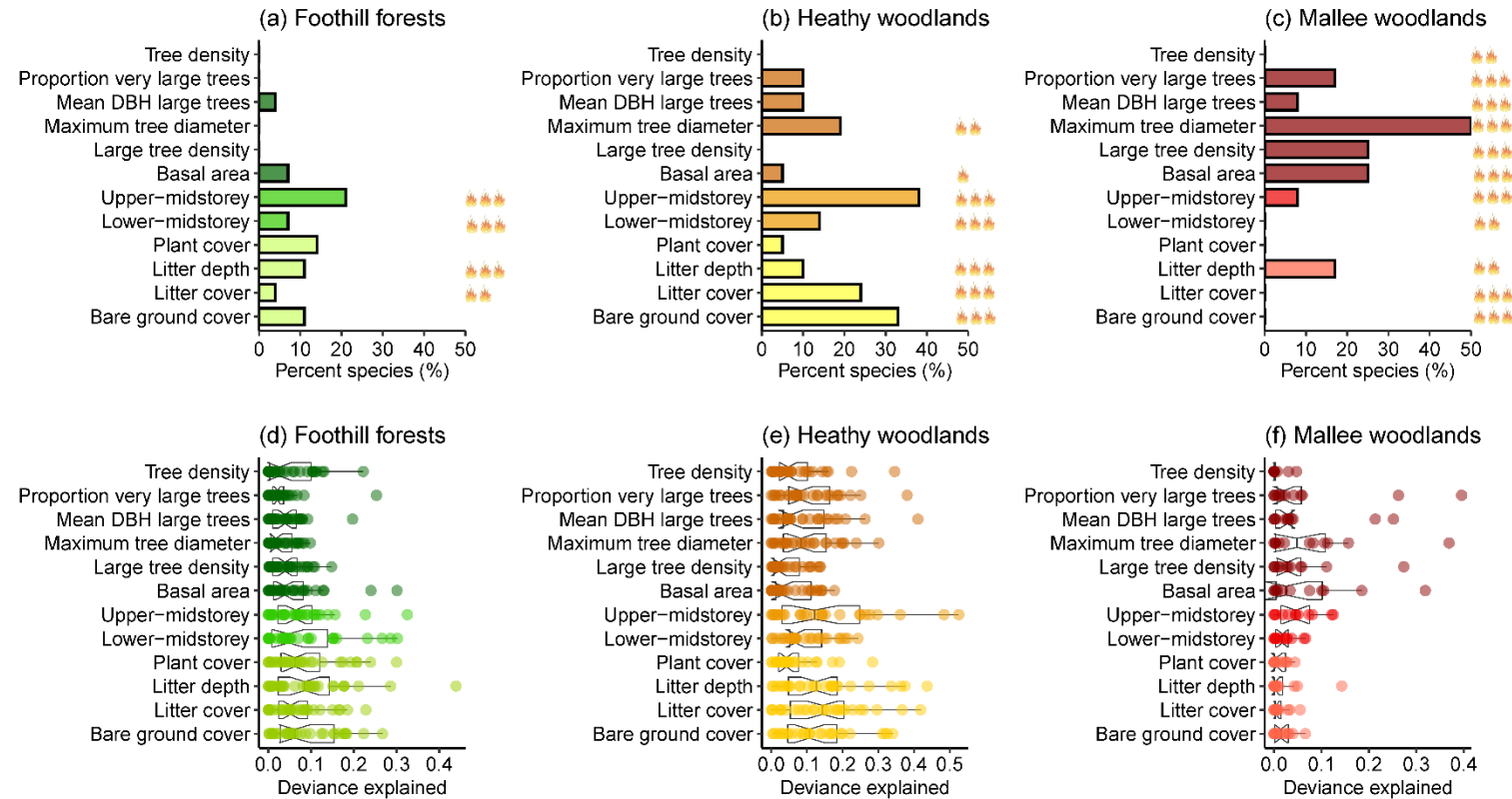


Figure 3.1. Influential habitat attributes for birds across an 80-year post-fire chronosequence in foothill forests (a,d,  $n = 28$  species), heathy woodlands (b, e,  $n = 21$ ), and (c) mallee woodlands (c, f,  $n = 12$ ). (a – c) Bars represent the percentage of species that were significantly ( $P < 0.05$ ) related to habitat attributes in each ecosystem, based on the three variables that had the strongest relationship with each species. (d – f) The deviance explained by models: boxplots represent the median and upper and lower quartiles for each habitat attribute; points represent individual species. Generalized additive models were built separately for each species/variable combination (i.e. univariate models). Colour tones represent habitat categories (darkest = canopy structure, intermediate = understorey vegetation, lightest = ground cover). Flame symbols represent significant relationships between habitat attributes and time since fire based on Rainsford et al. (2020). Single flame:  $P < 0.05$ , two flames:  $P < 0.01$ , three flames:  $P < 0.001$ .

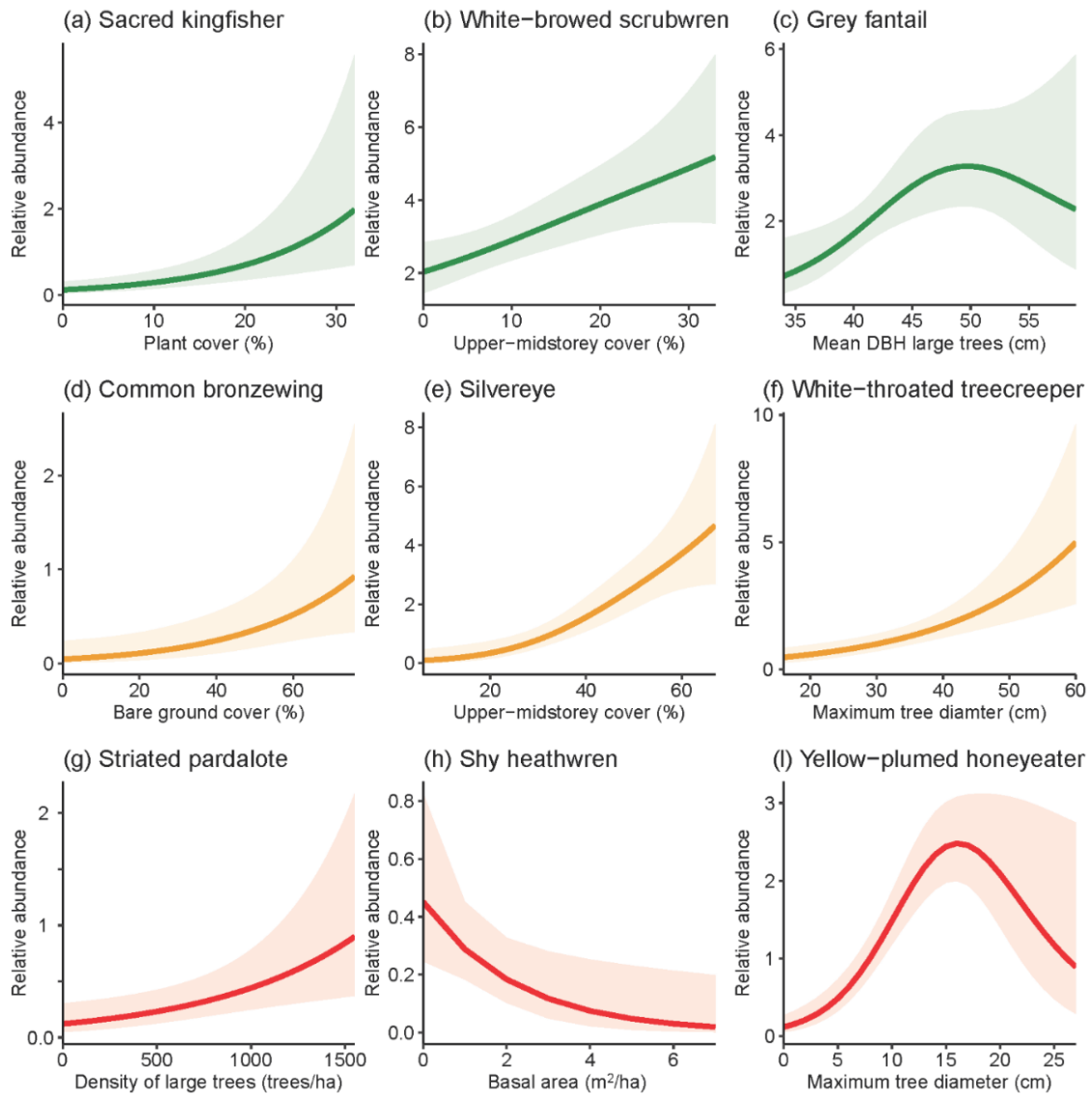


Figure 3.2. Responses of selected bird species to habitat structural components across an 80-year post-fire chronosequence in foothill forests (green plots, top row), heathy woodlands (orange plots, middle row) and mallee woodlands (red plots, bottom row). Lines are fitted generalized additive models of the relative abundance of species. Shaded areas indicated 95% confidence intervals.

Table 3.2. Bird species responses to habitat structural variables across an 80-year chronosequence in foothill forests, heathy woodlands and mallee woodlands. *P*-values and deviance explained (proportion) are from univariate generalized additive models for species relative abundances. The three strongest models for each species are presented. Significant relationships are indicated by bold font. Grey shading indicates species that occurred in more than one ecosystem.

Species name	Common name	Ecosystem	No. sites	Variable 1	Variable 2	Variable 3			
<i>Acanthagenys rufogularis</i>	Spiny-cheeked honeyeater	MW	40	Density of large trees	Upper-midstorey cover	Tree density			
				<i>P</i> -value	0.069	<i>P</i> -value	0.086	<i>P</i> -value	0.091
				Deviance	0.024	Deviance	0.073	Deviance	0.047
<i>Acanthiza apicalis</i>	Inland thornbill	MW	22	Litter depth	Upper-midstorey cover	Plant cover			
				<i>P</i> -value	0.054	<i>P</i> -value	0.151	<i>P</i> -value	0.243
				Deviance	0.010	Deviance	0.030	Deviance	0.024
<i>Acanthiza lineata</i>	Striated thornbill	FH	38	Plant cover	Upper-midstorey cover	Litter cover			
				<i>P</i> -value	0.273	<i>P</i> -value	0.438	<i>P</i> -value	0.435
				Deviance	0.192	Deviance	0.092	Deviance	0.091
<i>Acanthiza lineata</i>	Striated Thornbill	HW	19	Mean DBH of large trees	Proportion of very large trees	Lower-midstorey			
				<i>P</i> -value	0.052	<i>P</i> -value	0.051	<i>P</i> -value	0.061
				Deviance	0.187	Deviance	0.167	Deviance	0.135
<i>Acanthiza pusilla</i>	Brown thornbill	FH	35	Bare ground cover	Lower-midstorey	Upper-midstorey			
				<i>P</i> -value	<b>0.003</b>	<i>P</i> -value	<b>0.014</b>	<i>P</i> -value	<b>0.047</b>
				Deviance	0.267	Deviance	0.286	Deviance	0.088
<i>Acanthiza pusilla</i>	Brown Thornbill	HW	38	Bare ground cover	Litter cover	Litter depth			
				<i>P</i> -value	0.263	<i>P</i> -value	0.289	<i>P</i> -value	0.293
				Deviance	0.199	Deviance	0.177	Deviance	0.169

Species name	Common name	Ecosystem	No. sites	Variable 1	Variable 2	Variable 3			
<i>Acanthiza uropygialis</i>	Chestnut-rumped thornbill	MW	21	Density of large trees	Litter depth	Maximum tree diameter			
				<i>P</i> -value	<b>0.001</b>	<i>P</i> -value	<b>0.003</b>	<i>P</i> -value	<b>0.007</b>
				Deviance	0.111	Deviance	0.143	Deviance	0.106
<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	HW	33	Basal area	Density of large trees	Litter depth			
				<i>P</i> -value	0.257	<i>P</i> -value	0.382	<i>P</i> -value	0.389
				Deviance	0.047	Deviance	0.038	Deviance	0.026
<i>Anthochaera carunculata</i>	Red wattlebird	FH	23	Basal area	Litter depth	Tree density			
				<i>P</i> -value	<b>0.015</b>	<i>P</i> -value	0.055	<i>P</i> -value	0.057
				Deviance	0.130	Deviance	0.089	Deviance	0.091
<i>Cacomantis flabelliformis</i>	Fan-tailed cuckoo	FH	11	Litter depth	Bare ground cover	Plant cover			
				<i>P</i> -value	<b>0.039</b>	<i>P</i> -value	<b>0.003</b>	<i>P</i> -value	0.057
				Deviance	0.286	Deviance	0.183	Deviance	0.074
<i>Callocephalon fimbriatum</i>	Gang Gang	HW	9	Proportion of very large trees	Maximum tree diameter	Mean DBH of large trees			
				<i>P</i> -value	<b>0.012</b>	<i>P</i> -value	<b>0.011</b>	<i>P</i> -value	<b>0.014</b>
				Deviance	0.194	Deviance	0.204	Deviance	0.139
<i>Cinclosoma castanotum</i>	Chestnut quail-thrush	MW	22	Lower-midstorey	Litter cover	Tree density			
				<i>P</i> -value	0.228	<i>P</i> -value	0.436	<i>P</i> -value	0.507
				Deviance	0.027	Deviance	0.033	Deviance	0.002
<i>Climacteris erythrops</i>	Red-browed treecreeper	FH	12	Plant cover	Maximum tree diameter	Basal area			
				<i>P</i> -value	0.101	<i>P</i> -value	0.096	<i>P</i> -value	0.127
				Deviance	0.060	Deviance	0.069	Deviance	0.058
<i>Colluricincla harmonica</i>	Grey shrike-thrush	FH	34	Bare ground cover	Basal area	Litter depth			
				<i>P</i> -value	<b>0.039</b>	<i>P</i> -value	0.053	<i>P</i> -value	0.093

Species name	Common name	Ecosystem	No. sites	Variable 1	Variable 2	Variable 3			
<i>Colluricincla harmonica</i>	Grey Shrike-thrush	HW	33	Deviance	0.129	Deviance	0.128	Deviance	0.102
				Litter depth		Upper-midstorey cover		Litter cover	
				<i>P</i> -value	0.270	<i>P</i> -value	0.321	<i>P</i> -value	0.348
<i>Colluricincla harmonica</i>	Grey shrike-thrush	MW	23	Deviance	0.053	Deviance	0.008	Deviance	0.025
				Maximum tree diameter		Litter depth		Mean DBH of large trees	
				<i>P</i> -value	<b>0.017</b>	<i>P</i> -value	<b>0.049</b>	<i>P</i> -value	0.064
<i>Coracina tenuirostris</i>	Cicadabird	FH	9	Deviance	0.075	Deviance	0.050	Deviance	0.005
				Mean DBH of large trees		Density of large trees		Proportion of very large trees	
				<i>P</i> -value	0.206	<i>P</i> -value	0.233	<i>P</i> -value	0.302
<i>Cormobates leucophaea</i>	White-throated treecreeper	FH	38	Deviance	0.035	Deviance	0.086	Deviance	0.083
				Upper-midstorey cover		Maximum tree diameter		Basal area	
				<i>P</i> -value	0.223	<i>P</i> -value	0.346	<i>P</i> -value	0.549
<i>Cormobates leucophaea</i>	White-throated Treecreeper	HW	24	Deviance	0.108	Deviance	0.068	Deviance	0.027
				Maximum tree diameter		Mean DBH of large trees		Proportion of very large trees	
				<i>P</i> -value	<b>0.000</b>	<i>P</i> -value	<b>0.000</b>	<i>P</i> -value	<b>0.000</b>
<i>Corvus tasmanicus</i>	Forest raven	HW	10	Deviance	0.301	Deviance	0.411	Deviance	0.381
				Litter cover		Bare ground cover		Upper-midstorey	
				<i>P</i> -value	<b>0.018</b>	<i>P</i> -value	<b>0.046</b>	<i>P</i> -value	<b>0.046</b>
<i>Cracticus torquatus</i>	Grey butcherbird	MW	33	Deviance	0.200	Deviance	0.136	Deviance	0.152
				Lower-midstorey		Plant cover		Maximum tree diameter	
				<i>P</i> -value	0.109	<i>P</i> -value	0.104	<i>P</i> -value	0.306
				Deviance	0.063	Deviance	0.016	Deviance	0.010

Species name	Common name	Ecosystem	No. sites	Variable 1	Variable 2	Variable 3			
<i>Dacelo novaeguineae</i>	Laughing kookaburra	FH	12	Plant cover	Litter depth	Litter cover			
				<i>P</i> -value	<b>0.025</b>	<i>P</i> -value	0.050	<i>P</i> -value	0.137
				Deviance	0.239	Deviance	0.177	Deviance	0.150
<i>Eopsaltria australis</i>	Eastern yellow robin	FH	19	Plant cover	Density of large trees	Lower-midstorey			
				<i>P</i> -value	<b>0.021</b>	<i>P</i> -value	0.061	<i>P</i> -value	0.114
				Deviance	0.099	Deviance	0.077	Deviance	0.152
<i>Eopsaltria australis</i>	Eastern Yellow Robin	HW	20	Plant cover	Tree density	Upper-midstorey			
				<i>P</i> -value	0.161	<i>P</i> -value	0.337	<i>P</i> -value	0.346
				Deviance	0.063	Deviance	0.028	Deviance	0.026
<i>Hylacola cauta</i>	Shy heathwren	MW	20	Maximum tree diameter	Density of large trees	Basal area			
				<i>P</i> -value	<b>0.008</b>	<i>P</i> -value	<b>0.019</b>	<i>P</i> -value	<b>0.018</b>
				Deviance	0.113	Deviance	0.056	Deviance	0.101
<i>Lichenostomus chrysops</i>	Yellow-faced honeyeater	FH	38	Litter cover	Upper-midstorey cover	Basal area			
				<i>P</i> -value	0.215	<i>P</i> -value	0.403	<i>P</i> -value	0.410
				Deviance	0.185	Deviance	0.078	Deviance	0.301
<i>Lichenostomus chrysops</i>	Yellow-faced Honeyeater	HW	38	Lower-midstorey	Maximum tree diameter	Proportion of very large trees			
				<i>P</i> -value	0.236	<i>P</i> -value	0.259	<i>P</i> -value	0.325
				Deviance	0.007	Deviance	0.086	Deviance	0.065
<i>Lichenostomus leucotis</i>	White-eared honeyeater	MW	59	Proportion of very large trees	Maximum tree diameter	Mean DBH of large trees			
				<i>P</i> -value	<b>0.000</b>	<i>P</i> -value	<b>0.001</b>	<i>P</i> -value	<b>0.000</b>
				Deviance	0.262	Deviance	0.157	Deviance	0.213
<i>Lichenostomus ornatus</i>	Yellow-plumed honeyeater	MW	54	Maximum tree diameter	Proportion of very large trees	Basal area			

Species name	Common name	Ecosystem	No. sites	Variable 1	Variable 2	Variable 3			
				<i>P</i> -value	<b>0.000</b>	<i>P</i> -value	<b>0.000</b>	<i>P</i> -value	<b>0.000</b>
				Deviance	0.369	Deviance	0.395	Deviance	0.319
<i>Malurus cyaneus</i>	Superb fairywren	FH	15	Maximum tree diameter	Proportion of very large trees	Plant cover			
				<i>P</i> -value	0.090	<i>P</i> -value	0.100	<i>P</i> -value	0.193
				Deviance	0.045	Deviance	0.036	Deviance	0.054
<i>Malurus cyaneus</i>	Superb Fairywren	HW	34	Litter depth	Lower-midstorey	Proportion of very large trees			
				<i>P</i> -value	<b>0.016</b>	<i>P</i> -value	<b>0.030</b>	<i>P</i> -value	0.063
				Deviance	0.274	Deviance	0.115	Deviance	0.083
<i>Melithreptus lunatus</i>	White-naped honeyeater	FH	24	Plant cover	Upper-midstorey cover	Bare ground cover			
				<i>P</i> -value	0.060	<i>P</i> -value	<b>0.025</b>	<i>P</i> -value	0.097
				Deviance	0.174	Deviance	0.114	Deviance	0.076
<i>Melithreptus lunatus</i>	White-naped Honeyeater	HW	18	Maximum tree diameter	Basal area	Lower-midstorey			
				<i>P</i> -value	<b>0.004</b>	<i>P</i> -value	<b>0.020</b>	<i>P</i> -value	<b>0.023</b>
				Deviance	0.239	Deviance	0.144	Deviance	0.148
<i>Menura novaehollandiae</i>	Superb lyrebird	FH	11	Upper-midstorey cover	Maximum tree diameter	Density of large trees			
				<i>P</i> -value	<b>0.005</b>	<i>P</i> -value	0.066	<i>P</i> -value	0.108
				Deviance	0.325	Deviance	0.084	Deviance	0.051
<i>Oriolus sagittatus</i>	Olive-backed oriole	FH	8	Plant cover	Tree density	Upper-midstorey			
				<i>P</i> -value	<b>0.003</b>	<i>P</i> -value	0.183	<i>P</i> -value	0.211
				Deviance	0.207	Deviance	0.104	Deviance	0.038
<i>Pachycephala pectoralis</i>	Golden whistler	FH	27	Upper-midstorey cover	Lower-midstorey	Litter depth			
				<i>P</i> -value	<b>0.010</b>	<i>P</i> -value	<b>0.029</b>	<i>P</i> -value	0.050
				Deviance	0.121	Deviance	0.232	Deviance	0.152

Species name	Common name	Ecosystem	No. sites	Variable 1	Variable 2	Variable 3
<i>Pachycephala pectoralis</i>	Golden Whistler	HW	18	Upper-midstorey cover <i>P</i> -value Deviance	Maximum tree diameter <i>P</i> -value Deviance	Bare ground cover <i>P</i> -value Deviance
					<b>0.001</b> 0.082	<b>0.004</b> 0.061
<i>Pachycephala rufiventris</i>	Rufous whistler	FH	14	Plant cover <i>P</i> -value Deviance	Litter depth <i>P</i> -value Deviance	Upper-midstorey <i>P</i> -value Deviance
					0.101 0.126	0.069 0.096
<i>Pachycephala rufiventris</i>	Rufous Whistler	HW	33	Upper-midstorey cover <i>P</i> -value Deviance	Litter cover <i>P</i> -value Deviance	Litter depth <i>P</i> -value Deviance
					0.051 0.141	0.094 0.100
<i>Pardalotus punctatus</i>	Spotted pardalote	FH	38	Density of large trees <i>P</i> -value Deviance	Lower-midstorey <i>P</i> -value Deviance	Maximum tree diameter <i>P</i> -value Deviance
					0.321 0.108	0.545 0.040
<i>Pardalotus punctatus</i>	Spotted pardalote	MW	65	Bare ground cover <i>P</i> -value Deviance	Upper-midstorey cover <i>P</i> -value Deviance	Proportion of very large trees <i>P</i> -value Deviance
					0.162 0.010	0.233 0.003
<i>Pardalotus striatus</i>	Striated pardalote	FH	34	Basal area <i>P</i> -value Deviance	Mean DBH of large trees <i>P</i> -value Deviance	Tree density <i>P</i> -value Deviance
					<b>0.045</b> 0.091	0.060 0.079
<i>Pardalotus striatus</i>	Striated pardalote	MW	26	Density of large trees <i>P</i> -value Deviance	Basal area <i>P</i> -value Deviance	Maximum tree diameter <i>P</i> -value Deviance
					<b>0.007</b> 0.058	<b>0.003</b> 0.185
<i>Petroica boodang</i>	Scarlet robin	FH	12	Mean DBH of large trees	Density of large trees	Plant cover

Species name	Common name	Ecosystem	No. sites	Variable 1	Variable 2	Variable 3			
<i>Petroica boodang</i>	Scarlet Robin	HW	10	<i>P</i> -value	0.160	<i>P</i> -value	0.215	<i>P</i> -value	0.353
				Deviance	0.080	Deviance	0.148	Deviance	0.039
				Upper-midstorey cover		Bare ground cover		Litter depth	
				<i>P</i> -value	<b>0.004</b>	<i>P</i> -value	<b>0.018</b>	<i>P</i> -value	<b>0.015</b>
				Deviance	0.265	Deviance	0.169	Deviance	0.222
<i>Petroica phoenicea</i>	Flame robin	FH	32	Tree density	Density of large trees	Bare ground cover			
<i>Phaps chalcoptera</i>	Common Bronzewing	HW	8	<i>P</i> -value	0.054	<i>P</i> -value	0.188	<i>P</i> -value	0.126
				Deviance	0.111	Deviance	0.048	Deviance	0.059
				Upper-midstorey cover		Bare ground cover		Litter cover	
				<i>P</i> -value	<b>0.008</b>	<i>P</i> -value	0.340	<i>P</i> -value	<b>0.024</b>
				Deviance	0.362	Deviance	0.010	Deviance	0.259
<i>Phylidonyris pyrrhopterus</i>	Crescent Honeyeater	HW	36	Upper-midstorey cover	Bare ground cover	Litter cover			
<i>Platycercus elegans</i>	Crimson rosella	FH	37	<i>P</i> -value	<b>0.008</b>	<i>P</i> -value	<b>0.017</b>	<i>P</i> -value	<b>0.026</b>
				Deviance	0.249	Deviance	0.221	Deviance	0.185
				Lower-midstorey		Bare ground cover		Litter cover	
				<i>P</i> -value	0.097	<i>P</i> -value	0.189	<i>P</i> -value	0.360
				Deviance	0.151	Deviance	0.181	Deviance	0.121
<i>Platycercus elegans</i>	Crimson Rosella	HW	26	Upper-midstorey cover	Litter cover	Plant cover			
<i>Rhipidura albiscapa</i>	Grey fantail	FH	31	<i>P</i> -value	<b>0.004</b>	<i>P</i> -value	0.055	<i>P</i> -value	<b>0.013</b>
				Deviance	0.248	Deviance	0.148	Deviance	0.171
				Mean DBH of large trees		Upper-midstorey cover		Litter depth	
				<i>P</i> -value	<b>0.011</b>	<i>P</i> -value	<b>0.030</b>	<i>P</i> -value	0.142
				Deviance	0.197	Deviance	0.139	Deviance	0.091

Species name	Common name	Ecosystem	No. sites	Variable 1		Variable 2		Variable 3	
<i>Rhipidura albiscapa</i>	Grey Fantail	HW	37	Litter cover		Basal area		Mean DBH of large trees	
				<i>P</i> -value	0.100	<i>P</i> -value	0.122	<i>P</i> -value	0.136
				Deviance	0.119	Deviance	0.128	Deviance	0.088
<i>Sericornis frontalis</i>	White-browed scrubwren	FH	35	Litter depth		Upper-midstorey cover		Litter cover	
				<i>P</i> -value	<b>0.000</b>	<i>P</i> -value	<b>0.005</b>	<i>P</i> -value	<b>0.010</b>
				Deviance	0.439	Deviance	0.227	Deviance	0.167
<i>Sericornis frontalis</i>	White-browed Scrubwren	HW	29	Upper-midstorey cover		Litter cover		Bare ground cover	
				<i>P</i> -value	<b>0.000</b>	<i>P</i> -value	<b>0.000</b>	<i>P</i> -value	<b>0.002</b>
				Deviance	0.187	Deviance	0.277	Deviance	0.228
<i>Smicrornis brevirostris</i>	Weebill	MW	64	Upper-midstorey cover		Lower-midstorey		Plant cover	
				<i>P</i> -value	<b>0.026</b>	<i>P</i> -value	0.085	<i>P</i> -value	0.228
				Deviance	0.081	Deviance	0.037	Deviance	0.044
<i>Stipiturus malachurus</i>	Southern Emu-wren	HW	17	Lower-midstorey		Density of large trees		Basal area	
				<i>P</i> -value	<b>0.010</b>	<i>P</i> -value	0.114	<i>P</i> -value	0.120
				Deviance	0.214	Deviance	0.069	Deviance	0.068
<i>Strepera graculina</i>	Pied currawong	FH	29	Litter cover		Litter depth		Proportion of very large trees	
				<i>P</i> -value	0.121	<i>P</i> -value	0.152	<i>P</i> -value	0.163
				Deviance	0.051	Deviance	0.177	Deviance	0.023
<i>Strepera versicolor</i>	Grey currawong	FH	17	Plant cover		Litter cover		Maximum tree diameter	
				<i>P</i> -value	0.314	<i>P</i> -value	0.361	<i>P</i> -value	0.382
				Deviance	0.104	Deviance	0.031	Deviance	0.024

Species name	Common name	Ecosystem	No. sites	Variable 1	Variable 2	Variable 3
<i>Todiramphus sanctus</i>	Sacred kingfisher	FH	8	Plant cover	Upper-midstorey cover	Proportion of very large trees
				<i>P</i> -value	<b>0.001</b>	<i>P</i> -value 0.117
				Deviance	0.300	Deviance 0.069
<i>Zosterops lateralis</i>	Silvereye	FH	11	Litter depth	Lower-midstorey	Litter cover
				<i>P</i> -value	0.054	<i>P</i> -value 0.194
				Deviance	0.107	Deviance 0.050
<i>Zosterops lateralis</i>	Silvereye	HW	21	Upper-midstorey cover	Litter cover	Bare ground cover
				<i>P</i>	<b>0.000</b>	<i>P</i> -value <b>0.001</b>
				Deviance	0.525	Deviance 0.325

### 3.4.2 The response of individual species to habitat structure across ecosystems

Models were built for 17 species that occurred in more than one ecosystem (Table 3.1). Fifty-nine percent of these species responded to different habitat attributes in each ecosystem (Fig. 3.3). Twenty-nine percent of these species, responded to at least one common attribute across ecosystems and 12% of these species were not significantly related to any of the habitat attributes in each ecosystem. For one species, the golden whistler *Pachycephala pectoralis*, the strongest model in each ecosystem included the same attribute: upper-midstorey vegetation cover.

Only one species, the grey shrike-thrush *Colluricincla harmonica*, occurred at >20% of sites in all three ecosystems. In foothill forests, this species responded to bare ground cover, whereas in mallee woodlands, it responded to the size of canopy trees (Table 3.1, Fig. 3.4). In heathy woodlands, the grey shrike-thrush was not significantly related to any of the habitat variables. The shape of the response of grey shrike-thrush to habitat variables also differed between ecosystems (Fig. 3.4). The response to bare ground cover was positive in foothill forests (Fig. 3.4a), null in heathy woodlands (Fig. 3.4b) and a non-significant declining trend in mallee woodlands (Fig. 3.4c). The response to maximum tree diameter was non-significant in foothill forests (Fig. 3.4e) and heathy woodlands (3.4f) and positive in mallee woodlands (Fig. 3.4g).

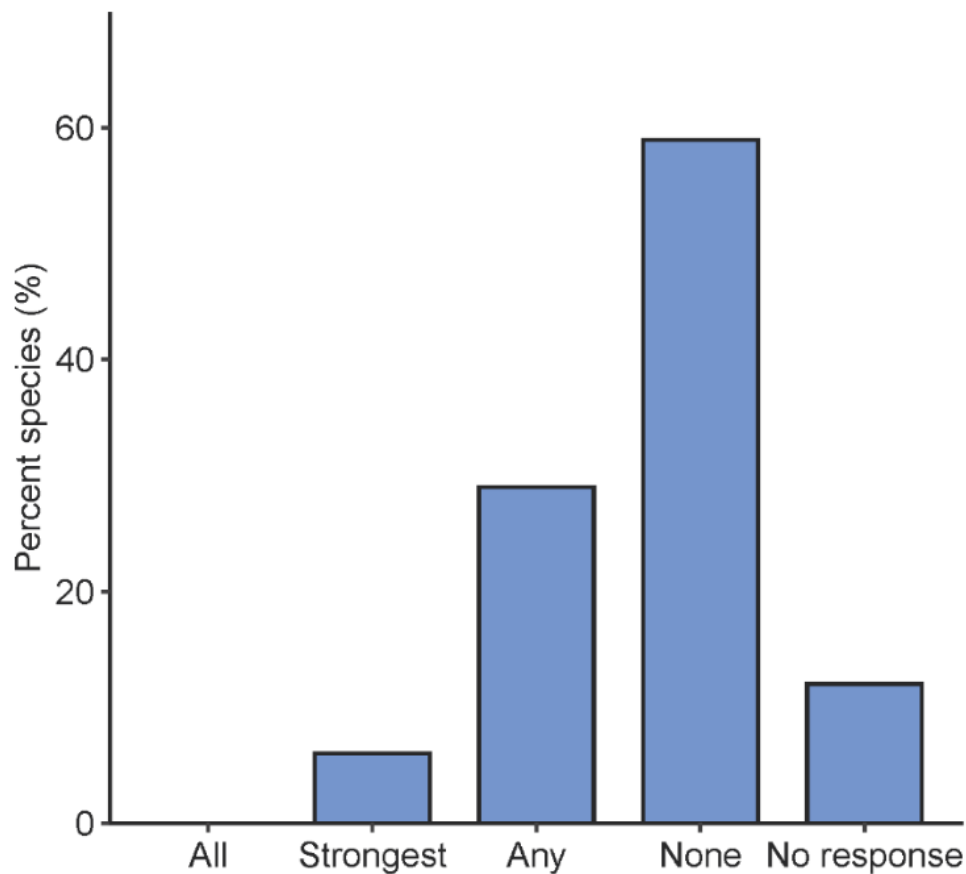


Figure 3.3. Summary of bird species' responses to habitat attributes across ecosystems. Bars represent the percentage of bird species modelled that occurred in more than one ecosystem (total of 17 species). 'All' = the species responded significantly to the same set of habitat attributes in each ecosystem. 'Strongest' = the strongest model for the species in each ecosystem was with the same habitat attribute. 'Any' = the species was significantly related to at least one habitat attribute that was the same in each ecosystem. 'None' = the species was related to none of the same attributes in each ecosystem. 'No response' = the species was not significantly related to any of the attributes in any ecosystem. Models were generalized additive models.

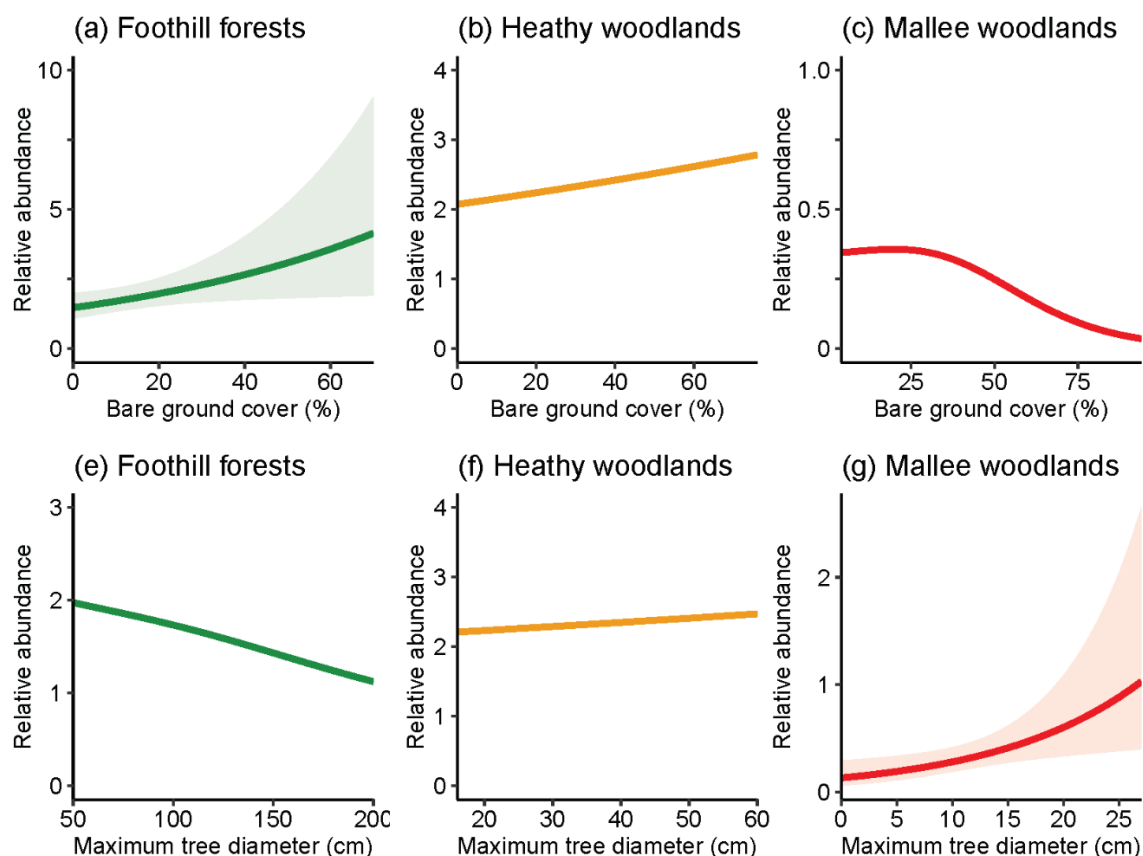


Figure 3.4. Response of the grey shrike-thrush *Colluricincla harmonica* to (a – c) bare ground cover and (e – g) maximum tree diameter in foothill forests (green lines), heathy woodlands (orange lines) and mallee woodlands (red lines). Lines are fitted from generalized additive models. Shaded areas represent 95% confidence intervals. Lines without shading indicate a non-significant relationship.

### 3.5 DISCUSSION

These findings demonstrate that, across an 80-year post-fire chronosequence, bird species in foothill forests, heathy woodlands and mallee woodlands respond to habitat attributes known to be related to time since fire (see Chapter 2, Rainsford et al. 2020), but these differed among ecosystems. In foothill forests and heathy woodlands, where canopy tree stems generally persist through fire, upper-midstorey vegetation was the most influential habitat attribute. In these ecosystems, several species responded to habitat attributes not related to time since fire (e.g. plant cover, large tree diameter). In mallee woodlands, where canopy

trees resprout basally, canopy tree attributes were the most important. Most species that occurred in more than one ecosystem responded to different attributes in each ecosystem. These findings highlight how the role of fire in shaping the distribution of faunal species can differ between ecosystems, and the need for fire management strategies to reflect these differences.

### **3.5.1 What do birds respond to post-fire: ground cover, midstorey or canopy?**

In foothill forests and heathy woodlands, birds responded strongly to upper-midstorey vegetation cover, because of two main characteristics of this stratum: (1) it is removed by fire and regenerates over time (Rainsford et al. 2020), leading to variation across the chronosequence; and (2) it provides important resources for birds (e.g. nest sites, nectar, invertebrates, fruit, shelter/roost sites) (McElhinny et al. 2006) (Fig. 3.5, Fig. 3.6a). Habitat attributes that are not related to time since fire were also influential for some species (e.g. plant cover, bare ground cover, Fig. 3.6b-c). Plant cover in forests is related to site-scale productivity (Small and McCarthy 2005) and provides habitat for ground-dwelling vertebrates and invertebrates (Brown 2001, McElhinny et al. 2006), and prey items for ‘perch-pounce’ predators such as the sacred kingfisher, laughing kookaburra *Dacelo novaeguineae* and eastern yellow robin *Eopsaltria australis*.

In mallee woodlands, the most limiting important habitat attribute across the chronosequence was maximum tree diameter. Previous studies in mallee woodlands have shown a strong relationship between bird species and time since fire (e.g. Taylor et al. 2012, Watson et al. 2012b), attributed to the correlation between tree size and time since fire (Haslem et al. 2011, Rainsford et al. 2020). Large trees provide important resources for birds (e.g. nectar, foliage, tree hollows) (Loyn and Kennedy 2009, Remm and Löhms 2011, Haslem et al. 2012, Bennett 2016), so variation in tree size through space and time drives variation in the abundance of birds associated with the resources provide by large trees.

Below, I discuss three main hypotheses to explain the observed differences between ecosystems, based on: (1) environmental conditions (productivity, climate); (2) plant regeneration traits; and (3) fire characteristics. These hypotheses are not mutually exclusive; it is likely a combination of the three that best explains the main findings.



Figure 3.5. Long-unburnt (79 years since fire) heathy woodlands vegetation. (a) Dense understorey vegetation dominated by *Leptospermum* species. (b) Flowers and invertebrates on prickly tea tree *Leptospermum continentale*.



Figure 3.6. Foothill forests vegetation. (a) Long unburnt (79 years since fire) vegetation with developed lower- and upper-midstorey. (b) Recently burnt (2 years since fire) *Eucalyptus* tree resprouting epicormically, regenerating low shrubs, patches of bare ground. (c) Recently burnt (2 years since fire) vegetation with high cover of low shrubs and little bare ground exposed.

### **3.5.2 Environmental conditions**

These three ecosystems occur in different climatic, topographic and geological settings, which can influence the distribution and rate of post-fire recovery of vegetation (Kenny et al. 2018). The direction and form of faunal species' responses to habitat structure and fire can vary in space and time according to environmental conditions (Nimmo et al. 2014, Puig-Gironès et al. 2017, Verdon et al. 2019). The rate of vegetation growth is slower in more arid climates such as mallee woodlands, than in more mesic areas like foothill forests, which could lead to greater variation in tree size across the chronosequence in mallee woodlands. However, it is more likely that the capacity for tree stems to persist through fire in foothill forests and heathy woodlands drives the differences between ecosystems in the most important habitat attributes for birds, post-fire.

### **3.5.3 Stand regeneration and biological legacies**

The type and extent of post-fire biological legacies have a key influence on the temporal and spatial variation in structural resources available to fauna. All ecosystems have biological legacies post-fire, and these habitat structures play an important role in ecosystem resilience, especially in post-disturbance recolonisation by fauna (Seidl 2014, Banks et al. 2017) and also in the provision of resources that are slow to develop (Haslem et al. 2012). The post-fire occurrence of large live trees is an important factor driving the differences between ecosystems in the role of tree size in shaping the distribution of birds.

In foothill forests and heathy woodlands, stringy-barked eucalypts resprout epicormically (Fig. 3.6b), resulting in rapid regeneration of canopy foliage and stand-persistence through fire. In these ecosystems, foliage is present in a range of vertical strata soon after fire, which can be used by birds for foraging, shelter and nesting. While there are directional post-fire changes in ecosystems dominated by epicormic resprouters (Haslem et al. 2016), this regeneration trait usually leads to rapid recovery of key resources, making these ecosystems

structurally resilient to many fires (Bennett 2016, Kelly et al. 2017b, Chergui et al. 2018, Collins 2020). As such, there was less variation in canopy tree structure across the chronosequence, resulting in fewer birds responding to this stratum compared to mallee woodlands.

To illustrate, I compare two species, both of which responded to the availability of large trees: the yellow-plumed honeyeater *Lichenostomus ornata* in mallee woodlands and grey fantail *Rhipidura albiscapa* in foothill forests. In mallee woodlands, the above-ground component is consumed by fire and regenerates from basal lignotubers. Thus, tree size (stem diameter, canopy height) increases with time since fire (Clarke et al. 2010, Haslem et al. 2011) and birds that have a strong association with large trees (e.g. yellow-plumed honeyeater) have a similarly strong association with time since fire. In foothill forests, the grey fantail also responded to tree size. In this ecosystem, however, the above-ground component of canopy trees persists through fire, large living trees are still standing post-fire and regenerate foliage rapidly via epicormic growth, and so the strong effect of habitat structure on the grey fantail will not correspond with a strong effect of time since fire.

This is further illustrated by the example of the grey shrike-thrush. This species preys on small vertebrates (e.g. lizards) and invertebrates on the ground. In foothill forests, bare ground exposes prey (e.g. basking lizards), creating favourable foraging conditions for the grey shrike-thrush. In mallee woodlands, some lizard species are also positively associated with bare ground (Nimmo et al. 2014). However, the most influential habitat attribute for the grey shrike-thrush was tree size. This species is likely responding to the availability of perch/nest/roost sites (i.e. large trees), which were present across the chronosequence in foothill forests, but not mallee woodlands (i.e. large trees are a limiting factor across the chronosequence on mallee but not foothills).

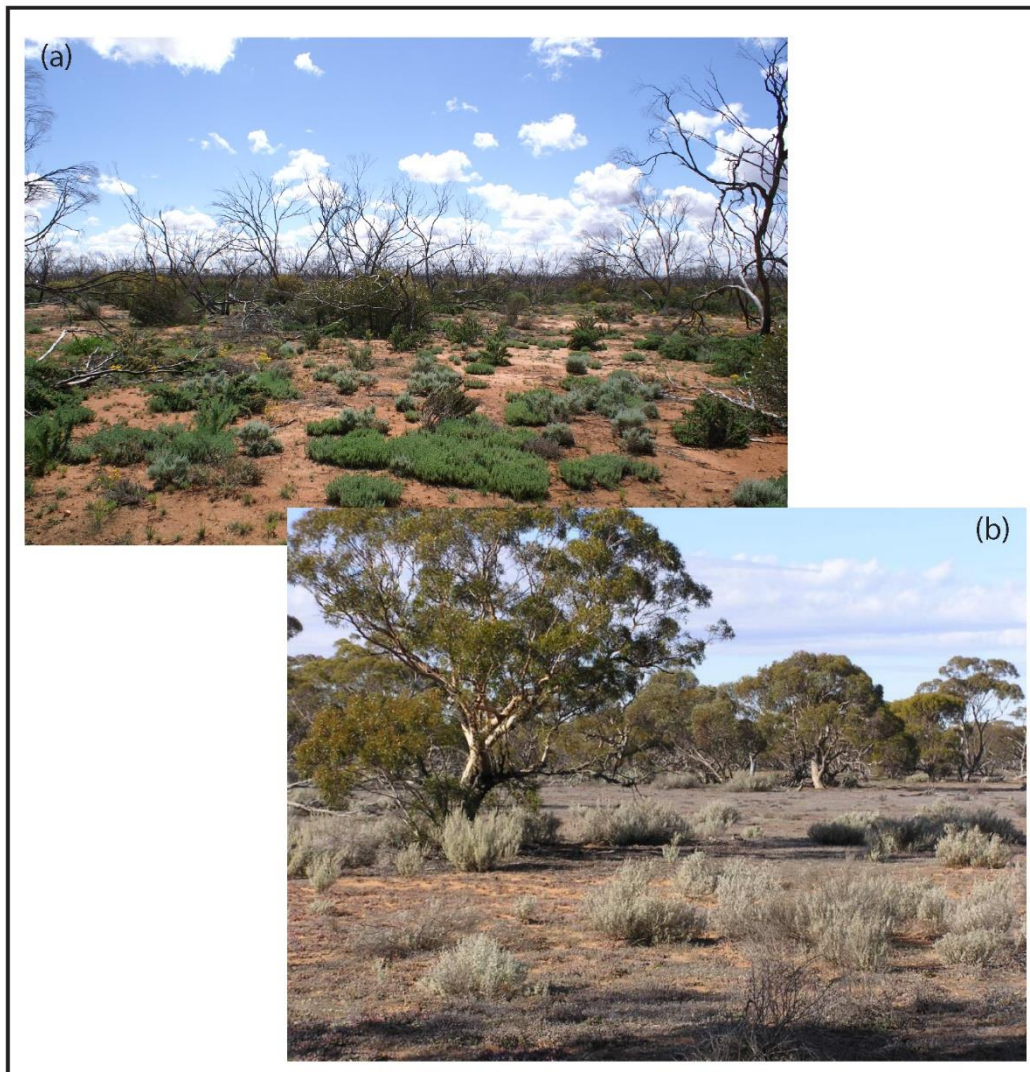


Figure 3.7. Mallee woodlands vegetation. (a) Recently burnt (<5 years since fire). (b) Long-unburnt (>40 years since fire). Credit: Mallee Fire and Biodiversity Project.

#### 3.5.4 Fire characteristics

Fire severity influences canopy foliage cover and the occurrence of birds following fire in *Eucalyptus* forests (Robinson et al. 2014, Haslem et al. 2016). By including only sites last burned by prescribed fire (less severe than wildfire) in foothill forests, I may have underestimated the influence of canopy structure on the bird community. However, I predict that the influence of habitat structure across a chronosequence of severe fires in foothill

forests will more closely resemble that of heathy woodlands (i.e. a stronger influence of midstorey cover with several species responding to canopy tree structure), than mallee woodlands where the canopy stratum is replaced by fire.

Testing this formally is an important next step, especially given the frequency of large severe fires is increasing in fire-prone regions world-wide (Keeley and Syphard 2019, Vitolo et al. 2019, Boer et al. 2020, Lizundia-Loiola et al. 2020). A further study using a whole-of-landscape approach encompassing a range of topographic positions (e.g. moist gullies to dry ridges, different aspects), variation in fire severity and time since fire gradients could reveal the role of canopy structure in shaping bird distributions across the foothill forests region.

The frequency of severe fires could also contribute to some observed differences between ecosystems. Several bird species in heathy woodlands were associated with canopy tree structural variables related to time since fire (maximum tree diameter and basal area) (Rainsford et al. 2020). Frequent severe fires can cause top-kill in epicormic resprouting trees driving reversion to basal resprouting (Catry et al. 2013, Collins 2020). The likelihood of top-kill depends, in part, on bark thickness (Clarke et al. 2013, Pausas and Keeley 2017), which varies between tree species in heathy woodlands.

### **3.5.5 Methodological limitations**

Some aspects of the methods may have influenced the results from this study. The use of different census methods in mallee woodlands (point-counts) and foothill forests and heathy woodlands (line transects) could potentially affect the types of species detected in each ecosystem if different species are more likely to be detected by one method. Observers differed between ecosystems which could also affect the types of species that were detected. However, the number and type of species recorded in each ecosystem was similar and models were built for the most common species which were typical of each ecosystem. Therefore, it

is considered unlikely that differences in survey methods between ecosystems contributed to the overall findings of this chapter.

### **3.5.6 Conservation implications**

Although the most limiting habitat attributes in the three ecosystems are known to be associated with time since fire (see Chapter 2, Rainsford et al. 2020), this pattern is strongest in mallee woodlands. The utility of temporal surrogates (e.g. time since fire, vegetation growth stages) to guide fire management will similarly differ between these ecosystems. In mallee woodlands, management categories based on temporal surrogates can represent landscape-wide variation in the abundance of birds reasonably well (Taylor et al. 2012). However, in foothill forests, such categories will likely represent variation in the abundance of mid-storey bird species, but not canopy-dwelling or ground-foraging species.

These findings support a growing body of research that shows that time since fire is a poor surrogate for bird occurrence in structurally resilient *Eucalyptus* forests (Sitters et al. 2014a, Kelly et al. 2017b). To better represent the distribution of bird communities in ecosystems like foothill forests, attributes used in fire management planning need to reflect the processes driving the distribution of habitat structure and bird species. This will require more than a single fire variable. Instead a more complex combination of fire and environmental attributes that includes, for example, fire severity, topography and the legacy of prior forest management.

Fire management strategies that aim to conserve the habitat of species in one setting may not be applicable to that species in other settings. The time window of occurrence of faunal species can vary across landscapes depending on post-fire habitat dynamics (Verdon et al. 2019). Management strategies for biodiversity conservation must reflect this diversity. For example, excluding fire to protect patches of older, large trees may conserve habitat for the grey shrike-thrush in mallee woodlands. However, in foothill forests, where the amount of

bare ground is important for the grey shrike-thrush, introducing fire by prescribed burning may be beneficial. These findings highlight the importance of explicitly considering ecological context in fire management strategies and the risks of applying knowledge from one region/ecosystem to another without verification of its applicability.

#### **4 HOW DOES FIRE MANAGEMENT SHAPE BIRD AND PLANT COMMUNITIES IN A HEATHY WOODLAND ECOSYSTEM?**

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Heathy woodland vegetation.

#### 4.1.1 Abstract

In ecosystems likely to experience more frequent severe fires, such as dry forests and woodlands, there is an urgent need to understand how fire management practices affect animal and plant communities. Species' life-history traits may help reveal the mechanisms driving the response of organisms to fire and how manipulating fire regimes may affect ecosystems. We used a field study, in a heathy *Eucalyptus* woodland in south-eastern Australia, to determine how: (a) individual species, (b) functional groups of species and (c) the composition of communities of birds and plants respond to time since fire. We then used these outcomes to evaluate the likely impacts of fire management on bird and plant communities as guided by two approaches based on: (1) tolerable fire intervals (TFIs), a concept based on plant life-history traits (e.g. reproductive age), and (2) the spatial arrangement of post-fire age-classes (based on vegetation growth stages). Species' life-history traits gave key insights into bird and plant responses to time since fire. Notable fire effects included: (a) an irruptive response of ground-foraging birds <5 years post-fire, (b) a plateau response ~50 years post-fire of lower-midstorey foraging birds, (c) a plateau response ~20 years post-fire of facultative-resprouting plants, and (d) an initial peak soon after fire followed by a decline in the richness of obligate-seeding species, and of shrubs and low shrubs. Post-fire age-classes represented distinct bird and plant communities, which can be attributed to species' life-history traits and successional changes in habitat conditions. The peak in species richness of several plant groups, coincided with the designated minimum TFI, whereas the peak in abundance of lower-midstorey foraging birds was later than the maximum TFI. Timing of prescribed burns based solely on TFIs and plant functional traits risks disadvantaging bird communities. Maintaining proportions of older age-class vegetation in the landscape to provide optimum habitat for populations of certain bird species, while introducing fire at sufficient frequency to prevent loss of plant and ground-foraging bird

species, can be achieved by fire management that uses a spatial representation of post-fire growth stages across the landscape. Incorporating additional complexity (e.g. topography) is also needed to represent components of biodiversity not strongly associated with time since fire.

## 4.2 INTRODUCTION

Conservation of biota in fire-prone ecosystems depends on knowing how, and when, populations and communities recover following fire (Turner 2010, Warchola et al. 2018). In ecosystems worldwide, fire regimes are changing, with uncertain consequences for the biota (Keeley and Syphard 2019, Vitolo et al. 2019, Nolan et al. 2020). Shifts in the frequency, severity, extent and timing of fires can threaten species and ecological communities with risk of local extinction (Bowman et al. 2011, Enright et al. 2015, Giljohann et al. 2015, Hanberry and Thompson Iii 2019, Stephens et al. 2019). Additionally, landscapes increasingly are managed to mitigate the consequences of severe fires (Stephens et al. 2013). There is an urgent need to understand how fire and fire management affect animals and plants in areas likely to experience more frequent severe wildfire, such as dry forest and woodland ecosystems.

For animals, persistence in fire-prone environments depends on their ability to capitalize on resources (for food, shelter, nesting), as they become available during the post-fire succession (Fox 1982, Nappi and Drapeau 2011, Barton et al. 2014, Sitters et al. 2014a, White et al. 2016, Gosper et al. 2019). For example, the black-backed woodpecker *Picoides arcticus* in western U.S.A. nests in fire-killed standing trees and occurs almost exclusively in recently burnt vegetation (Hutto et al. 2020). Knowledge of species' temporal responses to fire, and the mechanisms driving these responses, is crucial for conservation management (Jacquet and

Prodon 2009, Watson et al. 2012b, Doherty et al. 2017), but is poorly known for animal species in many ecosystems, or limited to the first decade post-fire (Hutto et al. 2020).

For plants, persistence in fire-prone landscapes depends on the ability of populations to recover from fire events, either through germination of seeds or resprouting survivors (Keeley et al. 2011). As such, the interval between fires is critical for both reproductive and resprouting success, but the required interval depends on a species' life-history (Menges 2007, Enright et al. 2015). Accounting for the different responses of taxa to fire is a complex challenge for fire management that aims to conserve biodiversity, including deciding the timing and placement of prescribed burns or fire suppression efforts. Fire planning has focused on the timing and spatial arrangement of fires and is guided generally by expert elicitation or analyses (Keith et al. 2007, Menges et al. 2017, Kelly et al. 2018).

Plant traits related to population persistence in fire-prone landscapes have been used to develop the concept of minimum and maximum tolerable fire intervals (TFIs) for ecosystems throughout the world (Noble and Slatyer 1980, Menges 2007, van Wilgen et al. 2011, Kraaij et al. 2013). The minimum tolerable fire interval is based on the number of years required post-fire for key plant species to successfully reproduce and set seed; while the maximum tolerable fire interval represents the age post-fire at which these key species begin to senesce (Cheal 2010, Kraaij et al. 2013). For example, in Victoria, Australia, fire managers quantify the proportions of landscapes that are either within, or outside, the recommended tolerable fire interval to decide where and when to carry out prescribed burns (York and Friend 2016). This approach, however, does not explicitly recognize the needs of other taxa (Clarke 2008). If the abundance of animals and plants in an ecosystem peak at different times post-fire, then landscape management guided by a concept based on plant traits alone will not necessarily benefit all taxa (Di Stefano et al. 2013).

A second concept in fire management, used to conserve multiple taxa across the landscape, is to plan spatially to maintain patches of vegetation with different fire-histories (Kelly et al. 2015, York and Friend 2016, Menges et al. 2017). Post-fire age-classes, determined by compositional and structural changes to vegetation, can be defined to represent key ‘growth stages’ in post-fire succession in an ecosystem (e.g. Cheal 2010). However, the assumption that such categories represent distinct successional communities has rarely been tested for animal taxa. Mostly, configurations of such fire age-classes are manipulated in landscapes to maximize a biodiversity index (e.g. geometric mean of species’ abundance) (Giljohann et al. 2015, Chick et al. 2019). The way in which the composition of an animal community changes over time post-fire, and the mechanisms driving such compositional change, remain key knowledge gaps for biodiversity conservation in dry forest and woodland ecosystems.

Recurrent fire has driven the evolution of various traits that enable species to persist in fire-prone landscapes (Keeley et al. 2011, Pausas and Keeley 2014, Pausas and Parr 2018, Nimmo et al. 2019). Relating life-history traits to species’ fire-responses can help reveal the processes that drive patterns of biodiversity across fire-prone landscapes (Keith et al. 2007, Jacquet and Prodon 2009, Penman et al. 2009, Clarke et al. 2015, Burgess and Maron 2016, Davis et al. 2016). Where generalisations can be made based on analyses of species’ life history traits, it will build understanding of how ecosystem structure and function change following fire (Gosper et al. 2019). This knowledge will help to identify species and ecosystem processes sensitive to more frequent fire, or benefit from more widespread prescribed burning, and thereby improve decision-making in fire management.

Here, we examine how bird and plant communities respond to fire in a heathy *Eucalyptus* woodland in south-eastern Australia. Specifically, we aimed to determine how: (a) individual species, (b) functional groups of species, and (c) the composition of communities of birds and plants respond to time since fire. We then used these outcomes to evaluate the likely impacts

of fire management on bird and plant communities of heathy woodlands as guided by two approaches: (1) tolerable fire intervals (TFIs), a concept based on plant life-history traits (e.g. reproductive age), and (2) the spatial arrangement of post-fire age-classes (based on vegetation growth stages).

## **4.3 METHODS**

### **4.3.1 Study location and climate**

The study area is part of the Great Otway National Park and Forest Park in the Otway Plains bioregion of southern Victoria, Australia (Fig. 1). The climate is temperate with mean annual rainfall ranging from 540 – 895 mm. The highest rainfall occurs in winter (August) and the hottest month is February (mean daily maximum 28°C) (Mount Gellibrand, station no. 0900351, Cape Otway lighthouse, station no. 090015; <http://www.bom.gov.au/>). The topography is gently undulating with elevation from ~ 40 to 250 m above sea-level.

### **4.3.2 Vegetation**

Heathy woodlands in south-eastern Australia mostly are confined to coastal areas, with some inland occurrences on nutrient-poor, deep sandy soils of quartzite gravel. In the study area, the canopy is low ( $\leq 10$  m) and dominated by brown stringybark *Eucalyptus baxteri* and western peppermint *Eucalyptus fasciata*, both of which are capable of resprouting epicormically following fire. The understorey consists of a diverse array of shrubs including austral grass tree *Xanthorrhoea australis*, heath tea-tree *Leptospermum myrsinoides*, prickly tea-tree *Leptospermum continentale* and silver banksia *Banksia marginata* (Victorian Government Department of Sustainability and Environment 2004). Fire regeneration traits vary between understorey species: tea trees resprout from basal lignotubers, austral grasstree resprouts apically, and silver banksia regenerates from seed. A dense understorey thicket forms over time, following disturbance (Figure 4.2b) (Rainsford et al. 2020).

### **4.3.3 Fire regime and fire history**

In heathy woodlands, wildfires typically occur in summer months while prescribed burning is carried out by fire managers during autumn and early spring. Wildfires occur at ~20 – 100 year-intervals (Murphy et al. 2013). In the study area, a wildfire occurred in 1939 and several wildfires also burned patches during the 1960s. Prescribed fire is employed by fire managers to achieve objectives relating to fuel reduction and, less often, biodiversity conservation. The timing of prescribed burns in Victoria is guided by minimum and maximum tolerable fire intervals (TFIs) for a particular vegetation type, based on the number of years required for key plant species to set seed (minimum TFI) and begin to senesce (maximum TFI) (Cheal 2010). Designated minimum and maximum TFIs for heathy woodlands are 12 and 45 years, respectively (Cheal 2010). Prescribed fires typically burn more patchily than wildfires, but in heathy woodlands, both fire types generally scorch the canopy (Figure 4.1b). Vegetation last burnt by either wildfire or prescribed fire were included as there were not enough sites within a single fire type to span the desired chronosequence.

Fire history of sites was determined by using spatial data maps supplied by the Victorian Department of Environment, Land, Water and Planning (DELWP) and analysed using the software ArcMap (ESRI 2011). Spatial data maps of fire perimeters post-1976 were created by using LANDSAT imagery, and pre-1976 by using historical records. The mapped time since fire was ground-truthed at each site by looking for signs of charring on eucalypt bark, epicormic resprouting and other structural features.

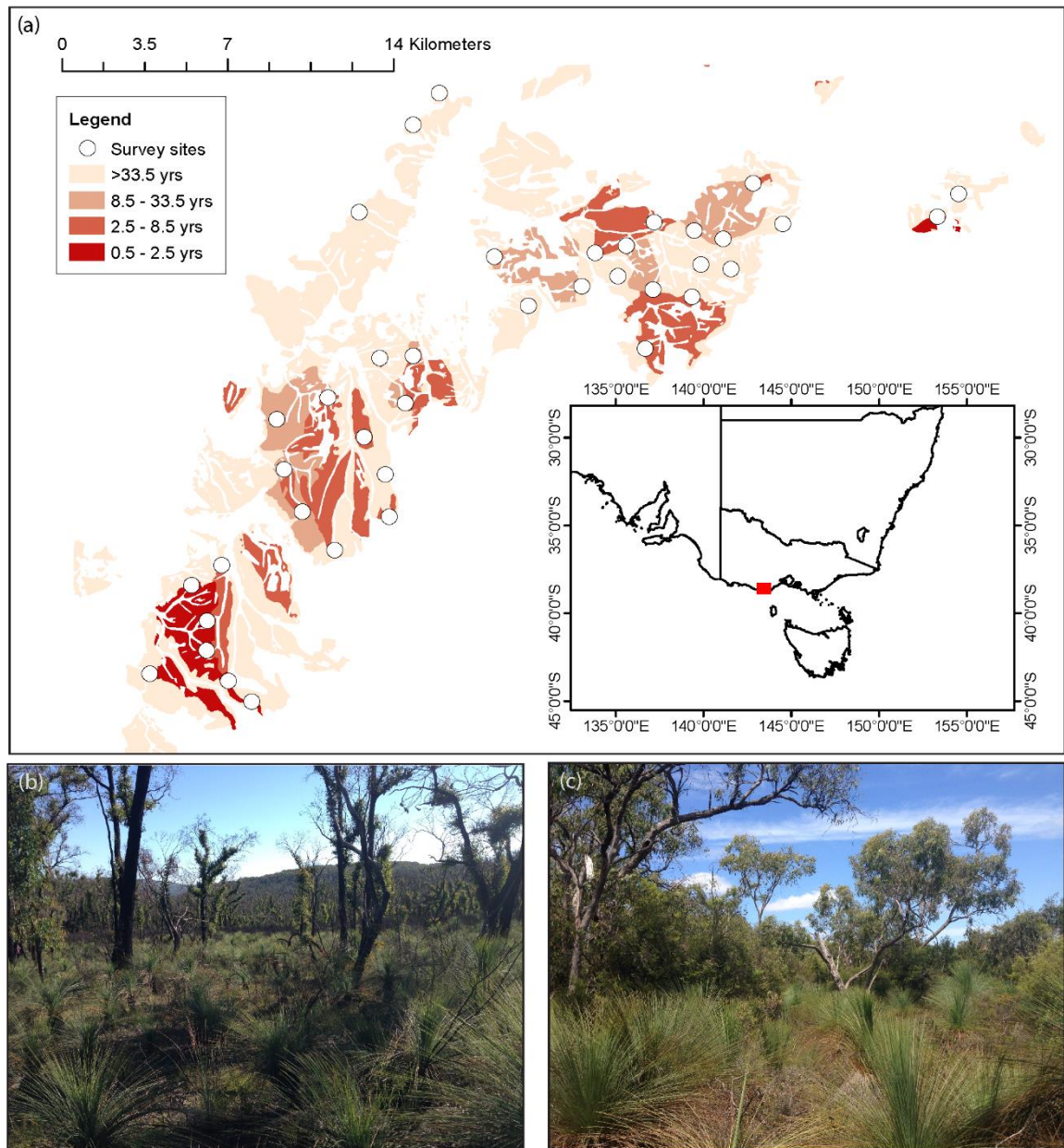


Figure 4.1. Heathy woodland study area and vegetation. (a) Map of the study area showing the extent of heathy woodlands, the location of study sites and distribution of fire age-classes (darker tones represent younger age-classes). Heathy woodland vegetation: (b) ~1 year after prescribed fire, showing a scorched canopy of *Eucalyptus* species resprouting epicormically, austral grass-tree resprouting apically; and (c) 51 years after fire with a well-developed midstorey dominated by *Monotoca glauca* and *Leptospermum* species.

#### **4.3.4 Study design**

We sampled diurnal birds and understorey vascular plants at 38 sites selected to span a chronosequence from 1 - 79 years post-fire. Sites were selected to evenly cover a range of post-fire 'age-classes': successional states based on the vegetation growth stages described by Cheal (2010). These were: 0.5 - 2.5 years (AC1), 2.5 - 8.5 years (AC2), 8.5 - 33.5 years (AC3), >33.5 years since fire (AC4) (Appendix 4.6.1). Sites were located away from gullies to avoid the influence of inherent differences in productivity and vegetation structure between gullies and slopes. The sites sampled a single ecological community (heathy woodlands EVC, Victorian Government Department of Environment and Sustainability 2004b), and were located at least 1 km apart to ensure sample independence.

#### **4.3.5 Data collection**

To survey bird and plant communities, I established a 250 m transect at each site that started at least 50 m from a road edge.

##### *4.3.5.1 Birds*

To sample bird communities at each site, a 2-ha plot was centred over the 250 m transect and surveyed by a single experienced observer (FR) a total of six times: three times during the austral autumn/winter and three times during spring/summer, between 2017 and 2018.

Surveys were conducted in clear weather within four hours of dawn, except for two winter survey rounds during which sites were each surveyed once in the morning and once in the afternoon. During surveys, all individuals either heard or seen over a 20-min period were identified to species level and recorded. The perpendicular distance (m) to all detections from the transect line were estimated to test for differences in detectability between sites (see Appendix 4.6.2). Nocturnal birds, raptors and swifts were recorded but excluded from all analyses.

#### 4.3.5.2 Understorey plants

Understorey vascular plants were sampled at each site by using three 10 m x 10 m plots: one at the start, mid, and end-point of the 250 m transect. All vascular plant species that were rooted within plots were identified to species level and the projected foliar cover (%) was estimated visually by a single observer (FR). The mean cover of the three plots was calculated for each species and used in analyses. Three plots were used to sample each site to increase coverage of potentially patchily distributed species. Because of uncertainty in the emergence time of geophytic orchids and lack of reproductive material to enable identification of grasses, these groups were excluded from analyses, except for forest wire grass *Tetrarrhena juncea* which was readily identified from vegetative material. Plant surveys were completed in the austral summer (between 7<sup>th</sup> Dec 2017 and 17<sup>th</sup> Jan 2018).

### 4.3.6 Data analysis

#### 4.3.6.1 Individual species

For individual species of birds and plants that occurred at  $\geq 7$  sites, we used generalised additive models (GAM) (Wood 2017) to predict changes in relative abundance with time since fire. For bird species, we used the reporting rate to represent relative abundance at sites. Reporting rate is the number of survey rounds during which a species was detected (here, from 0 – 6). It does not rely on counts of individuals, and so is less prone to biases caused by differences in detectability or flocking behaviour. Variation in reporting rate between sites is often a result of variation in the abundance of individuals between sites and so is a reliable proxy for relative abundance (Royle and Nichols 2003). Models were fitted using the Poisson error distribution. An observation-level random factor was used in this mixed-model framework if overdispersion of data was detected, following Harrison (2014).

For plants the mean projected foliar cover was modelled by using the beta error distribution. The beta distribution can overcome inherent problems with proportion data (i.e. bounding at

zero and one) that violate the assumptions of other distributions (Douma and Weedon 2019). For one species, silver banksia, using a beta distribution was problematic and a better model was fitted by using the Gaussian error distribution. The distribution of data supported this decision. GAMs were built by using the *mgcv* package in R (Wood 2017).

By assessing fitted response curves, species were each assigned to a generalized response curve as described by Watson et al. (2012). We then calculated the percentage of species with a significant relationship with time since fire, that resembled each response shape. Four response shapes were detected: ‘irruptive’ (abundance highest in the first few years following fire), ‘bell’ (initial increase followed by a decrease with time since fire), ‘incline’ (gradual increase with time since fire), and ‘plateau’ (initial increase followed by stability in later years post-fire). Non-significant relationships were classed as ‘NS’.

#### 4.3.6.2 *Community composition*

To test the influence of time since fire on the composition of bird and plant communities, first we classified sites into four post-fire age-classes (AC1-AC4) based on vegetation growth stages (Cheal 2010) (Section 4.3.4, Appendix 4.1). AC4 included two growth stages, ‘waning’ and ‘senescence’, because there were fewer sites in these categories and their vegetation structure is similar. We then used relative abundance/cover matrices for species and non-metric multidimensional scaling (NMDS) ordination analysis. NMDS represents ecological communities in lower-dimensional space, based on their dissimilarity (Legendre and Legendre 1998). We used the Bray-Curtis index to calculate dissimilarities as it is less sensitive to rare species than other techniques such as Euclidian distance. The NMDS was undertaken using the *metaMDS* function in the “*vegan*” package (Oksanen et al. 2019) and ordination plots. Non-parametric permutation tests (PerMANOVA, ADONIS in the ‘*vegan*’ package) were used to test for significant ( $P < 0.05$ ) effects of age-class on community

composition. Species detected at a single site only were removed from the analysis to reduce the leverage of rare or vagrant species.

#### 4.3.6.3 *Functional groups*

To test whether functional groups help explain bird and plant responses to time since fire, we classified species based on ecologically relevant traits (Table 4.1). Birds were classified according to: (a) typical foraging location (ground, lower-midstorey, upper-midstorey, throughout, aerial); (b) nest type (brood parasite, burrow, open, tree hollow); and (c) level of dietary versatility (low, intermediate, high), based on the number of food types (fruit, nectar or pollen, seeds, foliage or herbs, corms or tubers, terrestrial invertebrates, terrestrial vertebrates, carrion) that constitute  $\geq 1\%$  of total diet. To classify birds into functional groups, we used a combination of expert knowledge and a published database of Australian birds (Garnett et al. 2015).

Plant species were classified according to: (a) their fire regeneration trait, following the classification system of Clarke et al. (2015) (i.e. facultative resprouting, obligate resprouting, obligate seeding); and b) growth form (shrub 1-8 m, low shrub 0.1-1 m, herb, geophyte) (after Meers et al. 2010, Gosper et al. 2013b) (Table 4.1). We used a database of plant vital attributes for the Victorian flora (Cheal 2011) to determine fire regeneration traits of plant species. If a species' regeneration trait was not listed, it was classified based on congeneric species unless this was not available or there was inconsistency within the genus, in which case the species was not included in the functional group analysis.

We then used GAMs to model (a) the summed relative abundance (for birds) or cover (plants) of all species, and (b) the number of species within each functional group as a function of time since fire.

Table 4.1. Functional groups of birds and plants in heathy woodlands. Plant regeneration traits follow Clarke et al (2015). The classification system for plant growth forms was based on Meers et al. (2010) and Gosper et al. (2013). The number of species detected within each group is given. Individual species classifications can be found in Appendix 4.3.

Taxon	Category	Group	Description	Number of species
Birds	Foraging location	Ground	Takes most food from the ground. Includes species that perch in vegetation and swoop down to take prey from the ground, and species that forage from the ground.	11
		Lower-midstorey	Mostly forages in vegetation $\leq 3\text{m}$ above ground.	10
		Upper-midstorey	Mostly forages in vegetation $> 3\text{m}$ above ground. Includes species that forage amongst the canopy as well as those that fly out from within vegetation to take air-borne prey.	17
		Throughout	Forage throughout the range of vertical strata, from ground to the canopy.	5
		Aerial	Forages on the wing, above the canopy.	1
	Nest type	Brood parasite	Lays eggs in the nests of other species. Does not build a nest (cuckoos).	2
		Burrow	Tunnel in the ground.	1
		Open	Constructs nest outside of hollows or burrows.	34
		Hollow	Large or small cavity in a tree.	7
	Diet versatility <sup>†</sup>	Low	Only one food type that constitutes $\geq 1\%$ of the total diet.	19
		Intermediate	Two-three food type each constitute $\geq 1\%$ of the total diet.	20

Taxon	Category	Group	Description	Number of species
Plants	Regeneration trait	High	Four-six food types each constitute $\geq 1\%$ of the total diet.	5
		Facultative resprouter	Individuals regenerate either from seed or resprouting following fire.	43
		Obligate resprouter	Resprouts following fire but does not regenerate from seed.	4
		Obligate seeder	Individuals have no capacity to resprout following fire. Regeneration occurs via seed either stored in the soil seed bank or from survivors outside or inside the fire perimeter.	11
	Growth form	Shrub	Phanerophytes. Shrubs 1-8m.	22
		Low shrub	Chamaephytes. Shrubs 0.1-1m.	22
		Herb	Hemicryptophytes. Persistent buds at soil surface. Includes sedges.	21
		Geophyte	Seasonal reduction to below-ground storage organ.	2

<sup>†</sup> Food types include fruit, nectar or pollen, seeds, foliage or herbs, corms or tubers, terrestrial invertebrates, terrestrial vertebrates, carrion (Garnett et al. 2015).

## 4.4 RESULTS

We made 3975 detections of 44 species of diurnal bird (Table S4.6.3). The dominant bird families were the Meliphagidae (honeyeaters,  $n = 9$  species), Acanthizidae (thornbills,  $n = 4$ ), Artamidae (butcherbirds,  $n = 4$ ), and Pachycephalidae (whistlers,  $n = 4$ ). Widespread bird species included yellow-faced honeyeater *Lichenostomus chrysops* (38/38 sites), brown thornbill *Acanthiza pusilla* (38/38 sites), grey fantail *Rhipidura albiscapa* (37/38 sites) and crescent honeyeater *Phylidonyris pyrrhopterus* (36/38 sites).

We detected 67 species of vascular plants (Table S4.6.4). The most speciose plant families were the Fabaceae (peas and wattles,  $n = 8$  species), Cyperaceae (sedges,  $n = 7$ ), Ericaceae (heaths,  $n = 6$ ), Proteaceae ( $n = 4$ ), Asteraceae (daisies,  $n = 4$ ) and Dilleniaceae ( $n = 4$ ). Most species were capable of resprouting post-fire; 43 species were facultative resprouters and four species were obligate resprouters. Eleven species were obligate seeders. Five of the obligate seeders were from the Fabaceae and three from Asteraceae. Widespread species included the shrubs: prickly tea tree *Leptospermum continentale* (38/38 sites), heath tea tree *L. myrsinoides* (38/38 sites), austral grass-tree *Xanthorrhoea australis* (37/38 sites) and silver banksia *Banksia marginata* (37/38 sites), and the low shrubs: smooth parrot-pea *Dillwynia glaberrima* (38/38 sites) and erect guinea-flower *Hibbertia riparia* (38/38 sites).

We built models (GAMs) for 25 bird and 39 plant species that occurred at  $\geq 7$  sites. Five (20%) bird and twelve (31%) plant species were significantly related to time since fire (Fig. 4.2). We detected four types of generalized response curves: irruptive (13% of plants modelled, 4% of birds modelled), bell (8% of plants, 4% of birds), incline (3% of plants, 4% of birds) and plateau (8% of plants, 8% of birds). Outputs for all models are provided in Appendix 4.6.5.

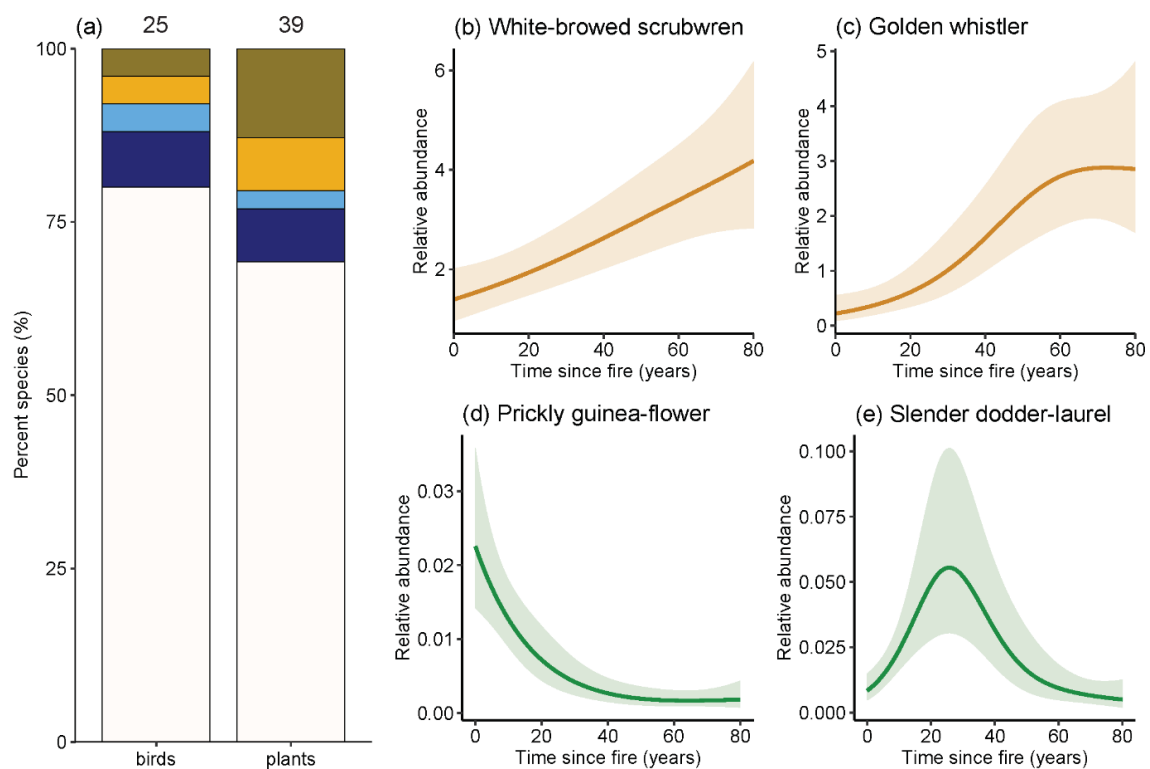


Figure 4.2. Generalized response curves from generalized additive models of the relationship between bird and plant species and time since fire in heathy woodlands. (a) The percentage of species modelled in each taxonomic group for which the response to time since fire resembled four generalized response curves (after Watson et al. 2012): ‘irruptive’ (dark brown), ‘bell’ (light brown), ‘incline’ (light blue) or ‘plateau’ (navy blue). Off-white bars represent non-significant responses. Numbers above bars indicate the number of species modelled in each taxon. (b – e) Examples of each response shape from bird (orange curves) and plant (green curves) species: (b) incline, (c) plateau, (d) irruptive, (e) bell. Lines are fitted from models and shaded ribbons indicate 95% confidence intervals.

Non-metric multidimensional scaling analyses and PerMANOVA showed there was a significant relationship ( $P < 0.01$ ) between post-fire age-classes and the composition of the bird and plant communities (Fig. 4.3). Clustering of age-classes in the ordination plots was more distinct when based on the bird community (Fig. 4.3a) than the plant community (Fig. 4.3c). Vectors of influential species revealed a strong influence of species traits on the composition of the bird communities (Fig. 4.3b). There were two notable features in the ordination: (1) the association of lower-midstorey foraging bird species (e.g. brown thornbill,

New Holland honeyeater, white-browed scrubwren *Sericornis frontalis*, silveryeye *Zosterops lateralis*) and upper-midstorey foraging species (golden whistler *Pachycephala pectoralis*, grey fantail *Rhipidura albiscapa*) with the oldest age-class (AC4, >33 years), and (2) the association of ground-foraging species (grey shrike-thrush *Colluricincla harmonica*, laughing kookaburra *Dacelo novaeguineae*, superb fairy-wren *Malurus cyaneus*, scarlet robin *Petroica boodang*, common bronzewing *Phaps chalcoptera*) with recently burned vegetation (AC1, <2.5 years).

Variation in plant community composition was greater between the oldest and youngest age-classes compared to the two intermediate age-classes (Fig. 4.3c). There was greater variation within age-classes in the plant community compared to bird community composition. Key influential plant species (Fig. 4.3d) included *Monotoca glauca*, which was associated with the oldest age-class (AC4); *Hibbertia fasciculata* and austral grass-tree, which were associated with intermediate age-classes (AC2, AC3); and tree everlasting *Ozothamnus ferrugineus* and austral bracken *Pteridium esculentum* which were associated with the youngest age-class (AC1).

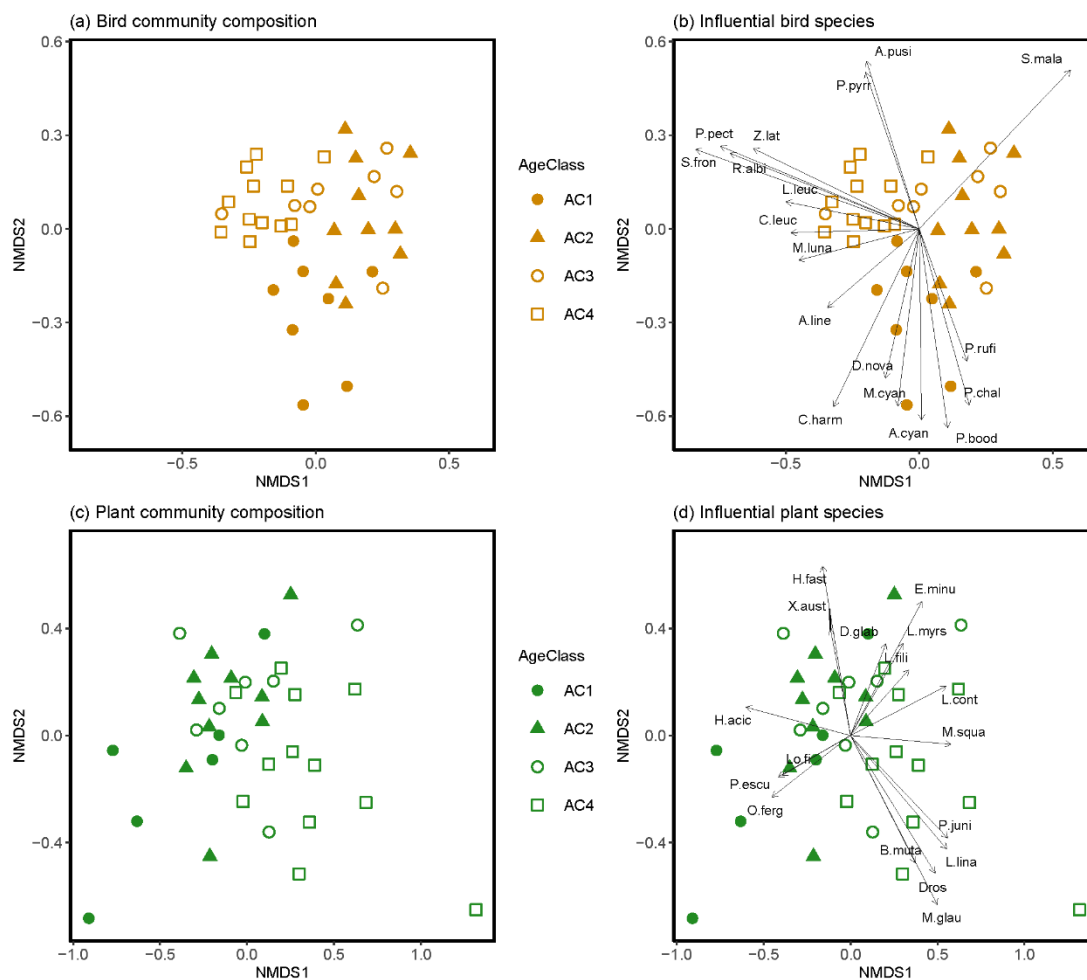


Figure 4.3. The influence of time since fire on the composition of bird (a – b) and plant (c – d) communities in heathy woodlands. Ordinations represent NMDS analyses on species relative abundance/cover matrices. Points represent sites. Symbols represent post-fire age-classes (AC1 = 0.5–2.5 years, AC2 = 2.5–8 years, AC3 = 8.5–33.5 years, AC4 = >33.5 years). The distance between sites represents the degree of dissimilarity between the composition of bird ( $n = 40$  species) and plant ( $n = 56$  species) communities. Arrows (b, d) represent vectors of influential species. The length of the vector represents the strength of the relationship. Species codes indicate the genus (capital letter) and the first four letters of the species name (e.g. A.pusi = *Acanthiza pusilla*). PerMANOVA showed a significant effect of post-fire growth stage on the composition of both the bird ( $P < 0.001$ ) and plant ( $P < 0.001$ ) communities. Species that occurred at a single site only were removed from the analyses.

Functional group analyses revealed a strong association between bird life-history traits and time since fire (Fig. 4.4). Ground-foraging species showed an irruptive response to time since fire, declining rapidly in the first 20 years after fire ( $P < 0.01$ , deviance = 35% Fig. 4.4a). The relative abundance of birds that forage in lower-midstorey vegetation increased with time since fire and plateaued at ~50 years post-fire ( $P < 0.001$ , deviance = 57%, Fig. 4.4b). Birds that forage in the upper-midstorey showed a non-significant positive trend and species that forage throughout the vertical strata did not respond to time since fire. The relative abundance of open-nest species increased with time since fire ( $P < 0.01$ , deviance = 22%, Fig. 4.4c). Hollow-nesting species were not significantly associated with time since fire. Relative abundance of birds with an intermediate level of dietary versatility increased linearly with time since fire ( $P < 0.001$ , deviance = 42%, Fig. 4.4d). Models of the number (richness) of species within each functional group generally were similar in shape to those based on the summed relative abundance of species.

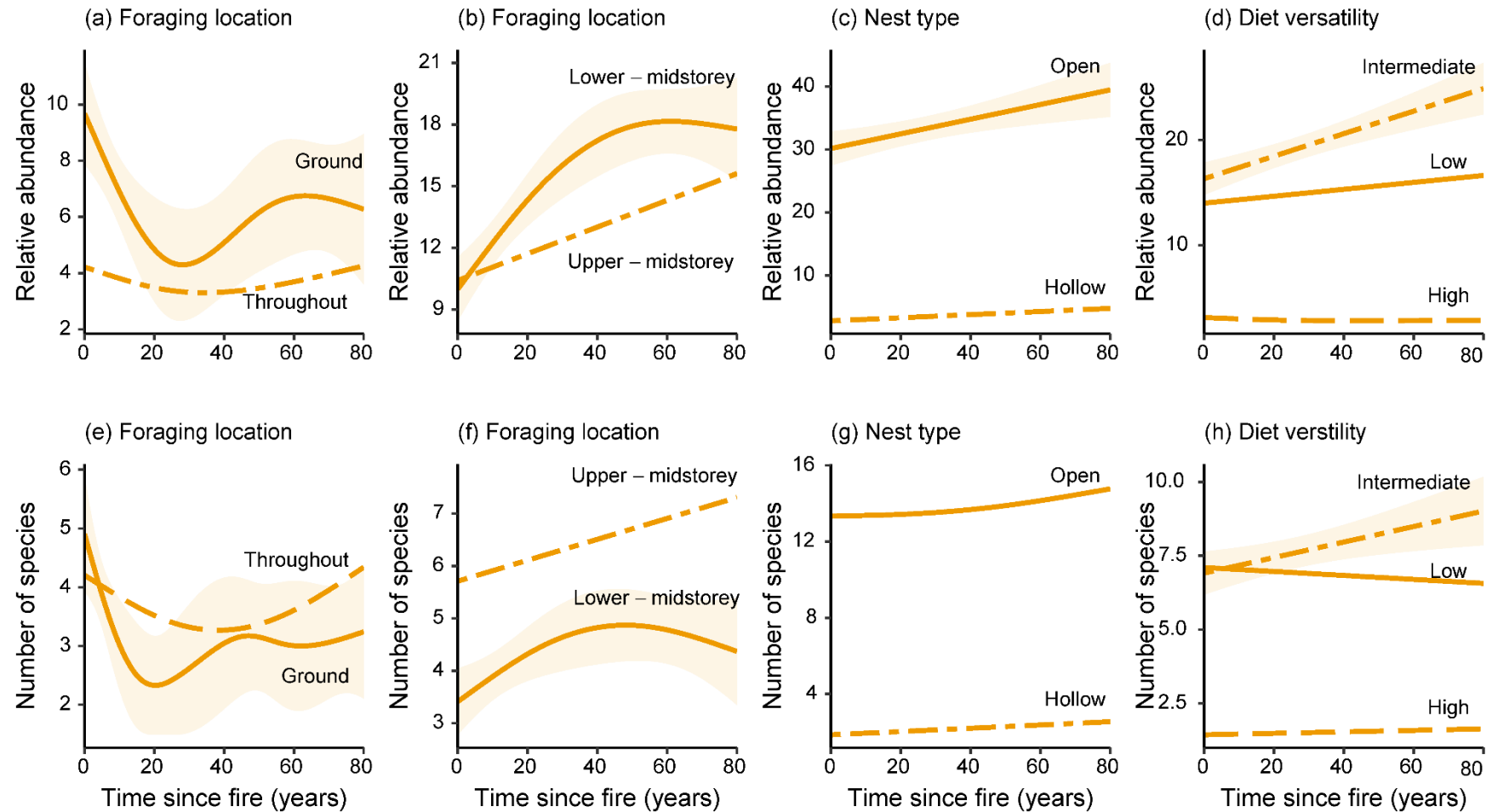


Figure 4.4. The influence of time since fire on the distribution of bird functional groups in heathy woodlands. Lines are fitted from generalized additive models of (a – d) the summed relative abundance and (e – h) the number of species per site within each functional group as a function of time since fire. Shaded areas represent 95% confidence intervals. Lines without shaded areas indicate non-significant relationships.

For plants, the relationship with time since fire for functional groups varied depending on the data used in the models (i.e. summed relative cover vs. species richness) (Fig. 4.5). The main effect of time since fire on facultative resprouters was a plateau in relative cover after ~20 years post-fire ( $P = 0.012$ , deviance = 24%, Fig. 4.5a). Species richness of this group showed a non-significant decline with time since fire (Fig. 4.5e). Cover of obligate resprouters increased with time since fire (Fig. 4.5b), although this was not significant, and the number of obligate-resprouting species showed no clear trend (Fig. 4.5f). For obligate-seeding species, the main effect of time since fire was a linear decrease in the number of species per site ( $P < 0.001$ , deviance = 32%, Fig. 4.5g). Cover of obligate seeders showed a (non-significant) bell-shaped response to time since fire, peaking at ~20 years post-fire (Fig. 4.5c). The relative cover of shrubs showed a plateau response ( $P < 0.01$ , deviance = 36%, Fig. 4.5d) and low shrub and herb cover were not significantly associated with time since fire. The number of species of shrubs ( $P < 0.01$ , deviance = 26%, Fig. 4.5h) and low shrubs ( $P < 0.01$ , deviance = 28%, Fig. 4.5h) showed irruptive responses to time since fire. Outputs of all functional group models are provided in Appendix 4.6.6.

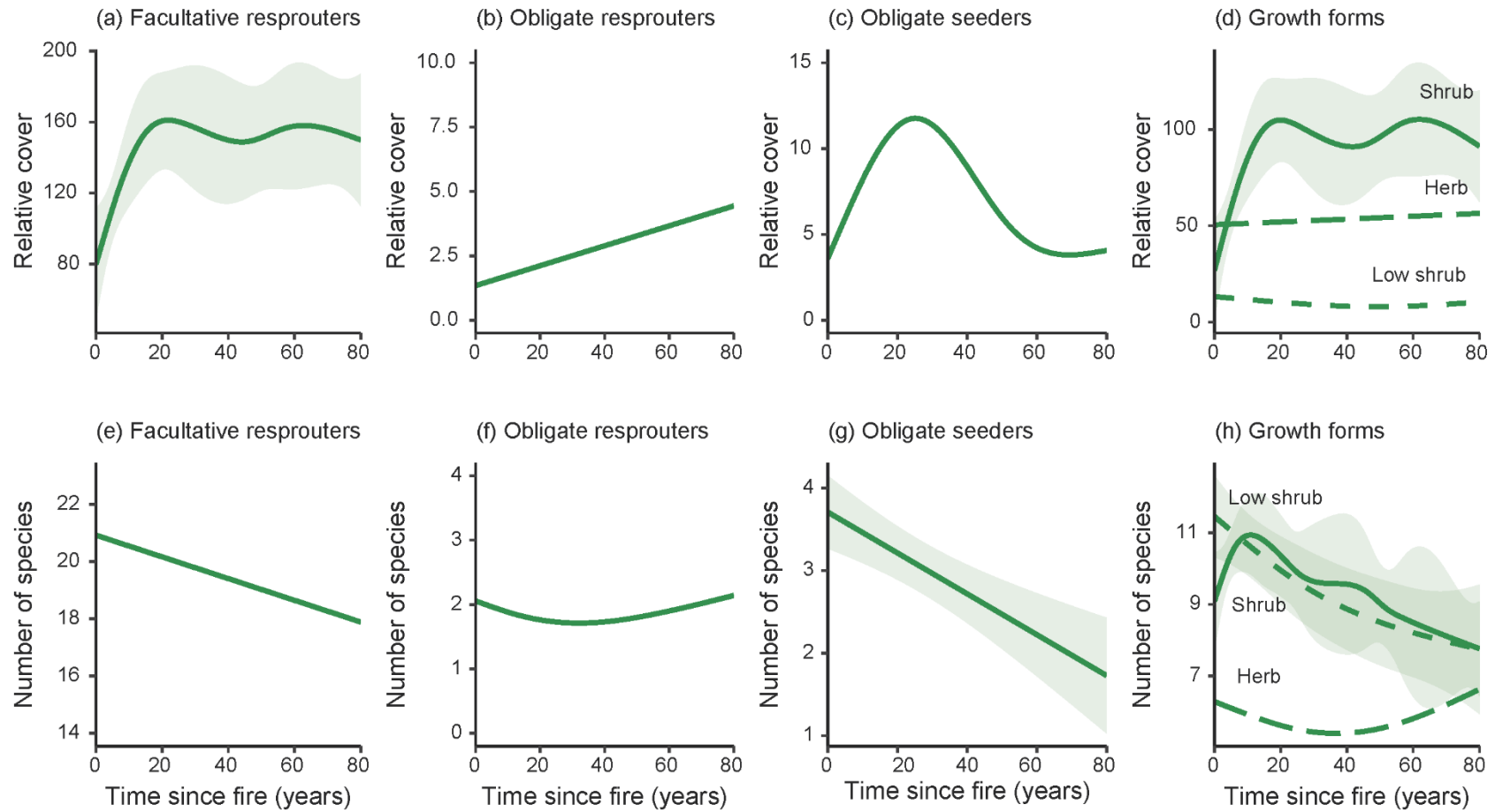


Figure 4.5. The influence of time since fire on the distribution of plant functional groups based on (a, b, c, e, f, g) regeneration traits and (d, h) growth form in heathy woodlands. Lines are fitted from generalized additive models based on the summed cover (a – d) and the number of species per site (e – h) of plants within each group as a function of time since fire. Shaded areas represent 95% confidence intervals. Lines without shaded areas indicate non-significant relationships.

## 4.5 DISCUSSION

These findings illustrate how the structure of bird and plant communities changes over time following fire in a heathy woodland ecosystem. Species' life-history traits gave key insights into the mechanisms driving post-fire community change. Notable fire effects included: (a) an irruptive response of ground-foraging birds, (b) a plateau response ~50 years post-fire of birds that forage in lower-midstorey vegetation, (c) a plateau response ~20 years post-fire of the cover of facultative-resprouting plants, and (d) an initial peak soon after fire followed by a decline in the richness of obligate seeding, shrub and low shrub species. Post-fire age classes represented distinct bird and plant communities. Variation in community composition between post-fire age-classes can be attributed to species' life-history traits and successional changes in habitat conditions.

There are implications for management practices in fire-prone landscapes. First, the timing of fires based on tolerable fire intervals (TFIs) can differentially affect taxa. For example, the peak in species richness of obligate seeders, shrubs and low shrubs, coincides with the minimum tolerable fire interval (TFI) for heathy woodlands (i.e. 12 years), whereas the peak in abundance of lower-midstorey foraging birds was later than the maximum TFI (i.e. 45 years) (Fig. 4.6). Second, the spatial arrangement of fires based on post-fire age-classes can influence the prevalence of fire-sensitive groups of species across the landscape. Applying fire to manipulate the distribution of age-classes across the landscape will alter the abundance of some types of species; however, for some others (e.g. hollow-nesting birds) such an approach to landscape management will have less influence.

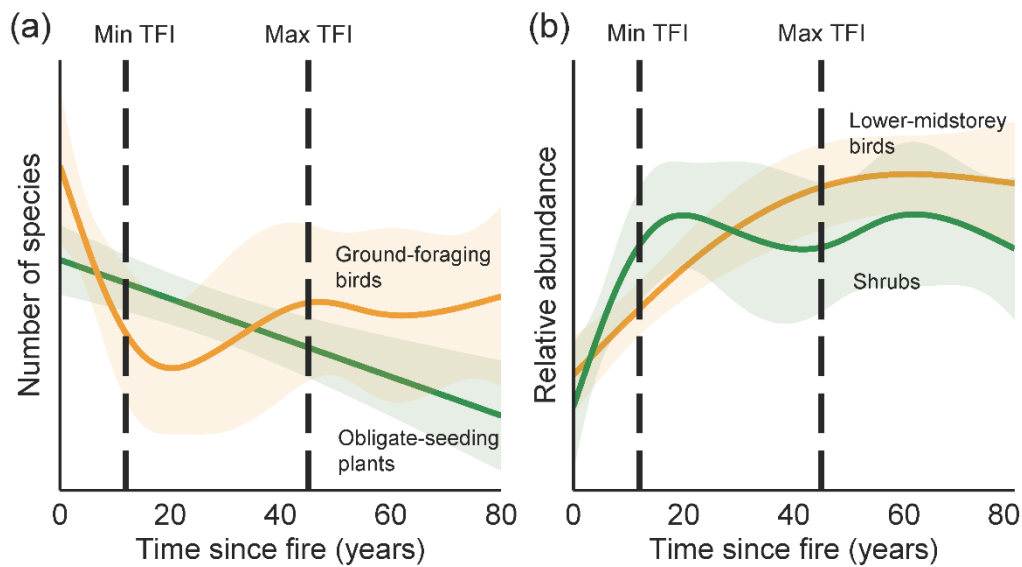


Figure 4.6. The response of bird and plant functional groups to time since fire and tolerable fire intervals (TFI) in heathy woodlands. (a) The number of species of ground-foraging birds and obligate-seeding plants. (b) the relative abundance of lower-midstorey-foraging birds and the relative cover of shrubs. Lines are fitted generalized additive models. Shaded areas represent 95% confidence intervals. Values on the y-axis are relative to each taxon.

#### 4.5.1 How does fire shape bird and plant communities?

The main effects of time since fire on the bird community were driven by the post-fire development of understorey vegetation structure, in line with the habitat accommodation model of post-fire faunal succession (Fox 1982). Species that forage in the lower-midstorey were more abundant in late-successional vegetation, and those that forage on the ground were more abundant in the first few years after fire, when the ground-layer habitat is open. Species that forage in the upper-midstorey were not significantly associated with time since fire, although there was a positive trend. This latter group is likely influenced by the degree of post-fire epicormic resprouting in *Eucalyptus* trees. Epicormic resprouting enables rapid regeneration of the upper-midstorey and canopy vegetation (Pausas and Keeley 2017), buffering the effect of time since fire on birds that forage in this stratum. This buffering effect

of epicormic resprouting trees means that the post-fire composition of the bird community was shaped primarily by the dynamics of the understorey vegetation structure.

Neither the richness nor abundance of hollow-nesting birds were related to time since fire in this study. This result contrasts with a study in a semi-arid *Eucalyptus* woodland dominated by obligate-seeding trees (Gosper et al. 2019) that showed a strong influence of time since fire on the abundance of hollow-nesting birds. Tree hollows are a limiting resource for many Australian faunal species because they take decades to develop and may be destroyed by fire (Haslem et al. 2012). There are two plausible hypotheses to explain this contrast: (1) because the stems of canopy trees in heathy woodlands are not killed by fire, the presence of tree hollows in this ecosystem is not strongly associated with time since fire, and so this nesting resource is not a limiting factor post-fire; and (2) hollow-nesting birds may forage within heathy woodlands but nest in adjacent vegetation types (e.g. wet forest, foothill forest). Further studies to determine the nesting behaviour of birds in heathy woodlands and the surrounding landscape would enhance fire management.

Key changes in the structure of the plant community over time since fire are attributed to: (a) increasing cover of facultative-resprouting and shrub species and (b) declining species richness of obligate-seeding, low shrub and shrub species. A decline in plant diversity over time following fire has been observed previously in several ecosystems (e.g. Keeley et al. 2005b, Penman et al. 2009, Gosper et al. 2013a, Fournier et al. 2020). When fire consumes above-ground biomass, light, nutrients and space become more accessible, facilitating germination of seeds and/or growth from resprouting buds, depending on species (Safford and Harrison 2004). Consequently, species richness often is high soon after fire. Then, over time, fewer species become dominant (e.g. austral grass tree, *Leptospermum* species) and exclude poorer competitors, driving down species richness.

Although there was evidence of directional change in the composition of the plant community over time post-fire, variation within post-fire age-classes indicates that factors additional to time since fire influence plant community composition in heathy woodlands. Multiple factors influence the temporal and spatial variation in plant communities in fire-prone landscapes, including primary productivity (Safford and Harrison 2004), climate and weather (Parra and Moreno 2018, Burrows et al. 2019), and other fire regime attributes (Keeley et al. 2005b, Kelly et al. 2017b). In this study, between-site differences in productivity likely influence the variation within age-classes in plant community composition. This could be a result of differences in topography (e.g. slope) or soils (e.g. depth of sand).

A key difference between the bird and plant community responses to time since fire was the decline in species richness of most plant functional groups versus the plateau response of lower-midstorey foraging birds. This presents a conundrum for conservation management in heathy woodland ecosystems with a risk of potential loss of: (a) floristic diversity in the longer-term absence of fire, and (b) bird species abundances if fire is too frequent.

#### **4.5.2 Implications for fire management**

Maintaining proportions of older age-class vegetation in the landscape to provide optimum habitat for populations of certain bird species, while introducing fire at sufficient frequency to prevent loss of plant species will involve careful planning and implementation. Fire management strategies, including the timing and placement of prescribed burns, will have greatest benefit if they incorporate biodiversity responses to fire along with reduction of wildfire risk (Driscoll et al. 2010).

Previous work on plant responses to fire in heathy woodland vegetation suggest that limiting the amount of older successional vegetation and introducing more fire into the landscape would benefit plant diversity (Duff et al. 2013, Chick et al. 2019). Our findings support this

proposition, which could be achieved by burning patches of vegetation toward the minimum tolerable fire interval (TFI) (e.g. at a frequency of ~12 - 20 years). However, by reducing the cover of understorey shrubs, this strategy would disadvantage substantial components of the bird community. Instead, maintaining stands of vegetation across the landscape at both the upper and lower TFIs may increase landscape biodiversity in heathy woodlands.

Maintaining proportions of the landscape at different fire ages to meet the needs of diverse taxonomic groups often is a goal of fire management (York and Friend, 2016, Menges et al. 2017). Previous studies have used diversity metrics based on species' abundances to test the effect of the spatial structure of post-fire age-classes on biota (Di Stefano et al. 2013, Kelly et al. 2015, Giljohann et al 2015). However, the assumption that post-fire age-classes represent distinct successional communities has rarely been tested for animal taxa. Here, we showed that post-fire age-classes (based on vegetation growth stages) in heathy woodlands represent distinct bird and plant communities. This can be attributed to responses associated with species' life-history traits (foraging behaviour in birds, fire-regeneration and life form in plants). Thus, there is a sound basis for employing a landscape mosaic approach to fire management based on a spatial representation of post-fire growth stages of vegetation to conserve bird and plant diversity in heathy woodlands.

Several components of the bird and plant communities were not related to time since fire (e.g. birds that forage throughout the strata, hollow-nesting birds, herb and low shrub species). The distribution of these groups is likely influenced by landscape heterogeneity unrelated to fire (e.g. driven by topography) or other components of the fire regime (e.g. between-fire interval, spatial configuration). Incorporating further complexity, additional to time since fire (e.g. topography, fire frequency), into a landscape mosaic approach to fire management may further benefit bird and plant diversity.

### **4.5.3 Concluding remarks**

By identifying the mechanisms that shape bird and plant communities post-fire, we can build a deeper understanding of how manipulating fire regimes influences components of biodiversity. Fire management guided by measures based on plant functional traits alone (e.g. TFI) can disadvantage faunal communities. Incorporating the responses of faunal communities to fire, by spatial representation of post-fire age-classes of greatest value to different faunal groups, should help conserve multiple taxa in fire-prone landscapes. However, further complexity additional to time since fire in landscape planning is needed to represent those components of ecosystems not strongly related to time since fire. This includes explicitly incorporating environmental gradients and topographic variation, as well as considering other temporal attributes of the fire regime (e.g. between fire interval), the spatial context of fire (e.g. amount or diversity of fire), and landscape context (e.g. surrounding vegetation types, connectivity).

## 4.6 APPENDICES

### 4.6.1 Post-fire age-classes in heathy woodlands

Table S4.6.1. Classification of post-fire age-classes to test the effects of time since fire on plant and bird communities in heathy woodlands. Vegetation growth stages described by Cheal (2010) are given, along with the time-since-fire range that each encompasses. The corresponding age-classes used in this study and the number of sites within each are also given. The stages ‘waning’ and ‘senescence’ were combined to reduce the number of categories and because of their structural similarity.

Vegetation Growth Stage (Cheal 2010)	Time since fire range (years)	Age-class	Number of sites
Juvenility	0.5 – 2.5	AC1	8
Adolescence	2.5 – 8.5	AC2	10
Maturity	8.5 – 33.5	AC3	8
Waning	33.5 - 55	AC4	6
Senescence	55 +	AC4	6

### 4.6.2 Detectability

During bird surveys, the distance (m) to all detections was estimated to the nearest metre, up to a maximum of 100 m using a laser range finder. For analysis we excluded all detections >40 m, as these were outside the 2-ha sample plot. We then used linear regression to test whether the perpendicular distance to detections declined with increasing midstorey cover (vegetation height = 1 – 4 m) within the 2 ha sample areas. Species were analysed individually, or (where data were lacking) grouped with species that were considered to have similar levels of detectability.

For most species and detectability groups (13/16), the distance to detection within the sample plots was not influenced by midstorey vegetation cover (Table S4.2). However, distance to detection decreased significantly with midstorey vegetation for brown thornbill *Acanthiza*

*pusilla*, grey fantail *Rhipidura albiscapa* and the groups: ‘canopy-foraging honeyeaters’, and ‘honeyeaters’, suggesting some individuals may have been undetected at sites with high midstorey vegetation cover.

Table S4.6.2. Detectability groups of species for linear regression analysis of the effect of midstorey vegetation cover (%) on species detectability (distance to detection) for bird species in and heathy woodlands.

Detectability group	R - squared	Estimate	SE	T – value	P – value
Arboreal perchers (Black-faced cuckoo-shrike, Dusky woodswallow, fan-tailed cuckoo, Horsfield’s bronze-cuckoo, Laughing kookaburra)	0.107	0.234	0.155	1.51	0.149
Brown thornbill (Brown thornbill, Buff-rumped thornbill)	0.033	-0.097	0.024	-4.13	<0.001
Canopy honeyeaters (Brown-headed honeyeater, White-naped honeyeater, White-eared honeyeater, Yellow-faced honeyeater)	0.016	-0.087	0.042	-2.06	0.040
Honeyeaters (Crescent honeyeater, New Holland honeyeater, Red wattlebird, Yellow-tufted honeyeater)	0.048	-0.330	0.078	-4.26	<0.001
Cockatoos (Gang, gang, Yellow-tailed black cockatoo)	0.170	0.230	0.15	2.00	0.059
Corvids (Australian magpie, Forest raven, Grey currawong, Pied currawong)	0.003	-0.057	0.22	-0.253	0.802
Eastern spinebill	0.018	-0.096	0.08	-1.21	0.229
Grey fantail	0.033	-0.126	0.06	-2.21	0.029
Grey shrike-thrush	<0.001	-0.018	0.07	-0.28	0.782
Ground	0.074	-0.182	0.17	-1.06	0.309

Detectability group	R - squared	Estimate	SE	T – value	P – value
(Brown quail, Common bronzewing, Rufous bristlebird, Spotted quail-thrush)					
Parrots	0.007	0.049	0.07	0.73	0.465
(Blue-winged parrot, Crimson rosella)					
Robins	0.063	0.168	0.09	1.80	0.078
(Eastern yellow robin, Scarlet robin)					
Small insectivores	0.002	0.035	0.07	0.50	0.621
(Silvereye, Spotted pardalote, Striated pardalote, Striated thornbill)					
Wrens	<0.001	0.007	0.03	0.22	0.824
(Southern emu-wren, Superb fairywren)					
White-browed scrubwren	0.001	-0.019	0.05	-0.35	0.729
Whistlers	<0.001	-0.001	0.05	-0.02	0.981
(Golden whistler, Olive whistler, Rufous whistler)					
White-throated treecreeper	0.020	0.085	0.08	1.01	0.320

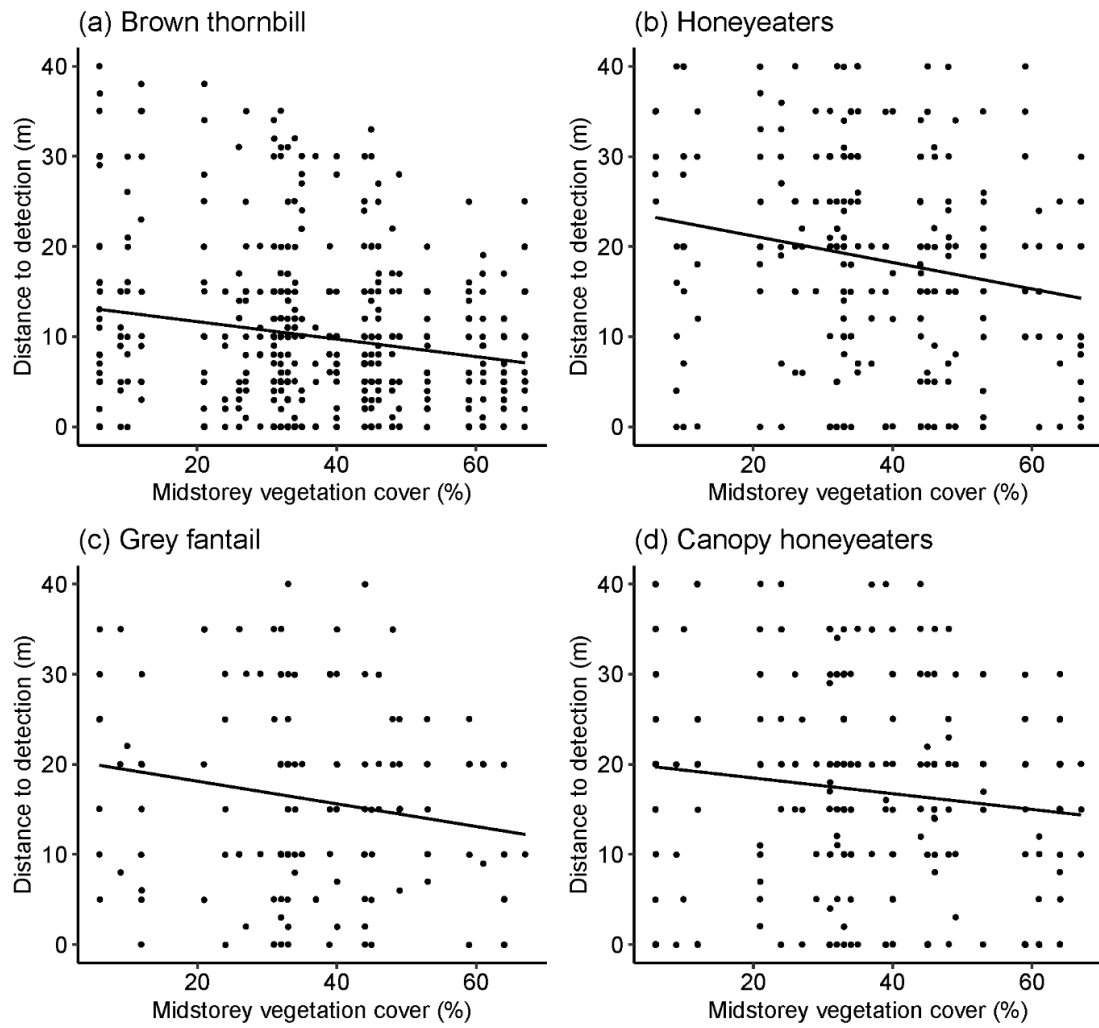


Figure S4.6.1. Significant ( $P < 0.05$ ) linear models of the relationship between the distance to detection of birds and midstorey vegetation cover in heathy woodlands. Points represent detections. Lines are fitted linear models.

#### 4.6.3 Bird species recorded at study sites in heathy woodlands

Table S4.6.3. Bird species recorded at study sites in heathy woodlands. Also given are the foraging location, nesting location, the number of food sources that each constitute at least 1% of the total diet, and the number of sites at which each species was recorded.

Family	Species name	Common name	Foraging location	Nesting location	No. food sources	Number of sites
Acanthizidae	<i>Acanthiza lineata</i>	Striated Thornbill	Mid-canopy	Mid-canopy	Two-three	20
	<i>Acanthiza pusilla</i>	Brown Thornbill	Low-mid	Low-mid	Two-three	38
	<i>Acanthiza reguloides</i>	Buff-rumped Thornbill	Low-mid	Low-mid	One	2
	<i>Sericornis frontalis</i>	White-browed Scrubwren	Low-mid	Low-mid	One	29
Alcedinidae	<i>Dacelo novaeguineae</i>	Laughing Kookaburra	Ground-low	Mid-canopy	Two-three	4
Artamidae	<i>Artamus cyanopterus</i>	Dusky Woodswallow	Aerial	Mid-canopy	Two-three	2
	<i>Cracticus tibicen</i>	Australian Magpie	Ground-low	Mid-canopy	Four-six	5
	<i>Strepera graculina</i>	Pied Currawong	Throughout	Mid-canopy	Four-six	5
	<i>Strepera versicolor</i>	Grey Currawong	Throughout	Mid-canopy	Four-six	4
Cacatuidae	<i>Callocephalon fimbriatum</i>	Gang Gang	Mid-canopy	Mid-canopy	Two-three	9
	<i>Calyptorhynchus funereus</i>	Yellow-tailed Black Cockatoo	Mid-canopy	Mid-canopy	Two-three	7
Campiphagidae	<i>Coracina novaehollandiae</i>	Black-faced Cuckoo-shrike	Mid-canopy	Mid-canopy	One	5
Climacteridae	<i>Cormobates leucophaea</i>	White-throated Treecreeper	Mid-canopy	Mid-canopy	One	24
Columbidae	<i>Phaps chalcoptera</i>	Common Bronzewing	Ground-low	Mid-canopy	One	8
Corvidae	<i>Corvus tasmanicus</i>	Forest Raven	Throughout	Mid-canopy	Four-six	9
Cuculidae	<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo	Mid-canopy	Brood parasite	One	1

Family	Species name	Common name	Foraging location	Nesting location	No. food sources	Number of sites
	<i>Chrysococcyx basalis</i>	Horsfield's Bronze-cuckoo	Throughout	Brood parasite	One	6
Dasyornithidae	<i>Dasyornis broadbenti</i>	Rufous Bristlebird	Ground-low	Low-mid	Two-three	4
Estrildidae	<i>Stagonopleura bella</i>	Beautiful Firetail	Low-mid	Low-mid	One	2
Maluridae	<i>Malurus cyaneus</i>	Superb Fairywren	Ground-low	Low-mid	One	35
	<i>Stipiturus malachurus</i>	Southern Emu-wren	Low-mid	Low-mid	One	17
Meliphagidae	<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	Throughout	Mid-canopy	Two-three	34
	<i>Anthochaera carunculata</i>	Red Wattlebird	Mid-canopy	Mid-canopy	Two-three	7
	<i>Lichenostomus chrysops</i>	Yellow-faced Honeyeater	Mid-canopy	Mid-canopy	Two-three	38
	<i>Lichenostomus leucotis</i>	White-eared Honeyeater	Mid-canopy	Low-mid	Two-three	7
	<i>Lichenostomus melanops</i>	Yellow-tufted Honeyeater	Mid-canopy	Low-mid	Two-three	1
	<i>Melithreptus brevirostris</i>	Brown-headed Honeyeater	Mid-canopy	Mid-canopy	Two-three	5
	<i>Melithreptus lunatus</i>	White-naped Honeyeater	Mid-canopy	Mid-canopy	Two-three	18
	<i>Phylidonyris novaehollandiae</i>	New Holland Honeyeater	Low-mid	Low-mid	Two-three	6
	<i>Phylidonyris pyrrhopterus</i>	Crescent Honeyeater	Low-mid	Low-mid	Two-three	36
Pachycephalidae	<i>Colluricincla harmonica</i>	Grey Shrike-thrush	Ground-low	Mid-canopy	Four-six	34
	<i>Pachycephala olivacea</i>	Olive Whistler	Low-mid	Low-mid	Two-three	4
	<i>Pachycephala pectoralis</i>	Golden Whistler	Mid-canopy	Mid-canopy	One	19
	<i>Pachycephala rufiventris</i>	Rufous Whistler	Mid-canopy	Mid-canopy	One	33
Pardalotidae	<i>Pardalotus punctatus</i>	Spotted Pardalote	Mid-canopy	Ground	One	4
	<i>Pardalotus striatus</i>	Striated Pardalote	Mid-canopy	Mid-canopy	One	2
Petroicidae	<i>Eopsaltria australis</i>	Eastern Yellow Robin	Ground-low	Low-mid	One	21

Family	Species name	Common name	Foraging location	Nesting location	No. food sources	Number of sites
	<i>Petroica boodang</i>	Scarlet Robin	Ground-low	Low-mid	One	10
Phasianidae	<i>Coturnix ypsilophora</i>	Brown Quail	Ground-low	Ground	Two-three	1
Psittaculidae	<i>Neophema chrysostoma</i>	Blue-winged Parrot	Ground-low	Mid-canopy	One	7
	<i>Platycercus elegans</i>	Crimson Rosella	Throughout	Mid-canopy	Two-three	26
Psophodidae	<i>Cinclosoma punctatum</i>	Spotted Quail-thrush	Ground-low	Ground	One	1
Rhipiduridae	<i>Rhipidura albiscapa</i>	Grey Fantail	Mid-canopy	Low-mid	One	37
Zosteropidae	<i>Zosterops lateralis</i>	Silvereye	Low-mid	Low-mid	Two-three	22

#### 4.6.4 Plant species recorded in at study sites in heathy woodlands

Table S4.6.4. Plant species recorded in at study sites in heathy woodlands. Also given are the post-fire regeneration trait, growth form and the number of sites at which each species was recorded.

Family	Species	Common name	Response trait	Growth form	Number of sites
Apiaceae	<i>Xanthosia huegelii</i>	Heath xanthosia	Resprouter	Herb	37
Asparagaceae	<i>Lomandra filiformis</i>	Wattle mat-rush	Resprouter	Herb	26
	<i>Thysanotus tuberosus</i>	Common fringe lily	Resprouter	Geophyte	1
Asphodelaceae	<i>Dianella revoluta</i>	Black-anther flax-lily	Resprouter	Low shrub	8
	<i>Xanthorrhoea australis</i>	Austral grass-tree	Resprouter	Shrub	23
Asteraceae	<i>Argentipallium blandowskianum</i>	Woolly everlasting	Obligate seeder	Herb	4

Family	Species	Common name	Response trait	Growth form	Number of sites
Casuarinaceae	<i>Coronidium scorpioides</i>	Button everlasting	Resprouter	Low shrub	9
	<i>Lagenophora stipitata</i>	Blue bottle-daisy	Obligate seeder	Herb	1
	<i>Ozothamnus ferrugineus</i>	tree everlasting	Obligate seeder	Shrub	3
	<i>Allocasuarina misera</i>	Small sheoak	Resprouter	Shrub	2
	<i>Allocasuarina paludosa</i>	Scrub sheoak	Resprouter	Shrub	2
Cunoniaceae	<i>Bauera rubioides</i>	Wiry bauera	Resprouter	Low shrub	15
Cyperaceae	<i>Caustis pentandra</i>	Thick twig-rush	Resprouter	Herb	2
	<i>Gahnia radula</i>	Thatch saw-sedge	Resprouter	Herb	4
	<i>Gymnoschoenus sphaerocephalus</i>	Button-grass	Resprouter	Herb	2
	<i>Isolepis marginata</i>	Tiny club-rush	Obligate seeder	Herb	19
	<i>Lepidosperma concavum</i>	Sandhill sword-sedge	Resprouter	Herb	22
Dennstaedtiaceae	<i>Lepidosperma filiforme</i>	Common rapier-sedge	Resprouter	Herb	21
	<i>Lepidosperma</i> sp. 2		Resprouter	Herb	13
	<i>Pteridium esculentum</i>	Austral bracken	Resprouter	Herb	4
Dilleniaceae	<i>Hibbertia acicularis</i>	Prickly guinea-flower	Resprouter	Low shrub	31
	<i>Hibbertia fasciculata</i>		Resprouter	Low shrub	22
	<i>Hibbertia procumbens</i>	Spreading guinea-flower	Resprouter	Low shrub	18
	<i>Hibbertia riparia</i>	Erect guinea-flower	Resprouter	Low shrub	38
Droseraceae	<i>Drosera</i> sp.		Resprouter	Geophyte	20
Elaeocarpaceae	<i>Tetratheca ciliata</i>	Pink bells	Resprouter	Low shrub	38
Ericaceae	<i>Acrotriche serrulata</i>	Honey-pots	Resprouter	Low shrub	7
	<i>Brachyloma ciliatum</i>	Fringed brachyloma	Resprouter	Low shrub	1
	<i>Epacris impressa</i>	Common heath	Resprouter	Shrub	18

Family	Species	Common name	Response trait	Growth form	Number of sites
	<i>Leucopogon virgatus</i>	Common beard-heath	Resprouter	Low shrub	7
	<i>Monotoca glauca</i>		Resprouter	Shrub	34
	<i>Monotoca scoparia</i>	Prickly broom-heath	Resprouter	Shrub	16
Euphorbiaceae	<i>Amperea xiphoclada</i>	Broom spurge	Resprouter	Low shrub	27
Fabaceae	<i>Acacia genistifolia</i>	Spreading wattle	Obligate seeder	Shrub	1
	<i>Acacia myrtifolia</i>	Myrtle wattle	Obligate seeder	Shrub	2
	<i>Acacia suaveolens</i>	Sweet wattle	Obligate seeder	Shrub	17
	<i>Daviesia ulicifolia</i>	Gorse bitter-pea	Resprouter	Shrub	1
	<i>Dillwynia glaberrima</i>	Smooth parrot-pea	Obligate seeder	Shrub	38
	<i>Gompholobium huegelii</i>	Common wedge-pea	Obligate seeder	Low shrub	32
	<i>Platylobium obtusangulum</i>	Common flat-pea	Resprouter	Low shrub	11
	<i>Sphaerolobium vimineum</i>	Leafless globe-pea	Obligate seeder	Low shrub	2
Goodeniaceae	<i>Goodenia lanata</i>	Trailing goodenia	Resprouter	Low shrub	38
Haloragaceae	<i>Gonocarpus tetragynus</i>	Common raspwort	Resprouter	Low shrub	11
Hypericaceae	<i>Hypericum gramineum</i>	Small St John's wort	Resprouter	Herb	3
Iridaceae	<i>Patersonia fragilis</i>	Short purple-flag	Resprouter	Herb	5
Lauraceae	<i>Cassytha glabella</i>	Slender dodder-laurel	Obligate seeder	Shrub	32
	<i>Cassytha melantha</i>	Coarse dodder-laurel	Obligate seeder	Shrub	6
Lindsaeaceae	<i>Lindsaea linearis</i>	Screw fern	Resprouter	Herb	23
Myrtaceae	<i>Leptospermum continentale</i>	Prickly teatree	Resprouter	Shrub	38
	<i>Leptospermum myrsinoides</i>	Heath teatree	Resprouter	Shrub	38
	<i>Melaleuca squarrosa</i>	Scented paperbark	Resprouter	Shrub	11
Pittosporaceae	<i>Billardiera mutabilis</i>	Common apple-berry	Resprouter	Shrub	2

Family	Species	Common name	Response trait	Growth form	Number of sites
Poaceae	<i>Tetrarrhena juncea</i>	Forest wire-grass	Resprouter	Herb	4
Polygalaceae	<i>Comesperma calymega</i>	Blue-spike milkwort	Resprouter	Low shrub	9
Proteaceae	<i>Banksia marginata</i>	Silver banksia	Resprouter	Shrub	37
	<i>Hakea ulicina</i>	Furze hakea	Resprouter	Shrub	5
	<i>Isopogon ceratophyllus</i>	Horny cone-bush	Resprouter	Low shrub	1
	<i>Persoonia juniperina</i>	Prickly geebung	Resprouter	Shrub	24
	<i>Empodisma minus</i>	Spreading rope-rush	Resprouter	Herb	30
Restionaceae	<i>Hypolaena fastigiata</i>	Tassel rope-rush	Resprouter	Herb	37
Rhamnaceae	<i>Spyridium parvifolium</i>	Dusty miller	Obligate seeder	Shrub	1
Rubiaceae	<i>Opercularia varia</i>	Variable stinkweed	Obligate seeder	Herb	1
Rutaceae	<i>Boronia nana</i>	Dwarf boronia	Obligate seeder	Low shrub	1
Stylidiaceae	<i>Stylidium graminifolium</i>	Grass triggerplant	Resprouter	Low shrub	3
Thymelaeaceae	<i>Pimelea humilis</i>	Common rice-flower	Resprouter	Low shrub	31
Violaceae	<i>Viola hederacea</i>	Ivy-leafed violet	Resprouter	Herb	1

#### 4.6.5 Individual species model outputs

Table S4.6.5a. Outputs of generalized additive models of bird species relative abundance in heathy woodlands as a function of time since fire. Significant responses are in bold.

Species name	Common name	Response shape	Deviance explained (prop)	P - value
<i>Acanthiza lineata</i>	Striated thornbill	ns	0.00	0.705
<i>Acanthiza pusilla</i>	Brown thornbill	ns	0.18	0.282
<i>Acanthorhynchus tenuirostris</i>	Eastern spinebill	ns	0.18	0.582
<i>Anthochaera carunculata</i>	Red wattlebird	ns	0.00	0.838
<i>Callocephalon fimbriatum</i>	Gang gang	ns	0.04	0.248
<i>Calyptorhynchus funereus</i>	Yellow-tailed Black Cockatoo	ns	0.08	0.254
<i>Colluricincla harmonica</i>	Grey Shrike-thrush	ns	0.23	0.286
<i>Cormobates leucophaea</i>	White-throated Treecreeper	ns	0.03	0.262
<i>Corvus tasmanicus</i>	Forest raven	ns	0.00	0.276
<i>Eopsaltria australis</i>	Eastern yellow robin	ns	0.01	0.502
<i>Lichenostomus chrysops</i>	Yellow-faced Honeyeater	ns	0.01	0.742
<i>Lichenostomus leucotis</i>	White-eared Honeyeater	ns	0.09	0.052
<i>Malurus cyaneus</i>	Superb fairywren	ns	0.13	0.152
<i>Melithreptus lunatus</i>	White-naped Honeyeater	ns	0.15	0.080
<i>Neophema chrysostoma</i>	Blue-winged Parrot	ns	0.01	0.526
<b><i>Pachycephala pectoralis</i></b>	<b>Golden whistler</b>	<b>Plateau</b>	<b>0.51</b>	<b>&lt;0.001</b>
<i>Pachycephala rufiventris</i>	Rufous whistler	ns	0.21	0.100
<b><i>Petroica boodang</i></b>	<b>Scarlet robin</b>	<b>Irruptive</b>	<b>0.32</b>	<b>0.032</b>
<i>Phaps chalcoptera</i>	Common bronzewing	ns	0.31	0.124
<i>Phylidonyris pyrrhopterus</i>	Crescent honeyeater	ns	0.22	0.080
<i>Platycercus elegans</i>	Crimson rosella	ns	0.06	0.090
<i>Rhipidura albiscapa</i>	Grey fantail	ns	0.25	0.168
<i>Sericornis frontalis</i>	<b>White-browed Scrubwren</b>	<b>Incline</b>	<b>0.21</b>	<b>0.001</b>
<i>Stipiturus malachurus</i>	<b>Southern Emu-wren</b>	<b>Bell</b>	<b>0.23</b>	<b>0.027</b>
<i>Zosterops lateralis</i>	<b>Silvereye</b>	<b>Plateau</b>	<b>0.46</b>	<b>&lt;0.001</b>

Table S4.6.5b. Outputs of generalized additive models of plant species relative abundance in heathy woodlands as a function of time since fire. Significant responses are in bold.

Species	Common name	Response shape	P - value
<i>Acacia suaveolens</i>	Sweet wattle	ns	0.161
<i>Acrotriche serrulata</i>	Honeypots	ns	0.977
<b><i>Amperea xiphoclada</i></b>	<b>Broom spurge</b>	<b>Irruptive</b>	<b>&lt;0.001</b>
<b><i>Banksia marginata</i></b>	<b>Silver banksia</b>	<b>Plateau</b>	<b>0.048</b>
<i>Bauera rubioides</i>	Wiry bauera	ns	0.545
<b><i>Cassytha glabella</i></b>	<b>Slender dodder-laurel</b>	<b>Bell</b>	<b>&lt;0.001</b>
<i>Comesperma calymega</i>	Blue-spike milkwort	ns	0.141
<i>Coronidium scorpioides</i>	Button everlasting	ns	0.332
<i>Dianella revoluta</i>	Black-anther flax-lily	ns	0.900
<i>Dillwynia glaberrima</i>	Smooth parrot-pea	ns	0.180
<b><i>Drosera sp.</i></b>		<b>Incline</b>	<b>0.031</b>
<i>Empodisma minus</i>	Spreading rope-rush	ns	0.353
<i>Epacris impressa</i>	Common heath	ns	0.129
<b><i>Goodenia lanata</i></b>	<b>Trailing goodenia</b>	<b>Irruptive</b>	<b>&lt;0.001</b>
<i>Gompholobium huegelii</i>	Common wedge-pea	ns	0.192
<i>Gonocarpus tetragynus</i>	Common raspwort	ns	0.222
<b><i>Hibbertia acicularis</i></b>	<b>Prickly guinea-flower</b>	<b>Irruptive</b>	<b>&lt;0.001</b>
<b><i>Hibbertia fasciculata</i></b>		<b>Irruptive</b>	<b>&lt;0.001</b>
<i>Hibbertia procumbens</i>	Spreading guinea-flower	ns	0.323
<i>Hibbertia riparia</i>	Erect guinea-flower	ns	0.707
<b><i>Hypolaena fastigiata</i></b>	<b>Tassel rope-rush</b>	<b>Bell</b>	<b>&lt;0.001</b>
<i>Isopogon ceratophyllus</i>	Horny cone-bush	ns	0.339
<i>Lepidosperma concavum</i>	Sandhill sword-sedge	ns	0.541
<i>Lepidosperma filiforme</i>	Common rapier-sedge	ns	0.151
<i>Lepidosperma sp. 2</i>		ns	0.753
<i>Leptospermum continentale</i>	Prickly teatree	ns	0.075
<b><i>Leptospermum myrsinoides</i></b>	<b>Heath teatree</b>	<b>Plateau</b>	<b>0.013</b>
<i>Leucopogon virgatus</i>	Common beard-heath	ns	0.856
<i>Lindsaea linearis</i>	Screw fern	ns	0.078
<b><i>Lomandra filiformis</i></b>	<b>Wattle mat-rush</b>	<b>Irruptive</b>	<b>&lt;0.001</b>
<i>Melaleuca squarrosa</i>	Scented paperbark	ns	0.443
<b><i>Monotoca glauca</i></b>	<b>Goldy wood</b>	<b>Plateau</b>	<b>&lt;0.001</b>
<i>Monotoca scoparia</i>	Prickly broom-heath	ns	0.318

Species	Common name	Response shape	P - value
<i>Persoonia juniperina</i>	Prickly geebung	ns	0.426
<i>Pimelea humilis</i>	Common rice-flower	ns	0.218
<i>Platylobium obtusangulum</i>	Common flat-pea	ns	0.917
<i>Tetratheca ciliata</i>	Pink bells	ns	0.338
<i>Xanthosia huegelii</i>	Heath xanthosia	ns	0.608
<b><i>Xanthorrhoea australis</i></b>	<b>Austral grass-tree</b>	<b>Bell</b>	<b>0.036</b>

#### 4.6.6 Functional group model outputs

Table 4.6.6a. Outputs from generalized additive models of bird functional group relative abundance and species richness as a function of time since fire in heathy woodlands.

Significant responses are in bold.

Trait group	Data type	AIC	Deviance explained (prop)	P - value
Foraging - ground	<b>Abundance</b>	<b>196</b>	<b>0.27</b>	<b>0.018</b>
	<b>Richness</b>	<b>130</b>	<b>0.29</b>	<b>0.024</b>
Foraging - lower-midstorey	<b>Abundance</b>	<b>194</b>	<b>0.56</b>	<b>&lt;0.001</b>
	<b>Richness</b>	<b>127</b>	<b>0.19</b>	<b>0.040</b>
Foraging - upper-midstorey	<b>Abundance</b>	<b>229</b>	<b>0.13</b>	<b>0.026</b>
	Richness	165	0.07	0.111
Foraging - throughout	Abundance	154	0.08	0.422
	Richness	100	0.01	0.840
Nest - open	<b>Abundance</b>	<b>248</b>	<b>0.22</b>	<b>0.003</b>
	Richness	173	0.06	0.311
Nest - hollow	Abundance	176	0.08	0.089
	Richness	120	0.04	0.210
Nest - brood parasite	<b>Abundance</b>	<b>51</b>	<b>0.11</b>	<b>0.038</b>
	<b>Richness</b>	<b>37</b>	<b>0.13</b>	<b>0.029</b>
Diet - low versatility	Abundance	225	0.04	0.228
	Richness	150	0.01	0.505
Diet - intermediate versatility	<b>Abundance</b>	<b>206</b>	<b>0.42</b>	<b>&lt;0.001</b>
	<b>Richness</b>	<b>149</b>	<b>0.16</b>	<b>0.011</b>
Diet - low versatility	Abundance	155	0.02	0.814
	Richness	88	0.01	0.576

Table 4.6.6b. Outputs from generalized additive models of plant functional group cover and species richness as a function of time since fire in heathy woodlands. Significant responses are in bold.

Trait/growth form	Data type	AIC	Deviance explained (prop)	P - value
Facultative resprouters	<b>Cover</b>	<b>397</b>	<b>0.24</b>	<b>0.012</b>
	Richness	204	0.09	0.070
Obligate resprouters	Cover	201	0.10	0.056
	Richness	116	0.04	0.633
Obligate seeders	Cover	264	0.06	0.443
	<b>Richness</b>	<b>111</b>	<b>0.32</b>	<b>&lt;0.001</b>
Shrubs	<b>Cover</b>	<b>378</b>	<b>0.36</b>	<b>0.002</b>
	<b>Richness</b>	<b>144</b>	<b>0.26</b>	<b>0.002</b>
Low shrubs	Cover	235	0.17	0.081
	<b>Richness</b>	<b>174</b>	<b>0.28</b>	<b>0.004</b>
Herbs	Cover	365	0.01	0.669
	Richness	157	0.08	0.354
Geophytes	Cover	214	0.10	0.052
	Richness	65	0.07	0.117

## 5 HOW DOES PRESCRIBED FIRE SHAPE BIRD AND PLANT COMMUNITIES IN A TEMPERATE DRY FOREST ECOSYSTEM?

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Prolific flowering of pink bells *Tetratheca ciliata* in a temperate dry forest seven years after a prescribed fire.

## 5.1 ABSTRACT

Prescribed fire is widely used in forest ecosystems to mitigate the impact of severe wildfires on human society and the environment by reducing fuel loads and limiting fire spread. To avoid detrimental effects of prescribed fire on conservation values, it is imperative to understand how prescribed fire affects a range of taxa with different adaptations to disturbance. Such studies will have greatest benefit if they extend beyond short-term impacts of burning. We used a field study to examine the effects of prescribed fire on birds and plants across a 36-year post-fire chronosequence in a temperate dry forest ecosystem in south-eastern Australia, and by making comparison with long-unburnt reference sites (79 years since wildfire). We modelled changes in the relative abundance of 22 bird and the cover of 39 plant species, and examined how individual species, functional groups, species diversity and community composition differed between sites with different fire history. For most bird and plant species modelled, relative abundance/cover at sites subject to prescribed fire did not change significantly with time since fire or differ from that of long-unburnt vegetation. When species were pooled into functional groups, time since fire had strong effects on birds that forage in the lower-midstorey, facultative-resprouting shrubs and obligate-seeding shrubs. Measures of alpha diversity did not differ between sites subject to prescribed fire and those in long-unburnt vegetation. Bird communities varied significantly between the youngest (0-3 years) and oldest (79 years) post-fire age-classes, driven by species associated with understorey vegetation. Plant community composition showed little evidence of a post-fire successional trajectory. The prevalence of bird species with broad habitat and dietary niches, plant regeneration through resprouting, and the characteristics of prescribed fire, make bird and plant communities in these temperate dry forests relatively resilient or resistant to the type of prescribed fire they have experienced in the last ~40 years. Application of prescribed fire will be most compatible with maintaining biodiversity by taking a landscape approach

that: 1) plans for a geographic spread of stands with a range of between-fire intervals (~15 – 80 years) to ensure provision of suitable habitat for all taxa, and 2) avoids burning in moist gullies to maintain their value as fire refuges.

## **5.2 INTRODUCTION**

Forest ecosystems worldwide are facing substantial changes in fire regimes (Halofsky et al. 2020, Nolan et al. 2020). Severe wildfires are becoming larger and more frequent in many regions, including tropical forests in Brazil (Lizundia-Loiola et al. 2020), dry forests in western U.S.A (Keeley and Syphard 2019), Mediterranean forests in southern Europe (Vitolo et al. 2019) and temperate forests in eastern Australia (Nolan et al. 2020). For example, from 2019 to early 2020 in Australia, wildfires burned >12 million ha of forests, destroying >2000 homes and putting multiple populations of animals and plants at risk of extinction (Boer et al. 2020, Lindenmayer and Taylor 2020, Ward et al. 2020). Much of the area burnt was temperate dry forest (Victorian Government Department of Environment, Land, Water and Planning 2020). Thus, even in dry forests with a long history of fire, there is a need to mitigate the threat of severe wildfires, not only to human life and property but also to prevent detrimental consequences for biodiversity.

A common method used to reduce the risk of large fires to human society and biodiversity values is to reduce fuel loads by using prescribed fire (Price et al. 2015, Stephens et al. 2019, Moreira et al. 2020). In temperate dry forests, prescribed fires generally are less intense and patchier than wildfires: they consume understorey vegetation and ground-layer fuels, and usually leave the canopy un-scorched (Penman et al. 2008, Fernandes 2018). Empirical data indicate that prescribed fire can reduce the extent of future wildfire in dry forests in south-eastern Australia, but with substantial variation between and within regions and vegetation communities (Price et al. 2015, Penman et al. 2020). Prescribed fire can also be used more

directly to achieve ecological goals, such as to promote plant regeneration and to create particular successional stages as habitats (Ryan et al. 2013).

Prescribed fire has diverse effects on biota, in part depending on the life-history of animals and plants. For example, it has been reported to increase food availability for some foraging guilds of birds (Pope et al. 2009, Fontaine and Kennedy 2012), destroy important structural resources for small mammals (Holland et al. 2017, Flanagan-Moodie et al. 2018), temporarily reduce understorey biomass (Gonzalez-Benecke et al. 2015), and stimulate regeneration of certain tree species (Hutchinson et al. 2012). There is an urgent need to understand how prescribed fire affects animals and plants in areas likely to be subject to more frequent severe fire.

In temperate dry forests of south-eastern Australia, studies of bird responses to fire suggest that species may be well adapted to recurrent fires: authors reported a relatively weak influence of time since last fire on species occurrences (Sitters et al. 2014a, Kelly et al. 2017b, Smith and Smith 2017) and a negative effect on functional diversity (Sitters et al. 2016). These studies included a mix of sites last burned by either prescribed fire or wildfire, which can have different effects on vegetation (i.e. habitat) structure (Haslem et al. 2016, Bassett et al. 2017). The frequency and season of prescribed fire in dry forests were shown to have limited effects on bird species (Loyn and McNabb 2015). There remains a knowledge gap concerning the longer-term effects on bird communities arising from prescribed fire in these forests, beyond the first few years post-fire.

Forest plants, in dry forests have evolved a range of traits (e.g. post-fire resprouting, fire-cued germination) that allow populations to persist in fire-prone environments (Pausas et al. 2004). Classifications based on plant functional traits, such as time to maturity and method of persistence, provide a useful framework to understand and predict species' responses to fire (Bradstock and Kenny 2003, Keith et al. 2007, Shedley et al. 2018). Studies in temperate dry

forests have shown that the influence of fire on understorey plant species varies between taxa based on species' life-history traits (Penman et al. 2008, Prior et al. 2016) and within taxa based on vegetation type (Foster et al. 2018). Plant regeneration from seed is often associated with species declining over time following fire and vulnerability to increased fire frequency, while post-fire resprouting is associated with species that increase post-fire (Penman et al. 2009, Enright et al. 2014).

Functional classification of plant species in relation to fire is further advanced than for animals. Animals are mobile for much of their life-cycle and adaptations for persistence that help them persist in fire-prone landscapes include those that are behavioral (e.g. fleeing fire, dietary versatility) (Pausas and Parr 2018). Functional of birds (e.g. nesting behavior, foraging guilds) have been used to estimate the time between fires needed for important resources to become available (Jacquet and Prodon 2009, Gosper et al. 2019) but have not been widely tested. Employing a functional approach to understanding the effects of prescribed fire on bird and plant communities in temperate dry forests will help address a key knowledge gap relating to how the widespread application of this management practice influences biodiversity.

Here, we assess the effects of prescribed fire on birds and understorey plants across a 36-year post-fire chronosequence in a temperate dry forests ecosystem to test how these diverse groups respond to such fire management. We modelled the responses of individual species, functional groups, community-wide indices and community composition to time since prescribed fire in a temperate forest in Victoria, Australia; and compared these with long-unburnt, but otherwise-similar, forest vegetation (i.e. 79 years since fire).

We address the general question: how does prescribed fire shape bird and plant communities in temperate dry forests? More specifically, we address questions relating to three levels of biodiversity: how do 1) individual species, 2) functional groups of species, and 3) the

composition of communities respond to prescribed fire; and how do these levels of biodiversity differ between sites subjected to prescribed fire and those in long-unburnt vegetation?

## **5.3 METHODS**

### **5.3.1 Study location, climate and vegetation**

The study took place in temperate dry forests, known as ‘foothill forests’, in Victoria, south-eastern Australia (Fig. 5.1). The generic term ‘foothill forests’ refers to temperate eucalypt forests that cover ~ 75 000 km<sup>2</sup> in Victoria and occur on the lower- to mid-slopes of the Great Dividing Range. Foothill forests include distinct ecological communities that differ in floristic composition, driven by topographic and climatic variation, ranging from wetter forest types in gullies to drier forests on slopes and ridges. The study area covered ~ 320 km<sup>2</sup> of the Big River State Forest in the Highlands Southern Fall bioregion (-37.516 S, 146.042 E) where the climate is temperate with a mean annual rainfall of ~ 850 mm. The highest monthly rainfall occurs in winter (August) and the hottest month is February (mean daily maximum ~ 29°C) (Lake Eildon, station no. 083023; <http://www.bom.gov.au/>). The topography is mountainous, often with steep slopes and densely vegetated gullies. Elevation ranges between ~ 450 and 950 m above sea-level.

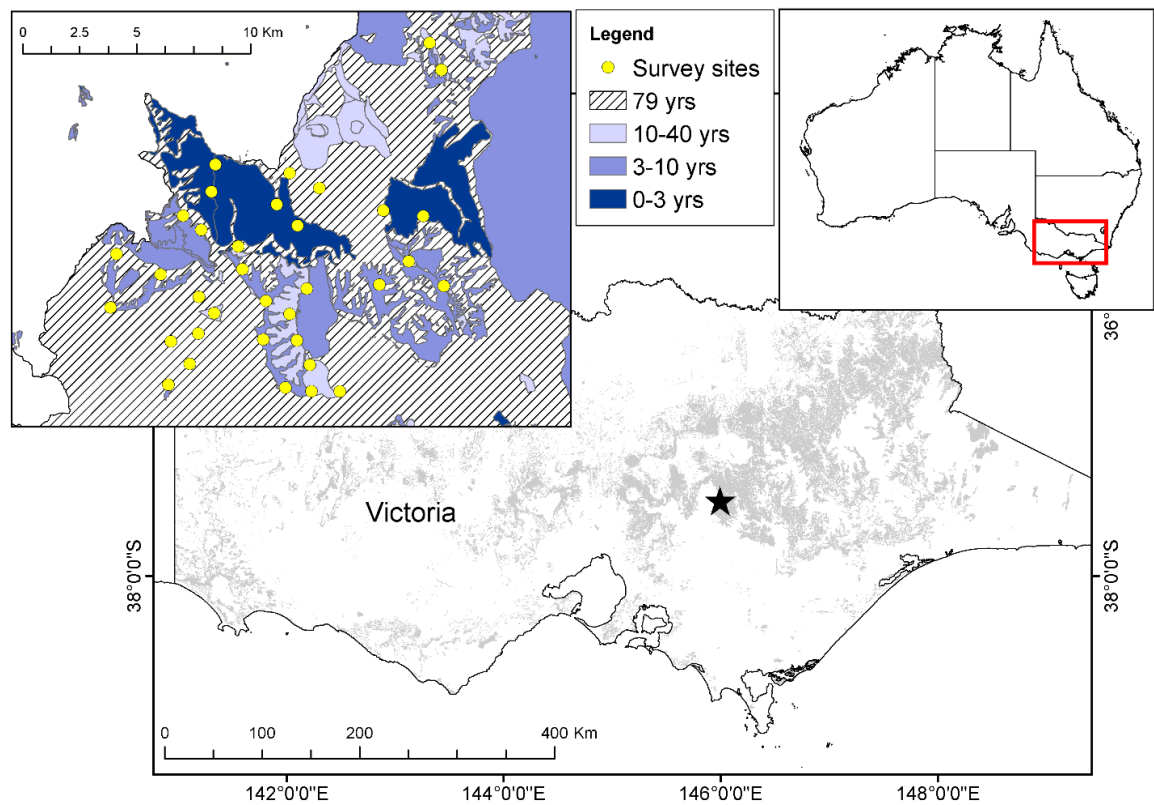


Figure 5.1. Distribution of foothill forests (shaded area in main panel) and locations of study area (star in main panel) in Victoria, Australia. Top left panel: shades of blue represent post-prescribed fire age classes: 0-3 years, 3-10 years, 10-40 years since prescribed fire. Simple hatch represents long-unburnt vegetation (79 years since wildfire). Yellow circles represent study sites.

The canopy of foothill forests reaches heights of 30 – 60 m and is often accompanied by a secondary tree layer of *Acacia* spp. To avoid topographic differences in vegetation composition and structure (i.e. between gullies and ridges), all sites were located within a single vegetation community, ‘herb-rich foothills forest’ (Victorian Government Department of Sustainability and Environment 2004). Sites were positioned on slopes at least 100 m upslope from a gully (riparian vegetation) and 50 m from the ridge top. The dominant canopy species were messmate stringybark *Eucalyptus obliqua*, mountain grey-gum *E. cypellocarpa*, broad-leaved peppermint *E. dives* and narrow-leaved peppermint *E. radiata*. Smaller trees

and shrubs constitute the understorey, including blackwood *Acacia melanoxylon*, silver wattle *A. dealbata*, prickly currant-bush *Coprosma quadrifida*, common cassinia *Cassinia aculeata*, and ferns such as austral bracken *Pteridium esculentum*. The ground layer consists of a rich cover of herbs.

### **5.3.2 Fire regime and fire mapping**

In foothill forests, wildfires typically occur in summer (Dec – Feb), whereas prescribed burns are undertaken in autumn and spring months. Large wildfires (> 10 000 ha) have occurred within the wider foothill forests region in 1939, 1962, 1983, 2003, 2005, 2006, 2009, 2014 and 2019 (Department of Environment, Land, Water and Planning 2015, Nolan et al. 2020). Mapped prescribed fires in the study area date from the 1970s to the year of surveys (Fig. 5.1). These generally are smaller: the mean fire size at the study sites was 658 ha (range = 44 – 1738 ha). Fire management and the interval between prescribed fires is guided by plant life-history, notably the time to maturity and senescence after fire (Cheal 2010); but in practice, fire intervals vary depending on local objectives and context. In general, prescribed burns in foothill forests do not scorch the canopy or kill canopy trees (McCarthy et al. 2017). Even severe wildfires in foothill forests are not stand-replacing. The stems of mature eucalypts generally persist through fire and resprout epicormically from buds protected by thick bark (Collins 2020).

To determine the fire history of sites we used spatial maps of fire history supplied by the Victorian Department of Environment, Land, Water and Planning (DELWP), and analysed by using the software ArcMap (ESRI 2011). Spatial maps of fire perimeters post-1976 were created by using LANDSAT imagery and pre-1976 by using historical records. The mapped time since fire was verified in the field by checking for charcoal on stringybark eucalypts, and other signs of past fire.

### 5.3.3 Study design

Diurnal birds and understorey vascular plants were systematically sampled at 29 sites selected to span a chronosequence from 1 - 36 years post-prescribed fire. A further nine sites last burned by wildfire in 1939 were sampled to represent a 'long-unburnt' state (79 years since fire). Sites were selected to ensure coverage of a range of post-fire 'age-classes': (sometimes called 'growth stages' or 'successional states') used by regional land managers (Table 5.1, Fig. 5.2). Although sites were distributed among four age-classes present in the study area (i.e. 0 – 3, 3 – 10, 10 – 40, >40 years post-fire), based on post-fire vegetation growth stages described by Cheal (2010), there was a gap in the chronosequence from 11 – 30 years post-fire. This was a consequence of the fire history of the study area, with no areas available that were last burned by prescribed fire during this period. Sites were located at least 1 km apart to ensure sample independence.

To survey the bird and plant communities at each site, we established a 250 m transect that ran along the contour of the slope and was at least 50 - 200 m from a road.

Table 5.1. The distribution of sites among post-fire age-classes.

Age class	Years since fire	Number of sites	Last fire-type
AC1	0 – 3	11	Prescribed burn
AC2	3 – 10	8	Prescribed burn
AC3	10 – 40	10	Prescribed burn
Long unburnt	79	9	Wildfire

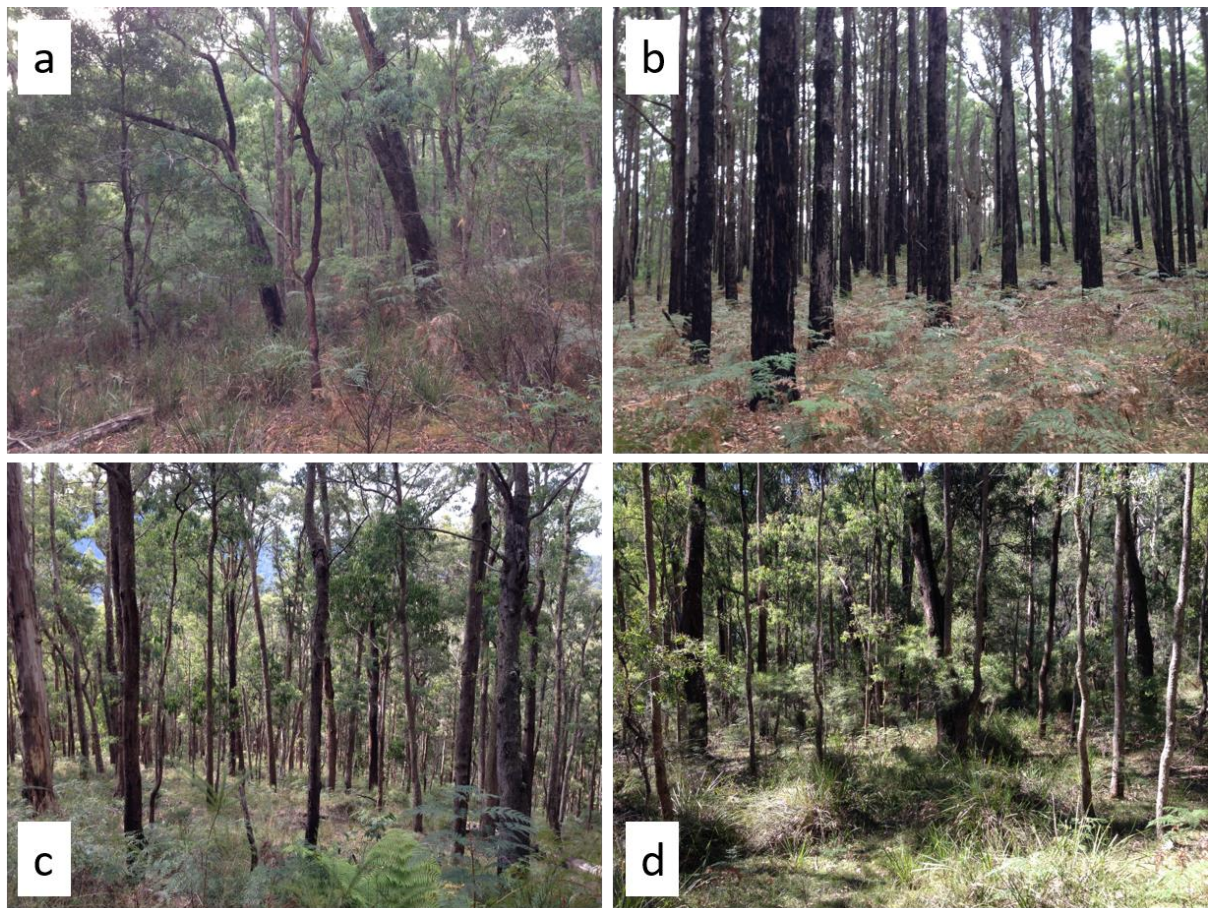


Figure 5.2. Foothill forests vegetation in four post-fire age-classes (AC). (a) long-unburnt: 79 years after wildfire. (b) AC1: 0-3 years after prescribed fire. (c) AC2: 3-10 years after prescribed fire. (d) AC3: 10-40 years after prescribed fire.

#### 5.3.3.1 *Birds*

At each site, a 2-ha plot centered over the 250 m transect was established and surveyed for birds by a single experienced observer (FR) a total of six times: three times during the austral autumn/winter and three times during spring/summer, between 2017 and 2018. Surveys were conducted in clear weather within four hours of dawn, except for two winter survey rounds during which sites were each surveyed once in the morning and once in the afternoon. Each survey was for a 20-min period and all individuals either heard or seen were identified to species level and recorded. The perpendicular distance (m) to each detection from the transect

line was estimated and used to test for differences in detectability between sites (see Appendix 5.6.1). Nocturnal birds, raptors and swifts were recorded but excluded from analyses.

#### 5.3.3.2 *Understorey plants*

Understorey vascular plants were sampled at each site by using three 10 m x 10 m plots: one at the start-, mid-, and end-point of the 250 m transect. All vascular plant species that were rooted within the plot were identified to species level and the projected foliar cover (%) was estimated visually by a single observer (FR). The mean cover from the three plots was calculated for each species and used in all analyses. Three plots were used to sample each site to increase spatial coverage of the site and to better detect patchily distributed species. Because of uncertainty in the emergence time of geophytic orchids and lack of reproductive material to facilitate identification of grasses, these groups were excluded from analyses, except for *Tetrarrhena juncea* (forest wire grass) which was readily identified from vegetative material. Floristic surveys were completed in the austral spring between 9<sup>th</sup> October and 10<sup>th</sup> November 2017.

#### 5.3.4 **Data analyses**

To account for potential issues of detectability, we first used linear regression to test for a relationship between the distance to detection of species (or groups of similar species) and midstorey vegetation cover (see Appendix 5.6.1). For several species/groups, there was a weak negative relationship between midstorey vegetation cover and distance to detection, suggesting that some individuals of these species may have been undetected at sites with high midstorey vegetation cover. To control for potential errors due to detectability, we used a presence/absence-based index (reporting rate) to compare the relative abundance of species between sites. Because it does not rely on counts of individuals, reporting rate is less prone to biases caused by differences in detectability or flocking behavior. This approach is a robust

alternative to model-based approaches (i.e. distance analysis) for which modelling assumptions cannot be met (Hutto 2016). Below we outline the approach used to address the key questions.

All analyses were conducted using the R statistical environment (R Development Team 2018).

#### *5.3.4.1 Individual species*

For individual species that occurred at  $\geq 25\%$  (8/29) of sites last burnt by prescribed fire, we used generalised additive models (GAMs) (Wood 2017) to predict changes in relative abundance (birds) and relative cover (plants) with time since fire. For bird species we used reporting rate, the number of survey rounds (out of 6) during which a species was detected. Variation in reporting rate of species between sites is often a result of variation in the abundance of individuals and so is a reliable proxy for relative abundance. For plant species, we used the mean projected foliar cover at sites.

We used a Poisson error distribution for bird models, and for plants we used the beta error distribution. The beta distribution is used to overcome inherent problems with proportion data (such as bounding at zero and one) that violate the assumptions of other distributions (Douma and Weedon 2019). The degrees of freedom of the smoothed term ( $K$ ) in the GAMs was set automatically during the model-fitting process. If overdispersion of Poisson-distributed data was detected, an observation-level random factor was used in a mixed-model framework, following Harrison (2014). GAMs were built by using the *mgcv* package in R (Wood 2017).

By visually assessing the fitted model for each species, we described the shape of the response-curve based on pre-defined generalized response curves (after Watson et al. 2012b). We then calculated the percentage of species with a significant relationship, that resembled each response shape. Four main response shapes were observed: ‘irruptive’ (abundance

highest in the first few years following fire), ‘bell’ (initial increase followed by a decrease with time since fire), ‘incline’ (gradual increase with time since fire), and ‘plateau’ (initial increase followed by stability in later years post-fire). Non-significant relationships were classed as ‘NS’. We also compared the explanatory power (deviance explained) of models between taxonomic groups by using boxplots.

We compared the relative abundance of species at post-prescribed fire sites with that for long-unburnt vegetation by using ‘age-class’ (AC) categories, representing the time since last fire (Table 5.1). Sites last burnt by a wildfire in 1939 were categorized as ‘long-unburnt’ (LU). For bird species, we used generalized linear models (GLMs), with the categorical variable ‘age-class’ as the explanatory variable, and a Poisson error distribution, to compare relative abundance between age-classes for species that occurred at  $\geq 25\%$  (10/38) of sites. For plant species, we carried out a similar approach, but built beta regression models by using the `betareg` function in the “betareg” R package (Zeileis et al. 2020). Beta regression models are analogous to GLMs but can incorporate proportion data. A Tukey HSD test was used to determine age-classes that differed significantly from long-unburnt vegetation. We then calculated the percentage of bird and plant species whose relative abundance differed significantly from long-unburnt vegetation in each age-class.

#### 5.3.4.2 *Functional groups*

We classified species into functional groups based on their life-history traits. For birds, we grouped species based on three functional traits (Table 5.2): (1) foraging location (ground, lower-midstorey, upper-midstorey, throughout), (2) nest type (open, hollow, burrow, brood parasite), and (3) diet versatility, the number of food types (fruit, nectar or pollen, seeds, foliage or herbs, corms or tubers, terrestrial invertebrates, terrestrial vertebrates, carrion) that each constitute at least 1% of the total diet (low: 1 food source, intermediate: 2-3 food sources, high: 4-6 food sources). For plants, we used two levels of classification, (1) fire-

regeneration trait and (2) growth form. Fire-regeneration traits were used to classify species into four groups following Clarke et al. (2015): facultative-resprouting (capacity to regenerate by resprouting or from seed), obligate-resprouting (regenerates by resprouting but no post-fire seeding), obligate-seeding (no capacity to resprout post-fire, regenerates from a seed bank) and fire-avoider (no post-fire resprouting or seeding). Four growth-form categories were used to group species: herbaceous plants (hemicryptophytes <1 m in Raunkiaer 1934), low shrubs, shrubs and understorey trees (Table 5.2). Both levels of classification were combined to group species (e.g. obligate-seeder shrubs).

To assign species to groups, we used a combination of the expert knowledge of the authors, a database of plant vital attributes (Cheal 2011), the Flora of Victoria online herbarium (Royal Botanic Gardens Victoria, vicflora.rbg.vic.gov.au) and a published database of Australian birds (Garnett et al. 2015). If the fire regeneration trait was unknown for plants, data for that species were not included in functional group analyses.

We summed the relative abundance/cover values of all species in each functional group for each site. We used GAMs to model changes in these values with time since prescribed fire, using a Gaussian error distribution. In a similar approach to that used for individual species, we compared the relative abundance/cover of functional groups between post-prescribed fire age-classes and long-unburnt vegetation by using GLMs and a Gaussian error distribution.

#### 5.3.4.3 *Species diversity and community composition*

To test the influence of prescribed fire on plant and bird communities, we compared (a) species diversity indices and (b) community assemblages between post-prescribed fire age-classes and long-unburned reference vegetation. First, for each taxonomic group at each site, we calculated two commonly used indices to represent alpha-diversity: species richness (total number of species recorded per site) and Shannon's diversity index, by using the "vegan" package in R. Then, we classified sites into post-fire age classes as above (AC1, AC2, AC3,

long-unburnt), and used GLMs to model changes in each index with time since fire (i.e. between post-fire age-classes).

Second, we used relative abundance/cover matrices and non-metric multidimensional scaling (NMDS) ordination to explore relationships between the composition of plant and bird communities and age-classes. NMDS represents ecological communities in lower-dimensional space, based on their dissimilarity (Legendre and Legendre 1998). We used the Bray-Curtis index to calculate dissimilarities between species' abundance values as it is less sensitive to rare species than other techniques, such as Euclidian distance. NMDS was carried out using the metaMDS function in the "vegan" package (Oksanen et al. 2019) and ordination plots. Non-parametric permutation tests (PerMANOVA, ADONIS in the 'vegan' package) were used to test for significant ( $P < 0.05$ ) effects of age-class on community composition. Species detected at a single site only were removed from the analysis to reduce the leverage of rare or vagrant species.

Table 5.2. Functional groups of bird and plant species used in analyses of the response of taxa to time since prescribed fire.

Taxon	Variable	Level	Description	Number of species
Birds	Foraging location	Ground	Mostly forages or takes prey from the ground.	12
		Lower-midstorey	Forages mostly in vegetation < 3m height.	5
		Upper-midstorey	Forages mostly in vegetation > 3m height (including canopy vegetation).	20
		Throughout	Forages throughout the vertical strata, from the ground to the canopy.	6
	Diet versatility <sup>†</sup>	Low	Species with high level of dietary specialization. Only one food type that contributes $\geq 1\%$ of total diet.	23
		Intermediate	Two – three food types each contribute $\geq 1\%$ of total diet.	16
		High	Four – six food types each constitute at $\geq 1\%$ of total diet.	4
	Nest type	Burrow	Nests in a burrow in the ground.	1
		Hollow	Nest in a cavity in a tree branch or trunk. Includes obligate and facultative cavity nesters.	9
		Open	Constructs a nest in the ‘open’, not in a cavity or burrow. Includes species that construct bowl, dome or saucer nests.	32
Plants	Fire regeneration trait	Brood parasite	Lays eggs in the nest of other species (cuckoos).	1
		Obligate seeding	Adult plants are killed by fire. Regeneration from seed.	17
		Obligate resprouter	Adults capable of surviving fire and resprouting. Includes basal, epicormic and rhizomal resprouting. Does not regenerate from seed.	14
		Facultative resprouter	Adults capable of surviving fire and resprouting, but regeneration also occurs from seed.	48

Taxon	Variable	Level	Description	Number of species
	Growth form	Herb	Herbaceous plants	26
		Low shrub	Shrubs, 0.1 – 1 m height	31
		Shrub	Shrubs, 1 – 8 m height	28
		Understorey tree	Small trees, > 8 m height	3

<sup>†</sup> Food types include: fruit, nectar or pollen, seeds, foliage or herbs, corms or tubers, terrestrial invertebrates, terrestrial vertebrates, carrion (Garnett et al. 2015).

## 5.4 RESULTS

We made a total of 4903 detections of diurnal birds from 43 species (Appendix 5.6.2). The most speciose bird families were the Meliphagidae (honeyeaters, 5 species), Acanthizidae (thornbills, 4 species) and Petroicidae (Australian robins, 4 species). The number of bird species recorded per site ranged from 13 – 29. The most frequently recorded species were striated thornbill *Acanthiza lineata*, white-throated treecreeper *Cormobates leucophaea*, yellow-faced honeyeater *Lichenostomus chrysops*, and spotted pardalote *Pardalotus punctatus*, which were recorded at all sites.

We recorded a total of 89 species of understorey vascular plants, including three species of understorey tree (mature height > 8 m), 28 shrubs (1 – 8 m), 31 low shrubs (0.1 – 1 m), 26 herbs and one geophyte (shield sundew *Drosera peltata*) (Appendix 5.6.3). The most speciose families were Asteraceae (daisies, 13 species) and Fabaceae (peas and wattles, 13 species). The number of plant species recorded per site ranged from 16 – 42. Some of the most widespread plant species were common heath *Epacris impressa*, austral bracken and pink bells *Tetratheca ciliata*.

Below we summarize the main findings in relation to the three levels of biodiversity.

### 5.4.1 Individual species

We built GAMs for 22 bird species and 39 plant species (9 shrubs, 6 low shrubs, 23 herbs, 1 geophyte). Significant responses ( $P < 0.05$ ) to time since prescribed fire were obtained for three bird species (14% of modelled species) and eight plant species (21%) (Fig. 5.3a). For birds, two types of generalized response curve were observed (Fig. 5.3a): incline (e.g. golden whistler *Pachycephala pectoralis*, Fig. 5.3c) and plateau (e.g. grey fantail *Rhipidura albiscapa*, Fig. 5.3d). For plants, significant responses to time since fire included three generalized response curves (Fig. 5.3a): irruptive (e.g. moth daisy-bush *Olearia erubescens*,

Fig. 5.3e), bell-shaped (8%) and incline (e.g. pink bells, Fig 5.3f). Overall, there was no substantial difference in the strength of models (i.e. deviance explained) between bird and plant species (Fig. 5.3b).

For most species in both taxonomic groups the relationship with time since prescribed fire was not significant (86% of modelled bird species, 79% of modelled plant species), due to high levels of variation in species abundances across the chronosequence. Model outputs for all species are given in Appendices 5.6.4 – 5.6.5.

We compared the relative abundance/cover of 25 bird and 41 plant species between post-prescribed fire age-classes and long-unburnt vegetation. The relative abundance of one bird species (white-browed scrubwren *Sericornis frontalis*, Fig. 5.4a) 0 – 3 years after prescribed fire (AC1) differed significantly from that of long-unburnt vegetation. For 7% (n = 3 species) of modelled plant species, relative cover differed significantly from long-unburnt vegetation at 4 – 10 years after prescribed fire (e.g. common cassinia, Fig. 5.4d). For several species, there were non-significant trends of relative abundance differing from long-unburnt vegetation in various age classes (e.g. silvereve *Zosterops lateralis*, Fig. 5.4b, brown thornbill *Acanthiza pusilla*, Fig. 5.4c, kurwan *Bursaria spinosa*, Fig. 5.4e, moth daisy-bush, Fig. 5.4f). For most bird and plant species, there was little difference with long-burnt vegetation for any post-fire age-class. All species model outputs are provided in Appendix 5.6.6 – 5.6.7.

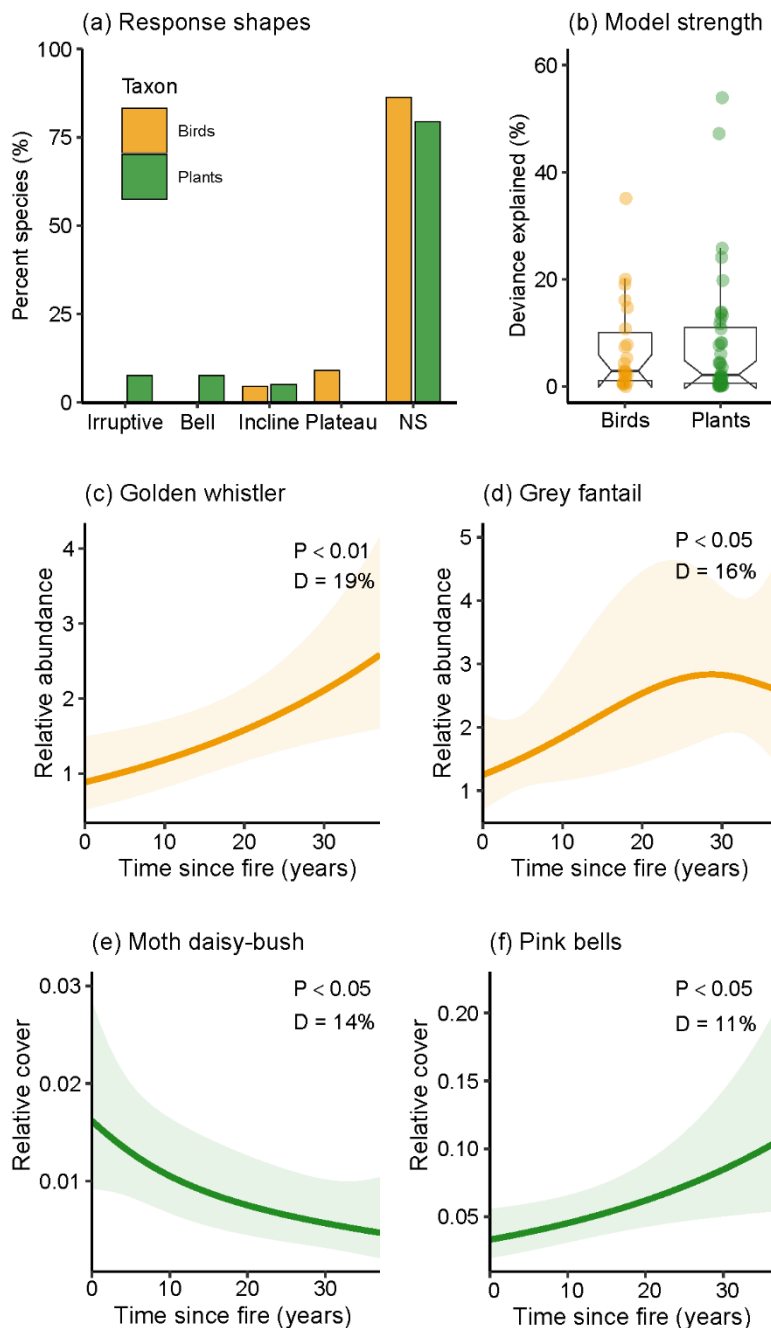


Figure 5.3. Responses bird and plant species to time since prescribed fire in foothill forests. (a) Percentage of plant and bird species for which the modelled response to time since prescribed fire resembled different types of generalized response-curves (after Whelan 2001 and Watson et al. 2012). 'NS' refers to non-significant relationships. (b) Explanatory power of generalized additive models of the relative abundance of bird ( $n = 22$ ) and relative cover of plant ( $n = 39$  species) species as a function of time since prescribed fire. Points represent the deviance explained (%) of models. Notch plots indicate the median, upper and lower quartiles and 95% confidence intervals for each taxonomic group. (c - f) Models of selected bird (orange lines) and plant (green lines) species to time since prescribed fire. Lines are fitted models. Shaded areas are 95 % confidence intervals.  $P = P$ -value,  $D =$  deviance explained.

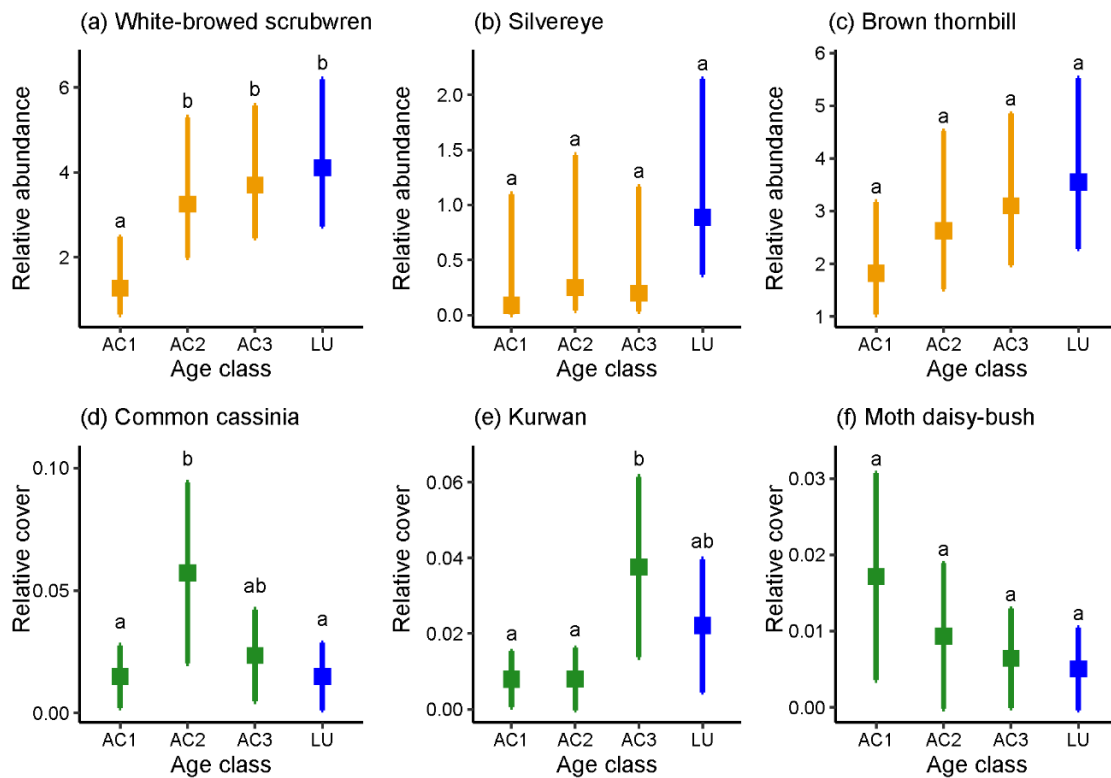


Figure 5.4. Relative abundance of selected bird (top panels) and relative cover of selected plant (bottom panels) species in post-fire age-classes (AC) in foothill forests. Points represent mean values ( $\pm$  SE). AC1 = 0-3, AC2 = 3-10, AC3 = 10-40 years since prescribed fire, LU = 79 years since wildfire. Generalized linear models with Poisson error distribution were used to model bird responses. Beta regression was used to model plant species responses to age classes. Letters above points indicate significant differences ( $P < 0.05$ ) determined by Tukey HSD.

## 5.4.2 Functional groups

The relative abundance or cover of several functional groups, for both birds and plants, was related to time since prescribed fire (Fig. 5.5). Upper-midstorey foraging birds increased in relative abundance linearly (incline response) with time since fire ( $P < 0.05$ , deviance explained = 16%, Fig. 5.5a), lower-midstorey foragers showed a plateau response ( $P < 0.001$ , deviance explained = 44%, Fig. 5.5a) and species with low diet versatility ( $P < 0.05$ , deviance explained = 23%, Fig. 5.5b) and open-nesting species ( $P < 0.05$ , deviance explained = 18%, Fig. 5.5c) both increased linearly (incline response) with time since fire. Facultative-

resprouting shrubs ( $P < 0.05$ , deviance explained = 30%, Fig. 5.5d) and obligate-seeding shrubs ( $P < 0.05$ , deviance explained = 25%, Fig. 5.5f) both showed a bell-shaped response to time since fire.

Relative abundance of one bird functional group, lower-midstorey foragers, differed significantly from that of long-unburnt vegetation in the youngest age class ( $P < 0.01$ , Fig. 5.6a). Relative cover of facultative resprouting shrubs was greater 4 – 10 years after prescribed fire than in the first three years following prescribed fire ( $P < 0.001$ , Fig 5.6d) and that of obligate resprouting shrubs was significantly greater in long-unburnt vegetation than in the first three years following prescribed fire ( $P < 0.05$ , Fig 5.6e).

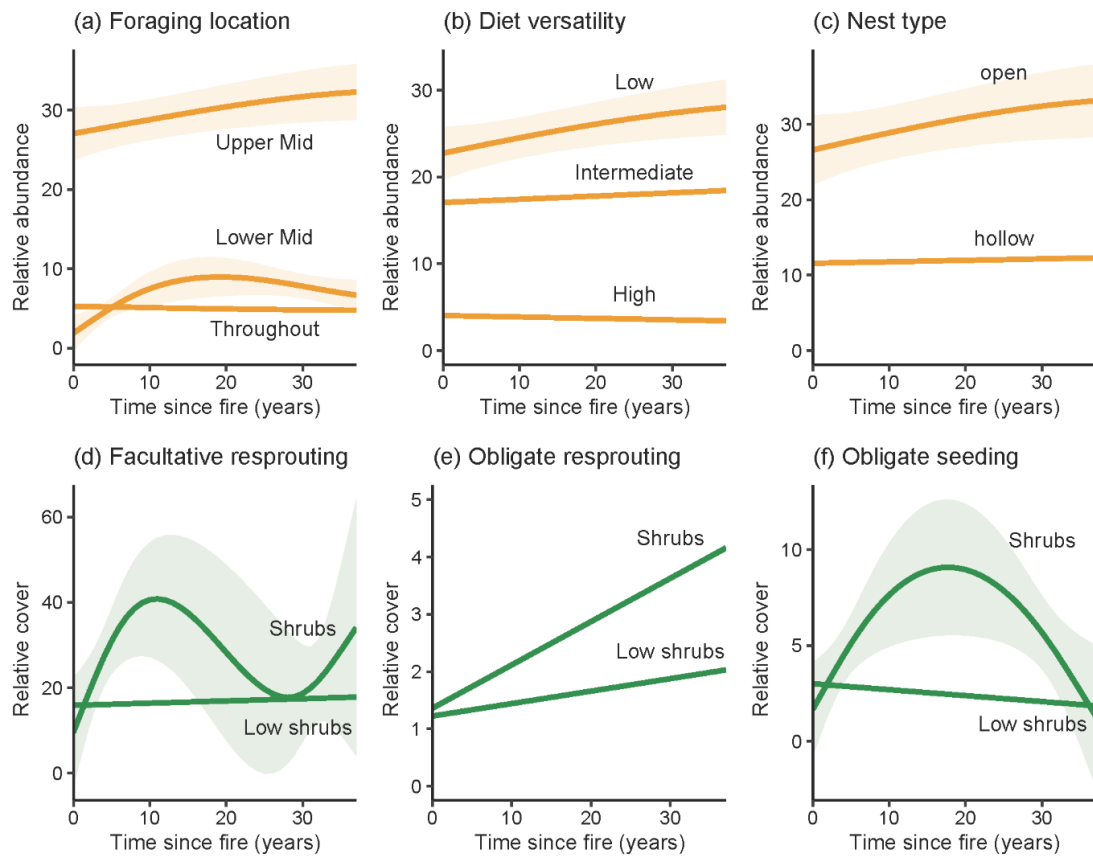


Figure 5.5. Response of functional groups of bird and (a – c) plant (d – f) species to time since prescribed fire in foothill forests. Birds were grouped according to (a) foraging location (upper-midstorey:  $n = 20$  species, lower-midstorey:  $n = 5$ , throughout:  $n = 6$ ), (b) diet versatility (low:  $n = 23$ , intermediate:  $n = 16$ , high:  $n = 4$ ) and (c) nest type (open:  $n = 32$ , hollow:  $n = 9$ ). Plants were grouped according to fire regeneration traits and growth form: (d) facultative resprouting shrubs ( $n = 11$  species) and low shrubs ( $n = 18$ ); (e) obligate resprouting shrubs ( $n = 9$ ) and low shrubs ( $n = 3$ ); (f) obligate seeding shrubs ( $n = 6$ ) and low shrubs ( $n = 6$ ). Lines are fitted responses from generalized additive models of the total relative abundance/cover of species in each group. Shaded areas are 95% confidence intervals. Lines without shaded areas indicate non-significant relationships.

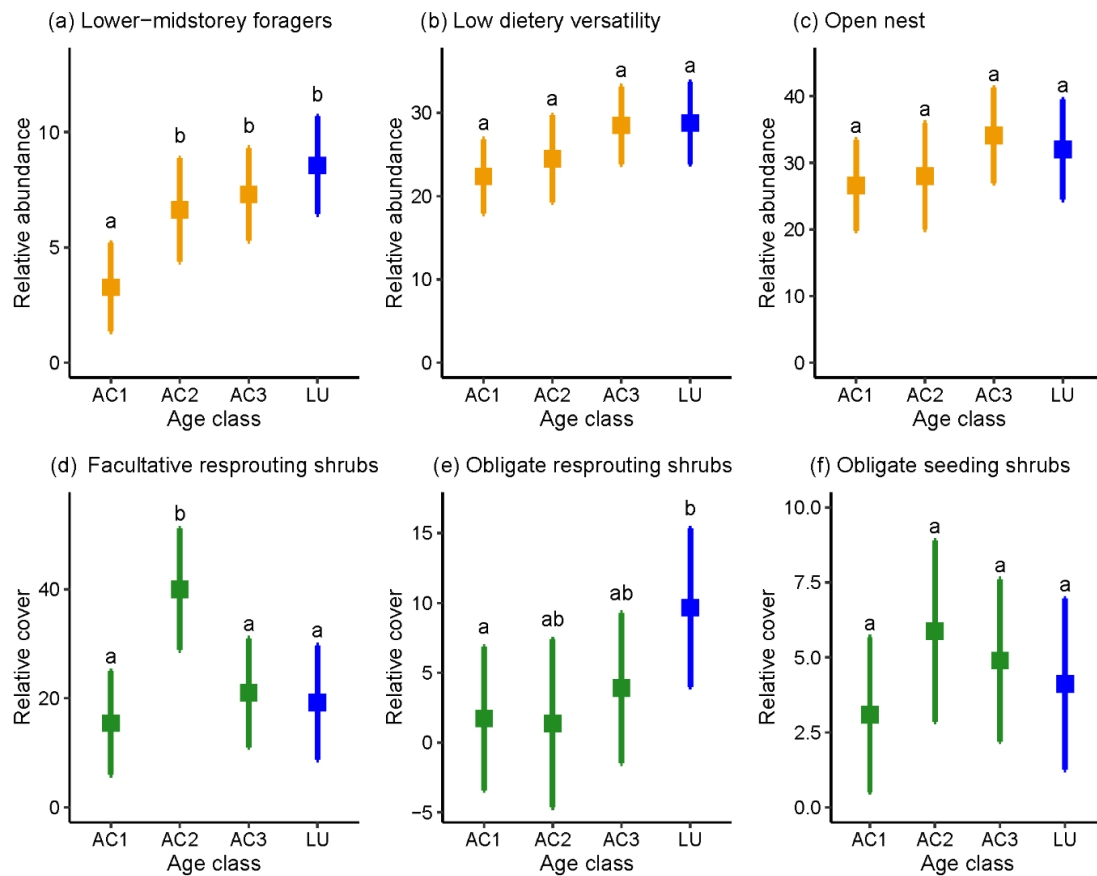


Figure 5.6. Response of selected bird (a – c) and plant (d – f) functional groups to post-fire age-classes (AC) in foothill forests. Points indicate mean  $\pm$  SE relative abundance of (a) lower-midstorey foraging birds, (b) birds with low dietary versatility, (c) open nest bird species, and mean  $\pm$  SE relative cover of (d) facultative resprouting shrubs, (e) obligate resprouting shrubs and (f) obligate seeding shrubs in post-fire age-classes. Letters indicate significantly different means ( $P < 0.05$ ) determined by Tukey HSD. AC1: 0-3 years, AC2: 3-10 years, AC3: 10-40 years since prescribed fire, LU: long-unburnt (79 years since wildfire).

### 5.4.3 Species diversity and community composition

Alpha diversity (species richness, Shannon's diversity) of both bird and plant species did not differ significantly between sites in post-prescribed fire age-classes and long-unburnt vegetation (Fig. 5.7).

NMDS ordination analyses showed some evidence of successional trajectories of bird and plant communities after prescribed fire (Fig. 5.8). This influence was stronger for birds ( $P = 0.01$ , PerMANOVA) than plants ( $P = 0.081$ ). Bird community composition showed most dissimilarity between AC1 (0-3 years post-fire) and long-unburnt vegetation (Fig. 5.8a). The main point of differentiation for plant communities was between AC2 (4 - 10 years post-fire) and long-unburnt (LU) vegetation (Fig. 5.8c). Vectors of influential bird (Fig. 5.8b) and plant (Fig. 5.8d) species showed some clustering of species within the ordinations. A key species cluster in the bird ordination is in the top right corner, in the direction of older age-classes. These species (white-browed scrub-wren, grey fantail, brown thornbill, golden whistler, fan-tailed cuckoo *Cacomantis flabelliformis*) typically are associated with well-developed understorey vegetation structure. A key feature of the plant ordination is the cluster of species to the right-hand side, in line with sites 4 - 10 years post-fire (AC2). These species include the facultative resprouter and obligate seeder species from the family Asteraceae, common cassinia (bell-shape response to time since prescribed fire, Appendix 5.6.5) and common fireweed *Senecio prenanthoides*, respectively.

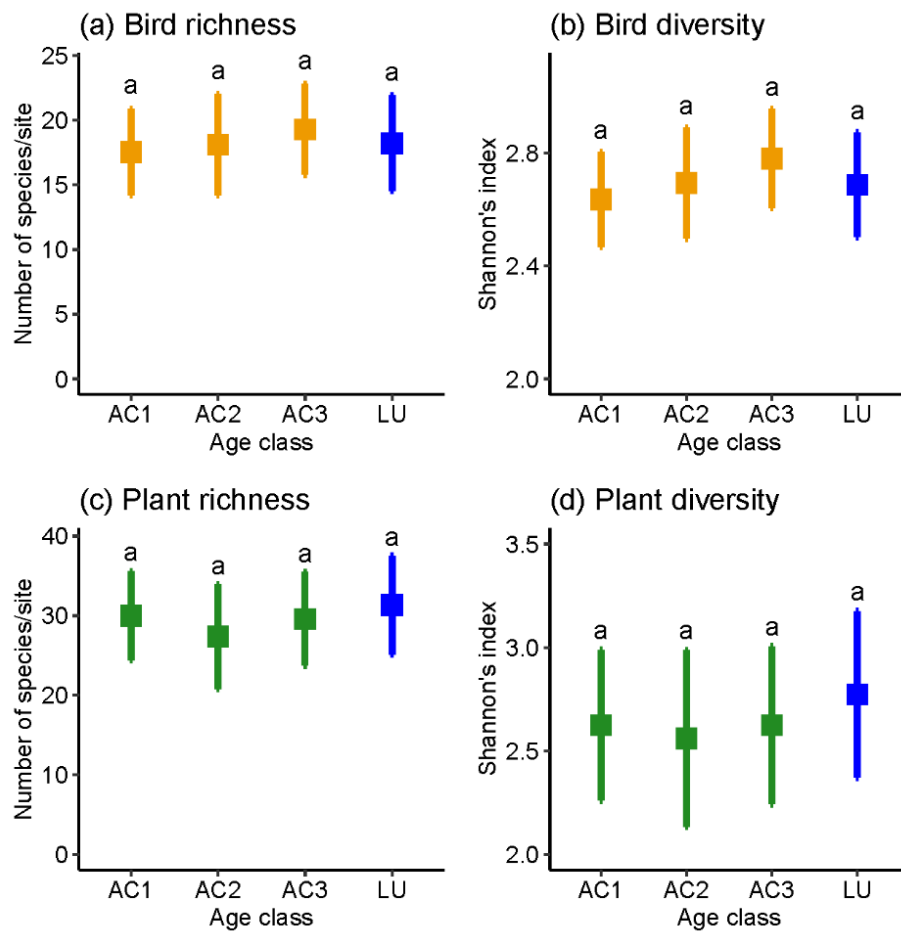


Figure 5.7. Response of bird and plant diversity indices to post-fire age-classes (AC) in foothill forests. Points indicate mean  $\pm$  SE of (a) bird species richness, (b) bird species diversity, (c) plant species richness, (d) plant species diversity. Letters indicate significantly different means ( $P < 0.05$ ) determined by Tukey HSD. AC1: 0-3 years, AC2: 3-10 years, AC3: 10-40 years since prescribed fire, LU: long-unburnt (79 years since wildfire).

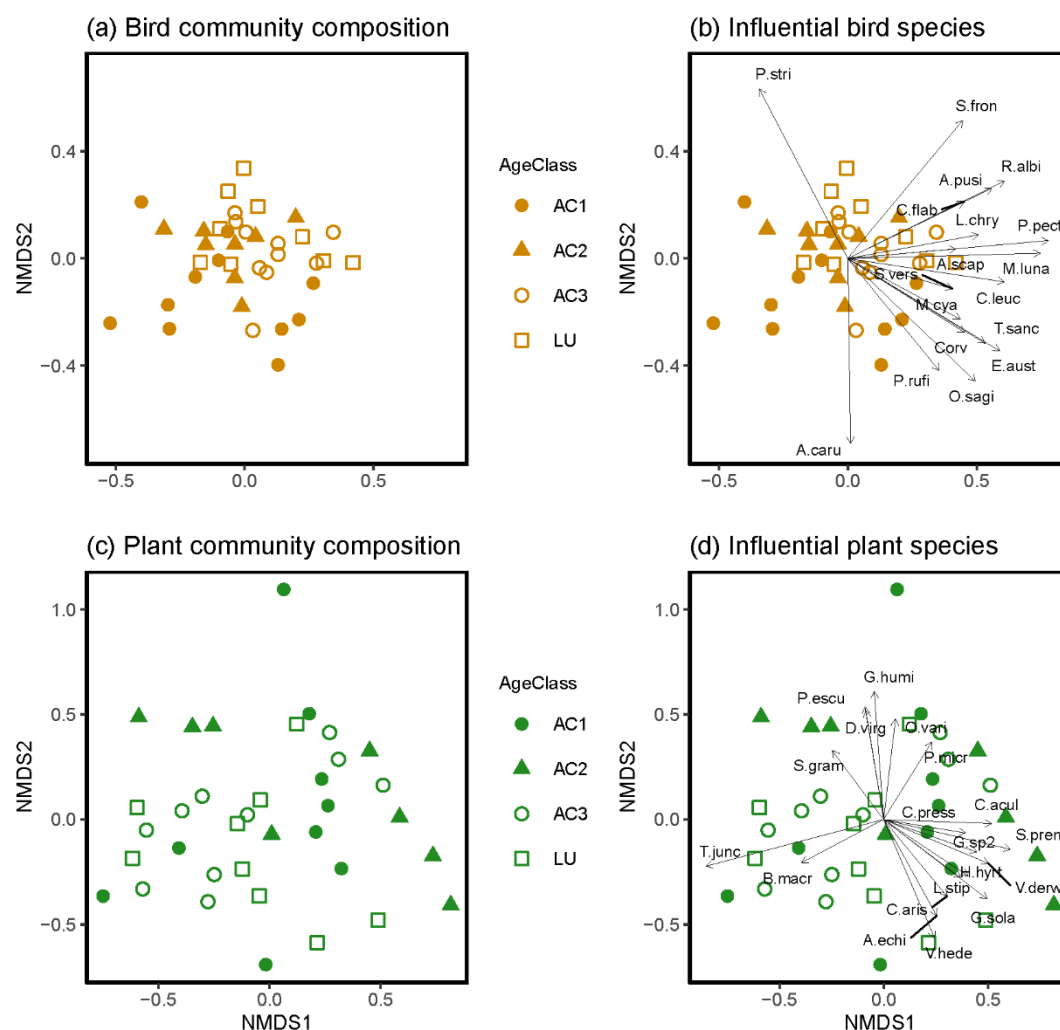


Figure 5.8. Non-metric multidimensional scaling (NMDS) ordinations showing similarity in bird (a – b) and plant (c – d) community composition between post-fire age classes in foothill forests. Colours and symbols represent time-since-fire age-classes: AC1 = 0-3, AC2 = 3-10, AC3 = 10-40 years since prescribed fire, ‘LU’ = 79 years since wildfire. (a) Bird community composition. (b) Bird community composition with arrows to represent vectors of influential species. (c) Plant community composition. (d) Plant community composition with arrows to represent vectors of influential species. PerMANOVA showed significant effects of post-fire age class on bird ( $P = 0.01$ ) but not plant ( $P = 0.081$ ) community composition. Species names are represented by capitalized generic name followed by the first four letters of the specific name (e.g. S.fron = *Sericornis frontalis*). Species lists are provided in Appendix 2-3.

## 5.5 DISCUSSION

Overall, our findings show a high level of resilience to prescribed fire by birds and plants in temperate dry forests. We showed that: (a) for most individual bird and plant species, relative abundance/cover was not significantly related to time since prescribed fire; (b) responses of functional groups of species to prescribed fire showed the strongest effects for lower-midstorey foraging birds, facultative-resprouting shrubs and obligate-seeding shrubs; (c) the abundance/cover of several functional groups in post-prescribed fire age-classes differed from that of long-unburnt vegetation; (d) measures of alpha diversity for both bird and plant species did not differ between post-prescribed fire age-classes and long-unburnt forest; and (e) variation in the composition of bird and plant communities was greatest between recently burnt and long-unburnt vegetation. Next, we discuss factors contributing to the apparent resilience of temperate dry forest plant and bird communities to prescribed fire, and the implications for fire management in these and other temperate forests.

### 5.5.1 Bird community response to prescribed fire

For birds, a strong effect of prescribed fire was on the abundance of species that forage in the lower-midstorey (<3 m above ground): abundance initially was low after fire, then increased before plateauing ~15 years after fire. Typically, animal species respond to structural changes in vegetation caused by fire, rather than fire *per se* (Pons and Clavero 2010, Sitters et al. 2014a). This understorey bird guild can be interpreted as responding positively to the development of understorey vegetation structure, which follows a similar post-fire trajectory of increasing height and structural complexity (Rainsford et al. 2020).

There also was a significant, but less-strong relationship between the abundance of both upper-midstorey foragers and dietary specialists with time since fire. Both of these guilds include grey fantail and golden whistler, insectivores that showed individual responses to fire which depend on a well-developed midstorey structure. Their responses are consistent with

previous studies in wooded ecosystems (e.g. (Davis et al. 2016). Diet specialization can influence species responses to fire (Santos et al. 2014). Species with more versatile diets may be less susceptible to a reduction in the diversity of available food resources after fire, as they can more easily switch between foods in response to prevailing conditions.

### **5.5.2 Plant community response to prescribed fire**

While some 20% of individual plant species showed a significant response to time since fire, a particularly clear functional effect was a ‘bell-shaped’ response by obligate-seeding shrubs (e.g. mountain hickory wattle *Acacia obliquinerva*) to time since fire. This fire response is typical in short-lived, woody species of Fabaceae and Asteraceae: propagule production reaches a peak at some point in the post-fire succession after which plant cover decreases as adults lose vigor (Keith 2012). For these obligate-seeding species, fire typically kills the mature plant and regeneration occurs from seed stored either in canopy or soil seed banks (Pausas and Keeley 2014). Obligate seeding in forest plants is associated with sensitivity to frequent and infrequent fire (Bradstock and Kenny 2003). Prescribed fire applied at appropriate intervals (~15 – 30 years) would allow enough time for fire-sensitive plants to reach maturity and then stimulate regeneration.

Similarly, there was a strong response of facultative-resprouting shrubs to time since fire. Several of these species (e.g. common cassinia, narrow-leaf bitter-pea *Daviesia virgata*, gorse bitter-pea *D. ulicifolia*), although they have the capacity to resprout, also display fire-cued regeneration from seed. This helps explain the similarity between the shapes of the response curves for obligate-seeding and facultative-resprouting shrubs. Plant species that display fire-cued germination may be at risk of senescence or decline in the absence of fire. For such species, introducing fire can potentially stimulate regeneration and local persistence. In contrast to these bell-shaped responses, the cover of obligate-resprouting shrubs tended to increase linearly, but non-significantly, with time since fire.

### 5.5.3 A resilient ecosystem?

Several factors contribute to the apparent resilience of birds and plants of these temperate dry forests to prescribed fire: (1) fire characteristics, (2) plant regeneration traits, and (3) environmental context.

Fire regime characteristics influence the post-fire occurrence of biota. Here, two main attributes likely influenced our findings: within and between-site variation in fire intensity, and the amount of forest burnt. First, prescribed fires typically burn more patchily than wildfires, leaving areas within the fire perimeter either unburnt or less severely burnt (Penman et al. 2007, McCarthy et al. 2017). These patterns influence the post-fire occurrence of plant species (Ooi et al. 2006), bird species (Dickson et al. 2009) and habitat attributes (Holland et al. 2017). If fire-sensitive plants and important habitat attributes are removed inconsistently by fire, it could mask the time-since-fire responses of biota.

Second, the size of a fire and therefore the distance to the burn edge can also influence the post-fire composition of community (Uys et al. 2006), depending on species' mobility and the rate of post-fire recolonization of sensitive species (Santos et al. 2009). In addition, the interval between multiple fires can have different effects on components of the vegetation (Penman et al. 2008, Kelly et al. 2017b), leading to differential legacy effects from past disturbance. Together, variation in these fire characteristics likely contributed to the relatively high level of variation in the cover/abundance of species within and between sites for a given age-class, and therefore to the muted responses to time since prescribed fire.

Variation in fire regeneration traits of plant species influence post-fire ecosystem trajectories. The prevalence in temperate dry forests of species with a capacity for post-fire resprouting means that many species are still present at sites immediately after fire, leading to rapid recovery of above-ground plant diversity and vegetation structure (Rainsford et al. 2020). In particular, *Eucalyptus* trees are capable of epicormic resprouting along trunks and branches

following fire, which enhances the rate of recovery of vegetation structure (Keith 2012, Collins 2020), and provides important resources (e.g. foraging substrates, refuge, nest sites) for birds soon after fire. Thus, the prevalence of regeneration through post-fire resprouting of major trees and shrubs is a key factor in the resilience of this ecosystem to prescribed fire.

Environmental context (e.g. topography, soil moisture, disturbance legacies) also influences ecosystem recovery following disturbance. In foothill forests, topographic complexity drives landscape-scale vegetation heterogeneity (Bassett et al. 2017) and influences the composition of bird communities (Robinson et al. 2016). Specifically, moist gullies in foothill forests support a higher bird abundance than adjacent slopes and ridges (Robinson et al. 2016). Gullies are less likely to burn during prescribed fire than slopes and ridges, particularly cooler patchy fires, and therefore may serve as post-fire refuges. Whether or not a gully was burnt could influence post-fire trajectories of bird species and communities on adjacent slopes, through a ‘spill over’ of gully residents to upslope sites. We do not have detailed fire mapping of historic fires in this study to compare such differences between study sites.

The apparent resilience of birds and plants to prescribed fire in this study may also be influenced by several aspects of the study design, including sample size along the post-fire chronosequence, the absence of less-common or rare species for which sample sizes were too low to model that are sensitive to fire, and there may also be species sensitive to fire that have already been greatly reduced in abundance or locally extirpated. However, by pooling species into functional groups, we were able to detect broader effects of prescribed fire on bird and plant communities. These trends were supported by the vectors for influential species in ordination analyses. Given the environmental and ecological characteristics of foothill forests and the patchy nature of prescribed fires, we consider these findings to be a realistic representation for this ecosystem.

Resilience of bird and plant communities to prescribed fire has also been documented for other forest ecosystems; for example, mixed-oak and conifer forests in the U.S.A (Hutchinson et al. 2005, Dickson et al. 2009, Stephens et al. 2019). In mixed-oak forests, resilience was attributed to the capacity of woody plants to resprout following fire, and to low fire intensity which left the canopy intact and limited the degree of change to understorey conditions (Hutchinson et al. 2005). In ponderosa pine forests, important habitat resources for birds survived prescribed fire and provided post-fire structural legacies (Dickson et al. 2009). In southern U.S.A., prescribed burning has been used to improve the conservation status of endangered bird species (Stephens et al. 2019). A commonality of these in dry forests from different continents is that prescribed fire does not completely reset the ecological succession to 'time zero'. Most plants regenerate rapidly and some key structural resources for fauna (e.g. large trees, woody debris) are present within the fire perimeter post-burn.

#### **5.5.4 Implications for management**

The muted response of bird and plant species in these dry forests indicate that it is feasible to carry out a planned program of prescribed burning to reduce wildfire risk, while ensuring conservation values are maintained or enhanced. We propose three important considerations to guide management.

First, the frequency at which prescribed fire is applied has consequences for at least three main functional groups: understorey-foraging birds, obligate-seeding shrubs and facultative-resprouting shrubs. Ensuring a fire interval of ~15 – 30 years across substantial areas will best accommodate the life-cycle of fire-sensitive understorey plant species and may stimulate regeneration of several shrub species, although many species of Fabaceae may persist in the soil seed bank beyond this interval. This interval is in line with the recommended minimum tolerable fire interval of 15 years (Cheal 2010) for this ecosystem. Burning below this

minimum interval puts fire sensitive plants at risk of local extinction if burnt before reaching reproductive maturity.

Second, adopting landscape-scale approach to fire management that incorporates a spatially heterogeneous fire history across the landscape, will best provide for the habitat requirements of all taxa. Importantly, this means fire management should not be based solely on the *minimum* fire interval needed for plant species to reach reproductive age, but actively plan to maintain forest stands in a range of age-classes up to the *maximum* fire interval (~ 150 years) for vegetation communities to persist (Cheal 2010). Such tracts of longer-unburnt vegetation will ensure the persistence and abundance of fire-sensitive functional groups, like dietary specialists, understorey birds; and structural habitat features such as large logs and dead trees sensitive to loss during prescribed fire (Holland et al. 2017, Flanagan-Moodie et al. 2018).

Third, topographic variation is a key consideration in landscape-scale planning for prescribed fire. Forest gullies contain distinct ecological communities to those on slopes and ridges, and their moister environment is more resistant to fire with the potential to serve as refuges for fauna during wildfires (Robinson et al. 2016). Limiting prescribed fire to slopes and ridges in these topographically complex forests will help preserve important gully refuges, both by not directly burning gully vegetation and by reducing the risk of gullies burning during wildfire.

Lastly, we identified bird and plant groups that are relatively sensitive to prescribed fire in foothill forests. These groups could be used as indicators of the successional state of plant and bird communities in ecological monitoring programs.

### **5.5.5 Concluding remarks**

By using a comprehensive approach involving analyses of the responses of individual species, functional groups and communities, we identified longer-term effects of prescribed fire on bird and plant communities in a structurally resilient forest. In particular, analyses of

functional groups gave important insights into the response to time since fire of several groups; notably, understorey-foraging birds, facultative resprouting shrubs and obligate seeder plants. These patterns were less evident from analyses of single species or community-wide diversity measures. Overall, bird and plant communities showed relatively high resilience to prescribed fire across a chronosequence of 36 years, which can be attributed to the patchiness of prescribed fires, the prevalence of plant regeneration through resprouting, and the effect of topographic complexity on burn patterns. Application of these findings requires a landscape-scale approach sensitive to forest topography, that will ensure the provision of suitable post-fire habitat for all taxa, both those resilient to fire and those that benefit from longer-unburnt forest vegetation.

## 5.6 APPENDICES

### 5.6.1 Detectability

In foothill forests, the main potential source of variation in detectability of birds between sites is understorey vegetation cover, which can reduce visibility and alter acoustics. We used a simplified distance analysis to test if there was an effect of understorey vegetation cover on the distance at which birds were detectable.

During bird surveys, the distance (m) to all detections was estimated to the nearest metre, up to a maximum of 100 m using a laser range finder. For analysis we excluded all detections >40 m, as these were outside the 2-ha sample plot. We then used linear regression to test whether the perpendicular distance to detections declined with increasing midstorey cover (vegetation height = 1 – 4 m) within the 2 ha sample areas. Species were analysed individually, or (where data were fewer) grouped with species that were considered to have similar levels of detectability (Table S5.6.1).

For most species and detectability groups (16/18), the distance to detection within the sample plots was not influenced by midstorey vegetation cover (Table S5.6.1). However, distance to detection decreased significantly with understorey vegetation for the groups: ‘*Melithreptus* honeyeaters’ and ‘parrots’ (Figure S5.6.1). Some individuals from these groups may have been undetected sites with high midstorey vegetation cover.

Table S5.6.1. Detectability groups of species for linear regression analysis of the effect of understorey vegetation cover (%) on species detectability (distance to detection) for bird species in foothill forest and heathy woodlands.

Detectability group	Model outputs of linear regression (distance to detection and understorey density)				
	R - squared	Estimate	SE	T – value	P – value
Brown thornbill (Brown thornbill, Buff-rumped thornbill)	<0.001	-0.025	0.070	-0.357	0.721
Corvids (Australian raven, Grey currawong, Pied currawong)	<0.001	-0.023	0.161	-0.15	0.885
Cuckoos (Fan-tailed cuckoo, Scared kingfisher, Black-faced cuckoo-shrike, Cicadabird)	0.018	0.172	0.139	1.24	0.220
Grey fantail	0.026	-0.161	0.102	-1.58	0.116
Grey shrike-thrush	0.016	-0.189	0.183	-1.03	0.307
Laughing kookaburra	0.028	0.277	0.420	0.66	0.520
Superb lyrebird	0.007	0.128	0.462	0.28	0.787
Melithreptus honeyeaters (Brown-headed honeyeater, White-naped honeyeater)	0.049	-0.226	0.112	-2.01	0.048
Misc. (Bassian thrush, Common bronzewing, Eastern spinebill, Spotted quail-thrush, Wonga pigeon)	0.057	-0.266	0.280	-0.95	0.357
Parrots (Australian king parrot, Crimson rosella, Yellow-tailed black cockatoo, Gang gang cockatoo)	0.043	-0.275	0.116	-2.38	0.019
Robins	<0.001	0.007	0.110	0.07	0.949

Detectability group	Model outputs of linear regression (distance to detection and understorey density)				
	R - squared	Estimate	SE	T – value	P – value
(Eastern yellow robin, Flame robin, Roes robin, Scarlet robin, Silvereye)					
Red wattlebird	<0.001	-0.007	0.200	-0.03	0.974
Wrens	<0.001	-0.030	0.080	-0.37	0.709
(Superb fairywren, White-browed scrub-wren)					
Spotted pardalote	<0.001	0.040	0.080	0.47	0.641
Striated pardalote	0.001	0.050	0.110	0.47	0.643
Striated thornbill	0.005	-0.070	0.060	-1.14	0.255
Treecreepers	<0.001	0.005	0.080	0.06	0.950
(Red-browed treecreeper, Varied sittella, White-throated treecreeper)					
Whistlers	0.007	0.089	0.090	0.94	0.348
(Olive-backed oriole, Golden whistler, Rufous whistler)					
Yellow-faced honeyeater	<0.001	-0.027	0.080	-0.32	0.743

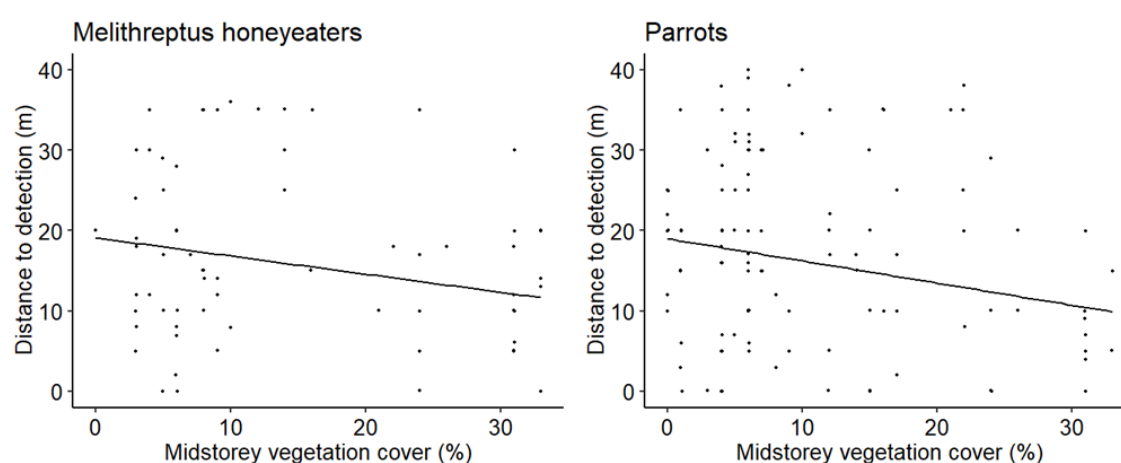


Figure S5.6.1. Significant ( $P<0.05$ ) linear models of the relationship between detectability (distance to detection) and midstorey vegetation cover for foothill forest birds: Melithreptus honeyeaters and parrots. Points represent individual detections. Lines are fitted linear model.

### 5.6.2 Bird species recorded at sites in temperate dry forests

Table S5.6.2. Bird species recorded during surveys, their functional groups and the number of prescribed fire and long unburnt sites at which they were recorded. Nomenclature follows Christidis and Boles (2008).

Family	Scientific name	Common name	Foraging location	Diet versatility (no. food items)	Nest type	Number of sites	
						Prescribed burns	Long-unburnt
Acanthizidae	<i>Acanthiza pusilla</i>	Brown Thornbill	Lower-midstorey	Two-three	Open	29	9
Acanthizidae	<i>Acanthiza reguloides</i>	Buff-rumped Thornbill	Lower-midstorey	One	Open	2	0
Acanthizidae	<i>Acanthiza lineata</i>	Striated Thornbill	Upper-midstorey	Two-three	Open	2	0
Acanthizidae	<i>Sericornis frontalis</i>	White-browed Scrubwren	Lower-midstorey	One	Open	26	9
Alcedinidae	<i>Dacelo novaeguineae</i>	Laughing Kookaburra	Ground	Two-three	Hollow	1	0
Alcedinidae	<i>Todiramphus sanctus</i>	Sacred Kingfisher	Ground	Two-three	Hollow	11	1
Artamidae	<i>Strepera versicolor</i>	Grey Currawong	Throughout	Four-six	Open	6	2
Artamidae	<i>Strepera graculina</i>	Pied Currawong	Throughout	Four-six	Open	0	1
Cacatuidae	<i>Callocephalon fimbriatum</i>	Gang Gang	Upper-midstorey	Two-three	Hollow	24	5
Cacatuidae	<i>Calyptrorhynchus funereus</i>	Yellow-tailed Black Cockatoo	Upper-midstorey	Two-three	Hollow	12	5
Campiphagidae	<i>Coracina novaehollandiae</i>	Black-faced Cuckoo-shrike	Throughout	One	Open	2	1
Campiphagidae	<i>Coracina tenuirostris</i>	Cicadabird	Upper-midstorey	One	Open	2	0

Family	Scientific name	Common name	Foraging location	Diet versatility (no. food items)	Nest type	Number of sites	
						Prescribed burns	Long-unburnt
Climacteridae	<i>Climacteris erythrops</i>	Red-browed Treecreeper	Upper-midstorey	One	Hollow	7	0
Climacteridae	<i>Cormobates leucophaea</i>	White-throated Treecreeper	Upper-midstorey	One	Hollow	7	2
Columbidae	<i>Phaps chalcoptera</i>	Common Bronzewing	Ground	One	Open	10	2
Columbidae	<i>Leucosarcia melanoleuca</i>	Wonga Pigeon	Ground	One	Open	29	9
Corvidae	<i>Corvus coronoides</i>	Australian Raven	Throughout	Four-six	Open	0	1
Cuculidae	<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo	Upper-midstorey	One	Brood parasite	1	0
Maluridae	<i>Malurus cyaneus</i>	Superb Fairywren	Ground	One	Open	4	2
Meliphagidae	<i>Melithreptus brevirostris</i>	Brown-headed Honeyeater	Upper-midstorey	Two-three	Open	7	4
Meliphagidae	<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	Lower-midstorey	Two-three	Open	11	4
Meliphagidae	<i>Anthochaera carunculata</i>	Red Wattlebird	Upper-midstorey	Two-three	Open	3	0
Meliphagidae	<i>Melithreptus lunatus</i>	White-naped Honeyeater	Upper-midstorey	Two-three	Open	19	4
Meliphagidae	<i>Lichenostomus chrysops</i>	Yellow-faced Honeyeater	Upper-midstorey	Two-three	Open	29	9
Menuridae	<i>Menura novaehollandiae</i>	Superb Lyrebird	Ground	One	Open	3	0

Family	Scientific name	Common name	Foraging location	Diet versatility (no. food items)	Nest type	Number of sites	
						Prescribed burns	Long-unburnt
Neosittidae	<i>Daphoenositta chrysoptera</i>	Varied Sittella	Upper-midstorey	One	Open	17	7
Oriolidae	<i>Oriolus sagittatus</i>	Olive-backed Oriole	Upper-midstorey	Two-three	Open	7	4
Pachycephalidae	<i>Pachycephala pectoralis</i>	Golden Whistler	Upper-midstorey	One	Open	1	1
Pachycephalidae	<i>Colluricincla harmonica</i>	Grey Shrike-thrush	Ground	Four-six	Open	6	2
Pachycephalidae	<i>Pachycephala rufiventris</i>	Rufous Whistler	Upper-midstorey	One	Open	27	7
Pardalotidae	<i>Pardalotus punctatus</i>	Spotted Pardalote	Upper-midstorey	One	Burrow	21	6
Pardalotidae	<i>Pardalotus striatus</i>	Striated Pardalote	Upper-midstorey	One	Hollow	12	2
Petroicidae	<i>Eopsaltria australis</i>	Eastern Yellow Robin	Ground	One	Open	29	9
Petroicidae	<i>Petroica phoenicea</i>	Flame Robin	Ground	One	Open	25	9
Petroicidae	<i>Petroica rosea</i>	Rose Robin	Upper-midstorey	One	Open	15	4
Petroicidae	<i>Petroica boodang</i>	Scarlet Robin	Ground	One	Open	10	2
Psittaculidae	<i>Alisterus scapularis</i>	Australian King Parrot	Upper-midstorey	Two-three	Hollow	24	8
Psittaculidae	<i>Platycercus elegans</i>	Crimson Rosella	Throughout	Two-three	Hollow	2	1
Psophodidae	<i>Cinclosoma punctatum</i>	Spotted Quail-thrush	Ground	One	Open	29	8
Ptilonorhynchidae	<i>Ptilonorhynchus violaceus</i>	Satin Bowerbird	Throughout	Two-three	Open	2	1
Rhipiduridae	<i>Rhipidura albiscapa</i>	Grey Fantail	Upper-midstorey	One	Open	24	7
Turdidae	<i>Zoothera lunulata</i>	Bassian Thrush	Ground	One	Open	0	1
Zosteropidae	<i>Zosterops lateralis</i>	Silvereye	Lower-midstorey	Two-three	Open	5	6

### 5.6.3 Plant species recorded at sites in temperate dry forests

Table S5.6.3. Plant species detected during flora surveys, response trait, growth form category and the number of sites last burned by prescribed fire or wildfire (79 years since fire) at which each species was recorded. Nomenclature follows Flora of Victoria (Royal Botanical Gardens Victoria).

Family	Species	Common name	Response trait	Growth form	Number of sites	
					Prescribed fire	Long-unburnt
Fabaceae	<i>Acacia dealbata</i>	Silver wattle	Obligate seeder	Shrub	20	4
Fabaceae	<i>Acacia melanoxylon</i>	Blackwood	Facultative resprouter	Understorey tree	6	3
Fabaceae	<i>Acacia mucronata</i>	Narrow-leafed wattle	Obligate seeder	Shrub	17	5
Fabaceae	<i>Acacia obliquinervia</i>	Mountain hickory wattle	Obligate seeder	Shrub	5	2
Rosaceae	<i>Acaena echinata</i>	Sheep's burr	Facultative resprouter	Low shrub	10	7
Ericaceae	<i>Acrotriche serrulata</i>	Honey pots	Facultative resprouter	Low shrub	14	4
Pteridaceae	<i>Adiantum aethiopicum</i>	Common maidenhair		Herb	0	2
Rubiaceae	<i>Asperula conferta</i>	Common woodruff	Obligate seeder	Low shrub	16	6
Asteraceae	<i>Asteracaea</i> sp. 1			Low shrub	12	6
Urticaceae	<i>Australina pusilla</i>	Shade nettle		Low shrub	0	1
Asteraceae	<i>Bedfordia arborescens</i>	Blanket leaf	Facultative resprouter	Shrub	1	1
Pittosporaceae	<i>Billardiera macrantha</i>	Purple apple-berry	Facultative resprouter	Shrub	7	5
Pittosporaceae	<i>Billardiera mutabilis</i>	Common apple-berry	Facultative resprouter	Shrub	6	1
Fabaceae	<i>Bossiaea prostrata</i>	Creeping bossiaea	Obligate seeder	Low shrub	2	0
Pittosporaceae	<i>Bursaria spinosa</i>	Kurwan	Facultative resprouter	Shrub	22	8

Family	Species	Common name	Response trait	Growth form	Number of sites	
					Prescribed fire	Long-unburnt
Asteraceae	<i>Cassinia aculeata</i>	Common cassinia	Facultative resprouter	Shrub	26	7
Ranunculaceae	<i>Clematis aristata</i>		Obligate resprouter	Low shrub	21	8
Polygalaceae	<i>Comesperma volubile</i>	Love creeper	Facultative resprouter	Low shrub	13	4
Rubiaceae	<i>Coprosma hirtella</i>	Rough coprosma	Obligate resprouter	Shrub	9	3
Asteraceae	<i>Coronidium scorpioides</i>	Button everlasting		Low shrub	4	2
Cyatheaceae	<i>Cyathea australis</i>	Rough tree-fern	Obligate resprouter	Shrub	1	3
Asteraceae	<i>Cymbonotus preissianus</i>	Austral bear's ear	Facultative resprouter	Herb	2	0
Fabaceae	<i>Daviesia ulicifolia</i>	Gorse bitter-pea	Facultative resprouter	Shrub	7	0
Fabaceae	<i>Daviesia virgata</i>	Narrow-leaf bitter-pea	Facultative resprouter	Shrub	12	3
Asphodelaceae	<i>Dianella tasmanica</i>	Tasman flax-lily	Facultative resprouter	Low shrub	26	9
Convolvulaceae	<i>Dichondra repens</i>	Kidney-weed	Facultative resprouter	Herb	1	1
Droseraceae	<i>Drosera peltata</i>	Sheild sundew	Facultative resprouter	Geophyte	11	3
Ericaceae	<i>Epacris impressa</i>	Common heath	Facultative resprouter	Shrub	24	9
Asteraceae	<i>Euchiton japonicus</i>		Facultative resprouter	Understorey tree	18	7
Santalaceae	<i>Exocarpos cupressiformis</i>	Cherry ballart	Obligate seeder	Herb	5	3
Rubiaceae	<i>Galium binifolium</i>	Reflexed bedstraw	Obligate seeder	Low shrub	19	6
Rubiaceae	<i>Galium</i> sp. 2		Obligate seeder	Herb	19	5
Gerianaceae	<i>Geranium solanderi</i>	Austral crane's bill	Facultative resprouter	Herb	17	6
Fabaceae	<i>Glycine clandestina</i>	Twining glycine	Obligate seeder	Low shrub	2	1
Haloragaceae	<i>Gonocarpus humilis</i>	Shade raspwort	Facultative resprouter	Shrub	29	9

Family	Species	Common name	Response trait	Growth form	Number of sites	
					Prescribed fire	Long-unburnt
Haloragaceae	<i>Gonocarpus tetragynus</i>	Common raspwort	Obligate seeder	Low shrub	6	2
Goodeniaceae	<i>Goodenia ovata</i>	Hop goodenia	Facultative resprouter	Low shrub	1	0
Fabaceae	<i>Hardenbergia violacea</i>	Purple coral-pea	Facultative resprouter	Low shrub	7	0
Monomiaceae	<i>Hedycarya angustifolia</i>	Djelwuck	Obligate resprouter	Shrub	1	0
Dilleniaceae	<i>Hibbertia obtusifolia</i>	Guinea flower	Facultative resprouter	Low shrub	3	2
Fabaceae	<i>Hovea heterophylla</i>	Common hovea	Obligate resprouter	Low shrub	9	3
Araliaceae	<i>Hydrocotyle hirta</i>	Hairy pennywort	Facultative resprouter	Herb	17	6
Hypericaceae	<i>Hypericum</i> sp.		Facultative resprouter	Herb	4	0
Fabaceae	<i>Indigofera australis</i>	Austral indigo	Facultative resprouter	Shrub	3	2
Asteraceae	<i>Lagenophora stipitata</i>	Blue bottle-daisy	Facultative resprouter	Herb	19	8
Asteraceae	<i>Leptinella filicula</i>	Mountain cotula	Facultative resprouter	Herb	4	1
Ericaceae	<i>Lissanthe strigosa</i>	Peach heath	Facultative resprouter	Low shrub	1	0
Asparagaceae	<i>Lomandra filiformis</i> subsp. 1		Obligate resprouter	Herb	13	1
Asparagaceae	<i>Lomandra filiformis</i> subsp. 2		Facultative resprouter	Herb	23	8
Asparagaceae	<i>Lomandra longifolia</i>	Spiny-headed mat-rush	Obligate resprouter	Herb	4	0
Proteaceae	<i>Lomatia fraseri</i>	Tree lomatia	Obligate resprouter	Shrub	5	1
Proteaceae	<i>Lomatia myricoides</i>	River lomatia	Obligate resprouter	Shrub	1	0
Juncacea	<i>Luzula</i> sp.		Facultative resprouter	Herb	12	3

Family	Species	Common name	Response trait	Growth form	Number of sites	
					Prescribed fire	Long-unburnt
Ericaceae	<i>Monotoca scoparia</i>	Prickly broom-heath	Obligate resprouter	Shrub	3	4
Oleaceae	<i>Notelaea ligustrina</i>	Privet mock-olive		Shrub	5	1
Asteraceae	<i>Olearia argophylla</i>	Musk daisy-bush	Obligate resprouter	Shrub	1	0
Asteraceae	<i>Olearia erubescens</i>	Moth daisy-bush	Facultative resprouter	Low shrub	22	4
Asteraceae	<i>Olearia lirata</i>	Snowy-daisy bush	Obligate seeder	Shrub	4	0
Asteraceae	<i>Olearia phlogopappa</i>	Dusty daisy-bush	Facultative resprouter	Shrub	6	4
Rubiaceae	<i>Opercularia varia</i>	Variable stinkweed		Herb	11	2
Oxalidaceae	<i>Oxalis</i> sp.			Herb	5	2
Thymelaeaceae	<i>Pimelea axiflora</i>	Bootlace bush	Obligate resprouter	Low shrub	2	3
Thymelaeaceae	<i>Pimelea ligustrina</i>	Tall rice-flower	Obligate seeder	Low shrub	1	0
Fabaceae	<i>Platylobium parviflorum</i>		Facultative resprouter	Low shrub	3	0
Araliaceae	<i>Polyscias sambucifolia</i>	Ferny panax	Facultative resprouter	Shrub	12	3
Dryopteridaceae	<i>Polystichum proliferum</i>	Mother shield-fern	Obligate resprouter	Shrub	5	4
Rhamnaceae	<i>Pomaderris aspera</i>	Hazel pomaderis	Facultative resprouter	Understorey tree	6	0
Phyllanthaceae	<i>Poranthera microphylla</i>	Small poranthera	Obligate seeder	Herb	16	6
Lamiaceae	<i>Prostanthera lasianthos</i>	Victorian christmas bush	Obligate seeder	Shrub	1	0
Dennstaed	<i>Pteridium esculentum</i>	Austral bracken	Facultative resprouter	Herb	29	9
Fabaceae	<i>Pultenaea juniperina</i>	Prickly bush-pea	Facultative resprouter	Low shrub	1	1
Pittosporaceae	<i>Rhytidosporum procumbens</i>	White marianth		Low shrub	1	0

Family	Species	Common name	Response trait	Growth form	Number of sites	
					Prescribed fire	Long-unburnt
Rosaceae	<i>Rubus parvifolius</i>	Small-leaf bramble	Facultative resprouter	Low shrub	5	3
Asteraceae	<i>Senecio prenanthoides</i>	Common fireweed	Obligate seeder	Herb	18	4
Celastraceae	<i>Stackhousia monogyna</i>	Creamy candles	Facultative resprouter	Herb	12	4
Caryophyllaceae	<i>Stellaria flaccida</i>	Forest starwort	Obligate seeder	Herb	2	2
Caryophyllaceae	<i>Stellaria pungens</i>	Prickly starwort	Facultative resprouter	Herb	7	2
Stylidiaceae	<i>Stylidium graminifolium</i>	Grass triggerplant	Facultative resprouter	Low shrub	23	5
Winteraceae	<i>Tasmannia lanceolata</i>	Mountain pepper	Obligate resprouter	Shrub	7	5
Poaceae	<i>Tetrarrhena juncea</i>	Forest wire-grass	Facultative resprouter	Herb	24	9
Elaeocarpaceae	<i>Tetratheca ciliata</i>	Pink bells	Facultative resprouter	Low shrub	27	9
Urticaceae	<i>Urtica incisa</i>	Scrub nettle		Shrub	0	1
Plantaginaceae	<i>Veronica calycina</i>	Hairy speedwell		Low shrub	2	1
Plantaginaceae	<i>Veronica derwentiana</i>	Derwent speedwell	Facultative resprouter	Low shrub	10	1
Plantaginaceae	<i>Veronica gracilis</i>	Slender speedwell	Facultative resprouter	Low shrub	4	0
Plantaginaceae	<i>Veronica plebeia</i>	Trailing speedwell	Facultative resprouter	Low shrub	4	1
Violaceae	<i>Viola betonicifolia</i>	Arrowhead violet	Facultative resprouter	Herb	29	9
Violaceae	<i>Viola hederacea</i>	Ivory-leaved violet	Obligate seeder	Herb	2	0
Campanulaceae	<i>Wahlenbergia stricta</i>	Tall bluebell	Facultative resprouter	Herb	11	4

#### 5.6.4 Bird species response to time since fire model outputs

Table S5.6.4. Model outputs for bird species relative abundance as a function of time since prescribed fire. Generalized additive models were fit for individual species that occurred at  $\geq 8$  prescribed burn sites. The shape of the response curve is based on generalised response curves described in Watson *et al.* 2012. Non-significant relationships were classed as ‘NS’.

Species name	Common name	Deviance explained (%)	P - value	Response shape
<i>Acanthiza lineata</i>	Striated Thornbill	0.7	0.896	Null
<i>Acanthiza pusilla</i>	Brown Thornbill	14.7	0.079	Null
<i>Anthochaera carunculata</i>	Red Wattlebird	2.7	0.321	Null
<i>Climacteris erythrops</i>	Red-browed Treecreeper	7.8	0.132	Null
<i>Colluricincla harmonica</i>	Grey Shrike-thrush	0.4	0.757	Null
<i>Cormobates leucophaea</i>	White-throated Treecreeper	10.8	0.254	Null
<i>Dacelo novaeguineae</i>	Laughing Kookaburra	7.4	0.187	Null
<i>Eopsaltria australis</i>	Eastern Yellow Robin	0.8	0.612	Null
<i>Lichenostomus chrysops</i>	Yellow-faced Honeyeater	20.0	0.207	Null
<i>Malurus cyaneus</i>	Superb Fairywren	49.8	0.041	Incline
<i>Melithreptus lunatus</i>	White-naped Honeyeater	5.3	0.138	Null
<i>Pachycephala pectoralis</i>	Golden Whistler	19.1	0.008	Incline
<i>Pachycephala rufiventris</i>	Rufous Whistler	0.0	0.861	Null
<i>Pardalotus punctatus</i>	Spotted Pardalote	2.0	0.693	Null
<i>Pardalotus striatus</i>	Striated Pardalote	3.0	0.451	Null
<i>Petroica boodang</i>	Scarlet Robin	0.5	0.732	Null
<i>Petroica phoenicea</i>	Flame Robin	2.3	0.423	Null
<i>Platycercus elegans</i>	Crimson Rosella	4.3	0.508	Null
<i>Rhipidura albiscapa</i>	Grey Fantail	16.1	0.040	Plateau
<i>Sericornis frontalis</i>	White-browed Scrubwren	35.1	0.005	Plateau
<i>Strepera graculina</i>	Pied Currawong	2.0	0.504	Null
<i>Strepera versicolor</i>	Grey Currawong	2.8	0.419	Null

### 5.6.5 Plant species response to time since fire model outputs

Table S5.6.5. Model outputs for plant species relative cover as a function of time since prescribed fire. Generalized additive models with beta error distributions were fit for individual species that occurred at  $\geq 8$  prescribed burn sites. The shape of the response curve is based on generalised response curves described in Watson *et al.* 2012. Non-significant relationships were classed as 'null'.

Species	Common name	Life form	Deviance explained (%)	P - value	Response shape
<i>Acacia dealbata</i>	Silver wattle	Shrub	8.2	0.071	Null
<i>Acacia mucronata</i>	Narrow-leafed wattle	Shrub	24.1	0.047	Bell
<i>Acaena echinata</i>	Sheep's burr	Low shrub	0.3	0.772	Null
<i>Acrotriche serrulata</i>	Honey pots	Low shrub	6.1	0.450	Null
<i>Asperula conferta</i>	Common woodruff	Low shrub	12.6	0.044	Irruptive
<i>Bursaria spinosa</i>	Kurwan	Shrub	53.9	<0.001	Incline
<i>Cassinia aculeata</i>	Common cassinia	Shrub	47.2	<0.001	Bell
<i>Clematis aristata</i>	Mountain clematis	Low shrub	1.3	0.444	Null
<i>Comesperma volubile</i>	Love creeper	Low shrub	0.7	0.634	Null
<i>Coprosma hirtella</i>	Rough coprosma	Shrub	2.0	0.462	Null
<i>Daviesia virgata</i>	Narrow-leaf bitter-pea	Shrub	13.3	0.580	Null
<i>Dianella tasmanica</i>	Tasman flax-lily	Low shrub	11.7	0.069	Null
<i>Drosera peltata</i>	Sheild sundew	Geo	0.2	0.835	Null
<i>Epacris impressa</i>	Common heath	Shrub	0.1	0.924	Null
<i>Euchiton japonicus</i>		Herb	3.6	0.539	Null
<i>Galium binifolium</i>	Reflexed bedstraw	Low shrub	4.4	0.555	Null
<i>Galium</i> sp.2		Herb	7.7	0.312	Null
<i>Geranium solanderi</i>	Austral crane's bill	Herb	13.8	0.038	Irruptive
<i>Gonocarpus humilis</i>	Shade raspwort	Low shrub	0.6	0.866	Null

### 5.6.6 Bird species response to post-fire age-classes

Table S5.6.6. Output of generalized linear models of individual species relative abundance in post-prescribed fire age classes.

Species name	Common name	Estimate	Deviance explained (%)	P - value
<i>Acanthiza lineata</i>	Striated Thornbill	0.054	3.7	0.789
<i>Acanthiza pusilla</i>	Brown Thornbill	0.367	14.9	0.240
<i>Anthochaera carunculata</i>	Red Wattlebird	-0.318	9.4	0.441
<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo	0.318	9.6	0.750
<i>Climacteris erythrops</i>	Red-browed Treecreeper	-0.375	8.9	0.665
<i>Colluricincla harmonica</i>	Grey Shrike-thrush	-0.221	11.6	0.512
<i>Cormobates leucophaea</i>	White-throated Treecreeper	-0.018	13.1	0.935
<i>Dacelo novaeguineae</i>	Laughing Kookaburra	-1.068	17.0	0.177
<i>Eopsaltria australis</i>	Eastern Yellow Robin	-0.886	6.0	0.179
<i>Lichenostomus chrysops</i>	Yellow-faced Honeyeater	0.235	21.2	0.416
<i>Malurus cyaneus</i>	Superb Fairywren	-0.192	4.3	0.710
<i>Melithreptus lunatus</i>	White-naped Honeyeater	-0.241	6.7	0.586
<i>Menura novaehollandiae</i>	Superb Lyrebird	18.609	29.7	0.995
<i>Pachycephala pectoralis</i>	Golden Whistler	0.000	14.4	1.000
<i>Pachycephala rufiventris</i>	Rufous Whistler	-2.079	21.0	0.046
<i>Pardalotus punctatus</i>	Spotted Pardalote	-0.033	1.3	0.876
<i>Pardalotus striatus</i>	Striated Pardalote	0.252	5.7	0.330
<i>Petroica boodang</i>	Scarlet Robin	0.829	7.0	0.256
<i>Petroica phoenicea</i>	Flame Robin	-0.192	1.8	0.598
<i>Platycercus elegans</i>	Crimson Rosella	-0.163	6.6	0.556
<i>Rhipidura albiscapa</i>	Grey Fantail	0.175	14.1	0.644
<i>Sericornis frontalis</i>	White-browed Scrubwren	0.937	42.5	0.005
<i>Strepera graculina</i>	Pied Currawong	-0.152	6.1	0.707
<i>Strepera versicolor</i>	Grey Currawong	0.031	3.1	0.968
<i>Zosterops lateralis</i>	Silvereye	1.012	27.6	0.409

### 5.6.7 Plant species response to post-fire age-classes

Table S5.6.7. Outputs from beta regression models of plant species relative abundance as a function of post-fire age-classes. The categorical variable 'age-class' had four levels based on time since fire: AC1: 0-3 years, AC2: 4-10 years, AC3: 11-36 years since prescribed fire, and long-unburnt: 79 years since wildfire.

Species	Common name	DF	Chi-square	P - value
<i>Acacia dealbata</i>	Silver wattle	2	4.64	0.200
<i>Acacia mucronata</i>	Narrow-leafed wattle	2	1.44	0.696
<i>Acaena echinata</i>	Sheep's burr	2	5.15	0.161
<i>Acrotriche serrulata</i>	Honey pots	2	3.41	0.333
<i>Asperula conferta</i>	Common woodruff	2	6.26	0.099
<i>Billardiera macrantha</i>	Purple apple-berry	2	1.81	0.613
<i>Bursaria spinosa</i>	Kurwan	2	19.20	<0.001
<i>Cassinia aculeata</i>	Common cassinia	2	11.87	0.008
<i>Clematis aristata</i>	Mountain clematis	2	4.32	0.229
<i>Comesperma volubile</i>	Love creeper	2	1.55	0.672
<i>Coprosma hirtella</i>	Rough coprosma	2	0.70	0.873
<i>Daviesia virgata</i>	Narrow-leaf bitter-pea	2	4.45	0.217
<i>Dianella tasmanica</i>	Tasman flax-lily	2	6.07	0.108
<i>Drosera peltata</i>	Sheild sundew	2	0.04	0.998
<i>Epacris impressa</i>	Common heath	2	45.60	<0.001
<i>Euchiton japonicus</i>		2	2.52	0.471
<i>Galium binifolium</i>	Reflexed bedstraw	2	1.33	0.723
<i>Galium</i> sp.2		2	4.40	0.222
<i>Geranium solanderi</i>	Austral crane's bill	2	4.49	0.213
<i>Gonocarpus humilis</i>	Shade raspwort	2	2.88	0.410
<i>Hovea heterophylla</i>	Common hovea	2	0.65	0.885
<i>Hydrocotyle hirta</i>	Hairy pennywort	2	1.78	0.619
<i>Lagenophora stipitata</i>	Blue bottle-daisy	2	2.54	0.467
<i>Lomandra filiformis</i> subsp. 1		2	1.58	0.665
<i>Lomandra filiformis</i> subsp. 2		2	11.47	0.009
<i>Luzula</i> sp.2		2	0.95	0.813
<i>Olearia erubescens</i>	Moth daisy-bush	2	9.09	0.028
<i>Olearia phlogopappa</i>	Dusty daisy-bush	2	1.07	0.785
<i>Opercularia varia</i>	Variable stinkweed	2	0.56	0.906

Species	Common name	DF	Chi-square	P - value
<i>Polyscias sambucifolia</i>	Ferny panax	2	1.45	0.695
<i>Poranthera microphylla</i>	Small poranthera	2	1.05	0.789
<i>Pteridium esculentum</i>	Austral bracken	2	0.60	0.897
<i>Senecio prenanthoides</i>	Common fireweed	2	1.88	0.597
<i>Stackhousia monogyna</i>	Creamy candles	2	0.32	0.956
<i>Stylidium graminifolium</i>	Grass triggerplant	2	2.55	0.467
<i>Tasmannia lanceolata</i>	Mountain pepper	2	2.78	0.426
<i>Tetrarrhena juncea</i>	Forest wire-grass	2	10.35	0.016
<i>Tetralthea ciliata</i>	Pink bells	2	3.79	0.285
<i>Veronica derwentiana</i>	Derwent speedwell	2	0.65	0.885
<i>Viola hederacea</i>	Ivory-leaved violet	2	1.48	0.686
<i>Wahlenbergia stricta</i>	Tall bluebell	2	0.51	0.917

## **6 DOES THE SPATIAL CONTEXT OF FIRE INFLUENCE THE ABUNDANCE OF BIRD SPECIES?**

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Morning fog through the trees in foothill forests.

## 6.1 ABSTRACT

Spatial and temporal attributes of fire regimes interact with environmental conditions to drive species distributions. Understanding how the spatial configuration of fire histories surrounding a site (e.g. proportion of vegetation at different fire ages) influences the abundance of species will help achieve more effective conservation planning in a range of fire-prone ecosystems. We compared the influence of time since fire and spatial measures of fire regimes on the relative abundance of bird species in two extensive ecosystems in south-eastern Australia: semi-arid ‘mallee’ woodlands and temperate ‘foothill’ forests. Both ecosystems are dominated by *Eucalyptus* trees, but differ in climate, topography and stand-regeneration patterns. We fitted sets of non-linear models for 21 species in mallee woodlands and 32 species in foothill forests that differed in the fire variables used (i.e. time since fire, area and diversity of successional vegetation classes) while controlling for environmental variation to address three questions: (1) Does the spatial configuration of fire histories influence the relative abundance of species at a site? (2) Does the relative influence of time since fire and spatial configuration of fire differ between ecosystems? (3) Do species’ preferences for post-fire successional vegetation differ between ecosystems? Model performance exceeded minimum thresholds for seven species in mallee woodlands and 18 in foothill forests. Overall, the influence of models that included a single measure of fire (time since fire or spatial context of fire variables) was similar between ecosystems. Models including both time since fire and a spatial measure of the fire regime generally outperformed models that included only time since fire, substantially so in foothill forests. The amount of late-successional vegetation was important for species in both ecosystems. More species were negatively associated with the amount of early successional vegetation in mallee woodlands than foothill forests. The spatial diversity of successional vegetation was important for more species in foothill forests than mallee woodlands. Maintaining landscape diversity of

successional vegetation in foothill forests can positively influence the abundance of some bird species. Incorporating landscape context of fire in conservation planning can help meet the habitat requirements for diverse species across whole landscapes, but the influence of spatial attributes differs between ecosystems.

## **6.2 INTRODUCTION**

Spatial and temporal attributes of fire regimes (e.g. area burnt, time since fire) interact with environmental conditions to influence the distribution of species in fire-prone regions worldwide (Lindenmayer et al. 2014, Burgess and Maron 2016, Puig-Gironès et al. 2017). Fire changes the composition and structure of vegetation by altering the recruitment and persistence of plants (Smith et al. 2016), influencing processes such as pollination (Carbone et al. 2019), and modifying patch dynamics (Alstad and Damschen 2016). Fire also influences the distribution of fauna by altering the availability of resources, such as food and shelter, both in space and through time (Fox 1982, Jacquet and Prodon 2009, Haslem et al. 2012, Hutto and Patterson 2016, Banks et al. 2017). Anthropogenic change to fire regimes is implicated in the current decline of numerous species, including many bird species (Connell et al. 2017, Stephens et al. 2019, Clarke 2020). Understanding how fire regimes, and their different components, influence species distributions is crucial for biodiversity conservation in fire-prone ecosystems.

Time since fire (Watson et al. 2012b, Hutto and Patterson 2016, Doherty et al. 2017), the spatial extent of fire (Lindenmayer et al. 2014, Berry et al. 2015) and the diversity of fire severity classes (Nappi and Drapeau 2011) are examples of temporal and spatial attributes that influence the distribution of biota. The challenge is to understand how the configuration of these attributes in landscapes influences species in a range of ecological settings. For example, a spatially diverse fire history can provide the habitat requirements for individual

species that require resources from different age-classes, or that track early successional vegetation (Hutto et al. 2020), thereby benefiting biodiversity in a range of ecosystems (Parr and Andersen 2006, Sitters et al. 2014b, Tingley et al. 2016, Beale et al. 2018). However, the relative importance of fire regime attributes differs between ecosystems, so problems can arise when knowledge of one system is transposed to another without verifying its applicability (Driscoll et al. 2010).

Identifying where generalizing between ecological settings may or may not be appropriate will aid conservation in fire-prone regions (Spies et al. 2012, Kelly et al. 2017a). For example, in North American boreal forests most bird species are associated with mid-to-late post-fire successional vegetation (Haney et al. 2008), compared to South African fynbos where a similar number of species is associated with early and late-successional vegetation (Chalmandrier et al. 2013), and North American conifer forests where many species are associated with early-successional vegetation (Hutto et al. 2020). Clearly, strategies to conserve bird species in these ecosystems are not directly interchangeable. There is a need to test the importance of different fire regime attributes in disparate ecosystems. In particular, the combined influence of two attributes, time since fire, and spatial context of fire on bird distributions has not been tested.

In semi-arid woodlands in south-eastern Australia, studies have demonstrated the importance of the spatial context of fire regimes for bird communities. In particular, the number of bird species and individuals in landscapes was associated with the amount of long-unburnt vegetation in an area (Taylor et al. 2012, Berry et al. 2015). Further, the proximity to unburnt vegetation enhanced post-fire occupancy of several species (Watson et al. 2012a). In contrast, in stringybark *Eucalyptus* forests in south-eastern Australia, few bird species were associated with time since fire (Sitters et al. 2014a, Kelly et al. 2017b), but bird species richness was positively associated with the spatial diversity of successional vegetation (Sitters et al.

2014b). These differences highlight two important considerations. First, ecological context is likely to influence how the spatial context of fire influences species in addition to time since fire. Second, the relative influence of fire regime attributes on biota is likely to differ between ecological settings.

Responses to fire regime attributes can also differ between species within ecosystems, depending on their habitat requirements. Kelly et al. (2017b) and Sitters et al. (2014a) correlated bird responses to fire and to habitat attributes in *Eucalyptus* forests but did not consider how species functional traits (e.g. foraging location, diet, etc.) might influence fire-responses. For example, species that nest in tree hollows (e.g. parrots) could be negatively affected by a large fire if hollows are destroyed by the fire (Gosper et al 2019); whereas, some species that forage on open ground (e.g. flame robin *Petroica phoenicea*) may be positively affected by fire if it creates suitable habitat by exposing open ground (Lindenmayer et al. 2014). The influence of temporal and spatial attributes of fire will likely differ between species, so it will be useful to identify those species for which fire attributes are important in different ecosystems.

In this study we test the influence of time since fire and spatial fire attributes (amount of recently burnt and long-unburnt vegetation, diversity of successional vegetation) on the distribution of birds in two extensive, *Eucalyptus*-dominated ecosystems in south-east Australia: semi-arid ‘mallee’ woodlands and temperate ‘foothill’ forests. These ecosystems differ in climate, topography, vegetation structure, bird community composition and, importantly, in the post-fire regeneration traits of the canopy trees (i.e. basal resprouting from lignotubers in mallee woodlands vs. epicormic resprouting from tree trunks and branches in foothill forests). Landscape management in these two regions is informed by knowledge of post-fire changes in vegetation structure and time to maturity and senescence of key plant species (York and Friend 2016). Testing the influence of the landscape context of fire on

species from these different ecosystems will uncover commonalities and contrasts in the role of fire between ecosystems and help identify areas where generalizations may or may not be appropriate.

Here, we address three questions: (1) Does the spatial context of fire influence the relative abundance of species? (2) Does the relative influence of time since fire and the spatial context of fire differ between ecosystems? (3) Do species preferences for post-fire successional vegetation differ between ecosystems?

## **6.3 MATERIALS AND METHODS**

### **6.3.1 Study locations**

There were two study areas; the first covers ~100 000 km<sup>2</sup> of mallee woodland vegetation, spanning parts of Victoria, South Australia and New South Wales; and the second ~75 000 km<sup>2</sup> of foothill forests in Victoria, Australia (Fig. 6.1). These ecosystems experience recurrent wildfires and are subject to active fire management including prescribed burning and wildfire suppression.

#### *6.3.1.1 Mallee woodlands*

The mallee woodlands ecosystem occurs in semi-arid south-eastern Australia where summers are hot and dry, and winters are mild (mean daily maxima January: 33°C, July: 16°C, mean annual rainfall: 286 mm, Mildura Airport, station no. 076031; <http://www.bom.gov.au>). The topography is flat and low-lying (<200 m above sea level) and soils are nutrient-poor and sandy. Aridity decreases from north to south (Haslem et al. 2010). A distinctive feature of mallee woodlands is the low canopy ( $\leq 10$  m) of multi-stemmed *Eucalyptus* trees that resprout from basal lignotubers after fire (Clarke et al. 2010). The generally sparse understorey is dominated by sclerophyllous shrubs, including *Acacia* species, chenopod species and the hummock grass *Triodia scariosa*. Mallee vegetation is highly flammable. Large wildfires

(>10 000 ha) occur roughly decadally in the region. Land managers undertake prescribed burning annually to achieve fuel reduction goals or maintain ecological values. Wildfires in mallee woodlands typically are stand-replacing (Clarke et al. 2010).

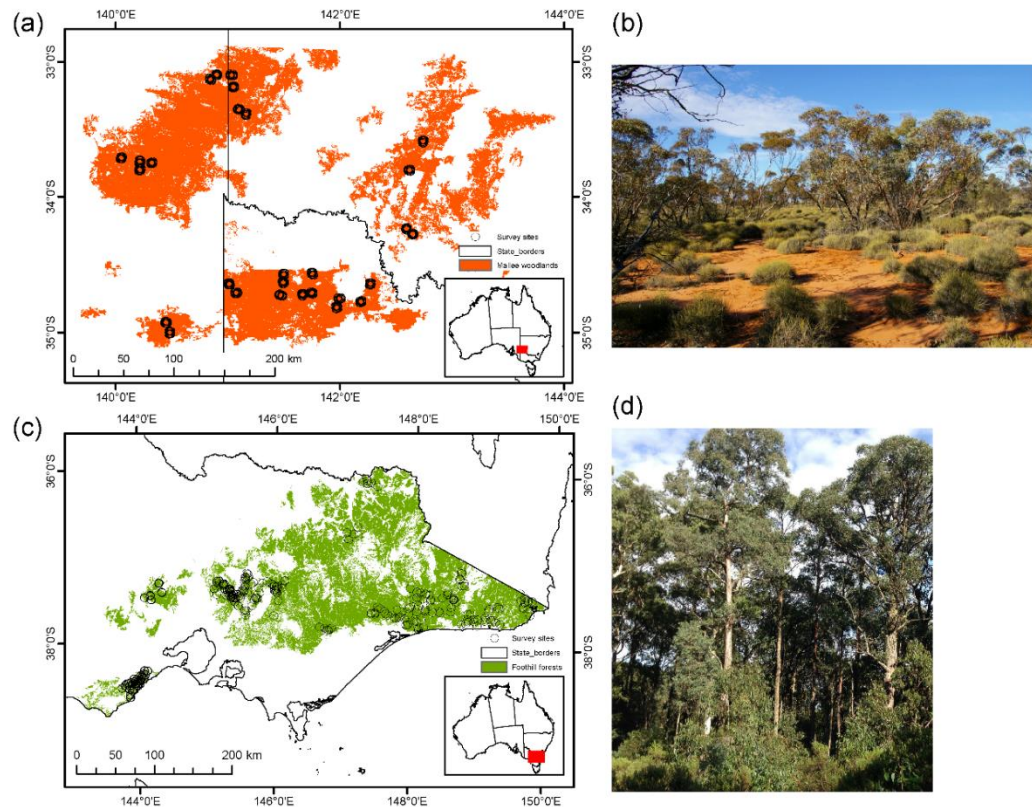


Figure 6.1. (a) The extent of mallee woodlands vegetation in the Murray-Mallee region, south-east Australia and locations of survey sites; (b) mallee woodlands vegetation (photo credit: MFBP); (c); the extent of foothill forests vegetation in Victoria and locations of survey sites (d); foothill forests vegetation (photo credit: FR).

### 6.3.1.2 Foothill forests

Foothill forests are temperate forests that occur on the low- to mid-slopes (<900 m above sea-level) of the Great Dividing Range in south-eastern Australia. Summers are hot and winters are cool and wet (Mean daily maxima January: 27°C, July: ~13°C [Willow Grove, Station

085283]; mean annual rainfall ranges from ~700 mm [Willow Grove] – 980 mm [Combienbar AWS, station no. 084143], <http://www.bom.gov.au>). The canopy (30 – 60 m height) is dominated by thick-barked *Eucalyptus* species on drier slopes and ridges, and smooth-barked *Eucalyptus* species in more mesic areas, like gullies. The understorey consists of a diverse array of shrubs and herbs that ranges from dense in mesic areas to sparse on exposed ridges. The foothill forests area experiences large wildfires (>10 000 ha) ~decadally, and prescribed burns are routinely carried out to achieve fuel hazard reduction and, occasionally, ecological objectives. Canopy trees persist through fire and trees resprout from protected epicormic buds along the trunk and branches. Fire also triggers *Eucalyptus* recruitment through seed germination.

### **6.3.2 Bird data**

To determine the responses of diurnal birds to fire regimes and environmental conditions (climate, topography, vegetation type), we used relative abundance data for birds collated during two multi-institutional research projects: Mallee Fire and Biodiversity Project (Watson et al. 2012) and Foothills Fire and Biota Project (Kelly et al. 2017b). Sites were stratified by time since fire. To minimize edge effects and the potential influence of adjacent non-target vegetation, we excluded sites at which >60% of the area within a 500 m buffer (81 ha) was non-target vegetation. This resulted in 555 sites in mallee woodlands and 458 sites in foothill forests.

Bird data were collected during systematic surveys that used either timed point counts or timed area searches (Watson et al. 2012b, Robinson et al. 2014, Sitters et al. 2014a, Loyn and McNabb 2015, Muir et al. 2015). All individuals heard or seen by an experienced observer within the defined survey area were identified to species level. Mallee woodlands were surveyed during 2006 and 2007 and foothill forests between 2009 and 2012. The relative abundances of species were calculated for each site by summing the total number of

detections over all survey rounds. We accounted for differences in survey effort between foothill forest sites by including the variables log(total survey time) and log(survey area) in analyses. Details of bird survey methods can be found in Appendix 6.6.1. Distance analyses performed on data from mallee woodlands and foothill forests showed that detectability was consistent among recently burnt and long unburnt vegetation at different topographic positions and was not affected by vegetation density (Watson et al. 2012b, Sitters et al. 2015). Therefore, we modelled species' relative abundances without explicitly accounting for detectability.

We used descriptive statistics to compare the composition of the bird communities in each ecosystem. We contrasted the dominant families, widespread species and the percentage of species in broad foraging and nesting groups in each ecosystem.

### **6.3.3 Environmental data**

We selected environmental variables representing three gradients that influence important ecological processes for birds: temperature, elevation and vegetation type (Table 6.1). We used the average annual temperature for mallee woodlands and the average daily maximum temperature for January (hottest month) for foothill forests. Different metrics were used to better represent the different gradients in each ecosystem (north-south in mallee, elevational + latitudinal in foothills). Elevation data were sourced from the Geoscience Australia, 1 second SRTM Digital Elevation Model (DEM) (<https://data.gov.au/dataset/>), resampled to 100 x 100 m using a bilinear sampling method in ArcGIS 10.3.1 and then merged to form a single layer for each study area. Vegetation classes for mallee woodlands were classified according to Haslem et al. (2010) as either *Triodia* Mallee, *Chenopod* Mallee or Heathy Mallee. For foothill forests, four vegetation classes were recognised following Cheal (2010): Foothill Forest, Grassy/Heathy Forest, Moist Forest and Tall Mixed Forest.

Table 6.1. Summary of explanatory variables included in species distribution models for birds in mallee woodlands (MW) and foothills forests (FF). The range of values in each ecosystem and a description of variables are given.

Category	Variable	Range of values		Description
		Mallee woodlands	Foothill forests	
Fire regime	Time since fire (years)	0 – 106	0 – 107	Number of years between the date of the bird survey and the most recent mapped fire at the site that preceded the survey.
	Amount early (ha)	0 – 81	0 – 81	The amount (ha) of vegetation classified as ‘early-successional’ [0 – 10 years since fire (MW), 0 – 4 years since fire (FF)] within a 900 x 900 m window, centered on the bird survey site.
	Amount late (ha)	0 – 81	0 – 81	The amount (ha) of vegetation classified as ‘late-successional’ [ > 35 years since fire (MW), > 40 years since fire (FF)] within a 900 x 900 m window, centered on the bird survey site.
	Spatial diversity of successional vegetation (index)	0 – 1.13	0 – 1.33	Shannon’s diversity index of post-fire successional states within a 900 x 900 m window, centered on the bird survey site. Successional states were: Mallee woodlands: 0 – 10, 11 – 35, > 35 years since fire. Foothill forests: 0 – 3, 4 – 10, 11 – 40, > 40 years since fire.
Environmental conditions	Temperature (°C)	15.4 – 17.4	19.4 – 28.5	MW: annual average daily maximum temperature; FF: average daily maximum temperature for January (hottest month).
	Elevation (m)	32 – 104	33 – 954	Metres above sea-level based on digital elevation model (DEM).

Category	Variable	Range of values		Description
		Mallee woodlands	Foothill forests	
	Vegetation class (categorical)	Triodia Mallee Chenopod Mallee Heathy Mallee	Foothill forest Grassy/heathy forest Moist forest Tall mixed forest	Groups of vegetation classes with similar floristic and structural composition and post-fire regeneration rate.

### **6.3.4 Fire data**

For mallee woodlands, fire data post-1972 were based on digitized annual fire scars as documented by Avitabile et al. (2013), and pre-1972 data were based on predictive mapping by Callister et al. (2016). For foothill forests, fire data were based on digitized annual fire scars from 1972 to 2016 and polygons of fire boundaries from 1903 to 1971 (DELWP 2016).

The environmental data and the annual fire data were supplied as, or converted to, gridded GIS layers with a resolution of 100 x 100 m.

### **6.3.5 Fire regime variables**

We investigated the influence of four fire regime variables on the relative abundance of birds in mallee woodlands and foothill forests (Table 6.1). These included three spatial attributes, amount of early successional vegetation (Amount early), amount of late successional vegetation (Amount late) and the spatial diversity of successional vegetation (Spatial diversity); and one temporal attribute, time since fire.

Time since fire was calculated as the number of years between the date of the bird survey and the most recent preceding mapped fire. To represent the spatial context of fire regimes, we categorized the vegetation into post-fire successional states based on the time since last fire. For mallee woodlands, these were calculated following Kelly et al. (2012): early: 0 – 10, mid: 10 – 35 and late: >35 years since fire. For foothill forests, successional states were based on Cheal (2010): early: 0 – 3, mid 1: 3 – 10, mid 2: 10 – 40, late: >40 years since fire. ‘Amount early’ and ‘Amount late’ were calculated as the summed area in each successional state within a 900 x 900 m window (81 ha) centered on the site. Spatial diversity was calculated using the Shannon diversity index of successional states within a 900 x 900 m window.

To select the window size for all spatial measures, we first ran a set of three exploratory models for all species in which the window size used to calculate spatial diversity varied (300

x 300 m, 900 x 900 m, 1900 x 1900 m windows). Overall, the explanatory power of models did not differ substantially between window sizes. For analyses presented here, we used a window size of 500 m as this was large enough to cover a range of values of spatial variables and the home range size of most common birds in these ecosystems.

### **6.3.6 Data analysis**

We used boosted regression trees (BRT) to model bird species responses to the environmental and fire variables. BRTs calculate the relative contribution of each predictor variable and are a superior method for modelling non-linear relationships (Elith et al. 2008). We built models for species that occurred at  $\geq 45$  sites. Models did not converge when the number of occurrences was less than this. For foothill forests, the variables log(survey duration) and log(survey area) were included in models to account for differences in survey effort between sites. Correlated predictor variables (Pearson's coefficient  $> 0.6$ ) were not included in the same model.

We built five sets of models that differed in the fire regime variables included (Table 6.2). Four of the models included a single fire regime variable: (1) time since fire, (2) Amount late, (3) Amount early, or (4) Spatial diversity. The fifth model included two fire regime variables, time since fire plus the spatial context variable with the highest relative contribution for that species (from models 2 – 3). All model sets included the three environmental variables to allow for detection of the influence of fire variables while controlling for environmental variation (see Table 6.2).

All calculations were undertaken using ArcMap 10.3.1 (ESRI 2016) and the R statistical environment (R Development Core Team 2018) with the raster (Hijmans 2017) and dismo (Hijmans 2016) packages. Models were built using the 'gbm.step' function in the dismo package, with tree complexity set at 3, learning rate set at 0.001, and bag fraction set at 0.75 following Kelly et al. (2017b).

Table 6.2. Explanatory variables included in groups of five boosted regression tree models to predict the relative abundance of bird species in mallee woodlands and foothill forests. Models were built to test the influence of a single measure of the fire regime (Models 1 – 4) and both time since fire and the spatial context of fire together (Model 5). Environmental variables were included to account for the effects of environmental gradients.

Model	Fire regime variables	Environmental variables
1	Time since fire	Temperature Elevation Vegetation type
2	Amount late successional	Temperature Elevation Vegetation type
3	Amount early successional	Temperature Elevation Vegetation type
4	Spatial diversity of successional vegetation	Temperature Elevation Vegetation type
5	Time since fire + best spatial context variable	Temperature Elevation Vegetation type

Below we outline the approach used to address the three main questions.

- 1) Does the spatial context of fire influence the relative abundance of species?

We assessed models of each species that included spatial measures of the fire regime and compared them to those models with only the site-based measure (i.e. time since fire).

- 2) Does the relative influence of time since fire and the spatial context of fire differ between ecosystems?

For models that included a single measure of the fire regime, we compared the deviance explained (%) attributable to each fire regime variable across species in each ecosystem by using notch plots. We considered that where the 95% confidence interval of a variable did not overlap with the median of another variable, there was a substantial difference between variables.

3) Do species preferences for post-fire successional vegetation differ between ecosystems?

We assessed species predicted responses to: (1) time since fire, (2) Amount young, (3), Amount old and 4) Spatial diversity of successional states using partial dependence plots. The peak of the response curve was used to determine species' associations with predictor variables. We then compared the percentage of species in each ecosystem (a) whose relative abundance peaked in either early, mid or late-successional vegetation; and the percentage of species that responded negatively, positively or null to (b) Amount old, (c) Amount young, and (d) Spatial diversity.

Model explanatory power was assessed by calculating (a) the total proportion of deviance explained and (b) the proportion of deviance explained attributable to each explanatory variable ( $\text{total dev} \times \text{variable contribution}/100$ ). Model predictive ability was assessed with the correlation coefficient between the observed and predicted values from 10-fold cross-validation (CV correlation coefficient). We considered models robust and informative if they exceeded a minimum threshold (i.e. CV correlation  $\geq 0.4$ ), following Francis et al. (2011). Only models that exceeded this threshold are presented here.

## 6.4 RESULTS

We collated data on relative abundance for a total of 66 diurnal bird species in mallee woodlands and 87 species in foothill forests. Although the species assemblages differed, the

functional composition of the bird communities was similar in both ecosystems based on species diet, foraging location and nest type (Fig. 6.2). Most species in both ecosystems feed on invertebrates (>75%, Fig. 6.2a). Most species forage in the upper-midstorey (> 30%, Fig. 6.2b), and most species construct a nest in the open (>75%, Fig. 6.2c).

The dominant bird families were similar in both ecosystems. In mallee woodlands, these were the Meliphagidae (honeyeaters, 17% of species), Artamidae (woodswallows and butcherbirds, 9%), Acanthizidae (thornbills, 8%) and Pachycephalidae (whistlers, 8%). In foothill forests, the most species-rich families were the Meliphagidae (16%), Acanthizidae (9%), Artamidae (6%), Cuculidae (cuckoos, 6%), Pachycephalidae (6%), Petroicidae (robins, 6%), and Psittaculidae (parrots, 6%).

The most widespread species in mallee woodlands (total sites = 555) were the yellow-plumed honeyeater *Lichenostomus ornatus* (54% of sites), spotted pardalote *Pardalotus punctatus* (46%) and white-eared honeyeater *Lichenostomus leucotis* (46%). The most widespread species in foothill forests (total sites = 458) were the spotted pardalote (83%), yellow-faced honeyeater *Lichenostomus chrysops* (83%), crimson rosella *Platycercus elegans* (80%) and striated thornbill *Acanthiza lineata* (79%). The rufous whistler *Pachycephala rufiventris*, spotted pardalote, striated pardalote *Pardalotus striatus* and white-eared honeyeater were recorded at >45 sites in both ecosystems. Species lists, foraging and nesting groups are provided in Appendices 6.6.2 – 6.6.3.

We built boosted regression tree models for 21 species in mallee woodlands and 32 species in foothill forests that occurred at  $\geq 45$  sites. Models for seven species in mallee woodlands and 18 species in foothill forests exceeded the minimum threshold for performance measures (cross validation correlation coefficient  $\geq 0.40$ ). Below, we address our three main questions.

- 1) Does the spatial context of fire influence the relative abundance of species?

Within mallee woodlands and foothill forests, the overall influence of models that included either time since fire or the spatial context of fire variables was similar (Fig. 6.3a-b). Models that included both time since fire and the spatial context of the fire regime generally outperformed models that included only time since fire (Fig. 6.3c-d). For one species in mallee woodlands, the striated pardalote, model performance measures were marginally higher when only time since fire was included (CV = 0.44, deviance = 39%, Table S6.6.4).

Including both time since fire and the spatial context of the fire regime increased model performance markedly for several species in foothill forests (Table S6.6.5). For example, for the silvereye *Zosterops lateralis*, model performance measures were below the minimum threshold when only time since fire was included (CV = 0.37, proportion of total deviance explained = 52%). However, the models exceeded the minimum threshold when either the amount of late (CV = 0.43, deviance = 61%) or amount of early-successional (CV = 0.55, deviance = 61%) vegetation, spatial diversity (CV = 0.47, deviance = 50%) or both time since fire and spatial context together (CV = 0.44, deviance = 60%) were included. Model outputs for all species are found in Appendices 6.6.4 – 6.6.5).

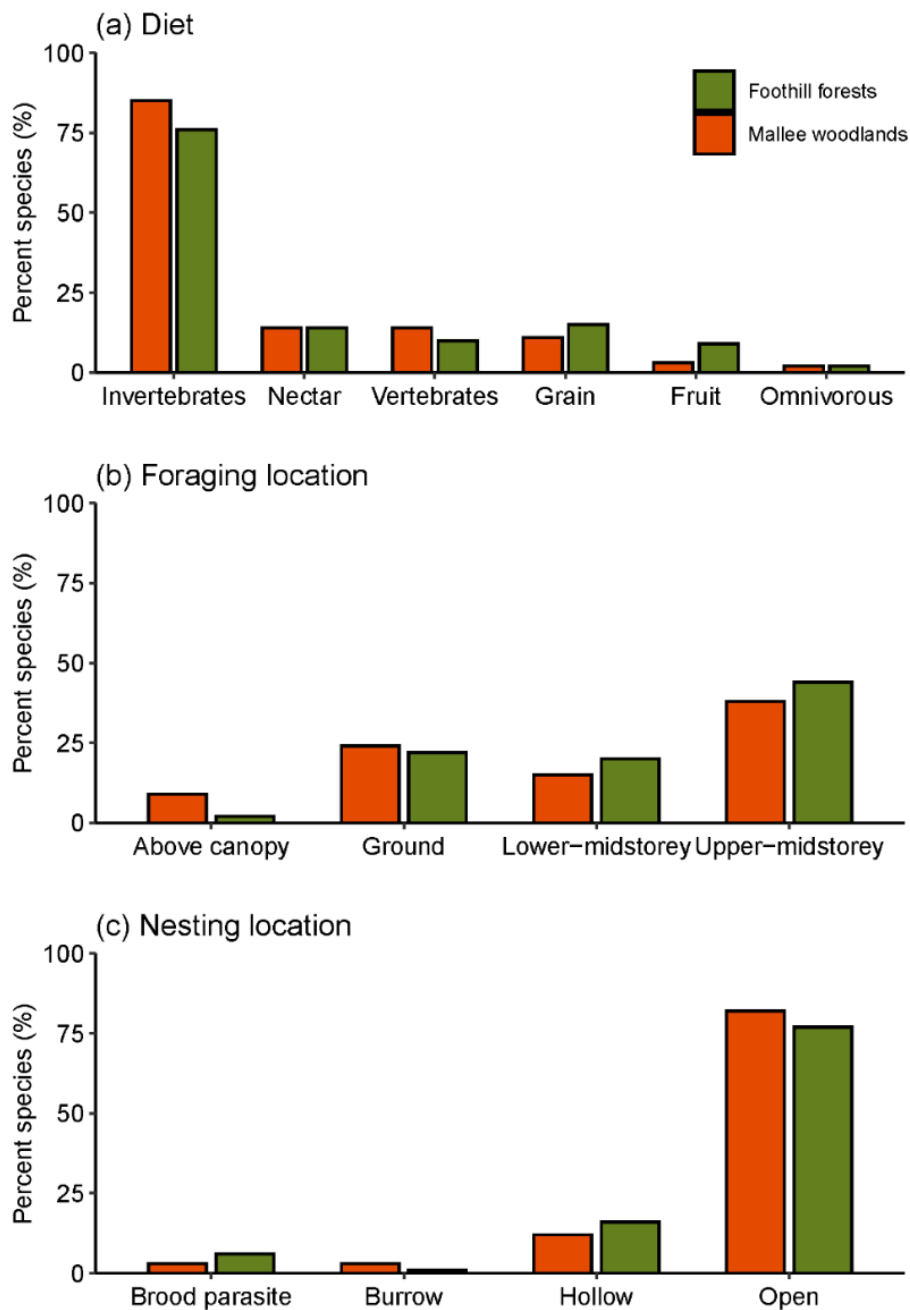


Figure 6.2. Functional composition of the bird communities in mallee woodlands ( $n = 66$  species) and foothill forests ( $n = 87$  species.) Bars show the percentage of species in functional groups based on (a) diet, (b) main foraging location, and (c) nest type. Diet groups were based on the main food source. If a species used more than one main food source (e.g. many honeyeaters consume nectar and invertebrates), it was counted in both groups. Foraging location was based on the stratum in which the species forages most of the time. 'Upper-midstorey' includes species that forage in the canopy. 'Open' nests refer to nests constructed outside hollows or burrows. 'Hollow' includes all size classes of hollow.

2) Does the relative influence of time since fire and spatial context of fire differ between ecosystems?

When models that included a single measure of fire regimes, the relative influence for fire variables was similar between ecosystems (Fig. 6.3a-b). However, trends displayed by some individual species suggest the relative influence of fire regime variables may differ between ecosystems. In mallee woodlands, time since fire and the amount of late successional vegetation had a very strong influence on one species, the yellow-plumed honeyeater (Table S6.6.4). In foothill forests the spatial diversity of successional vegetation, had substantial influence on at least three species (Table S6.6.5).

The relative difference between the overall influence of models that included *only* time since fire and those that included time since fire *and* spatial context of fire was greater in foothill forests than in mallee woodlands (Fig. 6.3c-d). In mallee woodlands, there was a marginal increase in model performance by adding landscape context to time since fire models, whereas in foothill forest, the increase was substantial. This increase was particularly strong for three species of canopy-foraging insectivores, the spotted pardalote (deviance attributed to time since fire + spatial context = 26%), white-naped honeyeater *Melithreptus lunatus* (28%) and striated pardalote (18%) (Table S6.6.5).

3) Do species preferences for post-fire successional vegetation differ between ecosystems?

Four of the seven species (57%) in mallee woodlands had their highest relative abundance in late successional state vegetation (Fig. 6.4a). Only the white-eared honeyeater was associated with early-successional vegetation. Relatively (Table S6.6.6) fewer species in foothill forests were associated with specific successional states (6/18, 33%) than in mallee woodlands (5/7, 71%). The superb fairywren *Malurus cyaneus* and white-naped honeyeater had highest relative abundance in early-successional vegetation (Table S6.6.7). For the striated thornbill,

relative abundance was highest in mid-successional vegetation, and for the golden whistler *Pachycephala pectoralis*, striated pardalote and yellow-faced honeyeater, this was highest in late-successional vegetation.

Most species in mallee woodlands (71%) responded negatively to the amount of early-successional vegetation (Fig. 6.4b), whereas in foothill forests most species (72%) showed a null response to this variable. A similar proportion of species responded positively to the amount of late successional vegetation in mallee woodlands (43%) and foothill forests (39%) (Fig. 6.4c).

In mallee woodlands, the relative abundance of only one species, the white-eared honeyeater, was positively associated with spatial diversity of successional vegetation. This species also responded negatively to both amount young and amount old. One other species, the yellow-plumed honeyeater, was negatively associated with spatial diversity and strongly positively associated with the amount of late successional vegetation. In foothill forests, seven species (39%) responded positively to spatial diversity of successional vegetation, including three species that forage on the ground as well as in low vegetation (buff-rumped thornbill *Acanthiza lineata*, grey shrike-thrush *Colluricincla harmonica*, superb fairy-wren).

Species response groupings can be found in Appendices 6.6.6 – 6.6.7.

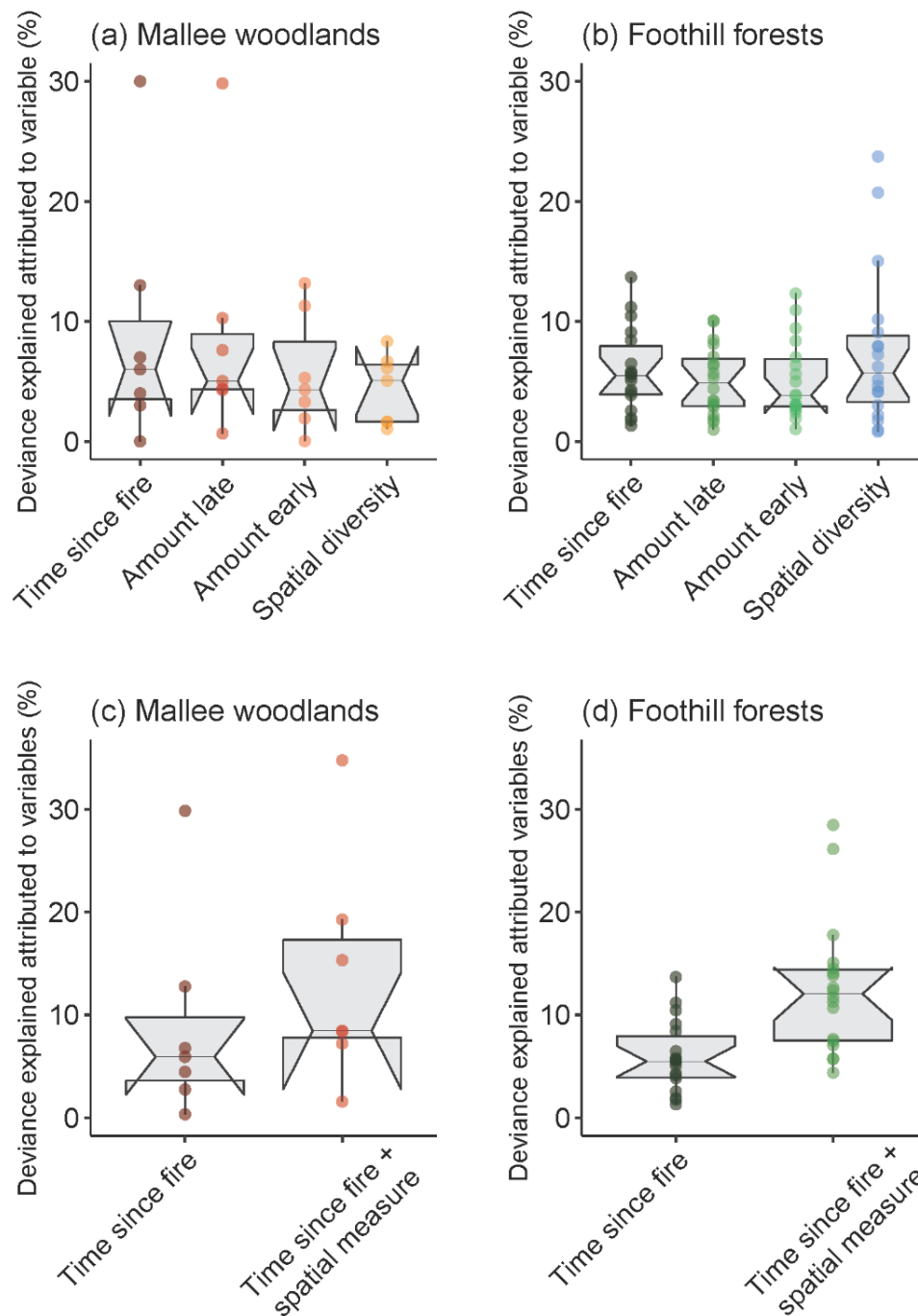


Figure 6.3. The influence of temporal and spatial measures of fire regimes on the relative abundance of bird species in mallee woodlands ( $n = 7$  species) and foothill forests ( $n = 18$  species). Points represent the deviance explained attributed to predictor variables from boosted regression tree models for individual species. (a – b) Models included a single measure of the fire regime. (c – d) Models included both time since fire plus the best spatial measure of fire variable. Notch plots indicate median and upper and lower quartiles and 95% confidence intervals for each predictor variable. All models included variables to represent environmental gradients (temperature, elevation, vegetation class).

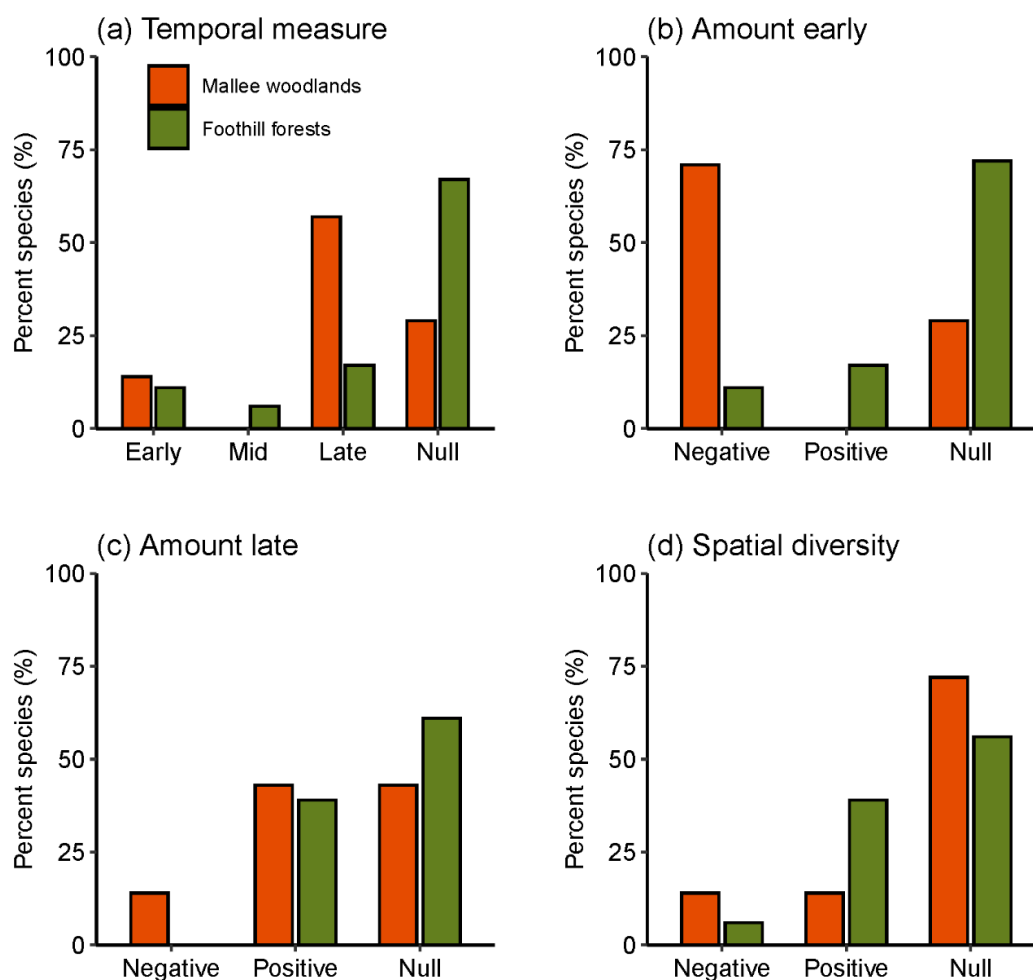


Figure 6.4. Responses of bird species to temporal and spatial aspects of fire regimes in mallee woodlands ( $n = 7$  species) and foothill forests ( $n = 18$ ). Bars represent the percentage of species modelled in each ecosystem a) whose relative abundance peaked in post-fire successional states (Early = 0-10 years since fire, Mid = 11-35 years since fire, late = >35 years since fire, Null = no response); and that responded positively, negatively or null to b) the amount of young successional vegetation; c) the amount of old vegetation; and d) to the spatial diversity of successional vegetation.

## 6.5 DISCUSSION

Fire histories beyond the site of occurrence can influence resource distribution and, subsequently, bird abundances in fire-prone ecosystems. Understanding how this influence varies between fire attributes, species and ecosystems will help improve conservation planning. Here, we addressed three key questions that aimed to improve this understanding.

We showed that: (a) overall, model performance was higher when time since fire and spatial context variables were included together, substantially so in foothill forests; (b) most species in mallee woodlands were associated with late-successional vegetation; (c) in foothill forests, most species were not associated with time since fire or the amount of early-successional vegetation, 39% were associated with the amount of late-successional vegetation and 39% were associated with spatial diversity of successional vegetation. These findings reflect variation among species both within and between ecosystems and highlight the need for nuance in understanding and managing biodiversity in fire-prone landscapes. In particular, we show that explicitly considering the spatial context of fire histories can improve understanding of how fire influences biota.

#### **6.5.1 Spatial context of fire**

Both mallee woodlands and foothill forests encompass broad climatic and environmental gradients that interact with fire regimes to shape the distribution of biota (Nimmo et al. 2014, Kelly et al. 2017b). Here, we showed that, when environmental conditions are held constant, the spatial context of fire regimes influence bird abundances. Spatial extent and configuration of fire influence species capacity to recolonize and persist in post-fire landscapes (Watson et al. 2012a, Lindenmayer et al. 2014, Nimmo et al. 2014). The importance of spatial diversity for birds depends on the ability of species to use the resources available in different successional states (Berry et al. 2015, Burgess and Maron 2016, Stillman et al. 2019). Despite the importance of large patches of long-unburnt vegetation for many species in woodland ecosystems (Taylor et al. 2012, Kelly et al. 2015, Davis et al. 2016), spatial heterogeneity (e.g. diversity of fire age-classes) can also positively influence species for which recently burnt vegetation in a landscape are unsuitable by facilitating recolonisation or *in situ* survival (Berry et al. 2015, Burgess and Maron 2016). Faunal species respond positively to spatial diversity because they depend on, or benefit from, multiple successional states to meet their

resource needs (Nappi and Drapeau 2011, Nimmo et al. 2019, Stillman et al. 2019). A common example of this is when animals exploit the foraging opportunities in recently burnt vegetation and use the dense cover of older vegetation for refuge or nesting (Lundie-Jenkins et al. 1993, Bliege Bird et al. 2013) (Lundie-Jenkins et al. 1993, Bliege Bird et al. 2013).

However, there is often variation between species in the influence of spatial diversity of fire. Some species respond negatively to spatial diversity because they need large intact areas of a particular successional state to maintain viable populations; for example, the yellow-plumed honeyeater in mallee woodlands (Berry et al. 2015). Here, relatively more bird species in foothill forests responded positively to spatial diversity than in mallee woodlands. This could be due to the stark structural differences in post-fire habitats between ecosystems. In mallee woodlands, there is much more contrast between early and late successional stages than in foothill forests, mainly due to the presence of biological legacies in the latter (Haslem et al. 2011, Rainsford et al. 2020). Another possibility is that early-successional post fire habitat in foothill forests could complement areas of later-successional states by providing different resources for birds, leading to greater bird abundances in spatially diverse landscapes. Species respond to departures from an ideal spatial configuration of successional states in various ways, such as population decline or local extirpation (Nimmo et al. 2019). It will be useful for conservation planning in these two ecosystems to understand more clearly how birds use spatially heterogeneous landscapes, in order to predict how species might respond to departures from an ‘ideal’ state.

We were able to build models only for the most common species in the two ecosystems. Therefore, we have omitted several threatened species known to depend on mid-late successional vegetation in mallee woodlands (Connell et al. 2017). We suggest that these species would not respond positively to spatial diversity due to the disproportionate importance of mid-late-successional vegetation. Our findings are representative of the most

common species from each ecosystem and likely reflect overall patterns of fire's influence on birds. Alternative modelling methods (e.g. MaxEnt) could be used to test the role of fire regimes on rare and threatened species.

A second limitation of our study is that the resolution of spatial fire data in current fire mapping does not always discern unburnt patches within fire boundaries that could act as refuges. For example, unburnt gullies can act as refuges for birds in fire-prone landscapes, influencing post-fire recolonisation of burnt areas (Robinson et al. 2014). If unburnt patches were present within a fire boundary, the importance of spatial diversity or amount of late-successional vegetation for some species may have been misrepresented (likely underestimated).

### **6.5.2 Structural resilience and post-fire abundance**

There are three potential explanations for the differences in the role of fire between ecosystems observed here: differences in bird traits, differences in post-fire stand-regeneration patterns (basal resprouting vs epicormic resprouting) and climatic differences. Many birds in fire-prone ecosystems are adapted to the habitat created by recurrent fires, as opposed to possessing specific morphological adaptations to fire itself (Pausas and Parr 2018). The similarity in dominant taxonomic and functional groups between the two ecosystems implies that these are not likely to drive differences in the importance of fire regime attributes between ecosystems.

Fire affects faunal species directly, through mortality and emigration, and indirectly, through changes in vegetation (habitat) structure (Sitters et al. 2014a, Stillman et al. 2019).

Consequently, the way in which vegetation in an ecosystem changes in response to fire will influence the fauna. First, canopy trees in mallee woodlands resprout basally following fire, making most fires stand-replacing, whereas in foothill forests, canopy trees resprout from

epicormic buds along the trunk and branches, leading to structural differences in post-fire habitats (Haslem et al. 2011, Haslem et al. 2016, Rainsford et al. 2020).

Second, climatic conditions affect plant growth rates, population dynamics and vegetation structural recovery; the more arid conditions in mallee woodlands make post-fire ecosystem recovery slower than in the more-mesic foothill forests (Haslem et al. 2016, Kenny et al. 2018). In mallee woodlands, development of structural resources used by fauna (e.g. large trees with cavities) take many years following fire (Haslem et al. 2011). Accordingly, the abundance of birds that use these resources, will increase with time since fire and, indeed most species were associated with late-successional vegetation (see also Watson et al. 2012b, Connell et al. 2017). In foothill forests, while several structural components (e.g. leaf litter depth, understorey vegetation) develop with time since fire (Haslem et al. 2016), others such as canopy tree stems persist through fire and are present in early successional states as biological legacies. These legacies mean that vegetation structure in foothill forests is more resilient to fire and fewer bird species are associated with specific successional states.

Differences in species associations with early-successional vegetation suggest there could also be differences in how large wildfires affect the bird communities. Most species in mallee woodlands were negatively associated with the amount of surrounding early-successional vegetation, and Watson et al. (2012b) showed that bird occurrence in recently burnt vegetation is influenced by proximity to unburnt patches. In contrast, in foothill forests, most species did not respond to the amount of early-successional vegetation, suggesting the bird community may be more resilient to large wildfires. This also is likely due to the presence of biological legacies and unburnt refuges.

### **6.5.3 Concluding remarks**

Fire regimes drive the distribution of birds in fire-prone landscapes, but the influence of fire regime attributes varies among species, both within and between ecosystems. While

generalizations across ecological settings can be useful, ecosystems differ structurally and functionally. Identifying situations where generalizations may or may not be applicable will help improve conservation strategies. Our findings highlight the need for a nuanced approach to fire management that considers the effects of both temporal and spatial aspects of fire regimes. Recognizing where differences occur will lead to better predictions of the impacts of fire on biota. A key finding is that a combination of both time since fire and the spatial context of the site can improve understanding of bird species distributions in fire-prone ecosystems. Maintaining landscape diversity of successional vegetation in foothill forests will positively influence the abundance of some bird species. More generally, incorporating the spatial context of fire in conservation planning will benefit in meeting the habitat requirements of diverse species; but with recognition that the role of spatial attributes can differ between ecosystems.

## 6.6 APPENDICES

### 6.6.1 Bird survey methods

Table S6.6.1. Survey methods for birds in projects contributing data on the avifauna of mallee woodlands and foothill forests. Total survey time is the summed time of all surveys across multiple survey rounds.

Ecosystem	Project	Total survey time (mins)	Survey area (ha)	Number of sites	Survey method
Mallee woodlands	Mallee fire and biota project	20	1.13	555	Point count
Foothill forests	Fauna refuges	120	0.57	192	Point count
	Gippsland Retrospective and HawkEye	40	2.00	124	Area search
	Otway Fire, Landscape Pattern and Biodiversity Study	80	1.58	129	Point count
	Otway HawkEye	80	1.58	23	Point count
	Fire Effects Study Areas	60-80	2.00	25	Area search

### 6.6.2 Bird species recorded in mallee woodlands

Table S6.6.2. Bird species recorded, and the number of sites at which they were recorded, in mallee woodlands. The main foraging stratum (lower-midstorey, upper-midstorey, throughout, above canopy), diet (invertebrates, fruit, nectar, seeds, vertebrates, omnivorous) and nest type (bowl, burrow, cup, dome, ground, hollow, hollow in termite nest, parasite) are given. Taxonomy for bird names follows (Christidis and Boles 2008).

Species	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Acanthagenys rufogularis</i>	Spiny-cheeked honeyeater	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in tree	170
<i>Acanthiza apicalis</i>	Inland thornbill	Acanthizidae	Lower-midstorey	Invertebrates	Dome in shrub	95
<i>Acanthiza uropygialis</i>	Chestnut-rumped thornbill	Acanthizidae	Lower-midstorey	Invertebrates	Dome in shrub	124
<i>Accipiter cirrocephalus</i>	Collared sparrowhawk	Accipitridae	Upper-midstorey	Vertebrates	Large bowl in tree	1
<i>Amytornis striatus</i>	Striated grasswren	Acanthizidae	Lower-midstorey	Invertebrates + seeds	Dome in shrub	39
<i>Anthochaera carunculata</i>	Red wattlebird	Meliphagidae	Upper-midstorey	Nectar	Cup in tree	30
<i>Artamus cyanopterus</i>	Dusky woodswallow	Artamidae	Upper-midstorey	Invertebrates	Bowl in tree	6
<i>Artamus personatus</i>	Masked woodswallow	Artamidae	Throughout	Invertebrates	Bowl in tree	20
<i>Artamus leucorhynchus</i>	White-browed Woodswallow	Artamidae	Above canopy	Invertebrates	Bowl in tree	12
<i>Barnardius zonarius</i>	Australian ringneck	Psittaculidae	Ground	Seeds + nectar	Hollow	56

Species	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Chrysococcyx basalis</i>	Horsfield's bronze-cuckoo	Cuculidae	Throughout	Invertebrates	Parasite	4
<i>Chrysococcyx osculans</i>	Black-eared cuckoo	Cuculidae	Upper-midstorey	Invertebrates	Parasite	1
<i>Cinclosoma castanotum</i>	Chestnut quail-thrush	Cinclosomatidae	Ground	Invertebrates	Ground	149
<i>Climacteris picumnus</i>	Brown treecreeper	Climacteridae	Upper-midstorey	Invertebrates	Hollow	10
<i>Colluricincla harmonica</i>	Grey shrike-thrush	Pachycephalidae	Ground	Vertebrates + invertebrates	Bowl in tree	181
<i>Coracina novaehollandiae</i>	Black-faced cuckoo-shrike	Campephagidae	Throughout	Invertebrates	Bowl in tree	13
<i>Corcorax melanorhamphos</i>	White-winged chough	Corcoracidae	Ground	Invertebrates	Bowl in tree	3
<i>Corvus bennetti</i>	Little crow	Corvidae	Throughout	Vertebrates + invertebrates	Large bowl in tree	4
<i>Corvus coronoides</i>	Australian raven	Corvidae	Throughout	Vertebrates + invertebrates	Large bowl in tree	7
<i>Corvus mellori</i>	Little raven	Corvidae	Upper-midstorey	Vertebrates + invertebrates	Large bowl in tree	2
<i>Cracticus nigrogularis</i>	Pied butcherbird	Artamidae	Throughout	Vertebrates + invertebrates	Bowl in tree	2
<i>Cracticus torquatus</i>	Grey butcherbird	Artamidae	Throughout	Vertebrates + invertebrates	Bowl in tree	138
<i>Daphoenositta chrysoptera</i>	Varied sittella	Neosittidae	Upper-midstorey	Invertebrates	Cup in tree	4

Species	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Dromaius novaehollandiae</i>	Emu	Casuariidae	Ground	Seeds + invertebrates	Ground	3
<i>Drymodes brunneopygia</i>	Southern scrub-robin	Petroicidae	Lower-midstorey	Invertebrates	Cup on ground	75
<i>Epthianura tricolor</i>	Crimson chat	Meliphagidae	Ground	Invertebrates	Cup in shrub	2
<i>Falco berigora</i>	Brown falcon	Accipitridae	Above canopy	Vertebrates	Large bowl in tree	2
<i>Falco cenchroides</i>	Kestrel	Accipitridae	Throughout	Vertebrates	Large bowl in tree	1
<i>Glossopsitta porphyrocephala</i>	Purple-crowned Lorikeet	Psittaculidae	Upper-midstorey	Nectar	Hollow	2
<i>Hylacola cauta</i>	Shy heathwren	Acanthizidae	Lower-midstorey	Invertebrates	Dome on ground	94
<i>Lalage tricolor</i>	White-winged triller	Campephagidae	Upper-midstorey	Invertebrates	Cup in tree	2
<i>Leipoa ocellata</i>	Malleefowl	Megapodidae	Above canopy	Invertebrates	Ground	1
<i>Lichenostomus cratitius</i>	Purple-gaped Honeyeater	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in tree	21
<i>Lichenostomus leucotis</i>	White-eared honeyeater	Meliphagidae	Lower-midstorey	Invertebrates	Cup in shrub	255
<i>Lichenostomus ornatus</i>	Yellow-plumed honeyeater	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in tree	301
<i>Lichenostomus plumulus</i>	Grey-fronted honeyeater	Meliphagidae	Upper-midstorey	Invertebrates	Cup in tree	36
<i>Lophochroa leadbeateri</i>	Major Mitchell's cockatoo	Cacatuidae	Lower-midstorey	Seeds + fruit	Large hollow	3
<i>Malurus lamberti</i>	Variegated fairy-wren	Maluridae	Ground	Invertebrates	Cup in shrub	31
<i>Malurus splendens</i>	Splendid fairy-wren	Maluridae	Ground	Invertebrates	Cup in shrub	25

Species	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Manorina melanotis</i>	Black-eared miner	Meliphagidae	Upper-midstorey	Invertebrates	Bowl in tree	15
<i>Melanodryas cucullata</i>	Hooded robin	Petroicidae	Ground	Invertebrates	Cup in tree	18
<i>Melithreptus brevirostris</i>	Brown-headed Honeyeater	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in shrub	54
<i>Merops ornatus</i>	Rainbow bee-eater	Meropidae	Above canopy	Invertebrates	Burrow	10
<i>Microeca fascinans</i>	Jacky winter	Petroicidae	Lower-midstorey	Invertebrates	Cup in tree	120
<i>Myiagra inquieta</i>	Restless flycatcher	Monarchidae	Upper-midstorey	Invertebrates	Cup in tree	5
<i>Oreoica gutturalis</i>	Crested bellbird	Oreicidae	Lower-midstorey	Invertebrates + seeds	Cup in shrub	103
<i>Pachycephala inornata</i>	Gilbert's whistler	Pachycephalidae	Upper-midstorey	Invertebrates	Cup in tree	25
<i>Pachycephala pectoralis</i>	Golden whistler	Pachycephalidae	Upper-midstorey	Invertebrates	Bowl in tree	37
<i>Pachycephala rufiventris</i>	Rufous whistler	Pachycephalidae	Upper-midstorey	Invertebrates	Cup in tree	45
<i>Pachycephala rufogularis</i>	Red-lored whistler	Pachycephalidae	Upper-midstorey	Invertebrates	Cup in tree	9
<i>Pardalotus punctatus</i>	Spotted pardalote	Pardalotidae	Upper-midstorey	Invertebrates	Burrow	256
<i>Pardalotus striatus</i>	Striated pardalote	Pardalotidae	Upper-midstorey	Invertebrates	Hollow	161
<i>Petrochelidon nigricans</i>	Tree martin	Hirundinidae	Above canopy	Invertebrates	Hollow	3
<i>Petroica goodenovii</i>	Red-capped robin	Petroicidae	Lower-midstorey	Invertebrates	Cup in shrub	23
<i>Phaps chalcoptera</i>	Common bronzewing	Columbidae	Ground	Seeds	Saucer in shrub	16
<i>Plectorhyncha lanceolata</i>	Striped honeyeater	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in tree	22
<i>Polytelis anthopeplus</i>	Regent parrot	Psittaculidae	Ground	Seeds	Hollow	4

Species	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Pomatostomus ruficeps</i>	Chestnut-crowned babbler	Pomatostomidae	Ground	Invertebrates	Dome in tree	12
<i>Pomatostomus superciliosus</i>	White-browed babbler	Pomatostomidae	Ground	Invertebrates	Dome in tree	49
<i>Psephotus varius</i>	Mulga parrot	Psittaculidae	Above canopy	Seeds	Hollow	38
<i>Psophodes nigrogularis</i>	Western whipbird	Psophodidae	Ground	Invertebrates	Cup in shrub	1
<i>Purnella albifrons</i>	White-fronted honeyeater	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in shrub	121
<i>Rhipidura leucophrys</i>	Willie wagtail	Rhipiduridae	Ground	Invertebrates	Cup in shrub	49
<i>Smicrornis brevirostris</i>	Weebill	Acanthizidae	Upper-midstorey	Invertebrates	Dome in tree	364
<i>Stipiturus mallee</i>	Mallee emu-wren	Maluridae	Ground	Invertebrates	Dome in shrub	9
<i>Strepera versicolor</i>	Grey currawong	Artamidae	Throughout	Omnivorous	Bowl in tree	24

### 6.6.3 Bird species recorded in foothill forests

Table S6.6.3. Bird species recorded, and the number of sites at which they were recorded, in foothill forests. The main foraging stratum (ground, lower-midstorey, upper-midstorey, throughout), diet (invertebrates, fruit, nectar, seeds, vertebrates, omnivorous), nest type (bowl, burrow, cup, dome, ground, hollow, hollow in termite nest, parasite) are given.

Species names	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Alisterus scapularis</i>	Australian king parrot	Psittaculidae	Upper-midstorey	Seeds	Large hollow	76
<i>Acanthiza lineata</i>	Striated thornbill	Acanthizidae	Upper-midstorey	Invertebrates	Dome in tree	382
<i>Acanthiza pusilla</i>	Brown thornbill	Acanthizidae	Lower-midstorey	Invertebrates	Dome in shrub	346
<i>Acanthiza reguloides</i>	Buff-rumped thornbill	Acanthizidae	Lower-midstorey	Invertebrates	Dome in shrub	172

Species names	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Acanthorhynchus tenuirostris</i>	Eastern spinebill	Meliphagidae	Lower-midstorey	Nectar + invertebrates	Cup in shrub	238
<i>Accipiter cirrocephalus</i>	Collared sparrowhawk	Accipitridae	Upper-midstorey	Vertebrates	Large bowl in tree	4
<i>Accipiter fasciatus</i>	Brown goshawk	Accipitridae	Upper-midstorey	Vertebrates	Large bowl in tree	9
<i>Anthochaera carunculata</i>	Red wattlebird	Meliphagidae	Upper-midstorey	Nectar	Cup in tree	260
<i>Artamus cyanopterus</i>	Dusky woodswallow	Artamidae	Upper-midstorey	Invertebrates	Bowl in tree	5
<i>Artamus superciliosus</i>	White-browed Woodswallow	Artamidae	Above canopy	Invertebrates	Bowl in tree	1
<i>Cacomantis flabelliformis</i>	Fan-tailed cuckoo	Cuculidae	Upper-midstorey	Invertebrates	Parasite	126
<i>Cacomantis pallidus</i>	Pallid cuckoo	Cuculidae	Throughout	Invertebrates	Parasite	11
<i>Cacomantis variolosus</i>	Brush cuckoo	Cuculidae	Upper-midstorey	Invertebrates	Parasite	37
<i>Callocephalon fimbriatum</i>	Gang-gang cockatoo	Cacatuidae	Upper-midstorey	Seeds	Large hollow	91
<i>Calyptorhynchus funereus</i>	Yellow-tailed black- cockatoo	Cacatuidae	Upper-midstorey	Seeds	Large hollow	21
<i>Chrysococcyx basalis</i>	Horsfield's bronze-cuckoo	Cuculidae	Throughout	Invertebrates	Parasite	7
<i>Chrysococcyx lucidus</i>	Shining-bronze cuckoo	Cuculidae	Upper-midstorey	Invertebrates	Parasite	66
<i>Cinclosoma punctatum</i>	Spotted quail-thrush	Cinclosomatidae	Ground	Invertebrates	Ground	25
<i>Climacteris erythrops</i>	Red-browed treecreeper	Climacteridae	Upper-midstorey	Invertebrates	Hollow	56
<i>Climacteris picumnus</i>	Brown treecreeper	Climacteridae	Lower-midstorey	Invertebrates	Hollow	22
<i>Colluricincla harmonica</i>	Grey shrike-thrush	Pachycephalidae	Ground	Vertebrates + invertebrates	Bowl in tree	367
<i>Coracina novaehollandiae</i>	Black-faced cuckoo-shrike	Campephagidae	Throughout	Invertebrates	Bowl in tree	102

Species names	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Coracina papuensis</i>	White-bellied cuckoo-shrike	Campephagidae	Upper-midstorey	Invertebrates	Bowl in tree	9
<i>Coracina tenuirostris</i>	Common cicadabird	Campephagidae	Upper-midstorey	Invertebrates	Saucer in tree	15
<i>Corcorax melanorhamphos</i>	White-winged chough	Corcoracidae	Ground	Invertebrates	Bowl in tree	17
<i>Cormobates leucophaea</i>	White-throated treecreeper	Climacteridae	Upper-midstorey	Invertebrates	Hollow	472
<i>Corvus coronoides</i>	Australian raven	Corvidae	Throughout	Vertebrates + invertebrates	Large bowl in tree	17
<i>Corvus mellori</i>	Little raven	Corvidae	Throughout	Vertebrates + invertebrates	Large bowl in tree	1
<i>Corvus tasmanicus</i>	Forest raven	Corvidae	Throughout	Vertebrates + invertebrates	Large bowl in tree	4
<i>Coturnix ypsilophora</i>	Brown quail	Phasianidae	Ground	Seeds	Ground	4
<i>Cracticus torquatus</i>	Grey butcherbird	Artamidae	Throughout	Vertebrates + invertebrates	Bowl in tree	29
<i>Dacelo novaeguineae</i>	Laughing kookaburra	Alcedinidae	Ground	Vertebrates + invertebrates	Large hollow	132
<i>Daphoenositta chrysoptera</i>	Varied sittella	Neosittidae	Upper-midstorey	Invertebrates	Cup in tree	33
<i>Dicaeum hirundinaceum</i>	Mistletoebird	Dicaeidae	Upper-midstorey	Fruit	Dome in tree	9
<i>Eopsaltria australis</i>	Eastern yellow robin	Petroicidae	Ground	Invertebrates	Cup in shrub	284
<i>Falcunculus frontatus</i>	Crested shrike-tit	Pachycephalidae	Upper-midstorey	Invertebrates	Cup in tree	14
<i>Gerygone mouki</i>	Brown gerygone	Acanthizidae	Lower-midstorey	Invertebrates	Dome in shrub	1
<i>Gerygone olivacea</i>	White-throated Gerygone	Acanthizidae	Lower-midstorey	Invertebrates	Dome in tree	3
<i>Glossopsitta concinna</i>	Musk lorikeet	Psittaculidae	Upper-midstorey	Nectar	Hollow	3

Species names	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Leucosarcia melanoleuca</i>	Wonga pigeon	Columbidae	Ground	Seeds + fruit	Saucer in tree	17
<i>Lichenostomus chrysops</i>	Yellow-faced honeyeater	Meliphagidae	Upper-midstorey	Invertebrates	Cup in shrub	400
<i>Lichenostomus fuscus</i>	Fuscous honeyeater	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in shrub	7
<i>Lichenostomus leucotis</i>	White-eared honeyeater	Meliphagidae	Upper-midstorey	Invertebrates	Cup in shrub	121
<i>Lichenostomus penicillatus</i>	White-plumed Honeyeater	Meliphagidae	Upper-midstorey	Invertebrates + nectar	Cup in tree	2
<i>Malurus cyaneus</i>	Superb fairywren	Maluridae	Ground	Invertebrates	Dome in shrub	283
<i>Manorina melanophrys</i>	Bell miner	Meliphagidae	Upper-midstorey	Invertebrates	Cup in shrub	2
<i>Meliphaga lewinii</i>	Lewins honeyeater	Meliphagidae	Lower-midstorey	Fruit	Cup in tree	17
<i>Melithreptus brevirostris</i>	Brown-headed honeyeater	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in shrub	103
<i>Melithreptus lunatus</i>	White-naped honeyeater	Meliphagidae	Upper-midstorey	Invertebrates + nectar	Cup in tree	146
<i>Menura novaehollandiae</i>	Superb lyrebird	Menuridae	Ground	Invertebrates	Dome in shrub	58
<i>Monarcha melanopsis</i>	Black-faced monarch	Monarchidae	Lower-midstorey	Invertebrates	Cup in tree	2
<i>Myiagra inquieta</i>	Restless flycatcher	Monarchidae	Upper-midstorey	Invertebrates	Cup in tree	6
<i>Myiagra rubecula</i>	Leaden flycatcher	Monarchidae	Upper-midstorey	Invertebrates	Cup in tree	22
<i>Neochmia temporalis</i>	Red-browed finch	Estrildidae	Ground	Seeds	Dome in shrub	14
<i>Neophema chrysostoma</i>	Blue-winged parrot	Psittaculidae	Ground	Seeds	Hollow	13
<i>Todiramphus sanctus</i>	Sacred kingfisher	Alcedinidae	Ground	Vertebrates + invertebrates	Hollow termite nest	38

Species names	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Oriolus sagittatus</i>	Olive-backed oriole	Oriolidae	Upper-midstorey	Invertebrates + fruit	Cup in tree	46
<i>Pachycephala olivacea</i>	Olive whistler	Pachycephalidae	Lower-midstorey	Invertebrates	Bowl in tree	2
<i>Pachycephala pectoralis</i>	Golden whistler	Pachycephalidae	Upper-midstorey	Invertebrates	Bowl in tree	287
<i>Pachycephala rufiventris</i>	Rufous whistler	Pachycephalidae	Upper-midstorey	Invertebrates	Cup in tree	197
<i>Pardalotus punctatus</i>	Spotted pardalote	Pardalotidae	Upper-midstorey	Invertebrates	Burrow	402
<i>Pardalotus striatus</i>	Striated pardalote	Pardalotidae	Upper-midstorey	Invertebrates	Hollow	260
<i>Petrochelidon nigricans</i>	Tree martin	Hirundinidae	Above canopy	Invertebrates	Hollow	3
<i>Petroica boodang</i>	Scarlet robin	Petroicidae	Ground	Invertebrates	Cup in shrub	121
<i>Petroica phoenicea</i>	Flame robin	Petroicidae	Ground	Invertebrates	Bowl in tree	70
<i>Petroica rodinogaster</i>	Pink robin	Petroicidae	Lower-midstorey	Invertebrates	Cup in tree	3
<i>Petroica rosea</i>	Rose robin	Petroicidae	Upper-midstorey	Invertebrates	Cup in tree	52
<i>Phaps chalcoptera</i>	Common bronzewing	Columbidae	Ground	Seeds	Saucer in shrub	15
<i>Phaps elegans</i>	Brush bronzewing	Columbidae	Ground	Seeds	Saucer in shrub	9
<i>Philemon citreogularis</i>	Little friarbird	Meliphagidae	Upper-midstorey	Nectar + invertebrates	Cup in tree	3
<i>Philemon corniculatus</i>	Noisy friarbird	Meliphagidae	Upper-midstorey	Nectar	Cup in tree	12
<i>Phylidonyris novaehollandiae</i>	New Holland honeyeater	Meliphagidae	Lower-midstorey	Nectar	Cup in tree	19
<i>Phylidonyris pyrrhopterus</i>	Crescent honeyeater	Meliphagidae	Lower-midstorey	Nectar + invertebrates	Cup in shrub	68
<i>Platycercus elegans</i>	Crimson rosella	Psittaculidae	Throughout	Seeds	Large hollow	393
<i>Psophodes olivaceus</i>	Eastern whipbird	Psophodidae	Ground	Invertebrates	Cup in shrub	17
<i>Ptilonorhynchus violaceus</i>	Satin bowerbird	Ptilonorhynchidae	Throughout	Fruit	Bowl in tree	30

Species names	Common name	Family	Foraging stratum	Diet	Nest	No. sites
<i>Pycnoptilus floccosus</i>	Pilotbird	Acanthizidae	Lower-midstorey	Invertebrates	Dome in shrub	11
<i>Rhipidura albiscapa</i>	Grey fantail	Rhipiduridae	Upper-midstorey	Invertebrates	Cup in shrub	414
<i>Rhipidura rufifrons</i>	Rufous fantail	Rhipiduridae	Lower-midstorey	Invertebrates	Cup in shrub	37
<i>Sericornis frontalis</i>	White-browed scrubwren	Acanthizidae	Lower-midstorey	Invertebrates	Dome in shrub	344
<i>Sericornis magnirostra</i>	Large-billed scrubwren	Acanthizidae	Lower-midstorey	Invertebrates	Dome in shrub	1
<i>Strepera graculina</i>	Pied currawong	Artamidae	Throughout	Omnivorous	Bowl in tree	178
<i>Strepera versicolor</i>	Grey currawong	Artamidae	Throughout	Omnivorous	Bowl in tree	43
<i>Trichoglossus moluccanus</i>	Rainbow lorikeet	Psittaculidae	Upper-midstorey	Nectar	Hollow	10
<i>Turnix varius</i>	Painted button-quail	Turnicidae	Ground	Seeds	Ground	11
<i>Zoothera lunulata</i>	Bassian thrush	Turdidae	Ground	Invertebrates	Cup in tree	15
<i>Zosterops lateralis</i>	Silvereye	Zosteropidae	Lower-midstorey	Fruit + invertebrates	Cup in shrub	188

#### 6.6.4 Model outputs fore bird species in mallee woodlands

Table S6.6.4. Boosted regression tree model outputs for birds in mallee woodlands. Model performance measures are cross-validation correlation coefficient and the percent deviance explained from boosted regression tree models of species relative abundance as a function of fire regime attributes and environmental conditions. Five models were built for each species in which the fire regime variables differed: four models included a single measure of fire (time since fire, amount of late successional vegetation, amount of early successional vegetation or spatial diversity of fire ages). The fifth model included both time since fire and the best spatial context variable. The deviance explained attributed to each explanatory variable (%) is given. Models were built for species that occurred at  $\geq 45$  sites. Models that exceeded minimum thresholds (CV correlation  $\geq 0.4$ ) are presented here (n = 7 species).

Species name	Model	CV correlation	Total deviance	Deviance explained attributed to variable (%)						
				Time since fire (years)	Amount late (ha)	Amount early (ha)	Spatial diversity	Temperature (°C)	Elevation (m)	Veg class
<i>Acanthiza apicalis</i>	Time since fire	0.52	34	0	-	-	-	15	4	16
	Amount late	0.45	35	-	1	-	-	14	4	16
	Amount early	0.50	34	-	-	0	-	15	4	16
	Spatial diversity	0.47	35	-	-	-	1	14	4	16
	TSF + spatial context	0.47	36	1	-	-	1	15	4	16
<i>Drymodes</i>	Time since fire	0.47	56	6	-	-	-	26	20	4
<i>brunneopygia</i>	Amount late	0.56	52	-	4	-	-	26	17	4
	Amount early	0.49	57	-	-	4	-	28	20	5
	Spatial diversity	0.50	50	-	-	-	2	25	17	5

Species name	Model	CV	Total	Deviance explained attributed to variable (%)						
				Time	Amount	Amount	Spatial	Temperature	Elevation	Veg
		correlation	deviance	since fire	late (ha)	early	diversity	(°C)	(m)	class
				(years)		(ha)				
	TSF + spatial	0.49	57	5	-	2	-	26	20	4
	context									
<i>Pardalotus punctatus</i>	Time since fire	0.42	33	4	-	-	-	19	9	1
	Amount late	0.42	31	-	4	-	-	19	7	0
	Amount early	0.41	32	-	-	3	-	20	9	1
	Spatial diversity	0.41	30	-	-	-	5	18	7	0
	TSF + spatial	0.44	33	3	-	-	5	17	7	0
	context									
<i>Pardalotus striatus</i>	Time since fire	0.44	39	7	-	-	-	17	5	10
	Amount late	0.41	38	-	8	-	-	16	5	9
	Amount early	0.37	35	-	-	2	-	16	5	11
	Spatial diversity	0.36	31	-	-	-	2	15	4	10
	TSF + spatial	0.40	38	6	-	2	-	16	4	10
	context									
<i>Lichenostomus leucotis</i>	Time since fire	0.54	50	13	-	-	-	22	11	4
	Amount late	0.49	46	-	10	-	-	21	9	5
	Amount early	0.48	44	-	-	5	-	24	11	4
	Spatial diversity	0.46	45	-	-	-	8	24	9	4

Species name	Model	CV	Total	Deviance explained attributed to variable (%)						
				Time	Amount	Amount	Spatial	Temperature	Elevation	Veg
		correlation	deviance	since fire	late (ha)	early	diversity	(°C)	(m)	class
				(years)		(ha)				
	TSF + spatial context	0.55	52	11	-	-	8	19	9	5
<i>Purnella albifrons</i>	Time since fire	0.26	24	3	-	-	-	15	6	1
	Amount late	0.35	29	-	5	-	-	15	7	1
	Amount early	0.35	40	-	-	13	-	17	8	1
	Spatial diversity	0.35	30	-	-	-	7	15	8	1
	TSF + spatial context	0.43	41	3	-	-	12	16	8	1
<i>Lichenostomus ornatus</i>	Time since fire	0.63	59	30	-	-	-	14	13	2
	Amount late	0.60	51	-	30	-	-	10	9	3
	Amount early	0.58	56	-	-	11	-	24	16	5
	Spatial diversity	0.51	48	-	-	-	6	20	17	5
	TSF + spatial context	0.63	62	28	-	-	6	13	12	3

### 6.6.5 Model outputs for bird species in foothill forests

Table S6.6.5. Boosted regression tree model outputs for birds in foothill forests. Model performance measures are cross-validation correlation coefficient and the percent deviance explained from boosted regression tree models of species relative abundance as a function of fire regime attributes and environmental conditions. Five models were built for each species in which the fire regime variables differed: four models included a single measure of fire (time since fire, amount of late successional vegetation, amount of early successional vegetation or spatial diversity of fire ages). The fifth model included both time since fire and the best spatial context variable. The deviance explained attributed to each explanatory variable (%) is given. Models were built for species that occurred at  $\geq 45$  sites. Models that exceeded minimum thresholds (CV correlation  $\geq 0.4$ ) are presented here (n = 18 species).

Species name	Model	CV correlation	Total deviance	Deviance attributed to variables								
				Time since fire (years)	Amount late (ha)	Amount young (ha)	Spatial diversity	Temperature (°C)	Elevation (m)	Veg class	Survey duration (mins)	Survey area (ha)
<i>Acanthiza lineata</i>	Time since fire	0.52	44	9	-	-	-	8	4	1	15	7
	Amount late	0.50	41	-	2	-	-	10	6	1	15	7
	Amount early	0.47	39	-	-	2	-	9	5	1	15	7
	Spatial diversity	0.49	39	-	-	-	1	9	5	1	16	7
	TSF + spatial context	0.55	45	9	-	2	-	8	4	1	15	6
<i>Acanthiza pusilla</i>	Time since fire	0.64	68	5	-	-	-	15	12	9	22	5
	Amount late	0.66	70	-	8	-	-	12	14	9	22	5
	Amount early	0.62	66	-	-	6	-	11	12	9	23	5
	Spatial diversity	0.64	67	-	-	-	8	10	12	9	23	5

Species name	Model	CV correlation	Total deviance	Deviance attributed to variables								
				Time since fire (years)	Amount late (ha)	Amount young (ha)	Spatial diversity	Temperature (°C)	Elevation (m)	Veg class	Survey duration (mins)	Survey area (ha)
	TSF + spatial context	0.64	70	4	8	-	-	12	12	8	22	5
<i>Acanthiza reguloides</i>	Time since fire	0.64	59	8	-	-	-	8	7	1	19	15
	Amount late	0.60	55	-	3	-	-	7	5	1	23	15
	Amount early	0.62	58	-	-	3	-	8	6	2	23	16
	Spatial diversity	0.60	55	-	-	-	4	6	5	2	22	16
	TSF + spatial context	0.62	59	7	-	-	4	7	7	1	18	14
<i>Colluricincla harmonica</i>	Time since fire	0.48	34	3	-	-	-	10	10	1	7	4
	Amount late	0.45	34	-	2	-	-	10	10	0	7	4
	Amount early	0.46	35	-	-	5	-	9	11	1	7	2
	Spatial diversity	0.46	35	-	-	-	5	9	11	0	7	3
	TSF + spatial context	0.47	38	2	-	-	5	10	11	1	7	3
<i>Cormobates leucophaea</i>	Time since fire	0.52	40	4	-	-	-	8	12	2	14	0
	Amount late	0.52	39	-	3	-	-	7	13	2	14	1
	Amount early	0.51	39	-	-	3	-	8	13	2	14	1
	Spatial diversity	0.52	37	-	-	-	3	7	11	1	14	0
	TSF + spatial context	0.53	42	4	3	-	-	7	12	2	14	0
	Time since fire	0.41	38	6	-	-	-	13	12	2	4	0

Species name	Model	CV correlation	Total deviance	Deviance attributed to variables								
				Time since fire (years)	Amount late (ha)	Amount young (ha)	Spatial diversity	Temperature (°C)	Elevation (m)	Veg class	Survey duration (mins)	Survey area (ha)
<i>Lichenostomus</i>	Amount late	0.45	40	-	10	-	-	13	9	2	5	1
<i>chrysops</i>	Amount early	0.42	38	-	-	7	-	13	10	2	5	1
	Spatial diversity	0.41	38	-	-	-	7	14	11	2	4	0
	TSF + spatial	0.49	42	5	9	-	-	11	9	2	5	1
	context											
<i>Lichenostomus</i>	Time since fire	0.48	57	1	-	-	-	13	24	3	15	1
<i>leucotis</i>	Amount late	0.55	54	-	1	-	-	12	23	3	15	0
	Amount early	0.59	55	-	-	4	-	12	21	3	15	0
	Spatial diversity	0.51	53	-	-	-	2	13	21	3	14	0
	TSF + spatial	0.49	60	1	-	4	-	14	22	3	15	0
	context											
<i>Malurus cyaneus</i>	Time since fire	0.45	37	11	-	-	-	7	10	3	5	1
	Amount late	0.43	35	-	5	-	-	7	12	3	5	3
	Amount early	0.41	36	-	-	6	-	7	11	3	5	3
	Spatial diversity	0.39	35	-	-	-	8	7	10	4	5	1
	TSF + spatial	0.43	37	10	-	-	5	5	8	3	5	0
	context											
<i>Melithreptus</i>	Time since fire	0.51	60	14	-	-	-	17	15	6	3	6
<i>lunatus</i>	Amount late	0.47	54	-	8	-	-	19	14	5	2	6
	Amount early	0.47	57	-	-	9	-	20	15	5	2	6
	Spatial diversity	0.44	53	-	-	-	21	14	10	3	3	2

Species name	Model	CV correlation	Total deviance	Deviance attributed to variables								
				Time since fire (years)	Amount late (ha)	Amount young (ha)	Spatial diversity	Temperature (°C)	Elevation (m)	Veg class	Survey duration (mins)	Survey area (ha)
	TSF + spatial context	0.60	62	10	-	-	18	14	11	3	3	2
<i>Pachycephala pectoralis</i>	Time since fire	0.46	44	6	-	-	-	12	14	6	7	0
	Amount late	0.48	46	-	7	-	-	10	14	6	8	1
	Amount early	0.43	46	-	-	8	-	10	13	6	8	0
	Spatial diversity	0.40	46	-	-	-	5	13	15	6	8	0
	TSF + spatial context	0.47	44	5	-	7	-	9	10	5	7	0
<i>Pachycephala rufiventris</i>	Time since fire	0.53	53	4	-	-	-	25	15	3	3	3
	Amount late	0.54	54	-	6	-	-	25	14	3	2	3
	Amount early	0.60	58	-	-	11	-	22	14	3	4	3
	Spatial diversity	0.58	54	-	-	-	10	24	13	4	2	1
	TSF + spatial context	0.50	56	3	-	11	-	22	13	3	3	2
<i>Pardalotus punctatus</i>	Time since fire	0.64	55	5	-	-	-	9	15	10	6	9
	Amount late	0.60	52	-	6	-	-	9	15	8	6	9
	Amount early	0.60	53	-	-	3	-	9	15	9	6	10
	Spatial diversity	0.61	51	-	-	-	24	8	13	3	3	1
	TSF + spatial context	0.62	54	3	-	-	23	8	12	3	3	2
<i>Pardalotus striatus</i>	Time since fire	0.58	49	6	-	-	-	20	12	3	3	4

Species name	Model	CV correlation	Total deviance	Deviance attributed to variables								
				Time since fire (years)	Amount late (ha)	Amount young (ha)	Spatial diversity	Temperature (°C)	Elevation (m)	Veg class	Survey duration (mins)	Survey area (ha)
	Amount late	0.58	51	-	6	-	-	20	13	4	3	5
	Amount early	0.55	49	-	-	4	-	21	13	4	3	4
	Spatial diversity	0.55	44	-	-	-	15	16	7	2	2	1
	TSF + spatial	0.56	46	3	-	-	15	16	8	2	2	1
	context											
<i>Phylidonyris</i>	Time since fire	0.67	74	10	-	-	-	46	11	6	1	0
<i>pyrrhopterus</i>	Amount late	0.56	77	-	4	-	-	50	14	7	2	0
	Amount early	0.63	74	-	-	3	-	49	14	7	2	0
	Spatial diversity	0.60	72	-	-	-	6	46	11	8	1	0
	TSF + spatial	0.68	76	10	-	-	5	45	10	5	1	0
	context											
<i>Platycercus elegans</i>	Time since fire	0.60	48	2	-	-	-	15	4	4	22	2
	Amount late	0.59	50	-	3	-	-	15	5	3	22	2
	Amount early	0.58	50	-	-	2	-	15	5	4	21	2
	Spatial diversity	0.58	49	-	-	-	2	15	5	4	22	2
	TSF + spatial	0.58	50	2	2	-	-	14	4	3	21	2
	context											
<i>Rhipidura albiscapa</i>	Time since fire	0.60	49	4	-	-	-	11	13	5	15	0
	Amount late	0.61	47	-	3	-	-	10	13	5	15	0
	Amount early	0.60	48	-	-	3	-	12	13	5	16	0
	Spatial diversity	0.58	43	-	-	-	1	10	12	5	16	0

Species name	Model	CV correlation	Total deviance	Deviance attributed to variables								
				Time since fire (years)	Amount late (ha)	Amount young (ha)	Spatial diversity	Temperature (°C)	Elevation (m)	Veg class	Survey duration (mins)	Survey area (ha)
<i>Sericornis frontalis</i>	TSF + spatial context	0.60	49	3	3	-	-	10	13	5	15	0
	Time since fire	0.52	42	6	-	-	-	10	7	5	14	1
	Amount late	0.52	42	-	2	-	-	11	8	5	14	1
	Amount early	0.50	38	-	-	1	-	9	6	5	15	1
	Spatial diversity	0.52	46	-	-	-	4	13	8	5	14	1
	TSF + spatial context	0.51	40	5	-	-	3	7	5	6	14	1
<i>Zosterops lateralis</i>	Time since fire	0.37	52	2	-	-	-	13	34	1	2	1
	Amount late	0.43	61	-	10	-	-	14	33	1	3	1
	Amount early	0.55	61	-	-	12	-	10	34	1	4	1
	Spatial diversity	0.47	50	-	-	-	9	9	28	1	2	1
	TSF + spatial context	0.44	60	1	-	12	-	10	33	1	4	1

### 6.6.6 The preferred successional vegetation for bird species in mallee woodlands

Table S6.6.6 The preferred successional vegetation for bird species in mallee woodlands based on the peak of species responses to time since fire (Null = no response, Early = 0–10, Mid = 10–35, Late = >35 years since fire), and species responses to amount young vegetation, amount old vegetation, and spatial diversity of post-fire successional states.

Species	Common name	Preferred successional vegetation	Amount young	Amount old	Response to spatial diversity
<i>Acanthiza apicalis</i>	Inland thornbill	Null	Null	Null	Null
<i>Drymodes brunneopygia</i>	Southern scrub-robin	Late	Negative	Positive	Null
<i>Lichenostomus leucotis</i>	White-eared honeyeater	Early	Negative	Negative	Positive
<i>Lichenostomus ornatus</i>	Yellow-plumed honeyeater	Late	Negative	Positive	Negative
<i>Pardalotus punctatus</i>	Spotted pardalote	Late	Negative	Null	Null
<i>Pardalotus striatus</i>	Striated pardalote	Late	Negative	Positive	Null

### 6.6.7 The preferred successional vegetation of bird species in foothill forests

Table S6.6.7. The preferred successional vegetation of bird species in foothill forests based on the peak of species responses to time since fire (Null = no response, Early = 0–3, Mid1 = 3–10, Mid2 = 10–40, Late = >40 years since fire), and species responses to amount young vegetation, amount old vegetation, and spatial diversity of post-fire successional states.

Species name	Common name	Preferred successional vegetation	Amount young	Amount old	Response to spatial diversity
<i>Acanthiza lineata</i>	Striated thornbill	Mid	Positive	Positive	Null
<i>Acanthiza pusilla</i>	Brown thornbill	Null	Null	Null	Null
<i>Acanthiza reguloides</i>	Buff-rumped thornbill	Null	Null	Null	Positive
<i>Colluricincla harmonica</i>	Grey shrike-thrush	Null	Negative	Null	Positive
<i>Dacelo novaeguineae</i>	Laughing kookaburra	Null	Null	Null	Positive
<i>Lichenostomus chrysops</i>	Yellow-faced honeyeater	Late	Positive	Positive	Null
<i>Lichenostomus leucotis</i>	White-eared honeyeater	Null	Null	Null	Null
<i>Malurus cyaneus</i>	Superb fairywren	Early	Null	Null	Positive
<i>Melithreptus lunatus</i>	White-naped honeyeater	Early	Null	Null	Positive
<i>Pachycephala pectoralis</i>	Golden whistler	Late	Null	Positive	Null
<i>Pachycephala rufiventris</i>	Rufous whistler	Null	Negative	Null	Positive
<i>Pardalotus punctatus</i>	Spotted pardalote	Null	Positive	Positive	Positive
<i>Pardalotus striatus</i>	Striated pardalote	Late	Null	Positive	Positive
<i>Phylidonyris pyrrhopterus</i>	Crescent honeyeater	Null	Null	Null	Null

Species name	Common name	Preferred successional vegetation	Amount young	Amount old	Response to spatial diversity
<i>Platycercus elegans</i>	Crimson rosella	Null	Null	Null	Null
<i>Rhipidura albiscapa</i>	Grey fantail	Null	Null	Positive	Null
<i>Sericornis frontalis</i>	White-browed scrubwren	Null	Null	Null	Negative
<i>Zosterops lateralis</i>	Silvereye	Null	Null	Positive	Null

## 7 SYNTHESIS

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Austral grass-tree *Xanthorrhoea australis* flowering ~6 months after a fire in heathy woodlands.

## 7.1 OVERVIEW

In this thesis I have explored how fire influences biodiversity in fire-prone ecosystems. The insights gained from this research will help address pertinent questions for biodiversity conservation in fire-prone ecosystems. A central theme of my research is that the influence of time since fire on ecological communities can differ among broad vegetation types, and that a broader perspective beyond using single measures of fire regimes (e.g. time since fire) is needed in fire management to help conserve biodiversity.

First, I outlined a conceptual framework that links fire management practices with understanding of relationships between fire and biota (Chapter 1). I then tested how time since fire influences bird and plant communities in ecosystems dominated by *Eucalyptus* trees with contrasting regeneration traits (Chapters 2,3,4,5). I investigated the role of species' life-history traits in bird and plant community responses to fire regimes and used these outcomes to explore how fire management practices may differentially affect bird and plant communities in structurally resilient forest ecosystems (Chapters 4 & 5). In this final chapter, I discuss the key findings of this work (see Table 7.1) and the implications for fire management. I also assess the results from this work, together with studies from the international literature, using a meta-analytical approach to explore the relationship between plant regeneration traits and the influence of time since fire on bird communities in forest ecosystems, across continents. Finally, I outline future directions for research that will further advance understanding of the ecological role of fire.

Table 7.1. The three research themes of this thesis, key questions, and main findings.

Research theme	Key questions	Key findings
The influence of time since fire on fauna	Does the post-fire development of faunal habitat differ between ecosystems? (Chapter 2)	<p>The number and type of habitat attributes that were significantly related to time since fire differed between ecosystems, in line with the regeneration traits of the canopy trees.</p> <p>More habitat attributes in mallee woodlands (basal resprouting) were related to time since fire than in foothill forests and heathy woodlands (epicormic resprouting).</p> <p>In foothill forests, only ground cover and understorey vegetation attributes responded significantly to time since fire, compared to all but one variable in mallee woodlands.</p>
	Does the influence of post-fire habitat structure on bird communities differ among ecosystems? (Chapter 3)	<p>Across an 80-year post-fire chronosequence, the most important habitat attributes for birds differed among ecosystems.</p> <p>In mallee woodlands, canopy structure attributes were the most important. In foothill forests, less species responded to habitat attributes overall. In both foothill forests and heathy woodlands, understorey vegetation and ground cover attributes were the most important.</p> <p>For most species of bird that occurred in multiple ecosystems, the most limiting habitat attributes varied among ecosystems.</p> <p>Over an 80-year chronosequence following fire, the most limiting habitat attributes for birds are those that are shaped by fire, but these can differ among ecosystems.</p>

Research theme	Key questions	Key findings
The influence of fire management practices on biodiversity in structurally resilient ecosystems	How does fire management shape bird and plant communities in a heathy <i>Eucalyptus</i> woodland? (Chapter 4)	<p>Species life-history traits gave key insights into the influence of time since fire and fire management practices on bird and plant communities.</p> <p>For birds, the peak in abundance of lower-midstorey foraging birds was later than the maximum tolerable fire interval, as currently specified for fire management.</p> <p>For plants, the peak in species richness of obligate seeders, shrubs and low shrubs, coincided with the minimum tolerable fire interval.</p> <p>Post-fire age classes based on vegetation growth stages represented distinct bird and plant communities.</p> <p>Timing of prescribed burns based solely on the life histories of plants will disadvantage bird communities. Maintaining stands of vegetation across the landscape at both the upper and lower TFIs will increase biodiversity in heathy woodlands. This can be achieved through a landscape-mosaic approach to fire management.</p>
	How does prescribed fire affect bird and plant communities in temperate dry forests? (Chapter 5)	<p>In a temperate dry forest ecosystem, the abundance of most bird species and the cover of most plant species at sites subject to prescribed fire did not differ from that of long-unburnt vegetation or change significantly with time since prescribed fire.</p> <p>Time since fire had strong effects on the relative abundance of birds that forage in the lower-midstorey, and on the relative cover of facultative-resprouting shrubs and obligate-seeding shrubs.</p>

Research theme	Key questions	Key findings
		<p>Community-wide diversity indices did not differ between sites subject to prescribed fire and long-unburnt vegetation. But there was significant variation in bird species assemblages between post-fire age-classes, particularly between the youngest (0-3 years post-fire) and oldest (&gt;40 years), driven by species typically associated with well-developed understorey vegetation structure. Plant community composition showed little evidence of a post-fire successional trajectory.</p> <p>Birds and plants in temperate dry forests showed a high level of resilience to prescribed burning. However, the interval between burns is important for certain species. Landscape-scale fire management should ensure the provision of suitable habitat for all taxa, both those resilient to fire and those that benefit from long-unburnt forest vegetation.</p>
The influence of spatial context of fire on birds	Does the spatial context of fire influence bird abundances? (Chapter 6)	<p>Species models that included both time since fire and a spatial measure of fire outperformed models that included only time since fire; and more so in foothill forests than in mallee woodlands.</p> <p>The amount of late-successional vegetation in the landscape was important for birds in both ecosystems. In mallee woodlands, most species were negatively associated with the amount of recently burnt vegetation. The spatial diversity of successional vegetation was important for more species in foothill forests than in mallee woodlands.</p> <p>Maintaining spatial diversity of successional vegetation in foothill forests can positively influence the abundance of some bird species. Limiting the occurrence of large wildfires will benefit several bird species in mallee woodlands. Incorporating the landscape context of fire in conservation planning can help meet the</p>

Research theme	Key questions	Key findings
		habitat requirements of diverse species across whole landscapes, but the role of spatial attributes can differ between ecosystems.

## **7.2 THE INFLUENCE OF TIME SINCE FIRE ON FAUNA**

In Chapter 2, I showed how the post-fire development of faunal habitat attributes across an 80-year post-fire chronosequence differs among ecosystems, based on the regeneration traits of the dominant canopy trees. In mallee woodlands, where canopy tree stems are killed by fire and resprout basally, all but one of the modelled habitat attributes were significantly related to time since fire. In foothill forests, where trees resprout epicormically, ground cover and understorey vegetation cover were related to time since fire, but attributes related to canopy tree structure were not.

In Chapter 3, I showed which habitat attributes were the most important for bird communities across the 80-year chronosequence and how these differed among ecosystems. Across the post-fire chronosequence, the most important habitat attributes for birds were those that were related to time since fire (from Chapter 2). In mallee woodlands, canopy tree structural attributes were the most important for the bird community. In foothill forests and heathy woodlands, understorey vegetation cover and ground cover attributes were the most important. For most species modelled, that occurred in multiple ecosystems, the influence of habitat attributes varied among ecosystems.

## **7.3 THE INFLUENCE OF FIRE MANAGEMENT PRACTICES ON BIRD AND PLANT COMMUNITIES**

In Chapter 4, I showed how fire and fire management practices influence bird and plant communities in a heathy *Eucalyptus* woodland in which canopy trees resprout epicormically. Compared to plants, fewer bird species were related to time since fire. Species' life-history traits gave key insights into the mechanisms driving community change over time post-fire. Successional change in the composition of the bird community followed post-fire changes in understorey vegetation structure and was driven primarily by changes in the abundance of

species that forage in the lower-midstorey. Fire management practices based on the life histories of plants (i.e. the use of tolerable fire intervals and vegetation growth stage structure) may differentially affect bird and plant communities. For both birds and plants, there was substantial variation in occurrence that was not explained by time since fire.

In Chapter 5, I tested the influence of prescribed fire on bird and plant communities across a 36-year post-fire chronosequence in a temperate dry forest in which canopy trees resprout epicormically). Overall, the bird and plant communities in these forests showed a high level of resilience to prescribed fire. However, analyses of functional groups of species revealed several components of the biota that may be vulnerable to the frequency of prescribed fire. If the interval between prescribed fires is too short, the abundance of birds that forage in the lower-midstorey will be limited. But, if the interval between fires is too long, the occurrence of plants that regenerate from seed may be limited. A landscape-scale approach that aims to maintain a spatially heterogeneous pattern of fire-histories to ensure habitat for all taxa, including those that rely on long-unburnt vegetation, will help conserve biodiversity in these forests.

#### **7.4 THE INFLUENCE OF THE SPATIAL CONTEXT OF FIRE ON BIRDS**

In Chapter 6, I investigated the influence of the spatial context of fire (i.e. the amount, diversity of successional vegetation in the landscape) on the abundance of bird species in mallee woodlands and foothill forests. Generally, models that included both time since fire and a spatial measure of fire outperformed models that included only time since fire, and substantially so in foothill forests. The amount of late-successional vegetation was important for species in both ecosystems. More species were negatively associated with the amount of early successional vegetation in mallee woodlands than foothill forests. The spatial diversity of successional vegetation was important for more species in foothill forests than mallee

woodlands. Incorporating the landscape context of fire in conservation planning can help meet the habitat requirements for diverse species across whole landscapes, but the influence of specific spatial attributes can differ between ecosystems.

Below, I discuss the implications of these findings in a cross-continental context, including a range of ecosystems from Australia, Europe and North America.

## **7.5 THE INFLUENCE OF PLANT REGENERATION TRAITS ON BIRD RESPONSES TO TIME SINCE FIRE: A CROSS-CONTINENTAL PERSPECTIVE**

In Australia, the distribution of epicormic resprouting species is driven by the combined effects of climate and fire (Clarke et al. 2015). Epicormic resprouting is common in savanna and forest ecosystems where annual rainfall is relatively high and is less common at the mesic and arid climatic extremes where basal resprouting and regeneration from seed tend to dominate (Clarke et al. 2015). As a result, it can be difficult to tease apart the relative influence of climate and plant regeneration traits on the relationship between bird communities and time since fire.

To test whether plant regeneration traits or climate were more influential in driving the responses of bird species to time since fire, I employed a meta-analytic approach whereby I assessed the results of this research together with studies from around the world. I predicted that in ecosystems that experience stand-replacing fires (i.e. tree stems are killed and resprout basally or regenerate from seed), the distribution of more bird species would be related to time since fire than in ‘structurally resilient’ ecosystems (i.e. tree stems resprout epicormically).

I searched the literature systematically for studies conducted in forest or woodland ecosystems around the world that reported the responses of multiple individual species of birds to time since fire (see Appendix 7.1 for details of methods). I then grouped studies

based on: (a) stand-regeneration system (stems killed by fire vs. stems survive fire), and (b) mean annual rainfall (high: >500 mm, low: <500 mm), and compared the percentage of species in each study that responded significantly to time since fire, between groups.

Globally, there were relatively few studies that modelled the relationship between bird species and time since fire and satisfied all selection criteria (Appendix 7.1). In total, I extracted data from 19 studies from three continents: North America (n = 11 studies), Australia (n = 7), and Europe (n = 1), and assessed the importance of time since fire in a total of 578 models for individual species. Time since fire was an important predictor of occurrence for a greater percentage of bird species in ecosystems that experience stand-replacing fires than in structurally resilient ecosystems (Fig. 7.1). All structurally resilient ecosystems were located in areas of high rainfall. Ecosystems that experience stand-replacing fires were located both in areas of high and low rainfall, but rainfall did not influence the percentage of species that was associated with time since fire.

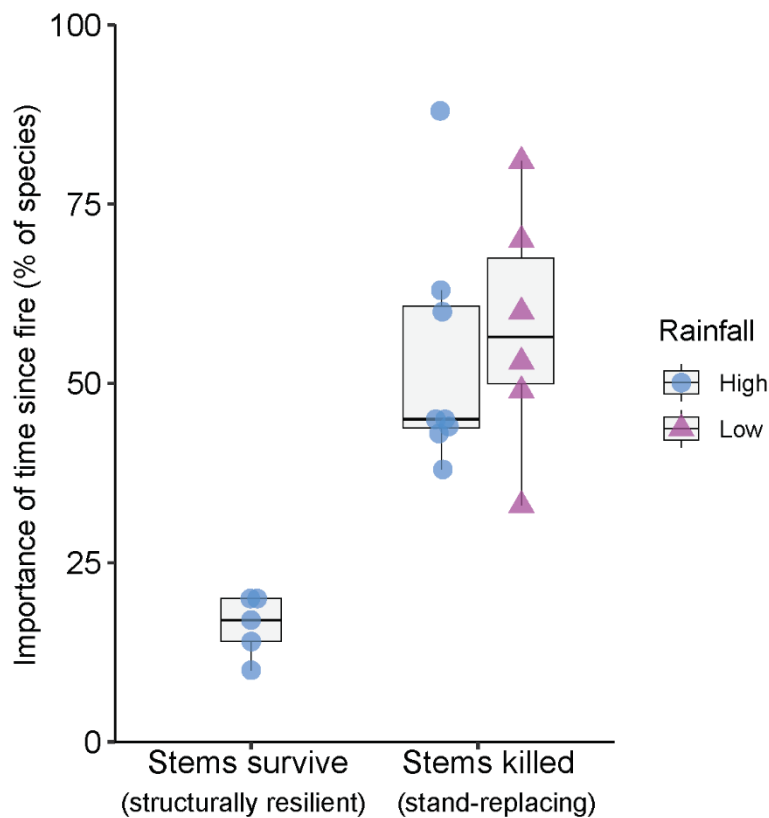


Figure 7.1. The influence of plant regeneration traits and mean annual rainfall on the response of bird species to time since fire. Points represent the percentage of bird species that responded to time since fire in individual studies. Boxplots indicate the median and upper and lower quartiles. Studies were grouped based on 1) stand-regeneration type (structurally resilient,  $n = 5$  studies; fires are stand-replacing,  $n = 14$ ), and 2) mean annual rainfall (high:  $>500$  mm,  $n = 13$  studies, low:  $<500$  mm,  $n = 6$ ).

Plant regeneration traits had a stronger influence on the importance of time since fire for bird species than annual rainfall, supporting the over-arching hypothesis of this thesis - that the influence of time since fire on faunal species depends on plant regeneration traits. Annual rainfall influences vegetation growth rates and the rate of post-fire ecosystem recovery. However, these findings show that globally, although the rate of post-fire regeneration may differ between ecosystems, the regeneration traits of the dominant trees determine the overall influence of time since fire on birds.

There are limitations to the approach used here, such as different modelling techniques used in studies, and additional variables included in several studies. However, this meta-analytic

approach provides key insights into how fire influences bird communities at a cross-continental scale.

## **7.6 BEYOND EUCALYPTS: STRUCTURAL RESILIENCE IN ECOSYSTEMS AROUND THE WORLD**

I expect that the key findings of this thesis, such as the limited influence of time since fire on faunal species, likely are applicable to other ecosystems dominated by epicormic resprouters. I found no published studies that reported the response of bird communities to time since fire in structurally resilient ecosystems outside Australia. However, a study of cork oak forests showed that the abundance of *Sylvia* warbler species changes over time following fire (Pons et al. 2012). Epicormic resprouting is the dominant regeneration trait in several forest ecosystems in the Mediterranean basin (e.g. cork oak *Quercus suber* forests) and Canary Islands (Canary Island pine *Pinus canariensis* forests) (Pausas and Keeley 2017).

Understanding the post-fire dynamics of the bird communities in these forests beyond the first few years following fire remains an important knowledge gap. However, there are commonalities in the influence of fire between these forests and stringybark-dominated *Eucalyptus* forests, suggesting that the role of fire in shaping faunal communities could be similar in epicormic resprouting ecosystems worldwide.

A recent study reported greater resilience to fire of vegetation (habitat) structure in cork oak forests compared to forests of obligate-seeding *Pinus* species (Chergui et al. 2018). Several studies have also shown that the structural resilience of cork oak forests results in muted effects of fire on the reptile community (Chergui et al. 2019, Chergui et al. 2020). Likewise, in Canary Island pine forests, the bird community was also shown to be relatively resilient to short-term effects (<3 years) of fire (Garcia-Del-Rey et al. 2010). The understorey vegetation in these forests is composed of various heathy shrubs that resprout or re-seed post-fire

(Garcia-Del-Rey et al. 2010, Chergui et al. 2019), suggesting that the post-fire development of understorey structure also resembles that of the stringybark *Eucalyptus* forests. Similarities in the post-fire dynamics of these diverse ecosystems with epicormic resprouters provides further support for the idea that plant regeneration traits have a dominant influence on the relationship between fauna and fire worldwide.

The use of prescribed fire for fuel management is increasing throughout the Mediterranean basin (Alcasena et al. 2018). It is crucial that the effects of prescribed fire and other fire management practices (e.g. suppression) on the biota of Mediterranean ecosystems, such as cork oak forests and Canary Island pine forests, are understood. The findings of this thesis provide a basis on which to build predictions of the potential effects of fire in these structurally resilient ecosystems. For example, I predict that, in these forests: a) the occurrence birds that forage throughout the vertical strata and those that forage in the canopy will not be related to time since fire, b) the occurrence of understorey birds will be related to the development of understorey vegetation and c) there will be substantial variation in the plant and animal communities that cannot be explained by time since fire. Testing these predictions will further advance understanding of the role of fire in structurally resilient ecosystems worldwide.

## **7.7 BEYOND TIME SINCE FIRE**

I have shown how the relationship between fauna and time since fire depends on plant regeneration traits. Several other factors, additional to time since fire, influence the distribution of species within ecosystems (e.g. environmental gradients, other fire regime attributes, past land-use). These factors could provide the additional complexity needed in fire science and management to understand the drivers of ecosystem structure and function.

The main implication for fire management from this work is that landscape categories based simply on time since fire do not reliably represent variation in faunal communities across time and space in all situations. In ecosystems that experience stand-replacing fires, time since fire can predict the occurrence of many species (Watson et al. 2012b). However, even in such situations, there is still a large amount of variation that is not explained by time since fire. For example, Watson et al. (2012) reported that the distribution of ~50% of bird species in mallee woodlands was not related to time since fire. In structurally resilient ecosystems (e.g. heathy woodlands, foothill forests), even less variation in bird communities can be attributed to time since fire (Chapters 4 & 5). Substantial variation in plant communities was also not attributed to time since fire. Below, I discuss some of the potential drivers of this additional variation in relation to the major findings of this thesis.

### **7.7.1 Environmental conditions**

At a region-wide scale (Chapter 6), temperature or elevation had the greatest influence on bird abundances in both mallee woodlands and foothill forests (see Appendix 6.3). Although environmental conditions are not directly amenable to fire management, they can moderate species' responses to fire (Nimmo et al. 2014, Burgess and Maron 2016, Robinson et al. 2016, Puig-Gironès et al. 2017, Verdon et al. 2019). Robinson et al. (2016) showed that, post-fire, forest gullies supported greater abundances of birds than adjacent slopes. Verdon et al. (2019) showed that the form of the relationship between a threatened bird species and time since fire differed between sites at higher and lower elevation. Factoring topographic position into fire management strategies could profoundly improve predictions of the landscape-scale effects of fire on biota. For example, if biodiversity values differ between similarly aged successional vegetation in gullies and on slopes, this should be reflected in a landscape classification system based on fire regime attributes, such as the vegetation growth stage structure. Further research into this area is needed to determine how to integrate topography

and time since fire into fire management planning. A simple recommendation for fire management is to avoid burning gully vegetation which generally supports higher value habitat and more abundant faunal communities than adjacent slopes.

Climatic gradients also shape the distribution of species (Kelly et al. 2017b) and may modulate the influence of fire on some species. For example, some faunal species are fire-sensitive only under certain climate conditions (Nimmo et al. 2014). Knowledge of the role of temperature in shaping species' distributions will become increasingly important for conservation management as the climate in many regions warms. If a species' sensitivity to fire is associated with warmer temperatures, a hotter climate could result in the species becoming fire-sensitive throughout a greater part of its range. This could have implications for the future conservation status of such species and points to the need for continued monitoring and evaluation. Predictions of species' responses to fire developed in this thesis are based on the conditions at the time of the surveys. However, whether these models will reliably predict species' responses to fire and habitat structure under future climate and fire regimes remains uncertain.

### **7.7.2 Other fire regime attributes**

Fire regime attributes other than time since fire can influence species' distributions in fire-prone ecosystems (Burgess et al. 2015, Kelly et al. 2017b). For example, in savanna ecosystems, the frequency and season of fires affect ecosystem structure (Murphy et al. 2010, Andersen et al. 2012), and in North American conifer forests, the habitat conditions created by severe fire are important for bird diversity (Nappi and Drapeau 2011, Hutto and Patterson 2016, Taillie et al. 2018). In structurally resilient forests, the long-term effects of fire severity on birds are less well understood. Fire severity has short-term (~2 years post-fire) effects on vegetation structure (Bassett et al. 2017) and bird diversity (Robinson et al. 2014) in foothill

*Eucalyptus* forests, and on bird diversity in Canary Island pine forests (Garcia-Del-Rey et al. 2010).

‘Foothill forests’-type vegetation constitutes a large proportion of the remaining forested area of south-eastern Australia, it is of high biodiversity value, and is some of the most fire-prone vegetation in the world. Understanding how fire severity shapes vegetation structure and faunal communities in foothill forests over longer time scales is crucial for conservation planning. Based on the findings of this thesis, I expect that the succession of bird communities following severe fire in foothill forests will resemble that of heathy *Eucalyptus* woodlands reported in Chapter 4.

The spatial context of fire was shown to be important for some bird species (Chapter 6). Previous studies have also reported the influence of spatial context. For example, in semi-arid woodlands in south-eastern Australia, the size of long-unburnt patches influenced the abundance of birds (Berry et al. 2015) and in conifer forests in western U.S.A. the spatial diversity of fire severity was positively associated with bird diversity (Tingley et al. 2016). However, a limitation of this study is that the spatial variables included (amount, diversity of successional vegetation) were based on time since last fire, which is a poor surrogate for bird communities in structurally resilient forests. Given the predictions for increased frequency of large, severe fires, and that fire severity can influence vegetation structure, how the spatial context of severe fire (e.g. spatial diversity of fire severity classes, area burnt by high severity fire) influences birds in structurally resilient forests remains a key knowledge gap.

An important next step is to determine how other aspects of the fire regime (e.g. fire severity, fire frequency) and environmental gradients (e.g. topography, temperature) interact with time since fire to influence biodiversity in structurally resilient forests. Ideally, studies should be designed in a way that facilitates the adoption of outcomes into fire management systems. These additional complexities could be incorporated into fire management systems currently

based on time since fire (e.g. vegetation growth-stage structure, Section 1.7) to better represent the variation in faunal communities across the landscape. For example, as the main point of difference in the composition of the bird communities in foothill forests is between recently burnt and long-unburnt vegetation, growth stages for this ecosystem could be simplified to these two categories (rather than 4+ categories). Further measures on which to base management categories could include topographic position (e.g. gully, non-gully) and fire severity (e.g. high, low/moderate). Fire managers could then calculate the proportion of the landscape within each category (e.g. the proportion of long-unburnt gully vegetation, or the proportion of non-gully vegetation burnt at high severity). This relatively simple advancement could improve fire management for biodiversity. Of course, further research is needed to test this idea.

## **7.8 PLANT-CENTRIC FIRE REGIMES MIGHT NOT ADEQUATELY CONSERVE ANIMALS**

Incorporating the needs of fauna into fire management planning remains a key challenge in fire-prone regions worldwide (Clarke 2008, Pausas 2019, Stephens et al. 2019, Clarke 2020). Often, fire managers use knowledge based on the life-histories of plants to guide plans to manipulate fire regimes, and assume that this will also protect animals by default (Clarke 2008). In this thesis, I have shown that: (a) between-fire intervals that enhance plant diversity may negatively impact bird communities (Chapter 4); and (b) in structurally resilient forests, landscape categories based on vegetation succession (e.g. vegetation growth stages) do not reliably represent successional changes in bird communities (Chapter 5). These findings indicate that, in structurally resilient forests, fire management frameworks that are based primarily on plant responses to fire will provide little guidance for planning fire regimes that will conserve animals. Instead, to conserve animals in fire-prone ecosystems, the processes

driving animal community dynamics must be explicitly considered in fire management practices.

North American ponderosa pine *Pinus ponderosa* forests offer a contrasting perspective. Following over a century of wildfire suppression in the U.S.A., there has been a recent paradigm shift in fire science and management to restore historical regimes, mainly through prescribed burning (Stephens et al. 2016). Historically, ponderosa pine forests experienced frequent, low-moderate severity fires. However, effective fire suppression changed the vegetation structure in these forests, leading to more frequent high-severity fires and reduced habitat for several threatened species (Stephens et al. 2019). In these forests, frequent low severity fires, achieved through prescribed burns, increase both plant diversity and populations of native wildlife (Kalies and Yocom Kent 2016). So, in this situation, fire regimes that are guided by plant responses to fire can also help to conserve faunal species. This contrasts with the *Eucalyptus* forests and woodlands studied here, where there is disparity between the fire-response of most fire-sensitive functional groups of plants and birds.

A similar contrast between the responses of birds and plants to fire was reported in semi-arid *Eucalyptus* woodlands in Western Australia. Plant diversity showed a ‘u-shaped’ response to time since fire whereas several bird guilds increased in abundance with time since fire (Gosper et al. 2013b, Gosper et al. 2019). These contrasts and commonalities between ecosystems highlight the need to test the influence of fire regimes and fire management practices on a range of taxonomic groups before generalising across systems.

Post-fire succession of animal communities is tied with the development of vegetation structure or provision of resources, but not necessarily with the succession of the plant community composition. The different evolution of animals and plants means that these taxa can be associated with different attributes of fire regimes. This creates a challenge for fire

management when there are expectations to reduce perceived risk from wildfires and preserve biodiversity. It can be tempting for fire management agencies to assume that, by default, meeting the needs of plants will meet the needs of animals and to design plans based primarily on fire regimes that will promote plant diversity. However, fire management policies and plans must incorporate the needs of multiple taxa. This will likely require ecosystem-specific approaches, rather than systems based on a single fire regime attribute (e.g. time since fire).

## **7.9 ECOLOGICAL KNOWLEDGE TO APPLICATION**

The conceptual model provided in Chapter 1 outlines the link between the way in which relationships between fire and biota are understood and how fire-prone landscapes are managed. I applied this framework to a case study of fire management in Victoria, Australia to reveal knowledge gaps that, once filled, may help improve conservation management. A common assumption of approaches to fire management, particularly in *Eucalyptus* forest ecosystems in Australia, is that the occurrence of species is driven by time since last fire. However, in this thesis I showed that, the influence of time since fire on bird communities differs between ecosystems dominated by trees that are epicormic resprouters (i.e. structurally resilient ecosystems) and an ecosystem dominated by trees that are basal resprouters (i.e. fires are stand-replacing). Also, in several ecosystems, there is substantial variation in animal and plant communities that is not related to time since fire.

This new knowledge of the role of fire in shaping faunal communities has implications for the way in which fire-prone landscapes are categorised and managed. In particular, the approach of using categories based simply on time since fire (e.g. growth stages, age-classes) as a common classification system to represent successional changes for forest management in all ecosystems (as is currently done in Victoria, Australia) needs to be reconsidered.

## 7.10 FUTURE DIRECTIONS

Despite the advances gained through the main findings of this thesis, knowledge gaps in relation to the ecology and management of fire in fire-prone ecosystems remain. Here, I outline four key areas for future research that will further advance the understanding gained from this thesis.

### 7.10.1 Drivers of species' distributions in structurally resilient ecosystems

I showed how a single measure of the fire regime (i.e. time since fire) poorly represents variation in the bird and plant communities in structurally resilient *Eucalyptus* forests.

However, management practices often are based on such measures. It is crucial to understand the processes that shape ecological communities in these forests and how these interact with time since fire. Important areas of further investigation include the influence of other fire regime attributes and environmental gradients on biota. Key research questions include the following:

- How do fire severity and topography interact with time since fire to influence biodiversity in structurally resilient forests? Are the successional trajectories of animal and plant communities different following high and low severity fires, and at different topographic positions? Is there more value in preserving long-unburnt vegetation in forest gully sites than on less productive slopes?
- How do large severe fires affect biodiversity? Is there a relationship between the extent and severity of fires and the rate of ecosystem recovery?
- What are the commonalities and differences between structurally resilient ecosystems throughout the world? Are the post-fire dynamics of bird communities similar in cork oak, Canary Island pine and stringybark *Eucalyptus* forests?

### **7.10.2 Spatial context of fire**

I showed that the spatial context of fire regimes can influence the abundance of bird species. The spatial context variables tested in this thesis are based on time since last fire. Following the directions outlined above in Section 7.10.1, a key next step is to test the influence of the spatial context of fire severity and environmental variables on animal and plant populations. Key questions include:

- How does the amount and diversity of fire severity classes surrounding a site influence species' distributions?
- Is there a critical threshold of the amount of severely burnt vegetation in the local area that limits population densities? E.g. which kinds of species experience increased or reduced populations in response to the amount of severely burnt vegetation?
- Is the spatial diversity of severity classes in structurally resilient forests important for species following fire, and if so, for how long? Is a particular severity class important for some species, or do they need a mixture of vegetation burnt at high and low severity in the local area? Which species traits are associated with spatially diverse fire regimes?
- What is the role of spatially diverse topography in influencing species' responses to fire? E.g. does the amount of gully vegetation in the local area influence population densities and does the fire history of the gully vegetation have an effect?

### **7.10.3 Threatened species**

A key knowledge gap that remains is how the findings of this thesis relate to the ecology of rare and threatened species in structurally resilient ecosystems. The findings were limited by the number of species for which there were sufficient data to run analyses, which were the most common and widespread species in each ecosystem. The most common species are also likely those that are the least vulnerable to the effects of fire. The functional group approach I

used in Chapters 4 and 5 gives insight into which kinds of species are likely to be influenced by time since fire. However, there are limitations to this approach. In foothill *Eucalyptus* forests of south-eastern Australia, forest owls are the main group of birds of conservation concern (based on a search for threatened species in Atlas of Living Australia, <https://www.ala.org.au/>). The life-history of owls (e.g. nocturnal, large home ranges, low population density) make this group difficult to study. The effects of fire on forest owls are largely unknown, so a fruitful area of research would be targeted studies of the fire ecology of these birds. Key questions include:

- How does the spatial context of fire and topography influence the distribution of forest owls?
- Do individuals use multiple seral stages or severity classes in their home range? Or is it more important to have large areas of homogenous fire history?
- What is the effect of large severe fires on individual owls – do they persist in burnt landscapes? If not, how long is needed before they return?

These questions could be addressed by locating owls in the wild and attaching tracking devices on individuals to understand their spatial ecology in relation to fire.

#### **7.10.4 Predicting species' distributions under future scenarios**

Finally, an important next step for this research is to use the models developed in this thesis to make predictions of species' distributions under future climate and fire management scenarios. In Chapter 6, I developed species distribution models as a function of both fire regime and important environmental variables. Making these models spatially explicit (i.e. mapped) will reveal important locations for species that could be targeted for conservation actions. Following this, species distribution models can be combined with computer simulations of future climate and fire management scenarios. These types of analyses can be

used to address questions relating to the conservation of species in fire-prone environments, including:

- How will the distribution of species change with increased average temperatures under current fire management regimes?
- How would alternative fire management strategies (e.g. more widespread or frequent prescribed burning, increased suppression efforts) affect the distribution of species under different climate change scenarios?

The outcomes of such future studies will be highly relevant to fire management and conservation planning. This knowledge will be valuable in forecasting how species may be impacted by climate change and fire management activities.

## **7.11 CONCLUDING REMARKS**

The influence of fire on biota differs between taxa and between ecosystems. Plant regeneration traits play a key role in modulating the influence of fire on faunal communities. Simple measures of fire regimes, such as time since fire (and other temporal surrogates), are limited in their ability to represent variation in ecological communities. Knowledge of species' life history traits can improve understanding of the mechanisms driving ecosystem change following fire. This understanding can be used to evaluate fire management practices and to make generalisations about the ecological impacts of changed fire regimes, including which species will be positively or negatively affected. To conserve species in fire-prone landscapes, fire management practices must be based on the processes that shape patterns of biodiversity through time and across space. Understanding this additional complexity will be crucial for biodiversity conservation in an increasingly fire-prone world.



## 7.12 APPENDICES

### 7.12.1 Methods for systematic search and meta-analysis

I searched two online databases (Web of Science, Google Scholar) using combinations of the following search terms: ‘bird’, ‘avian’, ‘time since fire’, ‘fire’, ‘succession’, ‘forest’, ‘woodland’. I then extracted data for analysis from articles that met the following criteria:

- Chronosequence or longitudinal study spanning  $\geq 5$  years with  $\geq 3$  sample points in time.
- Data were obtained from bird community surveys that aimed to detect all species present at sites, not just target species or groups. Studies that attempted to model all species within an ecosystem, should report both significant and non-significant results, reducing potential for publication bias (i.e. only significant results are published).
- The vegetation type in which the response was detected (including dominant canopy tree species) must be explicit so that the pattern of stand regeneration could be determined from the literature, if not stated in the article.
- A forest or woodland ecosystem (i.e. not a shrubland or grassland/prairie).
- For studies that including logging as a factor in the analyses, the independent effects of time since fire must be reported.
- The dataset was not used in another study sampled.

The data extracted from each article are provided in Table S7.1. Several notable studies of the relationship between bird species and time since fire were excluded from the analysis because they did not meet all the inclusion criteria. These are provided in Table S7.2.

Table S7.12.1. Articles from which data were extracted to test the influence of plant regeneration traits on the relationship between birds and time since fire. Information describing study authors, ecosystem characteristics, statistical methods and number of species is provided.

Author, year	Title	Canopy tree regeneration trait	Continent	Vegetation type	Rainfall	Range of years since fire	Model	No. species	Percentage for which TSF was 'important'	Definition of 'important'
Rainsford (Chapter 5).	How does prescribed fire shape bird and plant communities in temperate dry forests	Epicormic resprouting	Australia	Eucalypt forest	High	1 - 39	GAM	22	14	P-value <0.05
Rainsford (Chapter 4).	How do fire management practices influence bird and plant communities in a heathy <i>Eucalyptus</i> woodland	Epicormic resprouting	Australia	Heathy eucalypt woodland	High	1 - 79	GAM	25	20	P-value <0.05
Sitters et al. 2014a.	Associations between occupancy and habitat structure can predict avian responses to disturbance: Implications for conservation management	Epicormic resprouting	Australia	Eucalypt forest	High	1 - 70	GAMM	15	20	P-value <0.05
Smith and Smith 2017.	Influence of fire regime and other habitat factors on a eucalypt forest bird community in south-eastern Australia in the 1980s.	Epicormic resprouting	Australia	Eucalypt forest	High	1 - 42	GLM	21	10	TSF was included in the best model
Wills et al. 2020.	Wildfire and fire mosaic effects on bird species richness and	Epicormic resprouting	Australia	Eucalypt forest	High	1.5 – 9.5	Wilcoxon	18	17	P-value <0.05

Author, year	Title	Canopy tree regeneration trait	Continent	Vegetation type	Rainfall	Range of years since fire	Model	No. species	Percentage for which TSF was 'important'	Definition of 'important'
	community composition in south-western Australia									
Gosper et al. 2019.	Fire-mediated habitat change regulates woodland bird species and functional group occurrence.	Obligate seeding	Australia	Eucalypt woodland	Low	6 - 400	GAMM	30	33	P-value <0.05
Watson et al. 2012b.	Effects of time since fire on birds: How informative are generalized fire response curves for conservation management?	Basal resprouting	Australia	Eucalypt woodland	Low	1 - 164	GAMM	30	53	P-value <0.05
Hutto et al. 2020.	Patterns of bird species occurrence in relation to anthropogenic and wildfire disturbance: Management implications	Obligate seeding	North America	Conifer forests	Low	1 -32	Chi-square	68	49	P-value <0.05
Hutto and Patterson 2016.	Positive effects of fire on birds may appear only under narrow combinations of fire severity and time-since-fire.	Obligate seeding	North America	Conifer forests	Low	1 -10	Chi-square	50	60	P-value <0.05
Taillie et al. 2018.	Interacting and non-linear avian responses to mixed-severity wildfire and time since fire	Obligate seeding	North America	Conifer forests	High	1 -15	Hierarchical distance sampling	44	45	Significant effect of TSF

Author, year	Title	Canopy tree regeneration trait	Continent	Vegetation type	Rainfall	Range of years since fire	Model	No. species	Percentage for which TSF was 'important'	Definition of 'important'
Zlonis et al. 2019.	Burn severity and heterogeneity mediate avian response to wildfire in a hemi-boreal forest	Obligate seeding	North America	Conifer forests	High	0 - 5	GLMM	43	63	95% confidence intervals
Stephens et al. 2015.	Fire severity affects mixed broadleaf–conifer forest bird communities: Results for 9 years following fire	Obligate seeding	North America	Broadleaf-conifer forest	High	0 - 9	GLM	37	38	QAIC
Rush et al. 2012.	Fire severity has mixed benefits to breeding bird species in the southern Appalachians	Obligate seeding	North America	Mixed evergreen	High	0 - 20	CONTRA ST	9	44	AIC
Fontaine et al. 2009.	Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest	Obligate seeding	North America	Mixed evergreen	High	0 -100	Indicator species analysis	44	43	P-value <0.05
Simon et al. 2002.	Songbird abundance in clear-cut and burned stands: a comparison of natural disturbance and forest management	Obligate seeding	North America	Black spruce	High	0 - 27	GLM	10	60	P-value <0.05

Author, year	Title	Canopy tree regeneration trait	Continent	Vegetation type	Rainfall	Range of years since fire	Model	No. species	Percentage for which TSF was 'important'	Definition of 'important'
Schieck et al. 1995.	Differences in bird species richness and abundance among three successional stages of aspen-dominated boreal forests	Obligate seeding	North America	Aspen forest	Low	23 - 120	Kruskal-Wallis	40	70	P-value <0.05
Rose and Simons 2016.	Avian response to fire in pine-oak forests of Great Smoky Mountains National Park following decades of fire suppression	Obligate seeding	North America	Pine-oak forests	High	0 - 28	Hierarchical linear equations	24	88	TSF was included in the best model
Rey et al. 2019.	Effects of forest wildfire on inner-Alpine bird community dynamics	Obligate seeding	Europe	Pine-oak forest	Low	0 - 13	GLMM	37	81	TSF was included in the best model
Schwab et al. 2001.	Breeding songbird abundance related to secondary succession in the subarctic forests of western Labrador	Obligate seeding	North America	Aspen forest	High	0 - 135	GLM	11	45	P-value <0.05

Table S7.2. Notable studies of the relationship between birds and time since fire that were excluded from the analysis.

Author, year	Title	Vegetation type	Reason for exclusion
Lindenmayer et al. 2016.	Do temporal changes in vegetation structure additional to time since fire predict changes in bird occurrence?	Temperate rainforest Eucalypt forest Eucalypt woodland Heathland Shrubland Sedgeland	Several vegetation types that differ in fire response were included in the study. It was unclear how the bird responses to time since fire related to vegetation type.
Smucker et al. 2005.	Changes in bird abundance after wildfire: importance of fire severity and time since fire	Conifer forests	The chronosequence was too short (3 years).
Jacquet and Prodon 2009.	Measuring the postfire resilience of a bird–vegetation system: a 28-year study in a Mediterranean oak woodland.	Oak woodland	The canopy tree species were unclear. There seemed to be a mix of epicormic resprouters and obligate seeders.
Kelly et al. 2017.	Fire regimes and environmental gradients shape vertebrate and plant distributions in temperate eucalypt forests	Eucalypt forest	There was no indication of whether time since fire was ‘important’ for individual species’ models (boosted regression trees).
Haney et al. 2008.	Thirty Years of Post-Fire Succession in a Southern Boreal Forest Bird Community	Boreal forest	The article reported changes in bird abundances with time since fire, but with not measure of ‘importance’.

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